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Marine Algae of the Northern Gulf of California II: Rhodophyta

James N. Norris

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ABSTRACT

Norris, James N. Marine Algae of the Northern Gulf of California II: Rhodophyta. *Smithsonian Contributions to Botany*, number 96, xvi + 555 pages, 236 figures, 2014.— The present treatment constitutes a taxonomic study of the benthic marine red algae known in the northern Gulf of California. In all, 387 species of Rhodophyta belonging to two subphyla were found: the Rhodophytina, represented by 2 classes, 2 orders, 2 families, 7 genera, and 14 species; and Eurhodophytina, represented by 2 classes, 5 subclasses, 19 orders, 47 families, 133 genera, and 373 species (including varieties, forms, and possible new species); 71 species of red algae (~18%) are endemic to the Gulf of California. Together with the 133 species of Chlorophyta and Phaeophyceae, 520 marine algae are known in the northern Gulf. The systematic account includes the presently accepted taxon name, descriptions of the subphyla, classes, orders, families, genera, and species, with keys and illustrations to aid in their identification. Along with the taxon name are its basionym, synonyms, author(s), date and place of valid publication, type locality, relevant taxonomic studies, description, habitat, and distribution in the Gulf of California and, if applicable, in the eastern, central, and/or western Pacific. A remarks section includes information on taxonomy, nomenclature, ecology, distribution extensions and new records, and/or other problems or facts of interest. A new genus, 1 new subgeneric section, and 8 new species are described; 30 new combinations are proposed (listed in Appendix 1). A new name, *Rhodymenia huertae*, is chosen to replace an illegitimate name; a lectotype illustration is selected for *Laurencia paniculata* Kützing; 15 previously reported species are considered uncertain records; and 3 species are excluded from the Gulf's marine flora.

Cover images, left to right: Figures 170A (*Pugetia mexicana*), 231A (*Botryocladia datilensis*), 217 (*Predaea japonica*), and 219A (*Plocamium katinae*) from this publication.

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Marine Algae of the Northern Gulf of California II: Rhodophyta

James N. Norris

INTRODUCTION

The oceanography of the Gulf of California (Figure 1) has been described by Roden (1964), van Andel and Shor (1964), Álvarez-Borrego (1983, 2002), and Lavín and Marinone (2003), with overviews by Brusca (1980), Maluf (1983), Brusca et al. (2005), and Norris (2010). An atlas of the scientific cruises in the Gulf of California was given by Schwartzlose and Lluch-Cota (2003). The general features of the marine flora of the northern Gulf of California and its history of marine botanical exploration can be found in Norris (2010).

The systematic account of the Rhodophyta herein constitutes the companion volume of *Marine Algae of the Northern Gulf of California*; the first was the treatment of Chlorophyta and Phaeophyceae (Norris, 2010).

• • •

The intertidal and subtidal algal collections that form the basis for the present taxonomic study of the red algae were made during land- and ship-based field trips to the Baja California and Sonora coasts of the northern Gulf of California and Islas de la Cintura (Figures 2–8). These field trips and ship expeditions occurred while I was in residence as Station Director of Laboratorio de Biología Marina of the University of Arizona and Universidad de Sonora in Puerto Peñasco, Sonora (Norris, 2010) (Figure 6), and since 1975 after I came to work at the National Museum of Natural History. These were supplemented by the collections of E. Yale Dawson (Algal Collection, U.S. National Herbarium [US Alg. Coll.]; Allan Hancock Foundation Herbarium [AHFH], now Herbarium of the University of California, Berkeley [UC]) and those of Ivan M. Johnston and others that were included in the studies of W. A. Setchell and N. L. Gardner (Herbarium, California Academy of Sciences [CAS], now UC; US Alg. Coll.). The Gulf of California research was supported and encouraged by Robert W. Hoshaw, Donald A. Thomson, and John R. Hendrickson (University of Arizona), Michael Neushul (University of California, Santa Barbara), and Isabella A. Abbott (Stanford University and, later, University of Hawaii). Field explorations on the Sonora and Baja California coasts were made possible through support from National Science Foundation grants (BMS-73-07000-A01 and BMS-75-13960), USDC NOAA-04-5-158-20, and an American Philospohical Society grant (Penrose Fund no. 7530). The Islas de la Cintura (Midriff Islands) were surveyed during the cruise of the R/V *Dolphin* (Scripps Institution of Oceanography [SIO], University of California, San

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James N. Norris, Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C., USA; norrisj@si.edu.

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FIGURE 1. Map of the Gulf of California, with the Baja California peninsula to its west and mainland Mexico to the east. The area shown is the following: northern Gulf of California (dark shading) south to 28°N latitude (which is also the border between the Mexican states of Baja California and Baja California Sur), the southern Gulf of California (medium shading) to the Gulf's entrance between Cabo San Lucas and Cabo Corrientes, and the Pacific Mexican coasts of the Baja California, Baja California Sur, and Jalisco (light shading).

Diego [UCSD]) to the northern Gulf of California (Norris and Bucher, 1976, 1977) (Figure 3A–D).

Specimens were obtained from the intertidal and subtidal by me and Katina E. Bucher using scuba (Norris, 2010). Collection numbers are designated by the following prefixes:

JN	our field notebooks (Algal Collection, National Museum of Natural History, Smithsonian Institution);
EYD	notebooks of E. Yale Dawson (Algal Collection, National Museum of Natural History, Smithsonian Institution);
GJH	notebooks of George J. Hollenberg (Algal Collection, National Museum of Natural History, Smithsonian Institution);
JN and *HWJ*	H. William Johansen (Clark University; notebook with HWJ);
JS	notebooks of Joan G. Stewart (Scripps Institution of Oceanography, UCSD).

Methods for field collection of marine algal specimens and their subsequent preservation, mounting as herbarium specimens, and preparation for light microscope study are as given by Tsuda and Abbott (1985). Photomicrographs were made using an Olympus Q-5 digital camera mounted on a Zeiss Universal microscope; all images used herein were prepared using Adobe Photoshop PS-4 on a Macintosh Pro computer.

Specimens studied or examined, or referred to in this work are deposited in collections at the institutions listed below, which are abbreviated for subsequent mention in the text. Herbarium abbreviations herein follow the *Index Herbariorum* (Holmgren et al., 1990; Thiers, 2013).

AD	State Herbarium of South Australia, Adelaide, South Australia, Australia
AHFH	Herbarium of the Allan Hancock Foundation, University of Southern California, Los Angeles, California; Algae Collection moved to LAM, now UC
CAS	Herbarium of the California Academy of Sciences, San Francisco, California; now UC
CMMEX	Algae Herbarium of the Universidad Autónoma de Baja California, Facultad de Ciencias Marinas, Ensenada, Baja California, Mexico
CN	Herbier, Université de Caen, Laboratoire de Biologie, Caen, France
ENCB	Herbario, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico D.F., Mexico
L	Nationaal Herbarium Nederland, Leiden University, Leiden, Netherlands
LAM	Algal Herbarium of the Los Angeles County Museum, Los Angeles, California; now UC
LD	Botanical Museum, Lund, Sweden
MICH	Herbarium of the University of Michigan, Ann Arbor, Michigan
MLML	Marine Algae Collection, Marine Biological Collection (Museum), Moss Landing Marine Laboratories, California State University, Moss Landing, California
PC	Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris, France
TCD	Herbarium, School of Botany, Trinity College, Dublin, Ireland
UC	Herbarium of the University of California, Berkeley, California

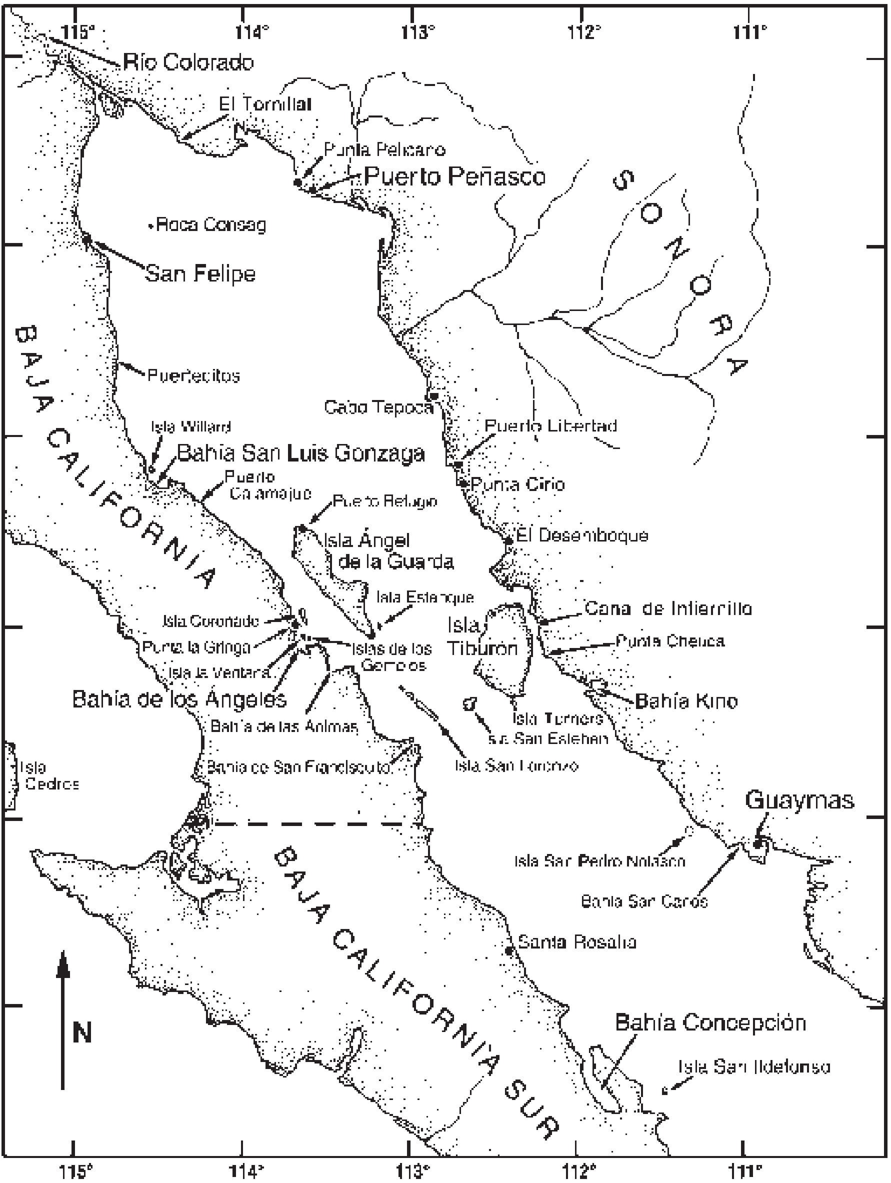


FIGURE 2. Map of the northern Gulf of California, Mexico, showing most of the locales (algal collection sites).

US Alg. Coll.	Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Several botanical and phycological references were invaluable throughout this study, notably the thorough AlgaeBase (http://www.algaebase.org), a database of information on marine, terrestrial, and freshwater algae that was developed and is updated and maintained by Michael and Wendy Guiry (Guiry and Guiry, 2007–2012); the second edition of *Taxonomic Literature* (referred to as TL-2) by Stafleu and Cowan (1976–1988) and its supplement volumes (Stafleu and Mennega, 1992–2000; Dorr and Nicolson, 2008, 2009); Stafleu (1972) on dates of publication of the extensive volumes of Engler and Prantl; *Botanical Latin* (Stearn, 2004); and *Composition of Scientific Words* (Brown, 1979). The citation of the authors of taxa names follows Brummitt and Powell (1992).

FIGURE 3. Some of the northern Gulf of California collecting sites. A–D. Isla Ángel de la Guarda: A. Puerto Refugio, south shore, low tide (April 1977). B. Roca Blanca, near the middle of Puerto Refugio (April 1974). C. Puerto Refugio, intertidal rock platform around point on west shore. D. Expansive alluvial fan on the island, above the cliff fronting the intertidal shore of Puerto Refugio (April 1977). E. Estero, Punta Sargento, Sonora, low tide (high tide covers the darker sand area) (February 1973). F. Estero, Bahía de Las Ánimas, Baja California, exposed at low tide (note that high tide covers up to leaves and green of mangroves (May 1972).

FIGURE 4. Desert coasts of the northern Gulf: A. Large cardón (*Pachycereus pringlei*), a cactus of the Sonoran Desert, on the shore near Punta Cheuca, Sonora (April 1976). B. Osprey flying in from the beach to add to its large nest of twigs, branches, and seaweeds—another seaweed collector in the northern Gulf, Punta Sargento, Sonora (February 1973). C. Low tide, showing intertidal habitats, Punta Willard, north of Bahía San Luís Gonzaga, Baja California (July 1973). D. Puerto Calamajue, Baja California (July 1973).

FIGURE 5. Land-based diving operations: A. Research vehicle set up to carry scuba air compressor, tanks, and diving equipment; collecting, photographic, and camping gear; and food and water for four week land-based diving operation; on the road to dive and collecting sites at Punta Cirio (south of Puerto Libertad), Sonora (June 1973). B. Scuba air compressor station to refill tanks, Punta Granito, Sonora (February 1973). C, D. Marine botanists James Norris and Katina Bucher during a break between scuba dives, Punta Cirio (November 1973). E. Jim Norris (aka “Santiago rojo,” as named by the Seri) working with Armando Torres and Angelita Torres at the Seri village, El Desemboque de San Ignacio, Sonora (February 1974).

Place and locality names of the land-based collection sites and ship-based cruise stations that are used herein (Figures 1, 2) are from the U.S. National Oceanic and Atmospheric Administration (NOAA) charts 21008, 21014, 21120, 21124, 21141, 21161, 21181, and 21182, Carta de Farod e Hidrografía de México F. H. 600, and the road, boating, and cruising sea guides to Baja California and the Gulf of California, particularly the work of Lewis (1971) and also Wheelock and Gulick (1975), Peterson (1998), Williams (2003), Cunningham (2004, 2006a, 2006b), Breeding and Bansmer (2009), and Rains (2013).

It is hoped this publication will encourage algal taxonomic and phylogenetic research as it makes available a taxonomic baseline for further biodiversity, marine botanical morphological and molecular systematics, and ecological investigations in the northern Gulf of California (Figure 2). Accurate identification of the marine algae is essential not only for molecular systematic and phylogenetic studies but also for ecological and conservation studies and ecosystem management of this biologically unique region. The taxonomic descriptions, particularly genera and species, presented herein are to be treated as hypotheses, and as such, it is encouraged that their taxonomic status will be tested using genetic molecular analyses and further morphological comparisons.

The biological uniqueness of the northern Gulf of California (Figures 3, 4, 6–8) is internationally recognized, and the islands

FIGURE 6. Playa Estación, Puerto Peñasco, Sonora: A. Low tide (arrow marks high tide line), one of the two daily (semidiurnal) tides that exposes the vast caliche shell-hash tidal platform below Laboratorio de Biología Marina (University of Arizona and Universidad de Sonora). B. Katy Bucher surveying the tidal platform; note the large Cumpleaños Tide Pool near the old “Casa Garcia” (seen above the shore).

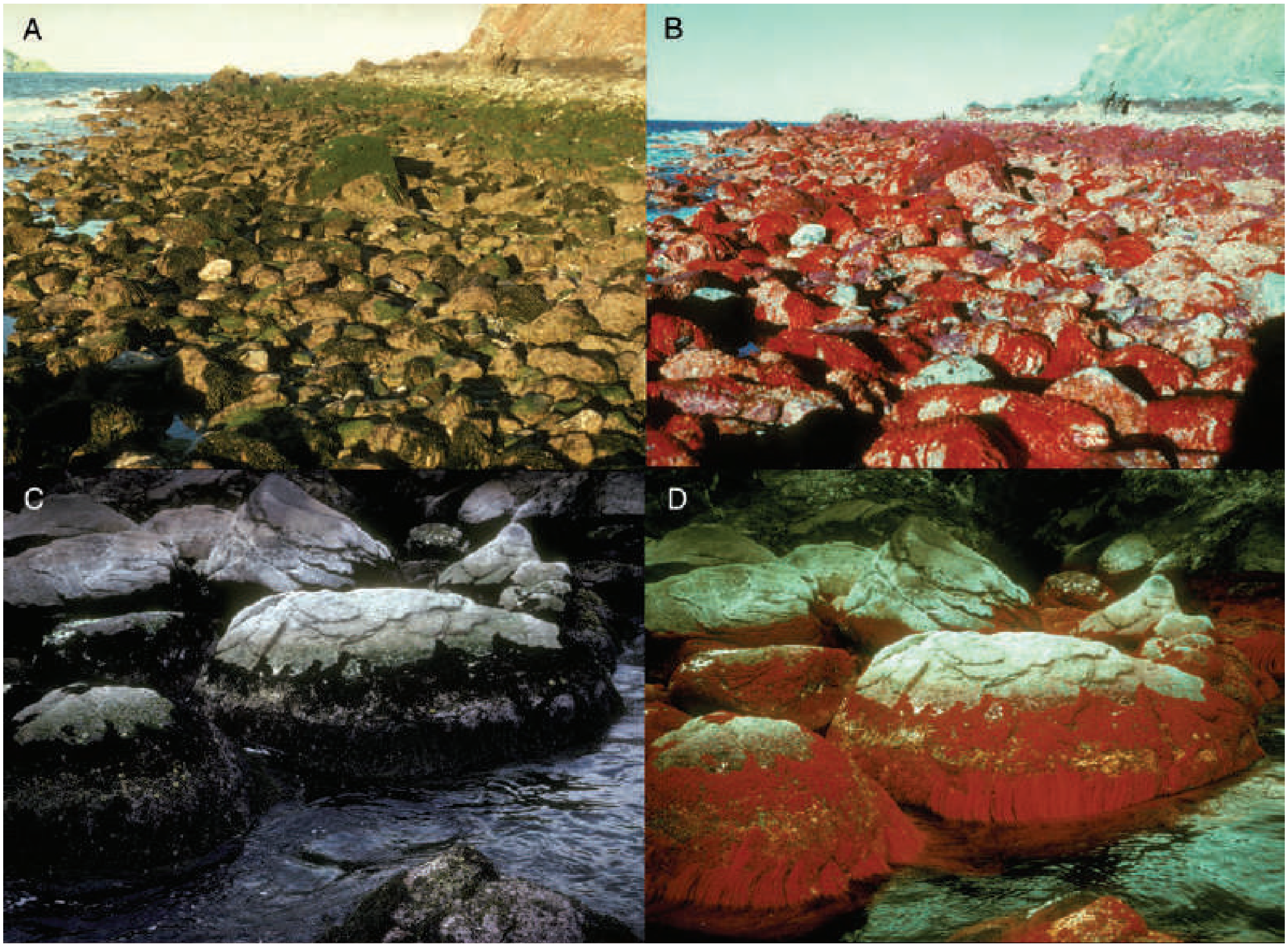
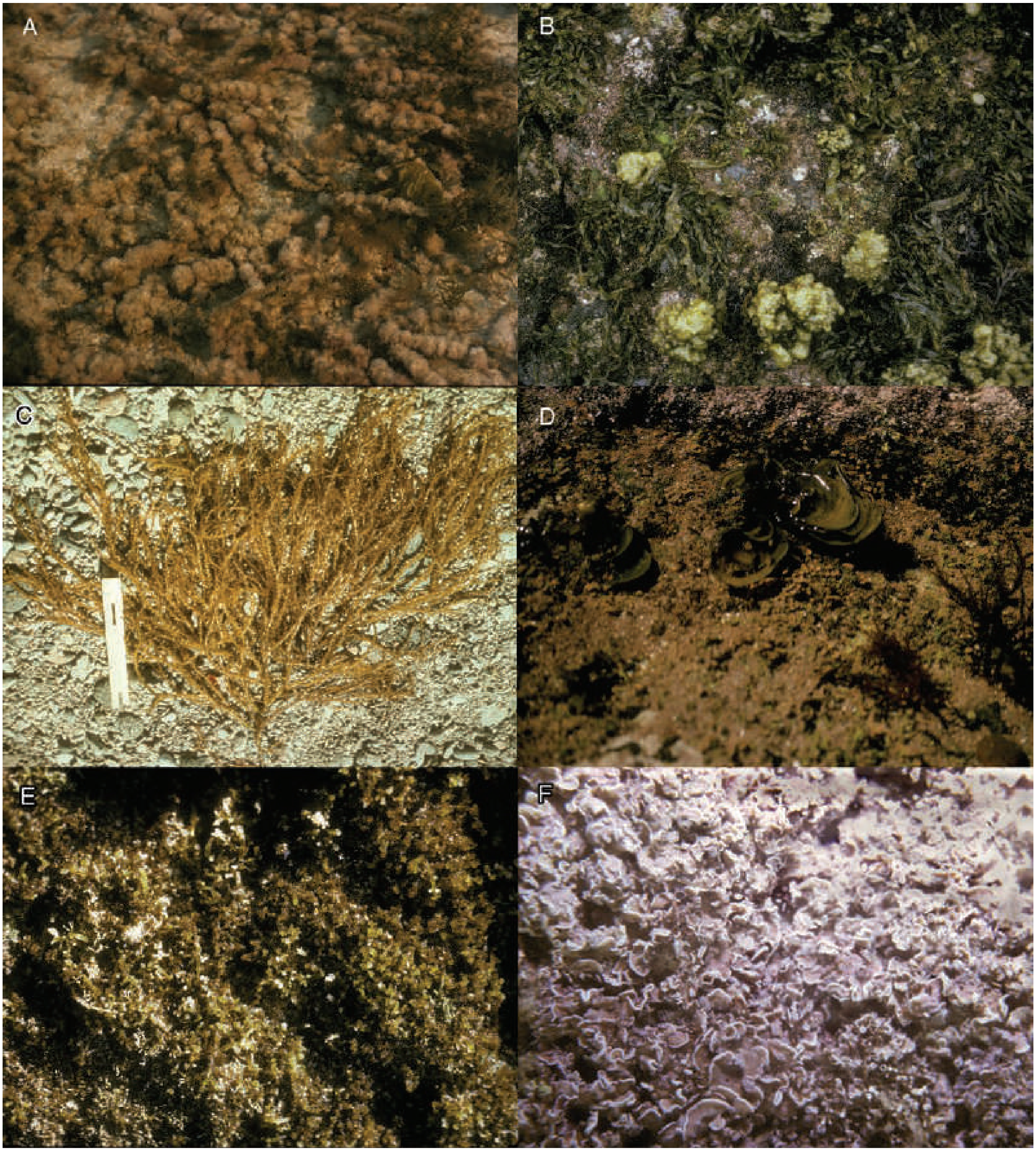


FIGURE 7. Punta Bufeo (about 3.2 km north of Bahía San Luís Gonzaga), one of the species-rich study sites on the east coast (Gulf coast) of Baja California. Comparison of the coverage of intertidal macroalgae using natural light (A, C) and with infrared photography (B, D), a nondestructive technique for identifying and quantifying algal coverage developed by M. Littler and Littler (1985). A, B. A rocky intertidal. C, D. Close-up of larger intertidal boulders. In each comparison, the contrasting natural light and infrared images show more extensive coverage using infrared by revealing the chlorophyll (in red colors) of the different algal species (photos by Diane Littler and Mark Littler).

FIGURE 8. (Opposite) Northern Gulf red algae: A. Dense clumps of epiphytic *Jania capillacea* covering *Sargassum,* Playa Estación, Puerto Peñasco (November 1973). B. *Corallina* and crustose corallines among *Chondracanthus* (blackish) and *Colpomenia tuberculata* and *C. phaeodactyla*; intertidal, Puerto Refugio, Isla Ángel de la Guarda (R/V *Dolphin* expedition, April 1974). C. *Tacanoosca uncinata*, a large specimen (scale of white ruler is 22.5 cm) of a species of economic potential, Bahía San Francisquito (May 1973). D. *Chondracanthus squarrulosus* (two on lower left) growing on crustose corallines, Puerto Refugio, Isla Ángel de la Guarda (M/V *Makrele* expedition, April 1969). E. *Palisada paniculata,* short growth form (note that the white tips indicate solar burn) that extensively covers the tidal platform, Playa Estación, Puerto Peñasco (July 1974). F. *Porolithon sonorense*, a crustose coralline endemic to the Gulf of California, on top of tidal platform, Playa Estación, Puerto Peñasco (November 1973).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and protected areas of the Gulf of California are a UNESCO World Heritage Site (http://whc.unesco.org/en/list/1182/). Conservation of its ecosystems' biodiversity is being provided by the several marine biosphere reserves, marine protected areas (for natural resources or flora and fauna), marine sanctuaries, and national marine parks in the Gulf of California (e.g., Case et al., 2002; Sala et al., 2002; Cartron et al., 2005; Enriquez-Andrade et al., 2005; Lluch-Cota et al., 2007; Danemann and Ezcurra, 2008; Brusca, 2010). It is increasingly important that we study the effects of climate change on seaweed communities and the ecosystem responses of primary productivity, species composition, and abundance to conserve and manage coastal ecosystems (Harley et al., 2012; Raven and Hurd, 2012).

Red Algae

PHYLUM RHODOPHYTA

Rhodophyta R. Wettstein, 1901:46.
Rhodophycophyta Papenfuss, 1946:218.

Members of the phylum (division) Rhodophyta, or "red algae," exhibit an extreme diversity of shapes, sizes, and forms, including unicells; coalescing cells; simple to branched pseudofilaments and uniseriate to multiseriate filaments; prostrate crusts; and erect, simple to branched terete, compressed or foliose forms that may be solid or hollow. In texture they can be soft and gelatinous or flaccid, semirigid, or cartilaginous or stony and hard (calcified). Many are considered to be beautiful, showing amazing branching patterns or cell arrangements and colors. In size the red algae can be microscopic, minute, or small to large, and some may be up to 3 meters or more in length (e.g., *Porphyra*; Guiry and Guiry, 2009–2011). Vegetative anatomy can be pseudofilamentous, filamentous, and nonfilamentous simple to complex forms of pseudoparenchymatous structure (Kylin, 1937, 1956; Dixon, 1973; Cole and Sheath, 1990).

Worldwide in distribution from both poles to the tropics, red algae grow in a wide variety of habitats, from the high intertidal to the deep subtidal. Some members, for example, certain crustose coralline algae, have been recorded growing at depths of 286 meters (927 feet) in tropical deepwater communities (Littler et al., 1985, 1986). The number of species of red algae is comparatively few at the poles and greatly increases in number and diversity toward the tropics.

Members of the Rhodophyta were initially grouped together on the basis of biochemical characters, i.e., their red pigments (Harvey, 1853, as Rhodospermeae). The degree of red coloring is variable among the species, from pale rose to dark red, sometimes blackish red or even greenish red. This color variation is due to accessory pigments, the phycobiliproteins, phycocyanin, phycoerythin, and allophycocyanin (organized in phycobilisomes), that mask in varying degrees the photosynthetic green pigments, chlorophyll *a* and *d* (note: Larkum and Kühl, 2005, suggested that a cyanobacterium associated with red algae may be the source of chlorophyll *d*). The chloroplasts of red algae lack external endoplasmic reticulum and contain unstacked thalakoids. Energy reserves, primarily floridean starch and galactoside floridoside, are stored in the cytoplasm. Cell wall composition is variable among the species, containing a mixture of cellulose and noncellulose polysaccharides, such as glucans, xylans, and galactans. Polysulphate esters are characteristic components of the cell walls. Some species are lightly to heavily calcified. The calcium carbonate is in the mineral form of calcite in the Corallinales P. C. Silva et Johansen (1986), some of the Peyssonneliales Krayesky, Fredericq et J. N. Norris (in Krayesky et al., 2009), and the Rhodogorgonales Fredericq, J. N. Norris et Pueschel (in Fredericq and Norris, 1995) and in the form of aragonite in some of the Nemaliales F. Schmitz (1892).

All red algae lack flagellated reproductive stages and centrioles in their life histories (Garbary and Gabrielson, 1990). Asexual reproduction is by nonflagellated spores that are either produced by vegetative transformation of a cell or developed within a sporangium. The sporangia may produce monospores (a single spore), bispores (two spores), tetraspores (four spores), or polyspores (many spores). The mobility of spores by amoeboid action and by gliding has been described for some red algal species in different classes (e.g., Pickett-Heaps et al., 2001; Ackland et al., 2007) and in the recently described "*Acrochaetium*-like" genus, *Rhodachlya* (West et al., 2008; Rhodachlyales, Rhodachlyaceae).

Sexual reproduction, varying from the relatively simple to highly specialized, characterizes the groups of red algae. Female reproductive structures in the Florideophyceae are differentiated into a carpogonial apparatus with a thread-like extension, the trichogyne. The one-celled carpogonium of the female reproductive apparatus becomes a zygote after fertilization. The zygote may divide to form carpospores or give rise to special filaments called gonimoblasts. Some or all of the cells of the gonimoblast develop into carposporangia. The mass of carposporangia, the gonimoblasts, and the specialized cell bearing them form the carposporophyte (diploid generation borne on the female gametophyte). Nonflagellate spermatia (male gametes) are produced by the spermatangia.

REMARKS. Among the benthic marine algae, the Rhodophyta, with more than 42 orders, contains the greatest number of species. Currently, more than 6,500 species of red algae are known, but there actually may be more than 12,000 species (Woelkerling, 1990). Most of the known red algal species are marine, and very few—less than 3% (or about 150 species)—are known from freshwater environments (Smith, 1950; Sheath, 1984, 2003). Even fewer red algae are terrestrial. Some, such as *Porphyridium cruentum* (S. F. Gray) Nägeli (1849; basionym: *Olivia cuenta* S. F. Gray, 1821; =*Porphyridium purpureum* (Bory de Saint-Vincent) K. M. Drew et R. Ross, 1965) form a gelatinous, blood-red-colored layer on damp soil or wood or walls with calcareous material or brickwork (Sheath and Sherwood, 2002). One genus, *Rufusia* D. E. Wujek et Timpano (1986), is described from Costa Rica and Panama and is only known in sloth hairs.

Benthic marine red algae are ecologically important. Almost all red algae are primary producers, with the exception of the very few parasitic species, providing food, oxygen, and structural habitat for herbivorous and omnivorous micro- to macroinvertebrates and fish, herbivorous sea turtles, and Galápagos marine iguanas. Herbivorous marine mammals, the manatees and dugongs, also ingest red algal epiphytes while grazing on seagrasses. Crustose corallines and calcified peyssonnelioids are important components in the buildup of layers of biotic (coral) reef structure. Others, as free-living rhodoliths or maerl, are harvested in coastal regions or sometimes dredged, crushed, and used as fertilizers or soil conditioners in agriculture and gardening (see discussion of Corallinales herein). Some red algal species are harvested in the field or grown in mariculture or aquaculture to be used as human foods or are used by the phycocolloid medical or cosmetic industries for their natural products, including antioxidants, cytotoxins, and other bioactive compounds (see, e.g., Naylor, 1976; Dawes, 1987; Ohno and Critchley, 1993; Jones, 2008; Zubia et al., 2009; Tierney et al., 2010; see also discussion of *Pyropia*, *Tacanoosca*, Gelidiales, and Gracilariales herein).

The Rhodophyta are one of the oldest groups of eukaryotic algae. Possible fossils of red algae may be from about 2 BYA (billion years ago) (Tappan, 1976). The noncalcified, filamentous *Bangiomorpha* N. J. Butterfield (2000), which resembles the living species of *Bangia*, originated about 1.2 BYA in the late Mesoproterozoic to early Neoproterozoic (Butterfield et al., 1990; Butterfield, 2000). It is generally accepted that the plastids of red (Rhodophyta), green (Chlorophyta), and "glaucophyte" algae share a common ancestry, having originated from a cyanobacterial endosymbiosis (Cavalier-Smith, 1986; Bhattacharya and Medlin, 1995; Delwiche et al., 1995; Delwiche, 1999, 2007; Moreira et al., 2000; Bhattacharya et al., 2004; Rodríguez-Ezpeleta et al., 2005; Yoon et al., 2006a, 2006b; Reyes-Prieto et al., 2007). The Rhodophyta is one of the three "primary" plastid-containing groups taxonomically classified within the kingdom Plantae Haeckel, 1866 (Cavalier-Smith, 1998) or more recently considered to be within the Archaeplastida Adl et al. (2005, 2012).

Pseudoparenchymatous red algae have been recognized and described from as early as the late Neoproterozoic, about 600–550 MYA (million years ago), and were apparently noncalcified when living (Xiao et al., 1998; Xiao and Knoll, 2000; Saunders and Hommersand, 2004). The simple pseudoparenchymatous red algae, such as *Wengania* (Zhang, 1989; Zhang et al., 1998), are among the earliest lineages near the base of the florideophytes, and the more complex pseudoparenchymatous species (e.g., *Thallophyca*) represent stem groups of the coralline algae (Johnson, 1960, 1961; Xiao et al., 2004). Calcifying red algae first appeared in the Paleozoic, 543–248 MYA (Brooke and Riding, 1998), and coralline red algae appeared in the Early Cretaceous of the late Mesozoic, 144–65 MYA, and through the Cenozoic, 65 MYA to present (Arias et al., 1995; Aguirre et al., 2000, 2010). Among the orders of class Florideophyceae, there is fossil evidence (Wray, 1977) that members of Corallinales may go back to the Cretaceous (130 MYA), and the Peyssonneliales and Gigartinales diverged from the Late Jurassic (160 MYA).

Red algal taxonomists have followed and continuingly modified the classification system of Schmitz (1889, 1892) and Kylin (1956). It traditionally has been accepted that there were two major groups of red algae, the Bangiophyceae and Florideophyceae (e.g., Schaffner, 1922; Papenfuss, 1955; Silva et al., 1996a; Abbott, 1999), with debate as to whether these groups should be classes or subclasses. For years the higher classification of the red algae remained in a state of flux (Dixon, 1973), with members of the Bangiophycidae considered to be polyphyletic (Müller et al., 2003, 2005b; Sutherland et al., 2011) and those of the Florideophycidae considered to be monophyletic (Gabrielson and Garbary, 1986, 1987; Garbary and Gabrielson, 1990).

More recently, three systems of higher classifications have been proposed on the basis of molecular, phylogenetic, and morphological analyses (e.g., Saunders and Hommersand, 2004; Adl et al., 2005, 2012; Yoon et al., 2006b). Saunders and Hommersand (2004) described the subkingdom Rhodoplantae G. W. Saunders et Hommersand with two phyla of red algae: (1) the Cyanidiophyta Moehn ex Doweld (2001), with a single class, Cyanidiophyceae Merola et al. (1981); and (2) the Rhodophyta to include three subphyla: Rhodellophytina Cavalier-Smith (1998), with the class Rhodellophyceae Cavalier-Smith (1998); Metarhodophytina (Magne) G. W. Saunders et Hommersand (2004), with the class Compsopogonophyceae G. W. Saunders et Hommersand (2004); and Eurhodophytina G. W. Saunders et Hommersand (2004), with the classes Bangiophyceae and Florideophyceae.

The major lineages of red algae proposed by Adl et al. (2005) in their system recognized the Rhodophyta as one of nine groups in the Archaeplastida. The Chlorophyta ("green algae") and Embryophyta (Plantae; "land plants") are within the Chloroplastida (Adl et al., 2012).

In a third system, Yoon et al. (2006b) considered the red algae to belong to a single phylum, the Rhodophyta, that contains two subphyla: (1) the subphylum Cyanidiophytina Yoon et al. (2006b), with a single class, the Cyanidiophyceae; and (2) a new subphylum, the Rhodophytina Yoon et al. (2006b), with six classes: Compsopogonophyceae, Stylonematophyceae Yoon et al. (2006b), Porphyridiophyceae Kylin (1937), Rhodellophyceae, Bangiophyceae, and Florideophyceae. Of these classes, the Bangiophyceae and Florideophyceae are herein treated as members of the subphylum Eurhodophytina.

Two of the three subphyla of the Rhodophyta are well represented in the northern Gulf of California: the Rhodophytina H. S. Yoon et al. with two of its classes; and the Eurhodophytina (Magne) G. W. Saunders et Hommersand, also represented by two of its classes. At present there are no members of the third subphylum, the Cyanidiophytina H. S. Yoon et al. known in the northern Gulf of California.

KEY TO THE SUBPHYLA OF RHODOPHYTA IN THE NORTHERN GULF OF CALIFORNIA

1a. Algae uniseriate to multiseriate pseudofilaments (initially uniseriate then becoming multiseriate within a thick gelatinous matrix); or erect or prostrate filaments (not pseudofilaments); disc-shaped or cushion-like; life histories biphasic or triphasic . . . . **Rhodophytina**

1b. Erect to prostrate, uniseriate to multiseriate filaments; or narrow to broad sheet-like blades; or structurally more complex forms, pseudoparenchymatous anatomy; life histories triphasic . . . . **Eurhodophytina**

PART I: SUBPHYLUM RHODOPHYTINA

Rhodophytina H. S. Yoon, K. M. Müller, Sheath, F. Ott, et D. Bhattacharya, 2006b:490.

The subphylum Rhodophytina includes red algae that are unicellular, pseudofilamentous, or multicellular. Cells have plastids of various morphologies and associations with differing organelles. Life histories are unknown for many species, but, where known, are either biphasic or triphasic.

Remarks. Two classes of the Rhodophytina are represented in the Gulf of California.

KEY TO THE CLASSES OF RHODOPHYTINA IN THE NORTHERN GULF OF CALIFORNI

1a. Algae uniseriate to multiseriate pseudofilaments (initially uniseriate then becoming multiseriate, with cells separated from each other within a thick gelatinous matrix) . . . . **Stylonematophyceae**

1b. Algae erect or prostrate filaments (not pseudofilaments); disc-shaped or cushion-like; life histories biphasic . . . . **Compsopogonophyceae**

PART IA. STYLONEMATOPHYCEAE

Stylonematophyceae H. S. Yoon, K. M. Müller, Sheath, F. Ott et D. Bhattacharya, 2006b:490.

Class Stylonematophyceae includes red algae that are unicellular, pseudofilamentous, or filamentous. Cells have plastids of various morphologies, with or without a pyrenoid. Golgi are associated with mitochondria and endoplasmic reticulum.

Asexual reproduction is by cell division or monospores.

Remarks. The class is currently composed of two orders: the Stylonematales, which is represented in the Gulf of California, and the more recent Rufusiales Zuccarello et J. A. West (in Zuccarello et al., 2008).

STYLONEMATALES

Stylonematales K. M. Drew, 1956b:73.

Chrootheceales F. D. Ott, 2009:554.

The Stylonematales is a monotypic order, with the characteristics of the family.

STYLONEMATACEAE

Stylonemataceae K. M. Drew, 1956b:73.

Chrootheceaceae F. D. Ott, 2009:555.

Goniotrichiceae G. M. Smith, 1933:120, *nom. superfl.* [see Silva, 1980: 83].

Algae of this family are usually uniseriate, simple to branched pseudofilaments; others may be multiseriate, branched pseudofilaments. Cells of the pseudofilaments are separate from each other within a conspicuous, thick gelatinous matrix. Growth is by intercalary cell divisions. Cells are variable in shape, ovoid, ellipsoid, or cylindrical, and uninucleate, with most having a single stellate chloroplast. Pit plugs are absent.

Asexual reproduction is by monospores and by direct metamorphosis of vegetative cells (with no apparent cell division) that function as spores and are released by dissolution or rupture of the enveloping gelatinous matrix. Sexual reproduction is unknown.

Two genera of the Stylonemataceae are reported in the northern Gulf of California.

KEY TO THE GENERA OF THE STYLONEMATACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. False-branched pseudofilaments of several globose cells, blue-green to brownish, within a broad gelatinous sheath .... ***Chroodactylon***

1b. Irregularly branched, uniseriate or multiseriate, pseudofilaments of mostly rectangular, reddish cells within a comparatively narrower gelatinous sheath .... ***Stylonema***

Chroodactylon Hansgirg

Chroodactylon Hansgirg, 1885:14.

Asterocytis (Hansgirg) Gobi ex F. Schmitz, 1896:324.

Algae are false-branched pseudofilaments. Pseudofilaments are composed of oval or elliptical cells that are enclosed within a broad, gelatinous sheath. Cells are arranged in an irregular uniseriate manner. Cells are 3.0–16 µm in diameter, 6.0–20 µm in length. Each cell contains a blue-green stellate, chloroplast, and a prominent pyrenoid. There is usually one false branch about every 200 µm of length of the pseudofilaments.

Asexual reproduction is by fragmentation and by monospores. Sexual reproduction has not been found.

One species is reported in the northern Gulf of California.

Chroodactylon ornatum (C. Agardh) Basson

Conferva ornata C. Agardh, 1824:104.

Chroodactylon ornatum (C. Agardh) Basson, 1979:67, pl. IX: fig. 52; Stewart, 1991:61; Yoshida, 1998:426, fig. 3-1D; Sheath and Sherwood, 2002:123; Brodie and Irvine, 2003:42, fig. 5.

Asterocytis ornata (C. Agardh) G. Hamel, 1924:451, figs. b–d; Tanaka, 1944:79, figs. 1–2; Tanaka, 1952:11, fig. 6; Phạm-Hoàng, 1969:68, fig. 2.2; Lewin and Robertson, 1971:236.

Hormospora ramosa Thwaites in Harvey, 1848b: pl. 213.

Chroodactylon ramosum (Thwaites) Hansgirg, 1885:19; Abbott and Hollenberg, 1976:283, fig. 225; Abbott, 1999:42, fig. 1A.

Goniotrichum ramosum (Thwaites) Hauck, 1885:517.

Asterocytis ramosa (Thwaites) Gobi ex F. Schmitz, 1896:314; Huerta-Múzquiz and Garza-Barrientos, 1975:7; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1986:420; González-González et al., 1996:302.

Algae forming filamentous tufts, blue-greenish in color, up to 5 mm tall; pseudofilaments of false branches, 300 µm (or more) in length, mostly about 25 µm in diameter; cells oval to adaxially compressed, about 15–18 µm in diameter; within thick gelatinous sheaths, sometimes up to 1(–3) mm thick (description after Abbott and Hollenberg, 1976).

Sexual reproduction unknown.

HABITAT. Epiphytic on *Compsonema secundum* f. *terminalis*; intertidal.

DISTRIBUTION. Gulf of California: Segundo Cerro Prieto, Bahía Kino; Bahía de La Paz. Central Pacific: Hawaiian Islands. Eastern Pacific: California; Isla Socorro (Islas Revillagigedo). Western Pacific: Vietnam; Japan.

TYPE LOCALITY. Lake Mälaren, bridge near Transberg, Stockholm, Sweden.

REMARKS. *Chroodactylon ornatum* is a widely distributed epiphyte, found on submerged plants and algae in marine, brackish, and freshwater habitats (Womersley, 1994; Sheath, 2003). Lewin and Robertson (1971), on the basis of morphological changes correlated with different salinities in culture, questioned if the marine and freshwater inhabitants were one or more species. However, most since then have accepted them as a single species (e.g., Schneider and Searles, 1991; Womersley, 1994).

Stylonema Reinsch

Stylonema Reinsch, 1875:40; Wynne, 1985b:502–503.

Algae are mostly microscopic or sometimes minute, consisting of cells embedded in a homogenous mucilaginous sheath that may be unbranched or pseudodichotomously to irregularly branched, uniseriate to multiseriate pseudofilaments, or some may form a monostromatic blade. Species are attached below by a typical cell or a slightly enlarged basal cell. Cells are usually quadrate with rounded corners, or occasionally oblong, and have a single stellate chloroplast with a large, central pyrenoid. Growth initially in the earliest stages of spore development may be apical, then becomes intercalary or diffuse as it grows.

Asexual reproduction occurs by transformation of the entire contents of vegetative cells into archeosporangia. Each archeosporangium releases a single archeospore (without a cell wall) by moving through the surrounding mucilaginous sheath or by dissolution of the sheath. Sexual reproduction is unknown.

REMARKS. Species of *Stylonema* are usually epiphytic or epizoic and are widely reported throughout temperate to tropical waters.

There are two species known in the Gulf of California.

KEY TO THE SPECIES OF *STYLONEMA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Pseudofilaments uniseriate below; above pseudofilament usually 1 cell (sometimes 2–3 cells) wide . . . . *S. alsidii*
1b. Pseudofilaments develop above a single basal cell becoming 2–6(–8) cells wide, usually with a single cell at the apex . . . . *S. cornu-cervi*

Stylonema alsidii (Zanardini) K. M. Drew

FIGURE 9A

Bangia alsidii Zanardini, 1839:136; 1841:217.

Stylonema alsidii (Zanardini) K. M. Drew, 1956b:72; Wynne, 1985b:503; Scagel et al., 1989:261; Mateo-Cid and Mendoza-González, 1991:18; Stewart, 1991:61; Mateo-Cid and Mendoza-González, 1992:19; Mendoza-González and Mateo-Cid, 1992:16; Serviere-Zaragoza et al., 1993a:484; Stout and Dreckmann, 1993:9; Mateo-Cid and Mendoza-González, 1994b:38; Mendoza-González et al., 1994:104; Bula-Meyer, 1995:32; Mendoza-González and Mateo-Cid, 1996b:64, 83, pl. 1: fig. 2; Abbott, 1999:44, fig. 1B,C; L. Aguilar-Rosas et al., 2000:130, 137; Mateo-Cid et al., 2000:63; CONANP, 2002:140; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Brodie and Irvine 2003:46, figs. 7, 8; Dreckmann et al., 2006:154; Mateo-Cid et al., 2006:55, 62; R. Aguilar-Rosas et al., 2006a:53, fig. 2A,B; Pacheco-Ruíz et al., 2008:205; Bernecker, 2009:CD-Rom p. 58.

Goniotrichum alsidii (Zanardini) M. Howe, 1914:75; Setchell and Gardner, 1924:741; Setchell and Gardner, 1930:151; Taylor, 1945:132; Tanaka, 1952:5, figs. 2, 3; Abbott and Hollenberg, 1976:280, fig. 222; Silva, 1979:315; R. Aguilar-Rosas, 1982:84; Schnetter and Bula-Meyer, 1982:108, pl. 9: fig. 1; Stewart and Stewart, 1984:142; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:421; Santelices and Abbott, 1987:8; Salcedo-Martínez et al., 1988:83; Sánchez-Rodríguez et al., 1989:41; Dreckmann et al., 1990:27, pl. 4: fig. 2; Ramírez and Santelices, 1991:164; González-González, 1993:441; León-Tejera and González-González, 1993:496; Mateo-Cid and Mendoza-González, 1994b:38; González-González et al., 1996:313; Riosmena-Rodríguez et al., 2005a:33; Fernández-García et al., 2011:65.

Goniotrichum elegans var. *alsidii* (Zanardini) Zanardini, 1873:457, pl. 96A.

Bangia elegans Chauvin, 1842:33.

Goniotrichum elegans (Chauvin) Zanardini, 1847: 249; Rosenvinge, 1909:75, figs. 15, 16; Kylin, 1937:44, fig. 17A; Kylin, 1941:3; Smith, 1944:161, pl. 35: figs. 1, 2; Dawson, 1953a:3; 1957c:13; 1961b:401; 1962b:184, 229, fig. 38a, b; Dawson et al., 1964:30, pl. 2: fig. B; Dawson, 1966a:14; Dawson and Neushul, 1966:174; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Garbary et al., 1980b:144; Pedroche and González-González, 1981:66; Stewart and Stewart, 1984:142; Santelices and Abbott, 1987:8; González-González et al., 1996:212.

Goniotrichum elegans (Chauvin) Le Jolis, 1863b:103; Kylin, 1925:6, fig. 1a,b; Dawson, 1944a:251.

Stylonema elegans (Chauvin) V. May, 1965:352.

Thalli minute epiphytes, 0.5–2.0 mm tall; pseudofilaments uniseriate in lower portions, 12–15 µm in diameter, occasionally becoming 2–3 cells wide in upper portions, 15–30 µm in diameter; simple or irregularly branched; attached by a single basal cell. Cells up to 10 µm in diameter, closely arranged within the thick, hyaline, gelatinous matrix of the pseudofilament.

Asexual reproduction as described for genus; monospores about 10 µm in diameter. Sexual reproduction unknown.

HABITAT. Epiphytic on various algae and sea grasses, including species of *Ulva*, *Bryopsis*, *Cladophora*, *Hincksia*, *Sphacelaria*, *Sargassum*, *Amphiroa*, *Jania*, *Botryocladia*, and *Branchioglossum*; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Tornillal (Gulfo de Santa Clara) to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: northern British Columbia to Todos Santos, Baja California Sur; Isla Guadalupe; Isla María Magdalena (Islas Marías; Islas Tres Marías); Jalisco to Chiapas; Costa Rica; Panama; Colombia; Peru; Chile; Rapa Nui (Easter Island); Isla Juan Fernández. Central Pacific: Hawaiian Islands. Western Pacific: Japan.

TYPE LOCALITY. Trieste, Gulf of Trieste (in northern part of the Adriatic Sea, near border with Slovenia), Italy.

REMARKS. *Stylonema alsidii*, usually growing as an epiphyte on other algae or epizoic on invertebrates, is widespread in temperate to tropical regions. Dawson (1953a, as "*G. elegans*") noted that some of the pseudofilaments of Gulf of California specimens of *S. alsidii* were occasionally, irregularly multiseriate in the lower portions, a condition not generally reported for the species elsewhere.

Stylonema cornu-cervi Reinsch

FIGURE 9B

Stylonema cornu-cervi Reinsch, 1875:40, pl. XV [Rhodophyceae]; Scagel et al., 1989:261; Yoshida, 1998:430, fig. 3-1H; Abbott, 1999:44, fig. 1D; Brodie and Irvine, 2003:49, fig. 9; R. Aguilar-Rosas et al., 2006a:55, fig. 3A–C.

Goniotrichum cornu-cervi (Reinsch) Hauck, 1885:519; Howe, 1914: 76; Kylin, 1925:6, fig. 1c–e; Kylin, 1937:41, fig. 17B; Tanaka, 1944:222, figs. 4, 5; Hollenberg, 1948:156; Tanaka, 1952:9, fig. 5; Dawson, 1961b:401; Dawson et al., 1964:30, pl. 63: fig. A; Dawson and Neushul, 1966:174; Abbott and Hollenberg, 1976:280, fig. 223; Hawkes et al., 1978:101; Garbary et al., 1981:146; Ramírez and Santelices, 1991:165; González-González et al., 1996:212.

Algae microscopic epiphytes; of pseudofilaments, irregularly pseudodichotomously branched, usually less than 1 mm tall, 15–100 µm in diameter; lower portions mostly uniseriate, above becoming 2–4 rows of cells (4–8 cells in cross section), narrowing to uppermost portion, usually with only a single cell at tip; attached by a distinctive basal cell, 6–9 µm in diameter by 10–14 µm long. Cells ovoid, 4–8 µm diameter; irregularly arranged within the thick, hyaline matrix of the pseudofilament.

Asexual reproduction as described for genus. Monosporangia not observed in Gulf specimens. Sexual reproduction unknown.

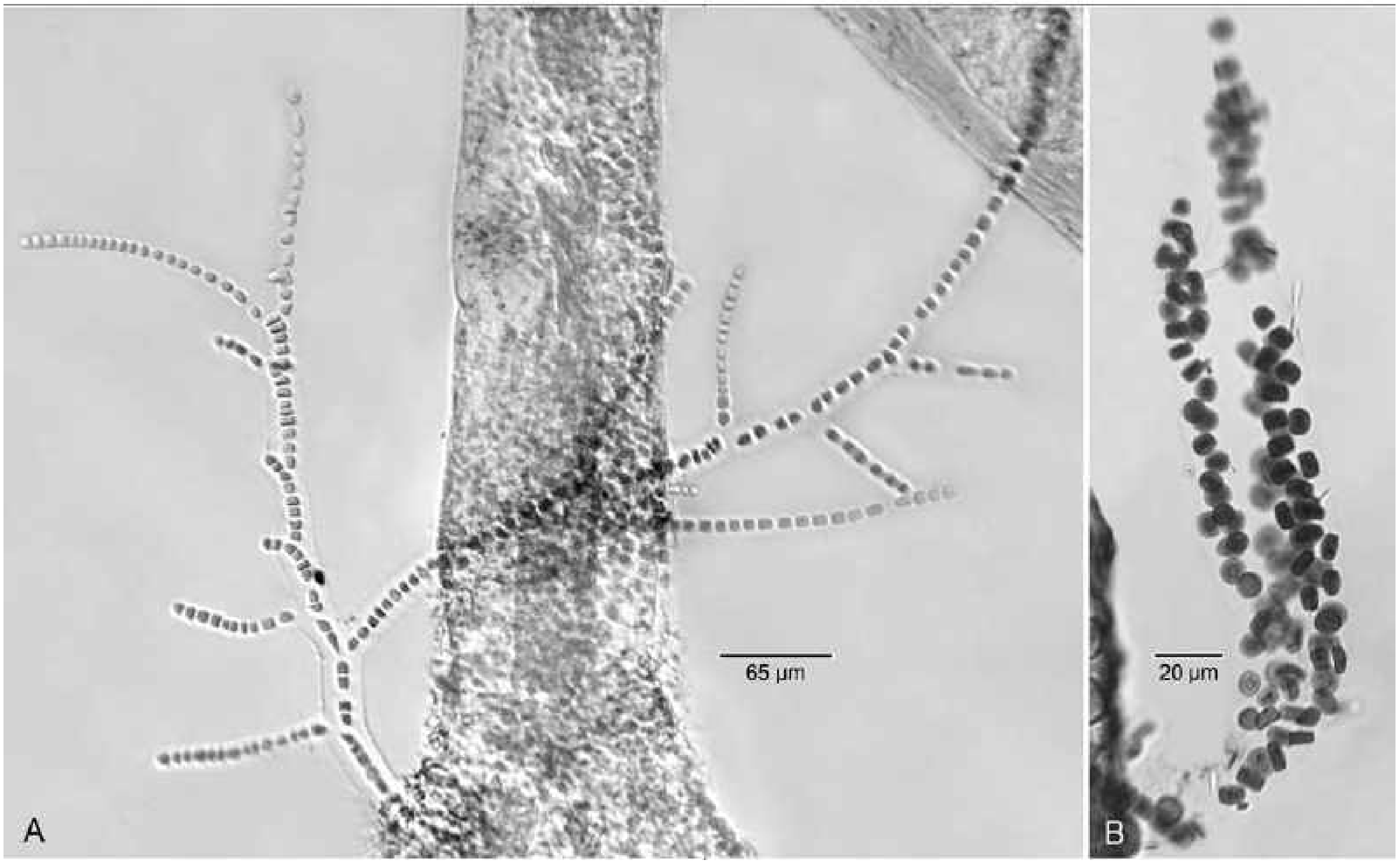


FIGURE 9. Species of *Stylonema*. A. *Stylonema alsidii:* Habit showing branching pseudofilament with cells enclosed in gelatinous matrix, regularly arranged and mostly uniseriate (*JN-4491b*, epiphytic on *Cladophora*, US Alg. Coll. microscope slide 4268). B. *Stylonema cornu-cervi:* Pseudofilament mostly multiseriate, with disc-shaped cells loosely and irregularly arranged in a gelatinous matrix, note the single basal cell and single cell at tip (*JN-4836,* epiphytic on *Anotrichium secundum,* US Alg. Coll. microscope slide 4974).

HABITAT. Epiphytic on *Anotrichium* and *Cladophora* and probably other algae; shallow subtidal, 5–15 m depths.

DISTRIBUTION. Gulf of California: Punta Robinson (vicinity of Puerto Libertad). Eastern Pacific: northern British Columbia to Cabo Punta Banda (Bahía de Todos Santos), Baja California; Peru; Chile; Isla Juan Fernández. Central Pacific: Hawaiian Islands. Western Pacific: Japan.

TYPE LOCALITY. Cres (northern island in Kvarner Gulf), Adriatic Sea, Croatia.

REMARKS. A new record for the Gulf of California, specimens of *Stylonema cornu-cervi* were found epiphytic on *Anotrichium* (*JN-4836*), and a *Cladophora* (*JN-4819b*) that was growing on *Digenea simplex*, both from Punta Robinson (east of Puerto Libertad), Sonora.

PART IB. COMPSOPOGONOPHYCEAE

Compsopogonophyceae G. W. Saunders et Hommersand, 2004:1503.

The class Compsopogonophyceae includes red algae with cells in which there is a Golgi-endoplasmic reticulum association and plastids with encircling thylakoids. Reproductive monosporangia and spermatia are produced by divisions by a curved wall through normal vegetative cells. Carpogonia, where known, are formed by the direct transformation of a vegetative cell. Life histories, where known, are biphasic.

REMARKS. Some of the members of the Compsopogonophyceae have lost the reproductive mode that is the accepted characteristic of this lineage (Nelson et al., 2003). However, as noted by Saunders and Hommersand (2004) this does not alter their overall taxonomic placement.

The class Compsopogonophyceae is represented by a single order in the Gulf of California.

ERYTHROPELTIDALES

Erythropeltidales Garbary, G. I. Hansen et Scagel, 1980b:149.

Algae are either crustose and discoid or erect and filamentous or erect and membranous. Species are found growing epi- and endophytic on various algae or sea grasses, epi- and endozoic on invertebrates, or saxicolous on rocks or other hard substratum. Structurally, the erect species are variable and may be (1) uniseriate to multiseriate filaments that are simple to irregularly branched, (2) membranous and saccate or ribbon-like and, although usually entire, some may be divided, or (3) prostrate and crustose, of uniseriate filaments that are irregularly branched that may tend to laterally coalesce. Cells have either a single stellate plastid or band- to cup-shaped parietal plastids and are with or without pyrenoids.

Asexual reproduction is by monospores that are cut off by an oblique or unequal curving wall through a vegetative cell. Sexual reproduction, where known, is by a carpogonium that is formed by direct transformation of a vegetative cell. Spermatia are produced by repeated divisions of vegetative cells by curved walls.

REMARKS. Zuccarello et al. (2011) proposed that the taxonomy of morphologically "simple" red algae—such as the Erythropeltidales, which can be difficult to distinguish—could be based on molecular studies.

One family occurs in the northern Gulf of California.

ERYTHROTRICHIACEAE

Erythrotrichiaceae G. M. Smith, 1933:120, 122; Smith, 1950:609 [see discussion of Silva et al., 1996a:912–915].

Erythropeltidaceae Skuja, 1939:33.

Algae of this family are entirely monostromatic, prostrate discs (*Erythrocladia*); partly prostrate with a basal disc and erect simple to branched filaments (*Erythropeltis*); crustose discs of radiating filaments that coalesce (*Sahlingia*); filamentous or ribbon-like to sheet-like (*Erythrotrichia*); or saccate and develop from a polystromatic disc that ruptures to form a monostromatic sheet (*Porphyropsis*).

Reproduction is by monospores that are divided from the vegetative cells by a curved wall.

REMARKS. A few members of the Erythrotrichiaceae are ribbon-like or saccate to sheet-like, but only filamentous and discoid species have been reported in the Gulf of California.

There are five genera represented in the northern Gulf of California.

KEY TO THE GENERA OF ERYTHROTRICHIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli entirely prostrate (without erect filaments); either discoid (1 cell layer) or cushion-like (1–3 cell layers); composed of laxly coalesced or free (not adjoined) branched prostrate filaments 2
1b. Thalli either a prostrate disc with erect filaments or erect and filamentous or ribbon-like, without a discoid portion . . . 3
2a. Irregularly shaped disc, with irregular margins; most marginal filaments not laterally coalesced; branching from submarginal cells; marginal cells not bifurcate; single parietal plastid with 1 central, usually irregular shaped pyrenoid . . . . *Erythrocladia*
2b. Compact disc shape of laterally coalesced filaments throughout; margins mainly entire; bifurcate marginal cells present; band-shaped or cup-shaped plastid, with circular pyrenoids . . . . *Sahlingia*
3a. Cells contain a single parietal plastid without pyrenoids; a few erect, free filaments above a distinct, discoid prostrate base . . . . *Erythropeltis*
3b. Cells contain a stellate plastid with a single pyrenoid; free filaments above a discoid base or with free filaments attached by basal cells (without a discoid base) 4
4a. Erect filaments above a discoid base . . . . *Porphyrostromium*
4b. Erect filaments attached by rhizoids (without discoid portion); thalli uniseriate and cylindrical or becoming multiseriate and compressed or flattened and ribbon-like . . . . *Erythrotrichia*

Erythrocladia Rosenvinge

Erythrocladia Rosenvinge, 1909:71.

Algae are microscopic to minute; filaments develop and radiate outward from the original spore and become irregularly branched and laxly coalesced centrally into a monostromatic disc. Disc remains monostromatic throughout or becomes polystromatic and has margins that are more or less entire or irregular with some extending free filaments. Growth is apical and at the margins in early stages of development and later becomes diffuse. Cells have a single parietal plastid with one central pyrenoid. Pit plugs are not present.

Asexual reproduction is by monospores and endospores. Monospores are formed by the division of a vegetative cell into two unequal portions, with the smaller developing into a sporangium. Asexual endospores are formed by repeated cleavage of a vegetative cell. Sexual reproduction is unknown.

There are two species of *Erythrocladia* reported in the Gulf of California, along with another somewhat similar discoid, prostrate epiphyte, a species of *Sahlingia*.

KEY TO THE SPECIES OF *ERYTHROCLADIA* AND *SAHLINGIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Endophytic within cell walls of other algae; filaments spreading out irregularly, later may become coalesced near center . . . . *Erythrocladia endophloea*

1b. Epiphytic on other algae; filaments centrally coalesced into a prostrate disc 2

2a. Irregular-shaped disc; margins uneven, with extending, elongated marginal cells (mostly not coalescing), each with a rounded tip (not bifurcate) . . . . *Erythrocladia irregularis*

2b. Disc shaped; margins more or less entire; filaments coalesced throughout; marginal cells mostly coalescing; marginal bifurcate cells present . . . . *Sahlingia subintegra*

Erythrocladia endophloea M. Howe

Erythrocladia endophloea M. Howe, 1914:81, pl. 30: figs. 1–7; Dawson et al., 1964:31, pl. 29: figs. G,H; Heerebout, 1968:143; Ramírez and Santelices, 1991:161; Schneider and Searles, 1991:180, fig. 212.

Erythrocladia recondita M. Howe et Hoyt, 1916:112, pl. 12: figs 1–5, pl. 13: fig. 1; Huerta-Múzquiz and Mendoza-González, 1985:46; González-González et al., 1996:199.

Algae minute; primarily endophytic growing between cell walls of other algae and sometimes also partly epiphytic. Initially of irregularly branched prostrate filaments, tending to form an incomplete network; later cells in central portions may partly coalesce into irregular discs, up to 180 μm in diameter, remaining mostly monostromatic. Filaments branch laterally, subdichotomously or irregularly, mostly from subterminal cells and remain free outward. In surface view: outer cells of filaments variously shaped; cells toward center portion ovoid to irregularly angular; outward mostly elongated; 4.0–14 μm in diameter.

Monospores 4–5 μm in diameter (description after Howe, 1914).

Habitat. Endo-epiphytic on *Halymenia* and probably other macroalgae; intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía de Las Ánimas; La Paz. Eastern Pacific: Peru.

Type Locality. On *Leptocladia peruviana*, dredged from 9 m depth; Bahía de Sechura, Departamento de Piura, northern Peru.

Remarks. *Erythrocladia endophloea* was recorded in the Gulf of California by Huerta-Múzquiz and Mendoza-González (1985, as "*E. recondita*"). It is also tentatively identified in/on a blade of *H. californica* from Bahía de Las Ánimas (*JN-3203b*, US Alg. Coll. microscope slide 4251).

Erythrocladia irregularis Rosenvinge

FIGURE 10A

Erythrocladia irregularis Rosenvinge, 1909:72, figs. 11, 12; Kylin, 1925:9, fig. 3A,B; Kylin, 1937:43, fig. 17C; Tanaka, 1944:93, fig. 14; Smith, 1944:166, pl. 37: fig.1; Dawson, 1944a:251; Tanaka, 1952:77, fig. 37; Dawson, 1953a:5; 1961b:402; Heerebout, 1968:141, figs. 1–4; Abbott and Hollenberg, 1976:284, fig. 226; Huerta-Múzquiz and Mendoza-González, 1985:46; Scagel et al., 1989:177; Stewart, 1991:61; Mateo-Cid and Mendoza-González, 1991:18; Ramírez and Santelices, 1991:161; Mateo-Cid and Mendoza-González, 1992:19; González-González, 1993:441; Serviere-Zaragoza et al., 1993a:483; León-Tejera and González-González, 1993:496; Mateo-Cid et al., 1993:46; Mateo-Cid and Mendoza-González, 1994b:38; Mendoza-González et al., 1994:104; González-González et al., 1996:309, 389; Mendoza-González and Mateo-Cid, 1996b:65, 83, pl. 1: fig. 5; Yoshida, 1998:432, fig. 3-1I; CONANP, 2002:140 [as "*Erythrotrichia irregularis*"]; Dreckmann et al., 2006:154; Mateo-Cid et al., 2006:55, 62; Pacheco-Ruíz et al., 2008:205; Zuccarello et al. 2010:366, fig. 3b–g, tbls. 1, 2.

Algae epiphytic, discoid, monostromatic (rarely distromatic), up to 300 μm across; adhering directly to host. Irregularly shaped discs; composed of prostrate filaments coalesced only in central portion; outward with uneven margins of irregularly branched filaments, mostly free from one another. Cells in central portion, polygonal, up to 8 μm; cells of margins, 3–4 μm in diameter and longer than wide; pyrenoids mostly irregularly shaped.

Asexual reproduction by subspherical monosporangia, formed in central portion of disc. Sexual reproduction unknown.

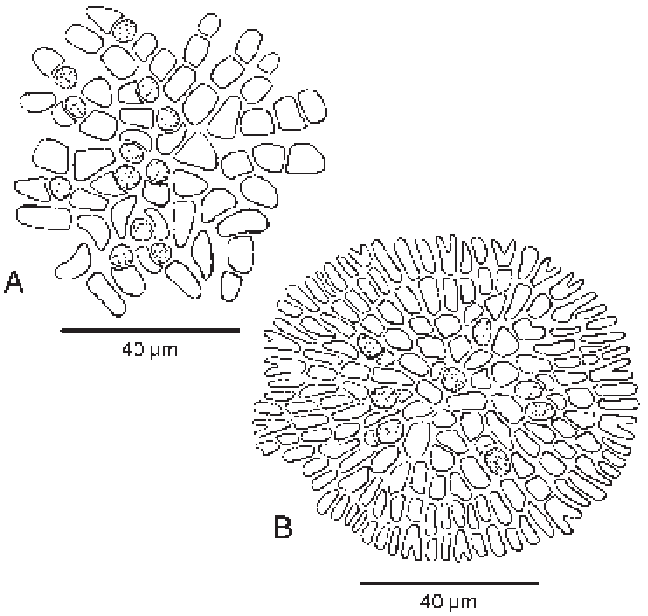


FIGURE 10. Species of *Erythrocladia* and *Sahlingia*. A. *Erythrocladia irregularis:* Prostrate disc with monospores (after Kylin, 1925: fig. 3a). B. *Sahlingia subintegra:* Prostrate disc with monospores (after Kylin, 1925: fig. 3g, as *Erythrocladia subintegra*).

HABITAT. Epiphytic on species of *Chaetomorpha, Dictyota* and probably other algae; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla Turner (off SE end of Isla Tiburón); Isla Estanque (Pond Island); Bahía Concepción to Bahía de La Paz; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Alaska to Todos Santos, Baja California Sur; Oaxaca to Chiapas; Chile. Western Pacific: Japan; Korea.

TYPE LOCALITY. Epiphytic on *Polysiphonia urceolata*; Møllegrund, about 0.8 km off Hirshals, Skagerrak, northern Denmark.

REMARKS. *Erythrocladia irregularis*, the lectotype of the genus (Kylin, 1956), has sometimes been considered to be conspecific with *Sahlingia subintegra* (e.g., Heerebout, 1968; Garbary et al., 1981, both as *Erythrocladia subintegra*). Morphologically *E. irregularis* differs primarily from *S. subintegra* in being irregular-discoid in shape, the result of having free (non-coalesced) marginal filaments that develop an irregular margin. Kornmann and Sahling (1985) and Kornmann (1989) also used development of the disc to further separate the two genera, with the early development of *Sahlingia* being a four-celled stage and a more regular disc shape with even margins.

Erythropeltis F. Schmitz

Erythropeltis F. Schmitz, 1896:313.

Algae epiphytic or epizoic; a prostrate monostromatic disc, with or without a few, short erect filaments. Growth from marginal cells. Cells irregularly arranged within disc; with a single parietal plastid. Monosporangia formed by oblique wall within a vegetative cell.

REMARKS. *Erythropeltis* is apparently a monotypic genus. Schmitz (in Schmitz et Hauptfleisch, 1896) originally described the genus as only being discoid (without erect filaments), having apparently overlooked the study of Berthold (1882a, 1882b), who had earlier described the generitype, *Erythrotrichia discigera,* as a disc with erect filaments (see also Batters, 1900; Rosenvinge, 1909; Silva et al., 1996a). Specimens identified as *Erythropeltis discigera* were cultured by Kornmann (1984) and Kornmann and Sahling (1985) and were found to have a heteromorphic life history of filamentous and discoid phases, which were both reproduced by monospores. Although *Erythropeltis discigera* is generally accepted as a species, it may be involved in the life history of *Porphyrostromium ciliare* (Brodie and Irvine, 2003). Further study is needed to clarify the generic status of *Erythropeltis*.

There is one species of *Erythropeltis* reported in the northern Gulf of California.

Erythropeltis discigera (Berthold) F. Schmitz

Erythrotrichia discigera Berthold, 1882a:511; Berthold, 1882b:25, pl. 1: figs. 15–18; Kylin, 1937:44, fig. 19A–C.

Erythropeltis discigera (Berthold) F. Schmitz, 1896:313, fig. 195; Dawson, 1944a:252; 1953a:6; 1961b:401; González-González et al., 1996:199; Brodie and Irvine, 2003:61.

Algae epiphytic; prostrate and discoid; spreading, up to 300 µm across; margins irregular; either without erect filaments or with a few short, erect filaments arising from the central portion of disc. Discoid portion monostromatic to polystromatic, of mostly polygonal cells, each with a single parietal plastid.

Monosporangia globose, cut off from originating cell by an oblique wall.

HABITAT. Epiphytic on *Sphacelaria* and probably on other algae; intertidal.

DISTRIBUTION. Gulf of California: Isla Tiburón (Islas de la Cintura).

TYPE LOCALITY. Epiphytic on *Cystoseira compressa;* Gulf of Naples, southwest coast of Italy, Tyrrhenian Sea, Italy.

REMARKS. The taxonomic status of *Erythropeltis discigera* is somewhat uncertain. Batters (1900) suggested *Erythrotrichia discigera* Berthold, the generitype of the genus *Erythropeltis*, may be a synonym of *Bangia ciliaris* Carmichael ex Harvey (in W. J. Hooker, 1833). Later, *Erythropeltis discigera* was also used as the type for another genus, *Erythrotrichopeltis* Kornmann (1984). Taxonomically, Kornmann (1984) also considered it conspecific with *Bangia ciliaris* Carmichael ex Harvey, making the combination *Erythrotrichopeltis ciliaris* (Carmichael) Kornmann (which is now *Porphyrostromium ciliare* (Carmichael ex Harvey) M. J. Wynne, 1986). Others have kept *Erythropeltis* and *Porphyrostromium* separate (e.g., Furnari et al., 2003), and Brodie and Irvine (2003), although recognizing *Erythropeltis discigera* as a distinct species, noted it may possibly be part of the life history of *Porphyrostromium ciliare*. Comparative morphological, molecular, and culture studies are needed on type locality *Erythropeltis discigera* and the Gulf of California *E. discigera* to elucidate their taxonomic status and possible relationship to *P. ciliare*.

Erythrotrichia Areschoug

Erythrotrichia Areschoug, 1850:435.

Algae are minute, erect, filaments that are uniseriate throughout, uniseriate only in the lower portion and multiseriate above, or multiseriate, flattened, and ribbon-like. They are unbranched or occasionally branched and attached by rhizoids from a basal cell or basal cells. Growth is usually apical in the initial stages of development and then becomes intercalary and diffuse. Each cell has a single, stellate plastid with a central pyrenoid. Pit plugs are absent.

Asexual reproduction is by monospores. An oblique wall is formed within the parent cell, dividing it into two unequal-sized cells; the smaller portion becomes the monosporangium that releases a single monospore. Sexual reproduction, where known, is by a three-celled gametophyte, with the apical cell initially producing a spermatangium by oblique division. Following the release of a single, very small, pale spermatium, the remaining contents of the apical cell differentiate into a carpogonium. Upon contact with a spermatium, the carpogonium fuses and develops a zygote that germinates directly on the gametophyte and develops a linear series of diploid cells that, in turn, produce monosporangia. Meiosis is likely somatic, occurring at the time of monospore germination.

Remarks. Species of *Erythrotrichia* are minute, often microscopic algae, and are usually epiphytic on various larger algae or sea grasses. Acknowledging the difficulty of separating these morphologically simple species, Zuccarello et al. (2010; 2011) noted future descriptions should include molecular and morphological data from standardized culture conditions.

There is one species in the southern Gulf, *Erythrotrichia ascendens* E. Y. Dawson (1953a), an epiphyte on *Galaxaura,* described from a beach approximately 8.05 km [5 miles] north of Cabo Pulmo, Baja California Sur.

Four other species of *Erythrotrichia,* including one with two taxonomic forms (*forma*), are currently known from the northern Gulf of California.

KEY TO THE SPECIES OF *ERYTHROTRICHIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Filaments cylindrical throughout; attached by a single basal cell 2
1b. Filaments cylindrical, compressed or flattened; attached by branched rhizoidal processes from lowermost basal cell . . . 4
2a. Lowermost basal cell elongated and tapering downward; penetrating cortical cells of algal host . . . . ***E. biseriata***
2b. Lowermost basal cell lobed (not tapered) at point of attachment on surface of algal host (not penetrating host) 3
3a. Filaments up to 3 mm long, 12–30 µm in diameter; monosporangia small, 5.0–10 µm in diameter . . . ***E. carnea* f. *carnea***
3b. Filaments shorter and narrower, mostly less than 1 mm long and 9.0–12 µm in diameter; monosporangia slightly larger, about 12 µm in diameter . . . . ***E. carnea* f. *tenuis***
4a. Cylindrical in lower portion and broadening in upper portion, up to 4(–8) rows of cells wide, with cells in transverse rows . . . . ***E. tetraseriata***
4b. Mostly cylindrical throughout; only 1–2 cells wide . . . . ***E. parksii* var. *minor***

Erythrotrichia biseriata Tak. Tanaka

FIGURES 11, 12A–C

Erythrotrichia biseriata Tak. Tanaka, 1944:86, fig. 8A–G; 1951:98; 1952:17, fig. 8A–G; Dawson, 1953a:7; 1954a:4; 1961b:401; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Kajimura, 1979:98; León-Tejera and González-González, 1993:496; González-González et al., 1996:200, 390; Serviere-Zaragoza et al., 2007:9 [as "*Erythrotrichia carnea.*"]

Algae epiphytic, unbranched, more or less erect filaments, 1–2 mm long, 10–26 µm diameter; attached by a lowermost basal cell penetrating cortical cells of algal host. Filaments initially uniseriate and remaining so in lower portions; later can become 2 cells wide by longitudinal divisions in portions of upper thallus (appearing more or less biseriate). Cells of filaments within gelatinous matrix, about 3–4 µm thick; cells usually not as long as wide, more or less quadrate with rounded corners; 8–15 µm long by 10–22 µm in diameter; chloroplast stellate with a central pyrenoid. Lowermost basal cell distinctive from above cells; elongated and more slender, tapering downward, 25 µm in length and 8 µm in diameter.

Asexual reproduction by ovate monospores, 6–8 µm by 5–7 µm; apparently cutoff laterally (see Tanaka, 1944: fig. 8G). Sexual reproduction unknown.

Habitat. Epiphytic on *Colpomenia*, *Halymenia*, and *Tacanoosca uncinata*; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Libertad; Bahía de Las Ánimas; Ensenada de San Francisco; Mazatlán. Eastern Pacific: Isla San Benedicto (Islas Revillagigedo); Baja California to Oaxaca. Western Pacific: Japan; Taiwan.

Type Locality. Hachijō-jima (Hatidyō Island), Izu islands, south of Tokyo, Japan.

Remarks. *Erythrotrichia biseriata* was listed as a synonym of *E. carnea* by Yoshida (1998) but without comment.

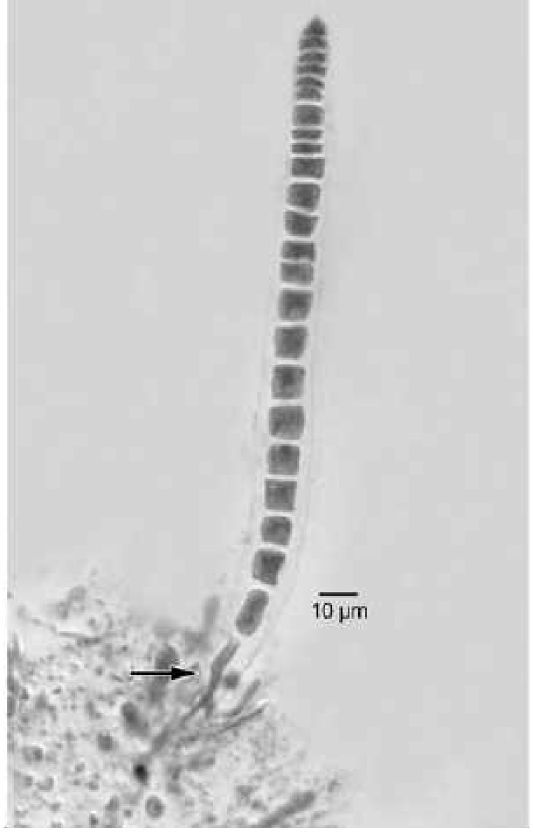


FIGURE 11. *Erythrotrichia biseriata:* Developing filament (not yet biseriate) with the characteristic, penetrating linear-elongate basal cell (arrow) (*JN-3203c*, epiphytic on *Halymenia,* US Alg. Coll. microscope slide 4251).

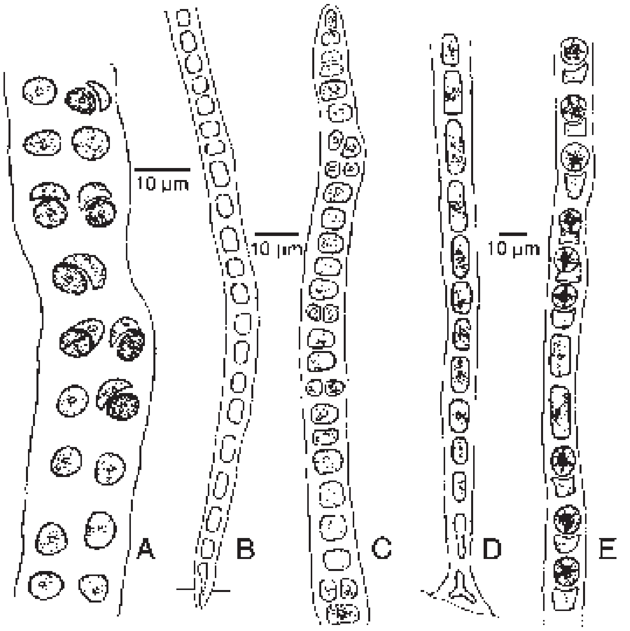


FIGURE 12. Species of *Erythrotrichia*. A–C. *Erythrotrichia biseriata:* A. Part of a filament with monosporangia. B. Basal portion of young filament with elongate basal cell. C. Upper part of biseriate filament (A–C after Tanaka, 1952: fig. 8E, F, H). D, E. *Erythrotrichia carnea* f. *tenuis:* D. Basal portion of young filament. E. Mature filament with monosporangia (D, E after Tanaka, 1944: fig. 13).

However, the species appears to be distinctive. The Gulf specimens referred to *E. biseriata* are apparently developing juveniles, with the characteristic long basal cell, that have not yet become two cells wide in the upper portions (see Tanaka, 1944: fig. 8F).

Erythrotrichia carnea (Dillwyn) J. Agardh

Conferva carnea Dillwyn, 1807:54, pl. 84.

Erythrotrichia carnea (Dillwyn) J. Agardh, 1883:15, pl. 19; Kylin, 1937:43, fig. 18B–D; Smith, 1944:164, pl. 35: figs. 3–7; Dawson, 1944a:252; Tanaka, 1944:92, fig. 13A; 1951:97, fig. 1A–D; 1952:14, fig. 7A; Dawson, 1953a:10; 1957c:13; 1959d:4; 1961b:401; 1962b:170, 229, fig. 6; 1963c:5; 1966a:14; Dixon and West, 1967:253, fig. 1A–D; Heerebout, 1968:151, figs. 5–11, 14–18; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Norris, 1973:8; Huerta-Múzquiz and Garza-Barrientos, 1975:7; Abbott and Hollenberg, 1976:286, fig. 228; Silva, 1979:315; R. Aguilar-Rosas, 1982:84; Stewart and Stewart, 1984:142; Huerta-Múzquiz and Mendoza-González, 1985:46; Santelices and Abbott, 1987:8; Salcedo-Martínez et al., 1988:83; Sánchez-Rodríguez et al., 1989:41; Dreckmann et al., 1990:27, pl. 4: fig. 1; Rocha-Ramírez and Siqueiros-Beltrones, 1991:26; Ramírez and Santelices, 1991:163; Mateo-Cid and Mendoza-González, 1991:18; González-González, 1993:441; Serviere-Zaragoza et al., 1993a:483; León-Tejera and González-González, 1993:496; Mendoza-González et al., 1994:105; R. Aguilar-Rosas and Aguilar-Rosas, 1994:519; Bula-Meyer, 1995:32; González-González et al., 1996:309; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Mendoza-González and Mateo-Cid, 1996b:65, 83; Hoffman and Santelices, 1997:200, fig. 50(1–4); Yoshida, 1998:433; Abbott, 1999:45, fig. 1E; L. Aguilar-Rosas et al., 2000:130, 137; Mateo-Cid et al., 2000:63; CONANP, 2002:140; León-Tejera and González-González, 2000:327, 329, 330; Riosmena-Rodríguez et al., 2005a:33; 2005b:102; Dreckmann et al., 2006:154; Mateo-Cid et al., 2006:50, 55, 62; Serviere-Zaragoza et al., 2007:9; Bernecker, 2009:CD-Rom p. 58; Fernández-García et al., 2011:61.

Conferva ceramicola Lyngbye, 1819:144, pl. 48D.

Erythrotrichia ceramicola (Lyngbye) Areschoug, 1850:435.

Algae epiphytic; unbranched, uniseriate filaments, 1–2(–3) mm long and 12–27 μm in diameter; attached by lowermost basal cell (narrower than above cells) with short lobes or with short rhizoidal outgrowths. Cells of filaments, as long as wide or tending to be longer than wide, 14–30 μm in length and 12–27 μm in diameter; possess a stellate plastid with large central pyrenoid.

Asexual reproduction by monosporangia cut off by oblique division at distal end of cell; monospores 5–10 μm in diameter. Sexual reproduction unknown.

HABITAT. Epiphytic on various algae, including species of *Chaetomorpha, Phyllodictyon, Dictyota, Sphacelaria, Padina, Amphiroa, Corallina, Gelidium, Gelidiopsis, Botryocladia,* and *Anotrichium*; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Mazatlan, Sinaloa to Jalisco. Eastern Pacific: Alaska to Chiapas; Isla Guadalupe; Isla San Benedicto (Islas Revillagigedo); Clipperton Island; Costa Rica; Colombia; Galápagos Islands; Peru; Chile; Rapa Nui (Easter Island; Isla de Pascua); Isla Juan Fernández. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea.

TYPE LOCALITY. Epiphytic on other algae; mouth of Loughor River, Glamorganshire (Loughor), Wales, United Kingdom (Brodie and Irvine, 2003:67) (epitype: Port Eynon, Gower, Wales [Zuccarello et al., 2011:635]).

REMARKS. In the upper Gulf of California, *Erythrotrichia carnea* has been reported on numerous host algal species (e.g., Mateo-Cid et al., 2006). Dawson (1966a) observed *E. carnea* to be mostly growing on deteriorating older algae in the vicinity of Puerto Peñasco.

Culture studies and molecular analysis of Zuccarello et al. (2011) yielded seven separate lineages of *E. carnea*, one of which (lineage 2) was close to the type locality and designed as an epitype. Although the other lineages could represent new genera, because of their simple morphologies they could not be separated, and Zuccarello et al. (2011) suggested they could be identified on the basis of their genetic and phylogenetic differences.

Erythrotrichia carnea f. *tenuis* Tak. Tanaka

FIGURE 12D,E

Erythrotrichia carnea f. *tenuis* Tak. Tanaka, 1944:92, fig. 13B–E; 1951:98; 1952:16, fig. 7B–E; Dawson, 1953a:10; Kajimura, 1979:98; González-González et al., 1996:200.

Algae epiphytic; composed of simple, unbranched, uniseriate filaments, up to 1.0 mm long and 9–12 μm wide. Cells slender, of varying lengths, mostly squarish to elongate, with rounded corners, 9–20(–30) µm long and 9–12 µm in diameter; have a stellate plastid with a pyrenoid.

Monosporangia more or less spherical, about 12 µm in diameter.

Habitat. Epiphytic on *Chaetomorpha, Padina,* and *Gelidium*; intertidal.

Distribution. Gulf of California: Cabo Pulmo. Eastern Pacific: Isla Guadalupe; Punta Santa Rosaliita ("Punta Santa Rosalía"), Baja California; Guerrero. Western Pacific: Japan.

Type Locality. Several syntype localities were listed by Tanaka (1944:92–93): "Ponape (Caroline Islands); Garanbi (Taiwan); and in Japan, Yonakuni Is. (Okinawa Pref.), Makurazaki (Satuma Prov.), Takamatu (Sanuki Prov.), Fukae (Gotō Islands), and Hinomisaki (Izumo Prov.)."

Remarks. Dawson (1953a) noted that most of the Mexican specimens, with filaments of smaller size and slender proportions, were in agreement with *Erythrotrichia carnea* f. *tenuis* Tak. Tanaka. Although known in the southern Gulf, its Gulf distribution is probably more widespread. Other Gulf records as "*E. carnea*" should be molecularly compared to the Japanese *E. carnea* f. *tenuis*, and their taxonomic status needs to be further evaluated.

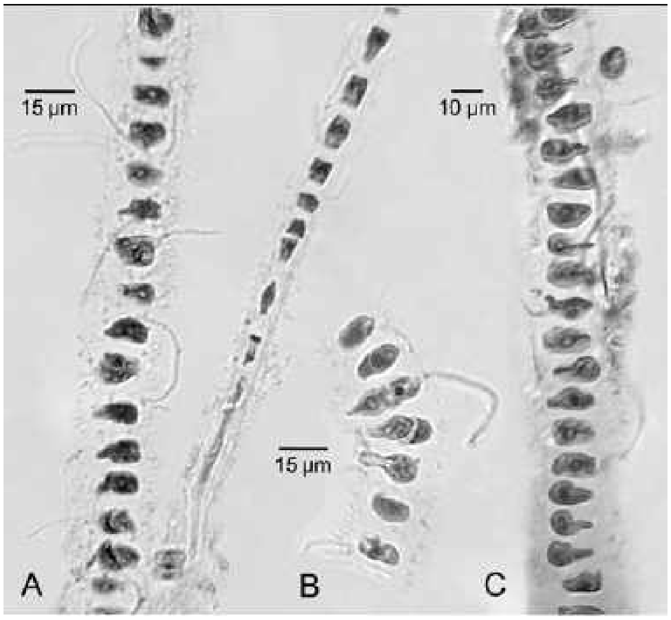


FIGURE 13. *Erythrotrichia parksii* var. *minor:* A–C. Portions of long unbranched, presumably female filament, some cells with "fertilization tubes" (*JN-5037*, US Alg. Coll. microscope slide 4276).

Erythrotrichia parksii var. *minor* N. L. Gardner

FIGURE 13

Erythrotrichia parksii N. L. Gardner var. *minor* N. L. Gardner, 1927a:239, pl. 24: figs. 6, 7; Scagel, 1957:125; Dawson, 1961b:401; Thom et al., 1976:271; Hawkes et al., 1978:100.

Algae epiphytic; erect filaments, up to 4 mm tall and 15–20 µm in diameter; attached by irregularly branched rhizoids from basal cell. Individual filaments more or less same diameter throughout; composed of cells more or less quadrate, varying in height (length) from much shorter to slightly taller than wide. Cells with a band-shaped chloroplast.

Monosporangia formed from vegetative cell.

Habitat. Epiphytic on *Colpomenia tuberculata* and likely other algae; mid to low intertidal.

Distribution. Gulf of California: Punta Pelícano, vicinity of Puerto Peñasco. Eastern Pacific: northern British Columbia to Washington.

Type Locality. Epiphytic on *Cryptosiphonia*; Neah Bay, Washington, USA.

Remarks. A new record for the Gulf of California, specimens (*JN-5037,* US Alg. Coll. slide 4276) from Puerto Peñasco generally agree with the description of *Erythrotrichia parksii* var. *minor* N. L. Gardner (1927a). Although smaller in length, the Gulf *E. parksii* var. *minor* is similar in diameter and has the characteristic monosporangia. Some structures interpreted as "female gametangia (?)" in the type material by Gardner (1927a) may possibly be "female" filaments with fertilization tubes (protoplasmic prolongations) that were also observed in our Puerto Peñasco specimen (Figure 13A–C). *Erythrotrichia parksii* var. *minor* had been considered to be conspecific with *E. carnea* (Desikachary et al., 1990), but for now the two are recognized to be morphologically distinct until needed culture and molecular studies can assess their relationship.

Erythrotrichia tetraseriata N. L. Gardner

FIGURE 14

Erythrotrichia tetraseriata N. L. Gardner, 1927a:240; Dawson, 1953a:12, pl. 1: fig. 5; 1961b:402; Dawson and Neushul, 1966:174; Abbott and Hollenberg, 1976:287, fig. 232; Pedroche and González-González, 1981:66; Pacheco-Ruíz and Aguilar-Rosas, 1984:71, 76; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:48; Serviere-Zaragoza et al., 1993a:483; R. Aguilar-Rosas and Aguilar-Rosas, 1994:519; González-González et al., 1996:200, 390, fig. 27.

Erythrotrichia californica Kylin, 1941:3, fig. 1A–D; Smith, 1944:165, pl. 36: figs. 4, 5; Dawson, 1944a:252; 1953a:8, pl. 1: fig. 1A–D; 1961b:401; Dawson and Neushul, 1966:174; González-González et al., 1996:200; Pacheco-Ruíz and Zertuche-González, 2002:467.

Algae epiphytic, unbranched filaments, 1.0–2.0(–4.0) mm long, attached below by short, branched rhizoidal cells. Filaments uniseriate in lower portions, 12–14 µm in diameter; upper portions 20–40 µm in diameter, multiseriate, of 4 or more cells; produced by successive longitudinal divisions. Cell shape slightly variable, usually shorter than wide; chloroplasts band(?) shaped.

Asexual reproduction by monosporangia. Monosporangia are cut off from cells in upper parts of filaments. Sexual reproduction unknown.

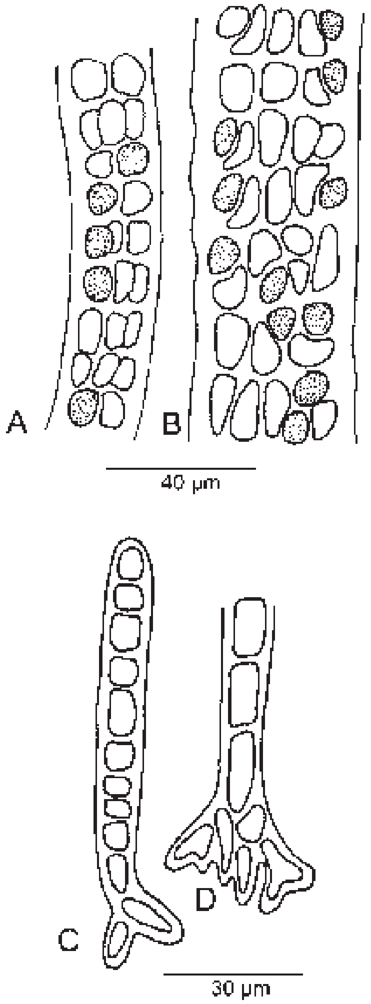


FIGURE 14. *Erythrotrichia tetraseriata:* A, B. Portion of mature filaments seen with sporangia. C. Young filament with attaching cells. D. Basal portion with multicellular attachment structure (A–D after Kylin, 1941: fig. 1A–D, as *Erythrotrichia californica*).

Habitat. Epiphytic on *Sphacelaria* and *Cladophora* and probably other algae; low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía de Los Ángeles; La Paz; Nayarit to Jalisco. Eastern Pacific: central California to Isla Magdalena, Baja California; Guerrero. Western Pacific: Korea.

Type Locality. Epiphytic on *Zostera marina*; San Pedro, Los Angeles County, southern California, USA.

Remarks. Although *Erythrotrichia tetraseriata* was considered conspecific with *E. carnea* by Desikachary et al. (1990), on the basis of morphological differences it is retained herein as a distinct entity until its taxonomic status can be evaluated by culture and molecular studies.

***Porphyrostromium* Trevisan**

Porphyrostromium Trevisan, 1848:100; Drew and Ross, 1965:97; Wynne, 1986:328–329.

Erythrotrichopeltis Kornmann, 1984:208.

Algae are composed of minute erect, filaments, only a few millimeters long, that arise from a prostrate, monostromatic, discoid base. Filaments are unbranched, initially uniseriate and cylindrical, but may become multiseriate and compressed to flattened, with cells in more or less longitudinal rows. Cells have a plastid, are without pit plugs, and are with or without a pyrenoid. Growth is diffuse throughout the thallus, although it is apparently apical during initial development.

Life histories are heteromorphic, with an erect phase (hair-like filaments) and a prostrate discoid phase. Asexual reproduction is by monospores, which develop by an unequal division (cytokinesis) of a vegetative cell. Monosporangia can be produced in both the erect filaments or prostrate discs. Gametophytes are monoecious with reproductive structures developed in the erect filaments. Carpogonia are formed with short trichogynes. After fertilization each carpogonium forms a zygosporangium that releases a single zygospore. Upon germination, it grows into the prostrate disc, which subsequently produces the erect hair-like filaments. Meiosis is presumably somatic. Spermatangia are formed by unequal division of vegetative cells, in which the smaller of the two resulting cells becomes a spermatangium that releases a single spermatium.

Remarks. Findings of Zuccarello et al. (2011) supported *Porphyrostromium* as a distinct genus, and they proposed that their taxonomy be based on molecular and culture studies.

KEY TO THE SPECIES OF *PORPHYROSTROMIUM* AND *ERYTHROPELTIS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Disc prostrate, monostromatic throughout (up to 300 µm in diameter); without or with erect, short, unbranched filaments from central portion of disc . . . . ***Erythropeltis discigera***

1b. Disc prostrate, monostromatic to pseudoparenchymatous; with erect, usually longer, unbranched filaments that are either cylindrical to compressed or flattened and ribbon-like 2

2a. Filaments cylindrical (uniseriate) becoming compressed above (2–4 cells wide) . . . . ***Porphyrostromium ciliare***

2b. Filaments initially uniseriate, broadening and becoming flattened, ribbon-like (4–8 cells wide) . . . . ***Porphyrostromium boryanum***

Porphyrostromium boryanum (Montagne) P. C. Silva

FIGURE 15A,B

Porphyra boryana Montagne, 1846b:150, pl. 3: fig. 2; Silva, 1952:300; Ardré, 1970:179, pl. 4: figs. 10, 11 [portion of Montagne's type specimen].

Porphyrostromium boryanum (Montagne) P. C. Silva in Silva et al., 1996a:914; Zuccarello et al., 2011:634, fig. 3e–h.

Porphyrostromium boryi (Montagne) Trevisan, 1848:100, *nom. illeg.* [see Silva in Silva et al. 1996a:914].

Erythrotrichia boryana (Montagne) Berthold, 1882b:25; Dawson, 1953a:7; 1961b:401; Heerebout, 1968:150, fig. 13; Garbary et al., 1980b:155; Stewart and Stewart, 1984:142; González-González et al., 1996:200.

Erythrotrichopeltis boryana (Montagne) Kornmann, 1984:221.

Algae small prostrate discs, up to 3 mm in diameter, epiphytic on flat portions or encircling cylindrical portions of small algae. Disc monostromatic to pseudoparenchymatous, with irregular margins. A few short filaments projecting above the surface of the discoid portion. Filaments initially uniseriate, broadening and becoming flattened, ribbon-like above, mostly 4–18 cells wide (90–170 μm in width). Cells of disc irregularly arranged; polygonal, with a single parietal plastid.

Monosporangia globose. Sexual reproduction unknown.

Habitat. Epiphytic on other algae.

Distribution. Gulf of California: Puerto Peñasco. Eastern Pacific: Isla Guadalupe; southern British Columbia to Bahía Asunción, Baja California; Peru.

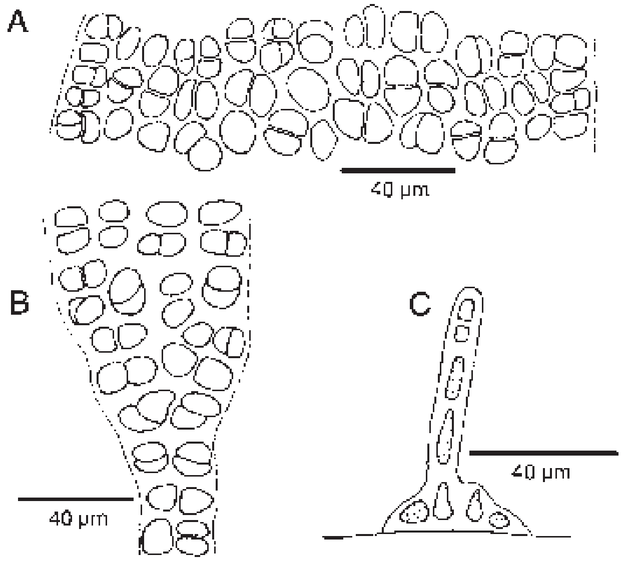


FIGURE 15. Species of *Porphyrostromium*. A, B. *Porphyrostromium boryanum:* A. Upper portion of thallus. B. Basal portion of thallus (A, B after Ardré, 1970: pl. 4: figs. 10, 11). C. *Porphyrostromium ciliare:* Young thallus showing development of the monostromatic basal disc (after Dawson, 1953a: pl. 1, fig. 2, as *Erythrotrichia ciliaris*).

Type Locality. On *Gelidium corneum*; Fort des Anglais, Algeria (Ardré, 1970).

Remarks. *Porphyrostromium boryanum* is not well known in the northern Gulf. Culture studies of Zuccarello et al. (2011) showed that mature flat thalli of *P. boryanum* can be considerabily larger, up to 4 mm wide and 1–3 cm in length. Silva (in Silva et al. 1996a:914) noted the correct name is *P. boryanum*, and that "*boryi* and *boryana* are two distinct epithets rather than orthographic variants" and not correctable to "*P. boryana*" (as done by Wynne, 1986; Scagel et al., 1989).

Porphyrostromium ciliare (Carmichael ex Harvey) M. J. Wynne

FIGURE 15C

Bangia ciliaris Carmichael ex Harvey in W. J. Hooker, 1833:316.

Porphyrostromium ciliare (Carmichael ex Harvey) M. J. Wynne, 1986:329; Zuccarello et al., 2011: fig. 3a-d.

Erythrotrichopeltis ciliaris (Carmichael ex Harvey) Kornmann, 1984:208.

Erythrotrichia ciliaris (Carmichael ex Harvey) Thuret, 1854:387–389; Thuret in Le Jolis, 1863a: Exsiccate No. 188 [see Sayer, 1975:357]; Thuret in Le Jolis, 1863b:103.

Erythrotrichia ciliaris (Carmichael ex Harvey) Batters, 1900:374; Dawson, 1953a [in part]:10, pl. 1: fig. 2; 1961b:401; González-González et al., 1996:200.

Algae microscopic prostrate discs, up to 350 μm in diameter; epiphytic on other compressed to flat algae or encircling some cylindrical small algae. Disc monostromatic to pseudoparenchymatous; with irregular margins; with few short filaments projecting above surface of the prostrate portion; filaments initially uniseriate in lower portion, 15–20 μm in diameter, above (distally) becoming 2–4 cells wide, 30–40 μm in diameter. Cells of disc irregularly arranged; polygonal, with a single plastid and a pyrenoid.

Monosporangia globose. Sexual reproduction unknown.

Habitat. Epiphytic on and encircling filaments of *Sphacelaria*; intertidal.

Distribution. Gulf of California: Isla Tiburón. Eastern Pacific: British Columbia to Punta Banda, Baja California; Isla Cedros (off central Baja California); Peru.

Type Locality. Epiphytic on *Zostera*; Appin, Argyll, Scotland, United Kingdom (Dawson, 1953a).

Remarks. *Porphyrostromium ciliare* is apparently known from only one northern Gulf collection, and its presence in the Gulf of California needs to be verified. The relationship of Gulf specimens referred to *P. ciliare* and *E. discigera* also needs to be investigated (see also Remarks under *Erythropeltis discigera*).

Sahlingia Kornmann

Sahlingia Kornmann, 1989:227.

Algae are compact, single-layered prostrate discs, composed of laterally adjoined, radiating, pseudodichotomously to irregularly branched prostrate filaments. Growth is by oblique divisions of the marginal cells in an alternating sequence. Intercalary growth can also occur in the central portions of the disc. Cells of the center and outward toward the margins are rectangular to irregular; bifurcate cells present in the outermost margin. Cells have several band-shaped or cup-shaped plastids, circular pyrenoids, and they lack pit plugs.

Monosporangia are produced by unequal division of vegetative cells within the central part of the disc. The smaller of the two resulting cells, separated by an oblique (curving) wall, becomes the monosporangium. Sexual reproduction is unknown.

REMARKS. Although it has been suggested that *Sahlingia* may be congeneric with *Erythrocladia*, Zuccarello et al. (2010) recently provided molecular support for their generic separation. In another study, Zuccarello et al. (2011) found "*Sahlingia*-like" discs in culture studies of some *Porphyrostromium*. The reported Gulf of California species will need to be cultured and molecularly tested to verify their taxonomy.

There is one species of *Sahlingia* in the northern Gulf of California.

Sahlingia subintegra (Rosenvinge) Kornmann

FIGURE 10B

Erythrocladia subintegra Rosenvinge, 1909:73, figs. 13, 14; Børgesen, 1924:268; Kylin, 1925:9, fig. 3C–G; Inagaki, 1935:41; Kylin, 1937:43, fig. 17D; Kylin, 1941:3; Dawson, 1944a:251; Smith, 1944:166, pl. 36: fig. 6; Dawson, 1945c:65; Hollenberg, 1948:156; Tanaka, 1952:75, figs. 35, 36; Dawson, 1953a:5; 1961b:402; 1961c:408, pl. 9: fig.2; 1962b:191, 229, fig. 53; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Huerta-Múzquiz and Garza-Barrientos, 1975:7; Abbott and Hollenberg, 1976:284, fig. 227; Schnetter and Bula-Meyer, 1982:109, pl. 11: figs. D, E; Pacheco-Ruíz and Aguilar-Rosas, 1984:71, 76; Mendoza-González and Mateo-Cid, 1985:28; Huerta-Múzquiz and Mendoza-González, 1985:46; Salcedo-Martínez et al., 1988:83; Dreckmann et al., 1990:27; Mateo-Cid and Mendoza-González, 1991:18; Stewart, 1991:61; Mendoza-González and Mateo-Cid, 1992:16; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:309, fig. 26; Yoshida, 1998:432, fig. 3-1J.

Sahlingia subintegra (Rosenvinge) Kornmann, 1989:227, figs. 1, 6–13; L. Aguilar-Rosas et al., 2000:130, 137; Mateo-Cid et al., 2000:63; Serviere-Zaragoza et al., 2007:11; Zuccarello et al., 2010:365, figs. 2b–g, tbls. 1, 2; Fernández-García et al., 2011:64.

Erythropeltis subintegra Kornmann et Sahling, 1985:224, fig. 8; Bula-Meyer, 1995:32.

Erythrocladia irregularis f. *subintegra* (Rosenvinge) Garbary, G. I. Hansen et Scagel, 1981:154.

Erythrotrichia polymorpha sensu Setchell and Gardner, 1924:741; González-González et al., 1996:200 [non *Erythrotrichia polymorpha* M. Howe, 1914:77].

Algae epiphytic, monostromatic and disc shaped, up to 300 µm in diameter, composed of prostrate, laterally coalesced filaments throughout; outermost cells mostly bifucate; margins entire, nearly even. Cells isodiametric or longer than wide, 2–5 µm wide and 5–12 µm long; pyrenoids circular.

Asexual reproduction by monosporangia, up to 15 µm in diameter, formed in central part of disc. Sexual reproduction unknown.

HABITAT. Epiphytic on various algae, including species of *Valoniopsis*, *Cladophora*, *Chaetomorpha*, *Dictyota*, *Polysiphonia*, and *Griffithsia*; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena; Nayarit to Jalisco. Eastern Pacific: Alaska to Baja California; Colima to Oaxaca; Isla Socorro (Islas Revillagigedo); El Salvador; Costa Rica; Isla Gorgona, Colombia; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: Japan; Vietnam.

TYPE LOCALITY. Epiphytic on *Polysiphonia urceolata*; Møllegrund, off Hirshals, Skagerrak, northern Denmark.

REMARKS. Heerebout (1968, as *Erythrocladia subintegra*) suggested that *Sahlingia subintegra* and *Erythrocladia irregularis* were conspecific. Later, *E. subintegra* was considered to be a taxonomic form (*forma*), as *E. irregularis* f. *subintegra* Garbary, G. I. Hansen et Scagel (1980). Since then, culture studies by Kornmann (1989) showed differences in development following germination and in the morphological characters of monospore size and the disc margins, thus separating the two, and recognizing *S. subintegra* with nearly even margins and *E. irregularis* with uneven, irregular margins.

The presence or absence of pyrenoids was noted to be an important generic character by Zuccarello et al. (2010). Pyrenoids are not always evident in some Gulf specimens referred to *S. subintegra*, possibly an artifact of preservation. This should be carefully studied, particularly in freshly collected specimens, as there may be more than one similar looking genus in the Gulf of California.

PART II: SUBPHYLUM EURHODOPHYTINA

Eurhodophycidae F. Magne, 1989:112.

Eurhodophytina (F. Magne) G. W. Saunders et Hommersand, 2004:1503.

Ultrastructurally, the Golgi apparatus (Golgi body), an organelle within eukaryotic cells, is found in an endoplasmic reticulum/mitochondrial association. Life histories, where known, are biphasic or triphasic. Pit plugs are present between cells in at least one stage of sexual life histories. (Diagnostic characters are after Saunders and Hommersand, 2004.)

The subphylum Eurhodophytina contains two classes; both are well represented in the northern Gulf of California.

KEY TO THE CLASSES OF THE EURHODOPHYTINA IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli uniseriate filaments or monostromatic or distromatic blades; cells without pit plugs; female reproductive structures comparatively simple . . . . **Bangiophyceae**

1b. Thalli simple to branched filaments, or terete, compressed or flat, unbranched to branched cylindrical, strap-shaped to broad blades; structurally simple to complex pseudoparenchymatous anatomy; cells with pit plugs; female reproductive structures complex . . . . **Florideophyceae**

PART IIA. BANGIOPHYCEAE

Bangiophyceae Wettstein, 1901:187

The class Bangiophyceae contains microscopic to macroscopic algae that are of diverse morphologies. They may be (1) unicellular; colonial masses of cells; (2) prostrate and disc shaped; (3) simple to branched filaments; or (4) narrow to broad foliose blades. Growth is by intercalary cell division (rarely apical). Cells are uninucleate, generally with 1 or 2 plastids (variously shaped parietal or disc-like plastids have been reported), and may be with or without pyrenoids. The cells contain chlorophyll *a* and one or more accessory pigments, including phycoerythrin and phycocyanin that occur in discrete submicroscopic units, the phycobilisomes. The predominance of one or the other of these pigments provides rose-colored (phycoerythrin) or grayish-red-colored (phycocyanin) thalli.

The reproductive structures of Bangiophycean algae are less complicated than those of the Florideophyceae. Asexual reproduction is mostly by monospores, archeospores, or neutral spores, produced by direct metamorphosis of a vegetative cell, or by divisions of vegetative cells. Sexual reproduction is unknown or at least not fully understood in most genera. Where reported, sexual reproduction involves simple zygotogsporangia that are formed by direct transformation of a vegetative cell. Spermatia are also similarly produced by divisions of a vegetative cell. Fertilized zygotosporangia develop zygotospores by divisions within the transformed cell. Zygotospores ("carpospores") of some species, e.g., *Porphyra*, *Pyropia*, and *Bangia*, produce an epizoic or endozoic, shell-boring, filamentous "*Conchocelis*-phase."

REMARKS. The large class Bangiophyceae with its subclass Bangiophycidae Wettstein (1901) contains two orders, most of which are marine species but a few species are known from freshwater.

The class is represented by some members of the Bangiales in the northern Gulf of California.

BANGIALES

Bangiales Nägeli, 1847:136 [as "Bangiaceae" (see Silva et al., 1996a:914)].

Bangiales F. Schmitz in Engler, 1892:15.

Algae are of a variety of morphological forms, discoid, filamentous, tubular, or foliose. In structure members are multicellular and lack a conspicuous gelatinous matrix. Growth is by intercalary cell division.

Asexual reproduction is by the formation of monospores, archospores, or neutral spores, formed by division of a vegetative cell and development of the resulting smaller cells into spores. What is apparently sexual reproduction (but difficult to interpret—fertilization has not been convincingly demonstrated) occurs in most members. The zygotosporangium forms zygotospores by division and redivision of the contents of a vegetative cell. Spermatia are also formed by the repeated division of a vegetative cell's contents.

REMARKS. Since some genera of the Bangiales were found to be polyphyletic (Müller et al., 2005a), at least 13 new or resurrected genera have been recognized (Sutherland et al., 2011).

A monotypic order, with some members, the Bangiaceae, reported in the Gulf of California.

BANGIACEAE

Bangiaceae Engler, 1892:16, *nom. cons.*; Silva, 1980:80 [for name conservation of Bangiaceae, see Silva, 1980:106; 1993b:707].

Porphyraceae Kützing, 1843:382 [as "Porphyreae"].

Members of this family are of two morphologies, either cylindrical, tubular filaments or flattened and blade-like. The foliose members may be monostromatic (one cell layer) or distromatic (two cell layers) throughout. Cells are uninucleate, usually with one or sometimes with two plastids, but at least one has multiple plastids. Plastids contain one pyrenoid.

Asexual reproduction is by repeated division of a vegetative cell into two or more smaller cells, each of which becomes a monospore. In assumed sexual reproduction, a zygotosporangium is formed by transformation of a vegetative cell, which by further divisions produces zygotospores. A short trichogyne has been reported in some, but this is in need of reinvestigation (Dixon, 1973). Spermatia are also formed by division and redivision within vegetative cells.

Culture studies have shown heteromorphic life histories involving macroscopic filaments (e.g., *Bangia*) or blades (e.g., *Porphyra*, *Pyropia*) and a microscopic, filamentous *Conchocelis*-phase inhabiting shells or other calcium carbonate substrate (Drew, 1949, 1954, 1956a; Kurogi,1953a, 1953b; Tseng and Chang, 1954, 1955a, 1955b; Iwasaki,1961; Conway and Cole, 1977). Additionally, the asexual stage of each of these phases may repeatedly reproduce itself asexually depending on environmental conditions, primarily photoperiod and temperature for *Bangia* and *Porphyra* (see summary in Dixon, 1973).

REMARKS. Molecular sequencing and phylogenetic analyses have elucidated many new taxa as well as the need for reevaluation of generic concepts in the Bangiales (e.g., Nelson et al., 2003, 2006; Niwa et al., 2003; Broom et al., 2004). The generic separation of two of the genera, *Bangia* and *Porphyra* C. Agardh (1824), is problematic as studies have revealed them in a monophyletic lineage (e.g., Stiller and Waaland, 1993; Oliveira et al., 1995; Müller et al., 2001a, 2001b; Milstein and Oliveira, 2005). Müller et al. (2003, 2005a) noted *Bangia* as well as *Porphyra* to be polyphyletic, and recently Sutherland et al. (2011)

provided molecular support for recognization of several genera, six of which were found within *Porphyra,* and there are probably more taxa in *Bangia*. Despite habit differences, there are no clear morphological or anatomical characters that support generic separations that are consistent with their phylogenetic relationships (Nelson et al., 2005; Zuccarello, 2011).

There are two genera of Bangiaceae currently known in the Gulf of California: the economically important genus *Pyropia* (e.g., Huerta-Múzquiz, 1961; Miyata and Notoya, 1997) and the cosmopolitan *Bangia*. The microscopic *Conchocelis*-phase has as yet remained undetected in the field in the Gulf of California.

KEY TO THE GENERA OF BANGIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus filamentous, cylindrical; uniseriate in lower portions and distally 2 or more cells wide; or multiseriate throughout, lower portions 4–6 cells wide, upward 6–20 cells wide . . . . ***Bangia***
1b. Thallus foliose; flat monostromatic blades . . . . ***Pyropia***

Bangia **Lyngbye**

Bangia Lyngbye, 1819:82.

Algae are erect and may form clumps of a few to many unbranched, cylindrical, purple-black to rusty-colored filaments, 2.0 mm to 35 cm long. Smaller or immature thalli are attached by a dilated basal cell, which in older thalli becomes supplemented by a dense base of filiform rhizoids that grow downward from lowermost cells of the filament. Filaments of cells may be (1) multiseriate, (2) uniseriate in juvenile thalli and remain so, or (3) initially uniseriate and become multiseriate and broader in the upper portions of older thalli. Cells have a large plastid with a single central pyrenoid.

Life histories, where known, involve an irregularly branched, microscopic, filamentous *Conchocelis*-phase that is developed from zygotospores of the *Bangia*-phase. Cells of *Conchocelis*-phase filaments contain a ribbon-shaped plastid, grow within calcareous shells (or other calcium carbonate substrates), and produce conchospores that germinate into the gametophytic *Bangia*-phase.

Reproductive cells, sporangia, and zygotosporangia or spermatangia, are formed by the differentiation of vegetative cells in the upper regions of *Bangia* filaments. Monosporangia or archeospores are produced on sporangial thalli, separate from the gametophytic thalli. Zygotosporangia are formed by direct transformation of vegetative cells into groups of 8 to 16 zygotosporangia. Spermatangia are formed by repeated division of vegetative cells into groups of 32–128 colorless, small spermatia.

REMARKS. *Bangia* species are mostly marine and are worldwide in distribution in subtropical to boreal regions. Taxonomically, species of *Bangia* are relatively simple filaments and have been separated primarily on filament diameter and karyotype. Molecular sequencing and phylogenetic analyses have revealed new taxa, for example, new genera *Minerva* W. A. Nelson, *Dione* W. A. Nelson (both in Nelson et al., 2005), and *Pseudobangia* K. M. Müller et Sheath (in Müller et al., 2005a) that closely resemble *Bangia*. In addition to a resolved *Bangia* clade that included *Bangia, Clymene* W. A. Nelson (in Sutherland et al., 2011), and *Porphyra*, nine other marine filamentous species of "*Bangia*" remain unresolved and may involve one or more genera (Sutherland et al., 2011). Similar methodologies applied to Gulf of California *Bangia* species are needed to elucidate their taxonomic status and phylogenetic relationships to other Bangiales.

Two species of *Bangia* are recorded in the northern Gulf of California, one known from Pacific Mexico and the other tentatively referred to a California species.

KEY TO THE SPECIES OF *BANGIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Filaments multiseriate throughout; 4–6 cells broad in lower portion, up to 20 cells wide in upper portion; simple (unbranched) or with short, spur-like branches basally . . . . ***B. enteromorphoides***
1b. Filaments uniseriate in basal portion, becoming multiseriate in upper portions; unbranched throughout . . . . ***B. vermicularis*?**

Bangia enteromorphoides E. Y. Dawson

FIGURE 16

Bangia enteromorphoides E. Y. Dawson, 1953a:13, pl. 1: fig. 8; 1961b:402; González-González, 1993:441; González-González et al., 1996:175, 384.

Algae of several minute, cylindrical to broadening filaments, up to 2 mm long, with broadly rounded apices; attached by a mass of rhizoids, epiphytic or partially endophytic on surface cells of host algae. Filaments about 20 µm in diameter, multiseriate at base, of 4 transverse rows of cells; usually unbranched or with a few spur-like branchlets in lower portion. Lowermost portions of filaments in rows of 4(–6) cells producing attachment rhizoids; upward with rows of 4–6 cells; upper portion becoming broader, up to 150 µm wide; cells squarish to more or less angular, in transverse rows of up to 20 cells. Thalli initially solid, but can become hollow above in larger specimens.

Asexual reproduction unknown. Spermatangia in groups of 16–32 with some apparently nonreproductive cells among them in fertile area of upper region of filaments. Carpogonia not known.

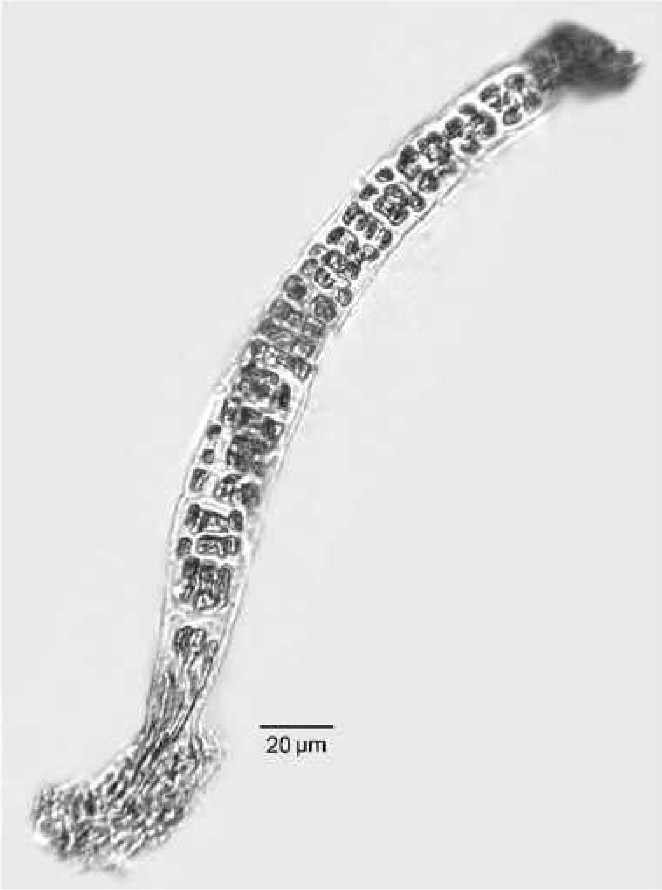


FIGURE 16. *Bangia enteromorphoides:* Rhizoids descending from the lower 4 basal cells; upward the axis is 4 cells across (entangled with *JN-3030b*, US Alg. Coll. microscope slide 8696).

Habitat. Entangled with *Asparagopsis* and epiphytic on *Gelidium*; low intertidal to shallow subtidal, down to at least 5 m depths.

Distribution. Gulf of California: Punta La Gringa, Bahía de Los Ángeles; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Oaxaca.

Type Locality. Epiphytic on *Gelidium sclerophyllum*; north of El Faro de Olas Atlas, Mazatlán, Sinaloa, Gulf of California, Mexico.

Remarks. Apparently little known or overlooked, *Bangia enteromorphoides* was described from the southern Gulf of California (Dawson, 1953a). A single small specimen (*JN-3030b*, US Alg. Coll. microscope slide 8696) from Punta La Gringa, probably a juvenile, shows the characteristic 4-celled row across the basal region and is tentatively referred to *B. enteromorphoides*. It is included in hopes that the species will again be collected and its generic and specific status will be further investigated.

Bangia vermicularis? Harvey

FIGURE 17

Bangia vermicularis Harvey, 1858:55, pl. 49: figs. A1–10; Kylin, 1941:4; Smith, 1944:167, pl. 37: figs. 4–6; Dawson, 1961b:402; Sheath and Cole, 1984:383; Scagel et al., 1986:128; Stewart, 1991:63; R. Aguilar-Rosas and Aguilar-Rosas, 1994:519; Pacheco-Ruíz et al., 2008:205; Lynch et al., 2008:609, figs. 7, 8.

Bangia fuscopurpurea [only Gulf of California and Pacific Mexico material] sensu Tanaka, 1950:165, fig. 3; 1952:23, pl. 2: fig. 2; Dawson, 1953a:13; 1961b:402; 1962b:210, 229, fig. 108; Abbott and Hollenberg, 1976:294, fig. 237; Silva, 1979:315; Pacheco-Ruíz and Aguilar-Rosas, 1984:71,76; Huerta-Múzquiz and Mendoza-González, 1985:48; González-González et al., 1996:302 [non *Bangia fuscopurpurea* (Dillwyn) Lyngbye, 1819:83].

Bangia atropurpurea sensu Mateo-Cid and Mendoza-González, 1994b:38; Mendoza-González et al., 1994:105; Hoffman and Santelices, 1997:206, fig. 52(1–5); Abbott, 1999:47, fig. 2A–E; Mateo-Cid et al., 2000:63 [non *Bangia atropurpurea* (Roth) C. Agardh, 1824:76; basionym: *Conferva atropurpurea* Mertens ex Roth, 1806:208; =*Bangiadulcis atropurpurea* (Roth) W. A. Nelson, 2007:885 (note that the taxonomic status of *Bangiadulcis* is uncertain; see Silva and Nelson, 2008:1352; Wynne and Schneider, 2010)].

Algae of several, often entangled filaments, dark red to purple-black, sometimes rusty brown, up to 3 cm long; usually growing in small to extensive patches. Filaments more or less cylindrical and unbranched; uniseriate at base and initially attached by a basal cell; later becoming attached by rhizoids descending from lowermost cells. Filaments mostly 40–60 μm in diameter, with cells usually wider than long. Uniseriate filaments become multiseriate in upper portions; filaments may be slightly constricted; cells may be as long as or longer than wide, sometimes arranged in more or less transverse rows. Cells about (4–)6–12 μm tall and (8.0–)10–15 μm in diameter; in upper portions, cells (12–)14–20 μm tall and 15–20 μm in diameter.

Asexual reproduction unknown in Gulf material. Carpogonium formed by transformation of vegetative cell. Spermatia 3–4 μm in diameter, formed by repeated divisions of vegetative cells.

Habitat. On rocks; high to upper mid intertidal.

Distribution. Gulf of California: Isla Partida; La Paz to Punta Arena; Mazatlán. Eastern Pacific: Alaska to Costa Rica; Chile. Western Pacific: Japan.

Type Locality. “Golden Gate” entrance to San Francisco Bay (Harvey, 1858) (probably below what is now the Golden Gate Bridge at Fort Point or the San Francisco Presidio [Silva, 1979]), San Francisco, San Francisco County, northern California, USA.

Remarks. There is a long history of taxonomic and nomenclatural debate over species limits and the number of species included in *Bangia*. Although often considered to be a single morphologically variable species, as “*B. fuscopurpurea,*” with a worldwide distribution, others have recognized that there are distinct taxa among populations of *Bangia*. Initially, Müller et al. (2003, as “*B. fuscopurpurea*”) concluded that the marine *Bangia* from the Pacific and Atlantic coasts of North America should be

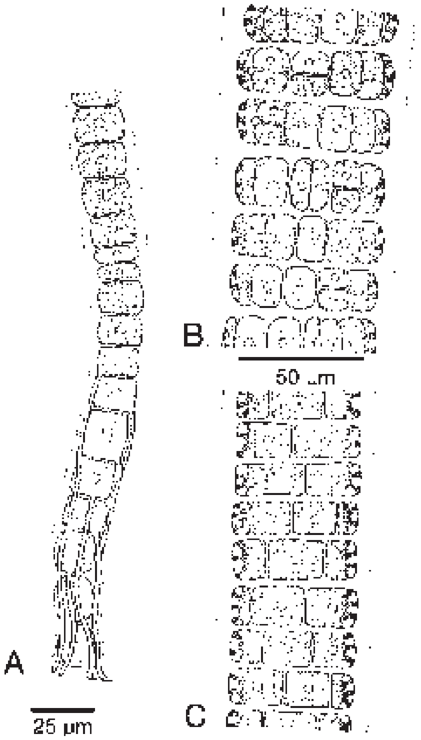


FIGURE 17. *Bangia vermicularis*?: A. Basal portion. B. Middle portion. C. Upper portions of thallus (A–C, after G. M. Smith, 1944: pl. 37, figs. 4–6).

referred to as a single entity until their phylogenetic relationships can be resolved (see also Müller et al., 1998) and later pointed out that *Bangia* as well as *Porphyra* are polyphyletic (Müller et al., 2005a). Müller et al. (2003) provided evidence that there are several distinct clades of specimens identified as "*B. fuscopurpurea* (Dillwyn) Lyngbye (1819)," and more recently, Sutherland et al. (2011) concluded that the genus to which the marine "*Bangia fuscopurpurea*" belongs remains unknown.

Earlier cytological studies by Cole et al. (1983) and Sheath and Cole (1984) indicated that there are two geographically separate, but similar looking, species (Smith, 1944) on the basis of their chromosome numbers (n): the northeastern Pacific *Bangia vermicularis* (n = 3) and the Atlantic "*B. atropurpurea*" (n = 4). However, *Bangia atropurpurea* (Roth) C. Agardh (1824) was subsequently shown to belong to a new freshwater genus (Müller et al., 2003) as *Bangiadulcis atropurpurea* (Roth) W. A. Nelson (2007); yet the taxonomic status of *Bangiadulcis* has been questioned by Silva and Nelson (2008).

All Gulf of California and Pacific Mexico material identified as "*B. fuscopurpurea*" needs to be reexamined. For now the Gulf of California material is tentatively referred to the Pacific Coast species, *Bangia vermicularis*. Although *B. vermicularis* and another northern California species, *B. maxima* N. L. Gardner (1927a), have been treated as synonyms included within "*B. fuscopurpurea*" by Abbott and Hollenberg (1976), Lynch et al. (2008: figs. 7, 8) noted that despite their morphological similarities, *B. vermicularis* and *B. maxima* were not particularly close phylogenetic relatives.

Dawson (1953a, as "*B. fuscopurpurea*") stated the Isla Partida specimens were a morphological variant in which cells in the lower portions of their filaments were longer than wide and less than 8 µm in diameter. These dimensions are much smaller than those of specimens from the Pacific coast of California, where *B. vermicularis* is typically characterized to have much wider and shorter cells in the lower portion that are about half as long as broad, 10–15 µm in diameter and about 5–12 µm long (Abbott and Hollenberg, 1976). The relationship of Gulf of California specimens, herein referred to *B. vermicularis* with a query, to the other species of *Bangia* and "*Bangia*-like" taxa needs further morphological and molecular evidence to elucidate their taxonomic status and relationships.

Pyropia J. Agardh

Pyropia J. Agardh, 1899:149, fig. 5a–d; Sutherland et al., 2011:1142.

Gametophytes are foliose, monostromatic, and of various shapes, including linear, lanceolate, ovate, orbicular or funnel-like, and mostly entire or sometime divided. Blades arise from a small discoid holdfast composed of rhizoidal cells produced from the basal cells. Color is variable between, and in some cases within, species and may be rose to dark red, purple, or green or combinations of these colors. Species range in size from a few centimeters to some that can be several meters in length, with blade margins that can be smooth, dentate, planar, undulate, or ruffled. Cells in most of the species have a single plastid, although some may have cells with two plastids. Pit plugs are absent.

Archeospores or neutral spores are known to be produced by the blades of a few of the species (Nelson and Knight, 1996; Nelson et al., 1999). The reproductive portions of the macroscopic gametophytes are either (1) monoecious with zygotosporangia (sensu Guiry, 1990b) or spermatangia produced by groups of cells; (2) monoecious and divided into zygotosporangial and spermatangial groups separated by a vertical or horizontal line; (3) monoecious with zygotosporangia or spermatangia intermixed in fertile portions of the blade; or (4) dioecious. Two of these groups develop continuous reproductive areas along the blade margins: zygotosporangia and spermatangia in species that are monoecious and sectored; and, zygotosporangia or spermatangia in dioecious species (after Sutherland et al., 2011).

The sporophytic, filamentous "*Conchocelis*-phase" is known in the life histories of some of the species. In nature, its branched, uniseriate filaments grow on and/or penetrate and grow in calcareous substrata such as shells, coral rubble, or crustose coralline algae. Cells of the "*Conchocelis*-phase" have parietal band-shaped to stellate plastids and pit plugs between the cells. Asexual reproduction, where known, is by conchospores or monospores produced by the filamentous sporophyte (e.g., Kapraun and Luster, 1980, as *Porphyra rosengurtii* J. Coll et J. Cox, 1977; which is now *Pyropia elongata* (Kylin) Neefus et J. Brodie in Sutherland et al., 2011).

REMARKS. The foliose gametophytes of *Pyropia* grow on hard substrata (such as rocks) or may be epiphytic or epizoic. Some species are short-lived (ephemeral) and seasonal, others live longer, through two or more seasons. Most of them are found in subtropical, temperate, or sub-boreal waters.

Pioneering culture studies by Drew (1949, 1956a) of *Porphyra umbilicalis* Kützing (1843), and by Kurogi (1953a, 1953b) and Tseng and Chang (1954, 1955a, 1955b) on *Porphyra tenera* Kjellman (1897; which is now *Pyropia tenera* (Kjellman) N. Kikuchi et M. Miyata in Sutherland et al., 2011) revealed heteromorphic life histories involving the foliose-phase and the filamentous *Conchocelis*-phase (see also Iwasaki, 1961; Conway and Cole, 1977). *Porphyra* was found to have the most primitive plastid genome known (Reith and Munholland, 1995; Reith, 1995). Molecular studies of some species of *Porphyra* revealed the genus to contain a polyphyletic assemblage of taxa that, although divergent at the molecular level, have converged on simple blade morphologies (e.g., Nelson et al., 2003, 2006). Sutherland et al. (2011) provided molecular phylogenetic evidence that the genus *Porphyra* should be based on *Porphyra purpurea* (Roth) C. Agardh (1824; basionym: *Ulva purpurea* Roth, 1797; e.g., Liu et al., 1994; Irvine and Brodie, 1997; Lindstrom and Fredericq, 2003, as *Porphyra rediviva* Stiller et Waaland, 1996; Bray et al., 2007) and restricted *Porphyra* to five species. The rest of the previously known species of "*Porphyra*" belong in six different genera: *Boreophyllum* S. C. Lindstrom, N. Kikuchi, M. Miyata et Neefus (in Sutherland et al., 2011), *Fuscifolium* S. C. Lindstrom (in Sutherland et al., 2011), *Lysithea* W. A. Nelson (in Sutherland et al., 2011), *Miuraea* N. Kikuchi, S. Arai, G. Yoshida, J. A. Shin et M. Miyata (in Sutherland et al., 2011), *Pyropia* J. Agardh (1899), and *Wildemania* De Toni (1890). There are more than 75 species previously in *Porphyra* that belong in *Pyropia*, a genus based on *Pyropia californica* J. Agardh (1899; which is now *Pyropia nereocyctis* (C. L. Anderson) S. C. Lindstrom in Sutherland et al., 2011; basionym: *Porphyra nereocystis* C. L. Anderson in Blankinship and Keeler, 1892; *Porphyra nereocystis* C. L. Anderson 1891, *nom. nud.*). Sutherland et al. (2011) noted there are another eight probable genera that are to be resolved in later studies.

Many species of *Pyropia*, including those of the Gulf of California—until recently called *Porphyra* (Sutherland et al., 2011; Zuccarello, 2011)—have a long history as food. It was eaten as early as AD 668 in coastal regions of the Korean peninsula and at least since AD 701 in Japan, where around AD 987 it was referred to as a common food (Miyata and Notoya, 1997). Korean texts mention cultivation of "*Porphyra*" as early as 1420, and it was probably introduced to China in 1429. It has been a traditional food since antiquity, with cultural and nutritional importance to indigenous people of the northeastern Pacific Coast (Turner, 2003).

The species of *Porphyra* and *Pyropia* may be the single most important seaweed food in the world. Since the 1950s the biology of "*Porphyra*" has been extensively studied because of its economic value to the mariculture industry in the production of nori or amanori (Japan and China), gim (Korea), or purple laver (England and Ireland) (e.g., Mumford and Miura, 1989; Miyata and Notoya, 1997; Yoshida, 1997). Today the major producers of nori are Japan, Korea, and China, with an annual market value of over US$2 billion. Although Gulf of California species may have economic potential, they are not currently being commercially grown or harvested (e.g., Zertuche-González, 1994). A species of *Pyropia*, or possibly *Porphyra*, from Baja California was noted by Huerta-Múzquiz (1961, as "*Porphyra perforata* var. *segregata*") to be of economic interest.

One species of foliose *Pyropia* has been reported in the southern Gulf from La Paz (Huerta-Múzquiz and Mendoza-González, 1985): *Pyropia perforata* (J. Agardh) S. C. Lindstrom in Sutherland et al. (2011), a California species recorded from Alaska to Pacific Baja California Sur (Dawson, 1953a; Abbott and Hollenberg, 1976; Huerta-Múzquiz, 1978; Pacheco-Ruíz and Aguilar-Rosas, 1984; Scagel et al., 1989; Mateo-Cid and Mendoza-González, 1994b:38; Pacheco-Ruíz et al., 2005b; all as *Porphyra perforata* J. Agardh, 1883). In addition to *Pyropia perforata* there are five other species also recorded from the Pacific coast of Mexico (R. Aguilar-Rosas et al., 2007b): *Pyropia gardneri* (G. M. Smith et Hollenberg) S. C. Lindstrom, *P. lanceolata* (Setchell et Hus) S. C. Lindstrom, *P. suborbiculata* (Kjellman) J. E. Sutherland, H. G. Choi, M. S. Hwang et W. A. Nelson, and *P. thuretii* (Setchell et E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas (all four new combinations in Sutherland et al. , 2011), and the newly described *P. raulaguilarii* Mateo-Cid, Mendoza-González et Sentíes (in Mateo-Cid et al., 2012).

Three species of *Pyropia* are present in the northern Gulf of California. All are monostromatic species, and two of them are endemic.

KEY TO THE SPECIES OF *PYROPIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades monoecious; broadly reniform to lanceolate; rose to purplish . . . . ***P. thuretii***
1b. Blades dioecious; linear to ligulate or oval to sometimes broader than tall 2
2a. Blades long, linear to ligulate, comparatively narrow, 0.3–1.2 cm wide; pale to bright rose; zygotosporangia in packets of 8; spermatia in packets of 128 . . . . ***P. pendula***
2b. Blades mostly wider, generally more than 2.0 cm, up to 4.0 cm in width; lanceolate to broadly oval; entire or divided; pale rose to greenish or purplish red; zygotosporangia in packets of 8; spermatia in packets of 64 . . . . ***P. hollenbergii***

Pyropia hollenbergii (E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas

Porphyra hollenbergii E. Y. Dawson, 1953a:14, pl. 13: fig. 1; 1959a:19; 1961b:402; González-González et al., 1996:257; Yoshida et al., 1997:8, fig. 3; Mateo-Cid et al., 2000:63; R. Aguilar-Rosas et al., 2007b:351, figs. 1–10; López-Vivas et al., 2011:520.

Pyropia hollenbergii (E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas in Sutherland et al., 2011:1143.

Porphyra perforata f. *segregata* sensu Dawson, 1944a:253 [non *Porphyra perforata* f. *segregata* Setchell et Hus in Hus, 1900:64, which is now *Porphyra segregata* (Setchell et Hus) V. Krishnamurthy, 1972:44].

Algae one to several, monostromatic blades, lanceolate or linear to ovate, sometimes obovate in lower portions with lanceolate upper portions, or broadening upward, often more or less divided (lacerated); 6–16(–22) cm long by 1.0–7.5 cm wide and 45–60 μm thick; pale rose to greenish rose or purplish red; attached by rhizoids from basal cells, 25–40 μm long and 18–28 μm wide, forming a discoid holdfast. Cells in surface view, with a thick cell wall, 12–20 μm in length, 8–12 μm wide; in transection, cells slightly elongated, 10–23(–30) μm tall and 8–20 μm wide.

Asexual reproduction unknown. Gametophytes dioecious. Zygotosporangia (“carposporangia”) in packets of 8 zygotospores, darker red than vegetative cells; forming continuous darker “reddish” patches along blade margins. Spermatangia on separate thalli; in packets of 64 spermatia; forming continuous whitish-yellowish margins on both sides of blade.

Habitat. On intertidal rocks; mostly high to mid intertidal.

Distribution. Gulf of California: Bahía Bocochibampo (west-northwest of Guaymas); Isla San Ildefonso to Bahía Agua Verde; Punta Arena (north of Cabo Pulmo).

Type Locality. On upper intertidal rocks; Bahía Agua Verde, Baja California Sur, Gulf of California, Mexico.

Remarks. *Pyropia hollenbergii* is apparently an endemic species, generally found from winter to spring. It primarily differs from other similar monostromatic, dioecious species of *Pyropia* by the number of packets of spermatia and its usually divided thallus with ruffled margins and purplish to rose to slightly greenish color (Dawson, 1953a). The life history phases of the Gulf *P. hollenbergii*, the foliose gametophytes and filamentous *Conchocelis*-phase, were found to be controlled by a combination of photoperiod and high water temperatures (López-Vivas et al., 2011).

The isotype of *Pyropia hollenbergii* shows variability in shape, from more or less lanceolate to broader, oval forms (*Porphyra hollenbergii*: *EYD-539-40*, US Alg. Coll.-56865). The broader forms of *Pyropia hollenbergii* can be somewhat similar to Gulf *Pyropia thuretii* but differ primarily in being dioecious, whereas *P. thuretii* is monoecious.

Pyropia pendula (E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas

FIGURE 18B

Porphyra pendula E. Y. Dawson, 1953a:16, pl. 13: fig. 2; 1961b:402; Espinoza-Avalos, 1993:333; González-González et al., 1996:258; Yoshida et al., 1997:11, fig. 3; López-Vivas and Riosmena-Rodríguez, 2000:45; L. Aguilar-Rosas et al., 2004:121, figs. 2a–c, 3–10; Nelson et al., 2006:250, 253, 254; Pacheco-Ruíz et al., 2008:205.

Pyropia pendula (E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas in Sutherland et al., 2011:1144.

Algae of monostromatic blades, pale to bright rose, attached by a very small discoid holdfast. Blades usually simple, sometimes divided near base, linear-ligulate and pendent, to 25 cm long, 3–12 mm wide; gradually becoming acuminate to apices, 45–50 μm thick; with ruffled margins. Cells irregularly shaped, to 11 μm in diameter in surface view; usually to 25 μm tall in transection.

Asexual reproduction unknown. Zygotosporangia (“carposporangia”) with packets of 8 zygotospores (“carpospores”) borne continuously along bright rose red margins and apices of blade. Spermatangia with packets of 128 spermatia; borne continuously along yellowish margins and apices of blade.

Habitat. On rocks; upper spray zone, and high to mid intertidal.

Distribution. Gulf of California: Isla Patos (off north end of Isla Tiburón) to Isla Partida Norte; Isla San Pedro Nolasco; Isla Carmén to Isla Espíritu Santo; Calerita to Punta Coyote (vicinity of Bahía de La Paz).

Type Locality. On shaded cliff rocks, upper intertidal spray zone; Isla Partida Norte (Isla Cordonazo), western island of Islas de la Cintura, Gulf of California, Mexico.

Remarks. *Pyropia pendula* is an endemic species of the Gulf of California, recognized in the field by its linear to lanceolate, often twisting, blades.

Pyropia thuretii (Setchell et E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas

FIGURE 18A,C,D

Porphyra thuretii Setchell et E. Y. Dawson in Smith, 1944 [May]:171, pl. 40: fig. 2; Setchell et E. Y. Dawson in Dawson, 1944a[July]:253; Doty, 1947:161; Dawson, 1953a:18; 1961b:403; Dawson et al., 1964:32, pl. 28; Norris, 1973:8 [with query]; Abbott and Hollenberg, 1976:302, fig. 246; Acleto O. and Endo, 1977:13, figs. 23–29; Garbary et al., 1981:185; Hawkes, 1982:98, figs. 7–11; Scagel et al., 1989:242; Rocha-Ramírez and Siqueiros-Beltrones, 1991:26, 32; Ramírez and Santelices, 1991:170; Lindstrom and Cole, 1992: 2069, tbls. 1–3; González-González et al., 1996:258; Yoshida et al., 1997:13, fig. 1; L. Aguilar-Rosas et al., 2000:130, 137; CONANP, 2002:136; L. Aguilar-Rosas and Aguilar-Rosas, 2003:159, figs. 2a–c, 3–10; Pacheco-Ruíz et al., 2008:205; Fernández-García et al., 2011:64.

Pyropia thuretii (Setchell et E. Y. Dawson) J. E. Sutherland, L. E. Aguilar-Rosas et R. Aguilar-Rosas in Sutherland et al., 2011:1145.

Porphyra leucosticta sensu Hus, 1902:199, pl. 20: figs. 1a–3b; Howe, 1911:499; González-González et al., 1996:258 [non *Porphyra leucosticta* Thuret in Le Jolis, 1863b:100; which is now *Pyropia leucosticta* (Thuret) Neefus et J. Brodie in Sutherland et al., 2011:1144].

Porphyra naiadum sensu Taylor, 1945:133 [in part; only Costa Rica specimens; non *Porphyra naiadum* C. L. Anderson in Blankinship and Keeler, 1892:148, which is now *Smithora naiadum* (C. L. Anderson) Hollenberg, 1959:3].

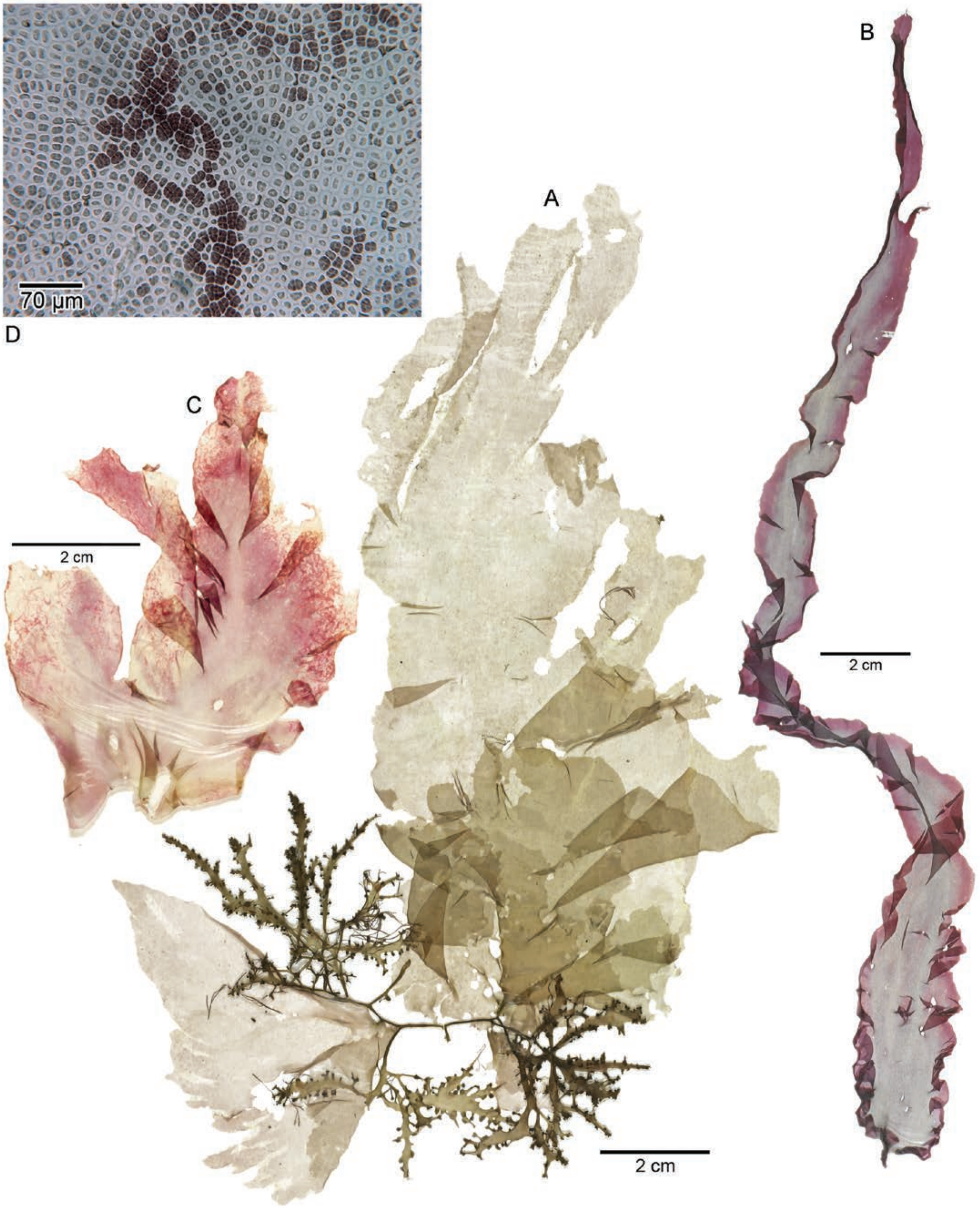

70 µm
D
B
A
C
2 cm
2 cm
2 cm

FIGURE 18. (Opposite) Species of *Pyropia*. A. *Pyropia thuretii:* Habit (*EYD-12546,* US Alg. Coll.-41997). B. *Pyropia pendula:* Habit (*JN-5194a*, US Alg. Coll.-160625). C. *Pyropia thuretii*: Habit, note reproductive regions with irregular streaks along blade margins (*JN-5194b*, US Alg. Coll.-160627). D. *Pyropia thuretii*: Surface view of cell arrangement within marginal reproductive area showing packets of darker zygotosporangia (*JN-5194b*, US Alg. Coll. microscope slide 4297).

Algae a single monostromatic blade, rose to purple, up to 6(–75) cm tall, attached by rhizoids from basal cells. Blades of Gulf specimens oval to broadly reniform, sometimes taller than broad, 25–40 µm thick, markedly cordate at base, with a short stipe. Cells in transection, subcubical to rectangular, 8–20 µm long by 4–10 µm wide; in surface view, polygonal, 10–15 µm long by 4–8 µm wide; with a single stellate plastid.

Asexual reproduction unknown. Gametophytes monoecious. Zygotosporangia in marginal bands with spermatangia lying in alternate streaks diagonal to blade margin. Zygotosporangia with zygotospores in packets of 8. Spermatia in packets of 64.

HABITAT. On rocks or occasionally epiphytic; high intertidal to shallow subtidal, down to 5 m depths.

DISTRIBUTION. Gulf of California: Rocas Consag; San Felipe to Bahía San Luís Gonzága; Puerto Refugio, Isla Ángel de la Guarda; Isla Patos (off north end of Isla Tiburón); Isla Partida; Ensenada Bocochibampo; Isla Carmen to Bahía de La Paz; Playa Pinitos to Playa Olas Altas (vicinity of Mazatlán), Sinaloa. Eastern Pacific: northern British Columbia to central California; Todos Santos (Baja California Sur); Costa Rica; Peru.

TYPE LOCALITY. On *Gracilariopsis andersonii* (as "*G. sjoestedtii*"); Pacific Grove, Monterey County, central California, USA (Dawson, 1944a; Smith, 1944); "floating in Carmel Bay, Monterey County, California" (UC-791973; Krishnamurthy, 1972:45).

Conchocelis-Phase of *Pyropia*

FIGURE 19

Conchocelis Batters, 1892:27, pl. 8; Drew, 1949:748; 1954:183; Tseng and Chang, 1954:287; 1955a:27; 1955b:375, pls. 1–7; Drew, 1955:373; 1956a:573; Hollenberg, 1958b:653, figs. 1–13; Hollenberg and Abbott, 1966:38; Richardson and Dixon, 1968:496.

Microscopic filamentous algae; growing on and perforating into calcareous substratum (such as old mollusk shells); forming pinkish patches. Uniseriate filaments (1.5–)4–6(–8) µm in diameter, highly variable, straight, curving, clavate, or irregular; branching opposite, alternate, or irregular; lateral branches sparse to dense; sometimes interwoven, forming a network. Portions of filaments notably swollen, 20–30 µm in diameter, of 2–10 cells (7.0–75 µm long) irregular-shaped, septate, simple to divided inflations. Cells more or less cylindrical, becoming tortuous to irregular, constricted at septae; pit plugs between cells; with a single parietal, band-shaped to stellate plastid.

Asexual reproduction by two known modes: (1) conchospores developed from conchosporangia, 13–15 µm in diameter, formed in inflated cells of the filaments, and usually superficial on calcareous shells; or (2) by protoplasts from a protothallus.

HABITAT. Within old mollusk shells, particularly bivalves, and other calcareous substratum; intertidal to subtidal.

DISTRIBUTION. Gulf of California: *Conchocelis*-phase not yet found in field collections.

GENERITYPE. *Conchocelis rosea* Batters, 1892:27, pl. 8.

TYPE LOCALITY. In empty shells of *Mya truncata* Linnaeus (truncate soft-shell clam) and *Solen vagina* Linnaeus (European razor clam); "dredged in 6–8 fathoms off Tan buoy, between the islands of Great Cumbrae and Little Cumbrae" (Batters, 1892:25), Millport, Firth of Clyde, western Scotland, United Kingdom.

REMARKS. In culture studies Drew (1949, 1954) and Kurogi (1953a, 1953b) observed spores from *Porphyra* developed into shell-penetrating *Conchocelis*-like filaments. Since then, the "shellboring" *Conchocelis*-phases or *Conchocelis*-like algae have been reported in the life histories of many other species of *Bangia, Porphyra,* and *Pyropia*. The *Conchocelis*-phases have been occasionally reported in nature, but because of their similar morphologies they are not easily distinguished, making it nearly impossible to associate it with the macro-phase of known species.

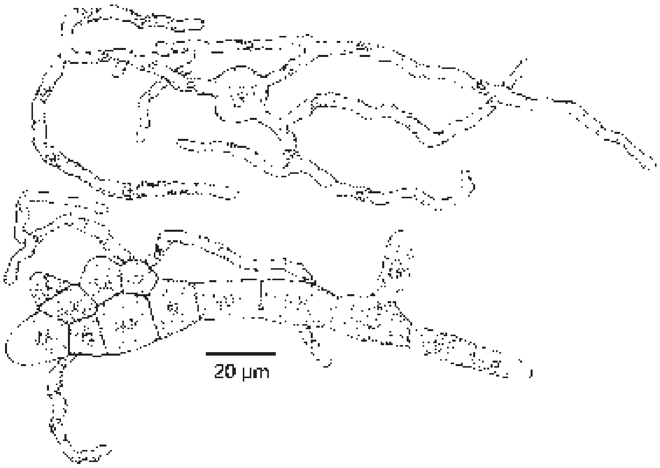


FIGURE 19. *Conchocelis*-phase: Habit of growing filaments developed from zygotospores of *Pyropia perforata* (after Hollenberg, 1958b: figs. 3, 9).

Molecular studies are needed to test their genetic relationships and whether the *Conchocelis*-phase is unique to certain genera or possibly species-specific. Culture studies on Gulf of California species of *Pyropia* and *Bangia* should reveal whether the expected *Conchocelis*-phases are involved in their life histories, as has been found in Gulf *P. hollenbergii* (López-Vivas et al., 2011).

PART IIB. FLORIDEOPHYCEAE

Florideophyceae Cronquist, 1960:438.
Florideophyceae Warming, 1884:43 [as "Florideae"].
Nemaliophyceae M. Shameel, 2001:245.

The class Florideophyceae is exemplified by an enormous diversity of forms; all are essentially filamentous and pseudoparenchymatous in structure. Thalli are formed by the aggregation of filaments, which are produced almost exclusively by the division of apical cells (Dixon, 1973); that is, growth is by apical cells that together with lateral initials form branched filaments in which the cells are linked throughout by pit connections. Intercalary cell division is also known, for example, in some species of the Delesseriaceae and Corallinaceae.

Algae are cylindrical to foliose and branched or unbranched. Two main types of construction are found: uniaxial (with a single axial filament) and multiaxial (with several to many axial filaments). Most thalli have erect and prostrate portions and are heterotrichous in organization. However, this is not found in the Ceramiales or in certain of the presumed parasitic genera. Cells are uninucleate or multinucleate and generally have several disc-shaped plastids.

Asexual reproduction is by monospores, bispores, tetraspores, or polyspores produced within sporangia that are borne lateral or terminal. Life histories, where known, are usually triphasic with gametophytes, carposporophytes, and tetrasporophytes. Most have a tetrasporophyte that develops tetrasporangia, producing four spores. The female gametophyte develops carpogonia, each with a trichogyne that is borne lateral or terminal on the carpogonial filaments ("branches"). Fertilization is initiated when spermatia attach to the trichogyne of a carpogonium, and the carposporophyte either develops directly from the carpogonium or from its derivatives. After fertilization, one to numerous special filaments called gonimoblasts are produced. Either all of the cells or only certain cells of the gonimoblast develop into carposporangia. Each carposporangium produces a single carpospore or, more rarely, a tetrad of carpospores. The female reproductive system is borne singularly or adjacent to others in sori, nemathecia, or conceptacles. Cystocarps are either naked or surrounded by involucral filaments or a pericarp. They are borne on the thallus surface or embedded within the cortical layers or in some species within the medulla. Spermatia are produced within spermatangia borne laterally or terminally in clusters, sori, or conceptacles or on spermatangial filaments.

REMARKS. The largest class of red algae is commonly referred to as the "Florideophyceae," a descriptive name. However, the correct typified name, although little used, is the Nemaliophyceae M. Shameel (2001), an elevation in rank of Nemaliophycidae T. A. Christensen (1978; see Silva in Silva et al., 1996a:911).

The majority of the class Florideophyceae, as in the Bangiophyceae, are marine species, occurring throughout the world's oceans from both poles to the equator. The Florideophyceae presently includes five subclasses that are well represented in the northern Gulf of California marine flora. The subclasses are currently divided into 28 orders, 19 of which are found in the northern Gulf.

KEY TO THE SUBCLASSES OF FLORIDEOPHYCEAE IN THE NORTHERN GULF OF CALIFORNIA

(AFTER SAUNDERS AND HOMMERSAND, 2004)

1a. Noncalcified crusts; zonate tetrasporangia; sexual reproduction unknown; pit plugs with single cap membrane but lack an outer cap layer . . . . **Hildenbrandiophycidae**
1b. Erect or crustose, calcified or noncalcified; ultrastructurally, pit plugs with or without cap layers 2
2a. Pit plugs with cap layers 3
2b. Pit plugs without cap layers and mostly without cap membranes (at least 1 member without cap layers and with cap membranes) 4
3a. Members noncalcified or some calcified (aragonite); ultrastructurally, pit plugs with 2 cap layers; tetrasporangia cruciately divided . . . . **Nemaliophycidae**
3b. Calcified (calcite) articulated and crustose corallines; pit plugs with 2 cap layers and the outer pit plug is dome shaped; tetrasporangia zonately divided . . . . **Corallinophycidae**
4a. Carposporangia terminal and sessile; carposporophyte developing outward; pit plugs without cap layers and membranes . . . . **Ahnfeltiophycidae**
4b. Triphasic life histories; carposporophyte developing directly from carpogonium or carpogonial fusion cell or indirectly from auxiliary cell (which received postfertilization diploid nucleus); pit plugs with membranes (with the exception of Gelidiales, which has a single cap layer) . . . . **Rhodymeniophycidae**

HILDENBRANDIOPHYCIDAE

Hildenbrandiophycidae G. W. Saunders et Hommersand, 2004:1504; Schneider and Wynne, 2007:201.

Algae are uncalcified crusts with upper surfaces that are usually smooth to slightly irregular or tuberculate, although a few have erect branches. Internally, the members are composed of a basal layer of laterally adhering, branched filaments and upper layers of laterally adhering, simple or branched, erect filaments. Ultrastructurally, the cells have pit plugs with a single cap layer and membrane.

Tetrasporangia are zonately or irregularly divided, are apomeiotic, and are borne within sunken, ostiolate conceptacles. Gametangial structures are unknown.

Remarks. The subclass Hildenbrandiophycidae has the characteristics of the Hildenbrandiales, an order that is represented in the northern Gulf of California.

HILDENBRANDIALES

Hildenbrandiales Pueschel et K. M. Cole, 1982:718; Pueschel, 1982:333.

Algae are entirely prostrate and encrusting or may have erect axes that arise from a crustose base. Thalli usually spread as they grow and can often cover extensive areas. Structurally, these crusts are thin and composed of strongly united filaments of rows of cells. Their lower surface is closely attached to the substratum without rhizoids. Ultrastructurally, the pit plugs have a single cap membrane but lack an outer cap layer.

Tetrasporangia are produced within characteristic sunken conceptacles. Tetrasporangia are elongated and zonately or irregularly divided. Sexual reproduction is unknown.

Remarks. Ultrastructural studies have shown single-layered pit plugs in *Hildenbrandia* (Pueschel and Cole, 1982; Pueschel, 1982, 1988b, 1989). This character and the presence of conceptacles that enlarge in a distinctive manner (i.e., by the continuous development of tetrasporangia, which are produced by the continuous conversion of vegetative cells that line the conceptacle wall and floor) make this order, with its single family, unique among the red algae. Culture studies of tetraspores have thus far yielded only sporophytes (Umezaki, 1969; DeCew and West, 1977a; Fletcher, 1983), and tetrasporangia remain the only reproductive structure known in the order.

The single family of the order, Hildenbrandiaceae, is represented in the northern Gulf of California.

HILDENBRANDIACEAE

Hildenbrandiaceae Rabenhorst, 1868:408 [as "Hildenbrandtiaceae"].

Algae are prostrate and entirely crustose or with simple or branched axes arising from the crustose base. The lower surface is without rhizoids but is closely and usually strongly adherent to the substratum. Internally, it is composed of small cuboidal cells in vertical rows. Basal rows are composed of small cylindrical cells, tightly crowded together. Erect rows (filaments) of the upper layers are composed of elongate cylindrical cells that form a cortex, with secondary pit connections usually present between cells. Ultrastructurally, the pit plugs have a single cap layer.

Vegetative reproduction is by propagules in freshwater species and apparently not by spores. Tetrasporangial conceptacles, the only known reproductive structures, are developed below the thallus surface in marine species, with tetrasporangia being continuously produced from the repeated conversion of vegetative cells of the surrounding conceptacle walls. Tetrasporangia are transversely to obliquely zonate or irregularly divided. Gametophytes are unknown.

Remarks. The Hildenbrandiaceae is generally recognized to include two genera: the presumably cosmopolitan *Hildenbrandia* and *Apophlaea* J. D. Hooker et Harvey (1845; see Saunders and Bailey, 1999), known from New Zealand and the sub-Antarctic islands. The species are almost exclusively marine, found from the high intertidal to subtidal in tropical to subpolar waters, but there is at least one widely distributed freshwater species (Sheath, 2003; Sherwood and Sheath, 2003).

Fungal hyphae of *Mycosphaerella* Johanson (1885; Ascomycetes) are often found penetrating the cell walls and into the conceptacle chambers of *Hildenbrandia* and *Apophlaea* (Kohlmeyer and Demoulin, 1981; Hawkes, 1983). Species of *Mycosphaerella* have also been described in other marine algae (e.g., Johnson and Sparrow, 1961), and the possible symbiotic fungal-alga association (Kohlmeyer and Hawkes, 1983) is apparently more common in the high intertidal. Other fungal-alga or fungal-cyanobacteria associations in marine habitats include members of the order Verrucariales Mattick ex D. Hawksworth et O. E. Erkisson (1986; Ascomycota, Eurotiomycetes), lichenized and nonlichenized fungi (Fletcher, 1980; Hawksworth, 2000), with some of the species found in coastal regions of Baja California and Sonora (e.g., Breuss and Bratt, 2000; Breuss, 2001). Other interesting marine fungal–alga associations on the eastern Pacific coast are found in the green alga *Blidinga minima* var. *vexata* (Setchell et N. L. Gardner) J. N. Norris (1971) from Alaska to California, and between a brown alga *Petroderma maculiforme* (Wollny) Kuckuck (1897; Wynne, 1969) and the lichen *Verrucaria tavaresiae* Moe (1997; Saunders et al., 2004), which occurs from Washington to California (Scagel et al., 1989) and Guerrero (Pedroche et al., 2008).

Hildenbrandia is the only genus of the Hildenbrandiaceae found in the Gulf of California.

Hildenbrandia Nardo

Hildenbrandia Nardo, 1834:676 [as "*Hildenbrandtia*"]; Pueschel, 1982:333; 1988b:25; 1989:625.

Algae are prostrate, coriaceous, noncalcified crusts, with smooth surfaces, and are usually irregular in outline. These firm crusts spread outward by peripheral growth, and their lower surface, without rhizoids, is strongly attached to the substratum. Anatomically, they are composed of small cells that are cylindrical or occasionally elongated in the direction of growth and in uneven or horizontal rows (horizontal stratification of the thallus is sometimes apparent). The hypothallus or basal layer is composed of firmly united, radially branched, horizontally spreading filaments; secondary pit connections are abundant (Pueschel, 1982, 1988b). The basal layer gives rise to the perithallus (upper layers), which is composed of compacted, vertical (erect) rows of sparsely branched filaments that adhere laterally to each other and form a pseudoparenchyma that is divided into transverse layers. Cells are cylindrical, mostly ~5 μm in diameter, uninucleate, with a single chloroplast. Adjacent cells of the filaments are joined by secondary pit connections, which are often abundant (Pueschel, 1988b). Pit plugs are unique in that they have a cap membrane but lack an outer cap layer.

Tetrasporangia are zonate, transversely to obliquely divided, but sometimes appearing cruciate or irregularly divided, and develop from the walls and floors of rounded to ovate, ostiolate conceptacles within the perithallus. The round to ovate or cylindrical conceptacle chambers become enlarged by repeated rounds of the conversion of vegetative cells lining the walls and floor into tetrasporangia. Conceptacles are with or without paraphyses. Sexual reproduction has not been convincingly shown for species of *Hildenbrandia* (Irvine and Pueschel, 1994), and gametangial structures remain unknown.

Remarks. There is one Pacific Mexico species, *Hildenbrandia dawsonii* (Ardré) Hollenberg (1971b; basionym: *H. canariensis* var. *dawsonii* Ardré, 1959), described from Punta Malamarrimo, Bahía Sebastián Vizcaíno, Baja California, that has been reported from San Juan Islands, Washington, to Baja California Sur (Abbott and Hollenberg, 1976) and in the southern Gulf of California from Nayarit to Jalisco (León-Álvarez and González-González, 1993; Mateo-Cid and Mendoza-González, 1992; Mendoza-González and Mateo-Cid, 1992; Mateo-Cid and Mendoza-González, 1994b).

Two species of *Hildenbrandia* are recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *HILDENBRANDIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts usually dark reddish brown to blackish; 250–450 μm thick; tetrasporangia irregularly divided, borne within immersed subspherical to compressed (wider than tall) conceptacles, with conspicuous paraphyses .... ***H. prototypus***
1b. Crusts lighter in color, rose to red; thinner, (50–)80–250 μm thick; tetrasporangia obliquely cruciate or irregularly divided, borne within immersed ovate conceptacles, without paraphyses .... ***H. rubra***

Hildenbrandia prototypus Nardo

FIGURE 20

Hildenbrandia prototypus Nardo, 1834:676; Taylor, 1945:166; Dawson, 1953a:95, pl. 7: fig. 4; 1959a:20; 1961b:413; 1966a:17; Denizot, 1968:196, fig. 196; Umezaki, 1969:17, fig.1; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:8,12; Abbott and Hollenberg, 1976:377 [in part; excluding *H. rosea*]; DeCew and West, 1977a:31, figs. 3–5, 8, 9; Huerta-Múzquiz, 1978:340; Pueschel and Cole, 1982:709, fig. 17; Schnetter and Bula-Meyer, 1982:123, pl. 16: fig. C; Huerta-Múzquiz and Mendoza-González, 1985:48; Ramírez and Santelices, 1991:228; Stewart, 1991:77; León-Álvarez and González-González, 1993:461 [in part]; González-González et al., 1996:317, 397; CONANP, 2002:141; Fernández-García et al., 2011:62.

Hildenbrandia rosea sensu Setchell and Gardner, 1924:787; Dawson, 1944a:265 [in part]; González-González et al., 1996:226 [non *H. rosea* Kützing, 1843:384, which is now *Hildenbrandia rubra* (Sommerfelt) Meneghini, 1841:426].

Algae crustose, reddish brown to blackish, spreading up to 2 cm, with a smooth surface; 250–450 μm thick; lower surface closely adherent to substratum, rhizoids lacking. Cells of erect filaments, squarish to slightly elongated, (2.5–)3–5 μm in diameter, arranged in compact vertical rows; secondary pit connections present.

Tetrasporangia irregularly divided, 15–22 μm long by 3.5–6.5 μm in diameter. Tetrasporangia borne inside immersed,

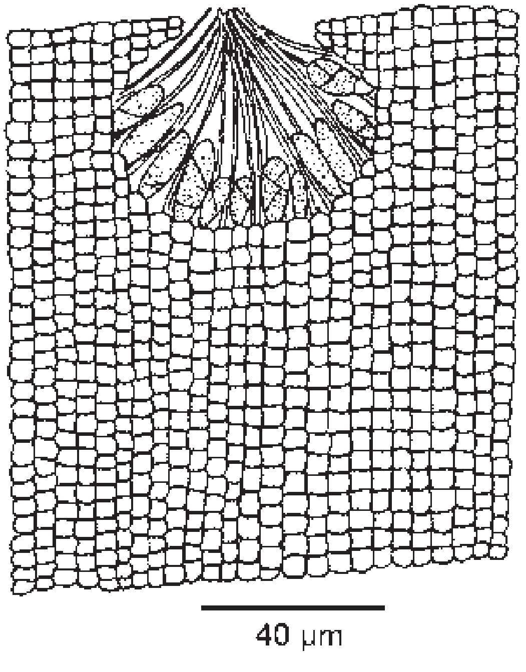


FIGURE 20. *Hildenbrandia prototypus:* Vertical section through crust showing a tetrasporangial conceptacle with irregularly divided sporangia among paraphyses (after Dawson, 1953a: pl. 7, fig.4).

subspherical to compressed (wider than tall), ostiolate conceptacles, 35–110 µm wide by 35–60 µm deep; with conspicuous paraphyses.

Habitat. On rocks; high to low intertidal.

Distribution. Gulf of California: Puerto Peñasco; Isla Turner, off SE end of Isla Tiburón (Islas de la Cintura); Isla Carmén; Cabeza Ballena; Nayarit to Jalisco; Isla María Magdalena and Isla María Cleofas (Islas Marías; Islas Tres Marias). Eastern Pacific: Alaska to Baja California; Isla Socorro and Isla Clarión (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador; Costa Rica; Panama to Colombia; Galápagos Islands; Chile.

Type Locality. Venezia, shore of Adriatic Sea, northeast Italy (Smith, 1944).

Remarks. Some have considered *Hildenbrandia prototypus* and *H. rubra* to be conspecific (e.g., Denizot, 1968) or *H. prototypus* to be conspecific with *H. rosea* Kützing (1843) (e.g., Abbott and Hollenberg, 1976). However, Irvine and Pueschel (1994) listed *H. prototypus* as a doubtful synonym of *H. rubra* since the type is unknown, and the tetrasporangial cleavage was not given in the original description of Nardo (1834). Thus, the taxonomic status of *H. prototypus* is somewhat uncertain. Until specimens, including types, can be critically studied, the Gulf material herein referred to *H. prototypus* differs in being thicker than *H. rubra*, (250–)270–500 µm, and dark reddish brown to blackish. Dawson (1953a) noted the cell sizes of Pacific Mexico *H. prototypus* were somewhat smaller than those reported from elsewhere in the world.

***Hildenbrandia rubra* (Sommerfelt) Meneghini**

Verrucaria rubra Sommerfelt, 1826:140.

Hildenbrandia rubra (Sommerfelt) Meneghini, 1841:426; Denizot, 1968:199; Pueschel and Cole, 1982:333, figs. 1–2, 17; Dethier, 1987:1842, fig. 8; Pueschel, 1988a:17, figs. 1–6; Mendoza-González and Mateo-Cid, 1992:17; León-Álvarez and González-González, 1993:461 [in part]; Serviere-Zaragoza et al., 1993a:483; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:47; Irvine and Pueschel, 1994:241, figs. 117B, 118B; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:105; González-González et al., 1996:397; Sherwood and Sheath, 1999:525; L. Aguilar-Rosas et al., 2000:130; Müller et al., 2005b:380; Mateo-Cid et al., 2006:55; Serviere-Zaragoza et al., 2007:10.

Hildenbrandia prototypus sensu Taylor, 1945:166 [in part]; Dawson, 1953a:95 [in part]; 1966a:17 [non *Hildenbrandia prototypus* Nardo, 1834:676].

Thallus crustose, noncalcified, rose to dark red, thin, (50–) 80–250 µm thick, and spreading up to 12 cm across, irregular in outline; upper surface more or less smooth; lower surface tightly adherent to substratum, rhizoids absent. Erect filaments, up to 100 µm long, of 10–30 cells arranged in compact, more or less vertical rows. Cells of perithallus, squarish to slightly elongated, 2.5–5.0 µm in diameter by 2.5–6.0(–7.0) µm tall; secondary pit connections present.

Tetrasporangia obliquely cruciate or irregularly divided, 15–25(–35) µm long by 8.0–12(–15) µm in diameter; borne within immersed, ovate conceptacles, 80–90 µm wide by 65–70 µm deep; paraphyses lacking.

Habitat. On rocks; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía La Choya (Bahía Cholla, vicinity of Puerto Peñasco); San Felipe to Bahía de Los Ángeles; Cabeza Ballena; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: British Columbia to Oregon; Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Socorro, Isla Clarión and Isla San Benedicto (Islas Revillagigedo); Michoacán to Oaxaca; Costa Rica; Panama; Galápagos Islands.

Type Locality. Saltdal, Nordland, Norway ("in lapidibus a fluxu maris inundatis ad litora Nordlandiae frequenter" [Sommerfelt, 1826:140]).

Remarks. The thin, mostly rose red to brownish red, Gulf of California specimens of Dawson (1953a, 1966a, both as "*H. prototypus*") are herein referred to *H. rubra*. *Hildenbrandia rosea* is sometimes accepted as a synonym of *H. rubra* (e.g., Silva et al., 1996a). However, Irvine and Pueschel (1994) listed both *H. rosea* and *H. prototypus* as doubtful synonyms of *H. rubra*. The type of *H. prototypus* is unknown, and its tetrasporangial cleavage was not given in the original description (Nardo, 1834), and the type of *H. rosea* Kützing (1843) was nonreproductive. Thus, the status of these taxa is uncertain, and Gulf specimens identified as "*H. prototypus*," "*H. rosea*," or "*H. rubra*," need to be critically reinvestigated taxonomically, in culture, and tested with DNA analyses with type locality materials.

Although another eastern Pacific species, *H. occidentalis* Setchell in Gardner (1917), described from northern California and reported from Alaska to Baja California, is recognized as a separate taxon by several phycologists (e.g., Abbott and Hollenberg, 1976; DeCew and West, 1977a; Dethier, 1987; Pueschel, 1988b; Scagel et al., 1989), Sherwood and Sheath (1999) found its separation from *H. rubra* was only partially supported.

NEMALIOPHYCIDAE

Nemaliophycidae T. A. Christensen, 1978:66; Guiry and Irvine, 1989:155; G. W. Saunders et Hommersand, 2004:1504; Schneider and Wynne, 2007:201.

Members of the subclass Nemaliophycidae are characterized by generally having a triphasic life history, and ultrastructurally, they have pit plugs with two cap layers.

Remarks. Recently, new orders and families were added to the Nemaliophycidae: Balliales H.-G. Choi, Kraft et G. W. Saunders (2000), Colaconematales J. T. Harper et G. W. Saunders (2002), Thoreales K. M. Müller, Sheath, A. R. Sherwood et Pueschel (in Müller et al., 2002), and on the basis of a new unique acrochaetioid algal genus, *Rhodachlya*, the Rhodachlyales G. W. Saunders, S. L. Clayden, J. L. Scott, K. A.West, U. Karsten et J. A.West (in West et al., 2008).

The subclass Nemaliophycidae is represented by four of its orders in the northern Gulf of California.

KEY TO THE ORDERS OF THE NEMALIOPHYCIDAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Algae filamentous, crusts of laterally fused filaments and erect fronds; life history diphasic, lacking a carposporophyte; single-cell carpogonium after fertilization directly produces tetrasporangial thallus; tetrasporangia repeatedly regenerated from a basal generative stalk cell (unique to the order); monosporangia not known . . . . **Palmariales**
1b. Algae either of uniseriate filaments or multiaxial with medullary and cortical layers; life histories triphasic or biphasic, with isomorphic, dimorphic, or heteromorphic phases; monosporangia present or absent 2
2a. Algae structurally complex (not a single row of axial cells); of filamentous medulla and cortex of loose anticlinal filaments, or compact, laterally adjoined filaments, or of cells fused to form a pseudoparenchymatous cortex; life histories triphasic with isomorphic, dimorphic, or heteromorphic phases . . . . **Nemaliales**
2b. Algae simple, unbranched to branched, uniseriate filaments 3
3a. Uniseriate filaments of two different kinds of members: one group has cells with 1 to several, discoid to band-shaped, parietal plastids without pyrenoids, tetrasporangia (monosporangia unknown), and biphasic life history; second group has cells with a single, stellate plastid and a central pyrenoid, primarily monosporangia, and triphasic life history . . . . **Acrochaetiales**
3b. Uniseriate filaments of cells with 1 or more lobed, spiral, or irregular (never stellate) parietal plastids, and with or wthout pyrenoids; monosporangia, life histories biphasic or triphasic . . . . **Colaconematales**

ACROCHAETIALES

Acrochaetiales Chemin, 1937:300.

Acrochaetiales Feldmann, 1953:12; Harper and Saunders, 2002:470 [emended description].

Algae are composed of uniseriate simple or branched filaments. Members occur in marine or freshwater habitats. There are two groups of marine species. Members of the first group have cells that may contain one but usually have several parietal discoid to band-shaped chloroplasts per cell and lack pyrenoids (i.e., *Rhodochorton* Nägeli, 1862); monosporangia are unknown in these members, asexual reproduction is primarily by tetrasporangia, and sexual reproduction, where known, involves a biphasic life history. In the second group each cell has a single stellate chloroplast with a single central pyrenoid; reproduction is primarily by monosporangia, and sexual reproduction, where known, involves a triphasic life history.

Members of the one family are known to occur in the Gulf of California.

ACROCHAETIACEAE

Acrochaetiaceae Fritsch ex W. R. Taylor, 1957:209–210, *nom. cons.*

Acrochaetiaceae Fritsch, 1944:258 [footnote], *nom. nudum*; Fritsch, 1945:737 [see Silva, 1980:20].

Chantransiaceae Kützing, 1843:180 [not including *Chantransia*; see Silva, 1952:261].

Rhodochortaceae Nasr, 1947:92, *nom. rej.*

Members of this family are mostly minute, uniseriate branched filaments, growing epiphytically, endophytically, or endo–epiphytically on various algae and sea grasses, endozoic or epizoic on invertebrates, or on hard substratum. Cells of the filaments are uninucleate and contain one chloroplast with one pyrenoid.

Asexual reproduction in most of the species is by monospores, but in some, it is by bispores or tetraspores. Sporangia are borne laterally or terminally. In some, the tetrasporophyte develops directly from the fertilized carpogonium (Stegenga, 1978). Sexual reproduction is apparently rare, and gametophytes are known in only a few genera (Abbott, 1962). The female reproductive apparatus is a one- to three-celled carpogonial branch. After fertilization the short-branched gonimoblast filaments produce carposporangia terminally. Cystocarps are exposed and naked without a surrounding envelope. Spermatangia are clustered on short-branched filaments.

Culture studies within this family have shown many interesting life histories (e.g., Stegenga, 1985b), with isomorphic and heteromorphic phases. Some culture studies have shown "*Acrochaetium*-like" phases to be involved in life histories of other, morphologically dissimilar species or even different genera (some even in other families). One of the earlier studies revealed an *Acrochaetium*-like phase of *Ganonema farinosum* (Liagoraceae) (von Stosch, 1965, as *Liagora farinosa*).

The Acrochaetiaceae is represented by one genus in the northern Gulf of California.

KEY TO THE UNISERIATE FILAMENTOUS RED ALGAE: GENERA OF ACROCHAETIACEAE (ACROCHAETIALES), COLACONEMATACEAE (COLACONEMATALES), AND RHODONEMATELLACEAE (PALMARIALES) IN THE NORTHERN GULF OF CALIFORNIA

1a. Cells of filaments with stellate chloroplasts containing a pyrenoid; asexual reproduction by monosporangia . . . . ***Acrochaetium* (Acrochaetiaceae)**
1b. Cells of filaments with a single parietal chloroplast or rarely with several parietal plastids 2

2a. Cells with a single parietal chloroplast and 1 pyrenoid; asexual reproduction by monosporangia . . . . ***Colaconema*** **(Colaconemataceae)**
2b. Cells with more than 1 parietal chloroplast, without pyrenoids; asexual reproduction by tetrasporangia (monosporangia lacking) . . . . ***Rhodonematella*** **(Rhodonematellaceae)**

Acrochaetium Nägeli

Acrochaetium Nägeli in Nägeli et C. E. Cramer, 1858:532; Harper and Saunders, 2002:470.

Algae are uniseriate filaments that are mostly microscopic, sometimes minute, and either epiphytic, endophytic, or endo-epiphytic (partly embedded within their alga host) or epizoic or endozoic on various invertebrates (notably hydrozoans, sponges, or mollusks) or growing on rocks or other hard substratum. Erect filaments are simple and unbranched or may be variously branched, irregular, secund, or opposite. Branch ends of some species may occasionally bear terminal unicellular hairs. Gametophytes are attached by a single cell or a monostromatic base. Cells contain a single stellate chloroplast with a central pyrenoid.

Life histories, where known, are triphasic, involving heteromorphic phases of sporophytes and gametophytes. Asexual reproduction is mainly by spherical monosporangia, borne terminally or laterally. In many species monospores are the only form of propagation known. Tetrasporangia, where known, are cruciately divided and terminal or lateral on erect filaments and branches. Sexual reproduction is apparently rare or unknown in many species. Gametophytes are monoecious or dioecious. Carpogonia (where known) are one-celled (lack a distinct carpogonial filament) and sessile or pedicellate. Postfertilization zygote does not divide but directly produces a small, globose carposporangium. Spermatangia produced in small clusters, with one to several spermatangia, and borne on long, hyaline stalks.

REMARKS. In the past *Acrochaetium* was generally accepted to represent a "form genus" in which, for convenience, species that resembled each other were all placed together within a broadly defined single genus, *Audouinella* Bory de Saint-Vincent (1823) by Woelkerling (1973a, 1973b). On the basis of the species studied, Pueschel (1989, 1990) concluded that they were polyphyletic. *Acrochaetium* has now been restricted to marine species that reproduce chiefly by monosporangia and contain stellate plastids (Y.-P. Lee and Lee, 1988); this generic concept has been supported by molecular analyses (Harper and Saunders, 2002). The freshwater species now are placed in *Audouinella*.

Dixon (1963) first suggested some members of the "*Acrochaetium* assemblage" may represent phases in the life history of other red algae. Since then, sporophytic *Acrochaetium*-like phases were grown from the germination of carpospores of *Liagora* and *Ganonema* species (von Stosch, 1965; Couté, 1971; Guiry and Irvine, 1989; Guiry, 1990a; Brodie and Norris, 1996) and species of *Tricleocarpa* (Magruder, 1984, as *Galaxaura*). Life history summaries have been provided by Hoshaw and West (1971), Dixon (1973), Norris and Kugrens (1982), and Hawkes (1990).

Further collections are needed for reevaluation of the species recorded in the Gulf of California in light of studies by Woelkerling (1971), Stegenga (1985b), Y.-P. Lee and Yoshida (1997), and Harper and Saunders (2002). Culture and DNA studies on Gulf of California species should further clarify their life histories and generic and specific status.

Presently, seven species of *Acrochaetium* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *ACROCHAETIUM* (ACROCHAETIALES; ACROCHAETIACEAE) AND *RHODONEMATELLA* (PALMARIALES; RHODOPHYSEMATACEAE) IN THE NORTHERN GULF OF CALIFORNIA

1a. Cells of filaments with parietal plastids (without pyrenoids); endo-epiphytic in/on Gulf of California foliose reds, *Halymenia* and *Kallymenia* . . . . ***Rhodonematella subimmersa***
1b. Cells of filaments with a stellate plastid containing a single pyrenoid; epiphytic, endophytic, or endo-epiphytic on various algae and sea grasses (species of ***Acrochaetium***) 2
2a. Filaments entirely endophytic *Porphyra* or *Asparagopsis*; originating from two hemispherical cells . . . . . ***A. porphyrae***
2b. Filaments may be partially endo-epiphytic or entirely epiphytic 3
3a. Filaments partially endophytic; creeping on host surface and sometimes between cortical cells of algal host ***A. bornetii***
3b. Filaments epiphytic; attached to surface layer of the alga host 4
4a. Basally attached by a prostrate single layer of cells (monostromatic) 5
4b. Attached by a single basal cell (not a prostrate monostromatic layer of cells) 6
5a. Branching mostly secund, sometimes alternate; filaments 600–800 µm in length . . . . ***A. seriaspora***
5b. Unbranched or only sparsely branched in lower portion, abundantly branched above; filaments longer, up to 1.5 mm in length . . . . ***A. secundatum***
6a. Initial basal cell produces prostrate filaments; entire thallus adheres to host surface, or with some upper branched filaments . . . . ***A. microscopicum***
6b. Initial basal attachment remains a single cell, with erect filament(s) growing from it 7

7a. Filament branching alternate or secund; monosporangia . . . . *A. arcuatum*
7b. Filament branching at first secund, later opposite, sometimes slightly arching; terminal monosporangia . . . *A. crassipes*

Acrochaetium arcuatum (K. M. Drew) C. K. Tseng

FIGURE 21A

Rhodochorton arcuatum K. M. Drew, 1928:165, pl. 37: figs. 1–3; Dawson, 1944a:255; González-González et al., 1996:264.

Acrochaetium arcuatum (K. M. Drew) C. K. Tseng, 1945:158, pl. 1: fig 1; Abbott and Hollenberg, 1976:310, fig. 251; Silva, 1979:316; Hawkes et al., 1978:96; Harper and Saunders, 2002:470.

Kylinia arcuata (K. M. Drew) Kylin, 1944:13; Papenfuss, 1947a:436; Dawson, 1953a:31; 1961b:405; Norris and West, 1967:112; Perestenko, 1996:45, pl. 6: figs. 10–12.

Chromastrum arcuatum (K. M. Drew) Papenfuss, 1945:321.

Audouinella arcuata (K. M. Drew) Garbary, G. I. Hansen et Scagel, 1983:12, fig. 2; Hansen and Garbary, 1984:174, figs. 1–9; Garbary, 1987:21; Scagel et al., 1989:144; González-González et al., 1996:175.

Algae epiphytic; erect filaments usually singular, occasionally 2 or more; at acute angles from host alga or sometimes almost decumbent; attached to host by a single, large, subglobose basal cell. Filaments up to 100 µm long, 5.0–5.5 µm in diameter, with irregularly secund or alternate branchlets; terminal cells may have long, hyaline hair-like cells. Cells mostly 7.5–8.5 µm in length, with a stellate plastid and a central pyrenoid.

Monosporangia borne lateral and terminal on main axis and branchlets. Sexual reproduction unknown.

Habitat. Epiphytic on *Sphacelaria*; intertidal.

Distribution. Gulf of California: Isla Turner (off SE end of Isla Tiburón). Eastern Pacific: Alaska to central California; Michoacán. Western Pacific: China (Hong Kong).

Type Locality. Epiphytic on *Pterosiphonia* spp. and *Polysiphonia* sp.; Moss Beach, San Mateo County, central California, USA.

Acrochaetium bornetii Papenfuss

Acrochaetium bornetii Papenfuss, 1945:313 [new name for *Chantransia corymbifera* Thuret (in Le Jolis, 1863b:107), which was based on two separate entities: Bornet et Thuret, 1876:16, pl. 5]; Dawson, 1953a:23; 1961b:403; Garbary, 1987:29; González-González et al., 1996:166 [non *Acrochaetium corymbiferum* (Thuret in Le Jolis, 1863b:107, *pro parte*) Batters, 1902:59].

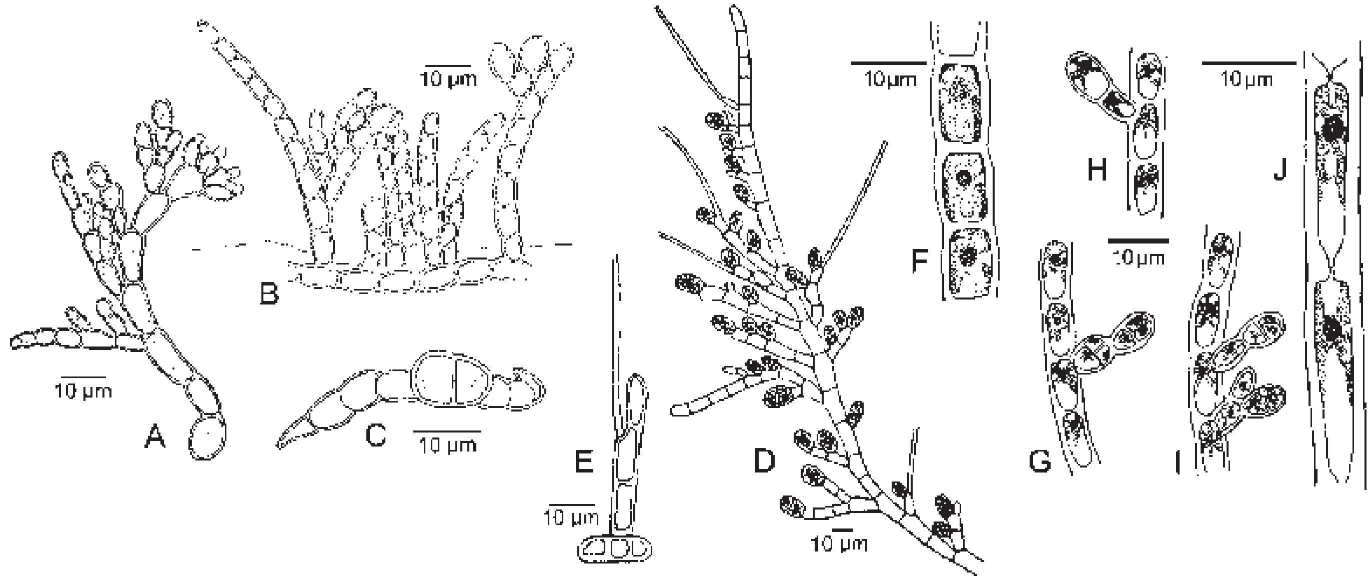


FIGURE 21. Species of *Acrochaetium*. A. *Acrochaetium arcuatum:* Mature thallus showing branching, monosporangia, and terminal spermatangia (after Drew, 1928: pl. 37, fig. 2, as *Rhodochorton arcuatum*). B, C. *Acrochaetium porphyrae:* B. An endophytic filament in host *Porphyra* issuing free erect branches, some bearing monosporangia. C. Germinating spore showing filaments bending down into the host that have developed from the two daughter cells of the spore (after Drew, 1928: pl. 46, figs. 71, part of 75, as *Rhodochorton porphyrae*). D–F. *Acrochaetium secundatum:* D. Filament with elongated, hair-like cells. E. Young filament (D, E after Kylin, 1944, fig. 11). F. Filament cells with stellate chloroplasts (after Dawson, 1953a: pl. 1, fig. 3, as *Kylinia secundata*). G–J. *Acrochaetium seriaspora:* Portions of several filaments of the type collection showing both solitary and seriate production of tetrasporangia (after Dawson, 1953a: pl. 2, figs. 2–5, type collection of *Kylinia seriaspora*).

Acrochaetium savianum sensu L. Aguilar-Rosas et al., 2000:130 [in part] [non *Acrochaetium savianum* (Meneghini) Nägeli, 1862:405, 414].

Algae endo-epiphytic; with erect branched filaments, up to 2 mm in length; of cells 6–7 µm in diameter, 30–70 µm long; branches few in lower portion, upper portions with many alternate to more or less secund branches.

Monospores ovate, 7–8 µm in diameter; sessile and singular, or 2–3 on a 1-celled pedicel. Gametophytes dioecious. Carposporangia and spermatangia in clusters, on short pedicels.

Habitat. On "*Helminthocladia*" (L. Aguilar-Rosas et al., 2000, as "*A. savianum*"); low intertidal to shallow subtidal.

Distribution. Gulf of California: Puertecitos. Eastern Pacific: San Pedro, southern California; Punta Pequeña, Bahía San Juanico, Baja California Sur.

Type Locality. On *Helminthocladia* (see Thuret in Bornet et Thuret, 1876:16, pl. 5); Belle-Ile-en-Mer, Morbihan, Brittany, northwest France.

Remarks. Some have treated *Acrochaetium bornetii* as a synonym of *A. savianum* (Meneghini) Nägeli (1862) (e.g., Wynne, 2005). Herein I follow Garbary (1987:29, 163) in recognizing these two as separate species, until the taxonomy of the Gulf species can be clarified.

Acrochaetium crassipes (Børgesen) Børgesen

FIGURE 22

Chantransia crassipes Børgesen, 1909:1, fig. 1.

Acrochaetium crassipes (Børgesen) Børgesen, 1915:20, figs. 11–13; Yendo, 1917:201; Taylor, 1928:134, pl. 28: fig. 16; Tseng, 1945:157; Phạm-Hoáng, 1969:86, fig. 2.18; Tanaka and Hirose, 1971:111; Kajimura, 1979:99; Pacheco-Ruíz et al., 2008:206.

Kylinia crassipes (Børgesen) Kylin, 1944:13; Papenfuss, 1947a:436; Dawson, 1953a:31; 1961b:405; 1963c:5.

Chromastrum crassipes (Børgesen) Papenfuss, 1945:321; Stegenga and Mulder, 1979:305, fig. 41; Stegenga and Kemperman, 1983:72, figs. 20–24.

Audouinella crassipes (Børgesen) Garbary, 1979:478, 490; 1987:49.

Rhodochorton microscopicum sensu Dawson, 1944a:254, pl. 41: fig. 3; González-González et al., 1996:264 [non *Rhodochorton microscopicum* (Nägeli ex Kützing) K. M. Drew, 1928:163, which is now *Acrochaetium microscopicum* (Nägeli ex Kützing) Nägeli in Nägeli and Cramer, 1858:532].

Algae epiphytic; of 1 or rarely 2 uniseriate filaments, abundantly branched; attached below by a single subglobose basal cell. Young thalli with short, 1- to 3-celled, secundly arranged branchlets; mature thalli usually with opposite, longer branches; branches or branchlets from almost every cell except the basal cell and terminal cells. Filaments frequently slightly arched. Apical cells occasionally with a long hyaline hair.

Monosporangia mostly terminal on short branchlets. Sexual reproduction unknown.

Habitat. Epiphytic on *Polysiphonia, Gelidium,* and probably other algae; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Isla Turner (off SE end of Isla Tiburón); Isla Rasa (with a query). Eastern Pacific: Bahía Sebastián Vizcaíno, Baja California Sur; Galápagos Islands.

Type Locality. Harbor, St. Thomas, U.S. Virgin Islands, Caribbean Sea.

Remarks. Specimens from Isla Rasa (Isla Raza; "Flat Island") were noted as probably belonging to *Acrochaetium crassipes* by Dawson (1953a, as "*K. crassipes*"). On the

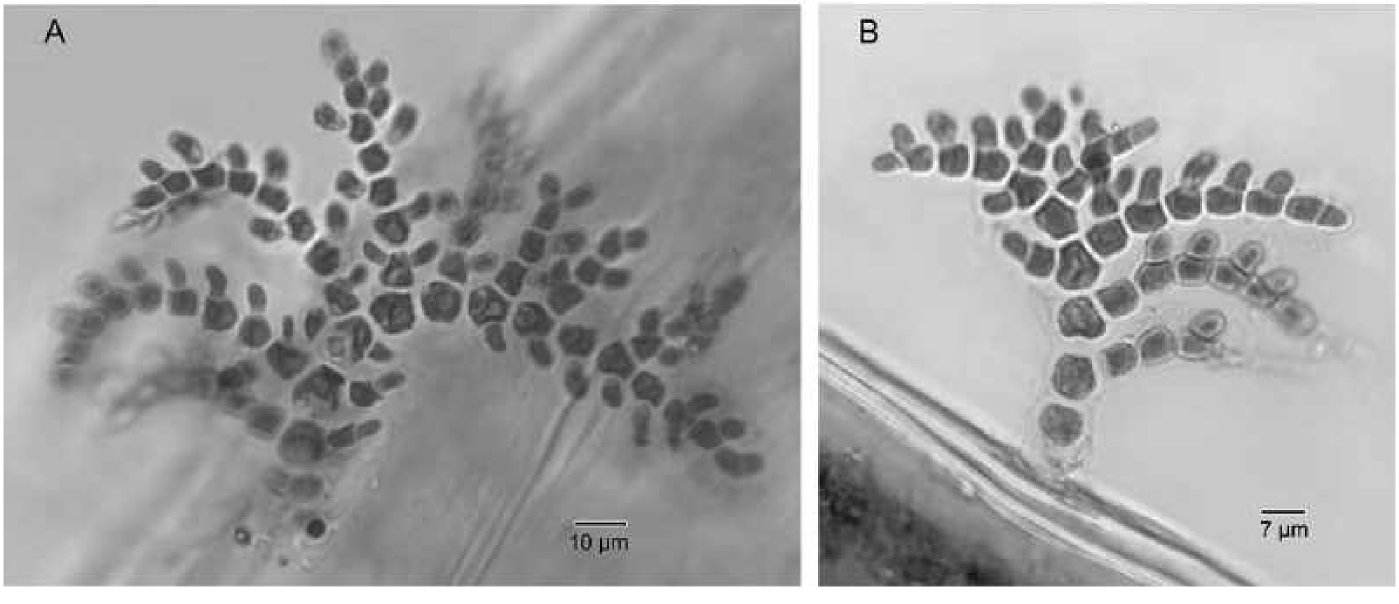


FIGURE 22. *Acrochaetium crassipes:* A, B. Habits of two minute epiphytes, each with a main axis from a single basal cell, at first secundly then oppositely branched, filaments slightly arched (*JN-4040b*, epiphytic on *Cladophora*, US Alg. Coll. microscope slide 4254).

basis of our collections, *A. crassipes* may now be recorded in the upper Gulf (*JN-4040b,* US Alg. Coll. microscope slide 4254) from Playa Hermosa and Playa Las Conchas (Playa Estación) (*JN-4082,* US Alg. Coll. microscope slide 4962), both in the vicinity of Puerto Peñasco, Sonora.

Woelkerling (1972, 1973a, as *Audouinella crassipes*) suggested *Acrochaetium crassipes* was synonymous with *A. microscopicum*. However, culture studies of *A. crassipes* (Stegenga and Mulder, 1979; Stegenga and van Wissen, 1979) revealed that although the gametophytes were similar looking in both, the two could be distinguished by the tetrasporophytes in their life histories, and Stegenga (1985b) has kept these two species separate (see also Garbary, 1987). For now, northern Gulf specimens are referred to *A. crassipes* until culture studies and molecular analyses can be carried out on Gulf material to ascertain their taxonomic and phylogenetic status.

Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli

Callithamnion microscopicum Nägeli ex Kützing, 1849:640.

Acrochaetium microscopicum (Nägeli ex Kützing) Nägeli in Nägeli et C. E. Cramer, 1858:532; Nägeli, 1862:403, figs. 24, 25; Okamura, 1932:87; Tseng, 1945:157; Hollenberg and Abbott, 1966:42, fig. 15; Lindstrom, 1977:86; Y.-P. Lee, 1987:30, fig. 14; Abbott, 1999:55, fig. 3G; L. Aguilar-Rosas et al., 2000:130, 137; Mateo-Cid et al., 2000:63; L. Aguilar-Rosas et al., 2002:234; Mateo-Cid et al., 2006:55, 62; Y.-P. Lee, 2008:169, figs. A–D.

Chantransia microscopica (Nägeli ex Kützing) Berthold, 1882a:512.

Rhodochorton microscopicum (Nägeli ex Kützing) K. M. Drew, 1928:163; González-González et al., 1996:264.

Chromastrum microscopicum (Nägeli ex Kützing) Papenfuss, 1945:322; Stegenga and Kemperman, 1983:299, figs. 37–38(type material), 41.

Kylinia microscopicum (Nägeli ex Kützing) Kylin, 1944:13; Papenfuss, 1947a:437; Dawson, 1953b:125; 1961b:405.

Audouinella microscopica (Nägeli ex Kützing) Woelkerling, 1971:9, 33, figs. 10, 23A; Garbary, 1979:479; Lindstrom et al., 1986:5; Garbary, 1987:116; Scagel et al., 1989:147; Mateo-Cid and Mendoza-González, 1997:56, pl. 1: fig. 2; Yoshida, 1998:465.

Algae minute epiphytes; with erect upper portions, up to 40(–100) μm tall; covering area up to 250 μm on host's surface; branched 1–3(–4) orders, with branches of similar or unequal length; original spore, 8.0 μm long and 7.0–8.0 μm in diameter, persisting after germination; attached by a basal cell directly to host's surface layer or partly endophytic within host's cortical cells. Cells squarish to barrel shaped, 6.0–9.0 μm tall and 8.0–12 μm in diameter; with a stellate plastid and 1 pyrenoid. Terminal cells of filaments without or with hairs up to 55 μm long.

Monosporangia sessile or terminal, on short branchlets; 20–24 μm in diameter. Sexual reproduction unknown.

HABITAT. Epiphytic on *Cladophora*, *Chaetomorpha*, *Sphacelaria*, and *Sargassum*; intertidal.

DISTRIBUTION. Gulf of California: Piedras del Burro (Gulfo de Santa Clara) to Puertecitos; Punta Arena (north of Cabo Pulmo). Eastern Pacific: Alaska to Bahía Sebastián Vizcaíno, Baja California; Oaxaca. Western Pacific: Korea; Japan.

TYPE LOCALITY. "In sinu neapolitano" (Kützing, 1849); Golfo di Napoli, Italy, Mediterranean Sea (Silva et al., 1996a:99). Others have listed the type locality as Torquay, Devon, England, UK (Hamel, 1927, 1928; Woelkerling, 1972; Woelkerling and Womersley, 1994; Athanasiadis, 1996b), and the type in Kützing collections (L) is from England (Guiry and Guiry, 2012).

REMARKS. *Acrochaetium microscopicum* was reported in the northern Gulf of California by L. Aguilar-Rosas et al. (2000) and Mateo-Cid et al. (2006). Although the species is reportedly widespread in temperate to tropical seas (e.g., Børgesen, 1915, 1927, 1931; Taylor, 1960; Wynne, 2005), Garbary (1987) noted there is much confusion on the taxonomic identification and application of the epithet "*microscopicum*." Some Pacific Mexico specimens may have been identified following the descriptions of "*Acrochaetium microscopicum*" by Hollenberg and Abbott (1966) and Abbott and Hollenberg (1976); however, Garbary (1987) noted that their descriptions of California material represent a different species.

Woelkerling (1972) suggested another species, *A. crassipes,* was conspecific with *A. microscopicum*. On the basis of culture studies, Stegenga (1985b) noted that Woelkerling's species concept was too broad and that similar-looking gametophytes were involved in the life histories of tetrasporophytes that could be differentiated. For now, the two are considered distinct entities, with both species recorded in the Gulf of California.

Acrochaetium porphyrae (K. M. Drew) G. M. Smith

FIGURE 21B,C

Rhodochorton porphyrae K. M. Drew, 1928:188, pl. 46: figs. 70–75.

Acrochaetium porphyrae (K. M. Drew) G. M. Smith, 1944:179, pl. 40: figs. 8, 9; Sparling, 1971:237; Norris and Abbott, 1972:90; Abbott and Hollenberg, 1976:317, fig. 259; Silva, 1979:316; L. Aguilar-Rosas and Aguilar-Rosas, 1993:202.

Chromastrum porphyrae (K. M. Drew) Papenfuss, 1945:325.

Kylinia porphyrae (K. M. Drew) Papenfuss, 1947a:438; Dawson, 1953a:30; 1961b:405.

Colaconema porphyrae (K. M. Drew) Woelkerling, 1971:9, 50, figs. 20, 27B.

Audouinella porphyrae (K. M. Drew) Garbary, 1979:479, 490; Garbary et al., 1983:42, fig. 17; Scagel et al., 1986:125; Tam et al., 1987:532, figs. 1–19; Garbary, 1987:141; Scagel et al., 1989:148; Ramírez and Santelices, 1991:180; Womersley, 1994:71.

Algae endophytic; in the Gulf of California, forming small reddish patches within *Asparagopsis*. Filaments originating from two hemispherical cells (Figure 21C); branching irregularly, pinnately, and mostly divaricately; spreading prostrate on the surface and between cells of algal host; occasionally with erect branches of 1 or more cells, sometimes with short branchlets. Cells of endophytic filaments usually broader in middle and narrower at ends; to 10 μm in diameter; erect filament cells, 5–8 μm in diameter; with a stellate plastid and single central pyrenoid.

Monosporangia borne terminally and laterally on erect filaments and branchlets. Sexual reproduction unknown.

HABITAT. Endo-epiphytic on *Asparagopsis*; subtidal, down to 5 m depths.

DISTRIBUTION. Gulf of California: Puerto Calamajue. Eastern Pacific: southern Alaska to northern Baja California; Chile.

TYPE LOCALITY. Land's End, San Francisco, San Francisco County, northern California, USA.

REMARKS. *Acrochaetium porphyrae* is now reported in the northern Gulf of California. Specimens of this species, collected at Puerto Calamajue, Baja California (*JN-4637b,* US Alg. Coll. microscope slide 4259), were growing on *Asparagopsis taxiformis*, apparently a new host for this species. Elsewhere in the northeastern Pacific, this endo-epiphyte is most commonly found on *Porphyra* (Abbott and Hollenberg, 1976). It had been reported in central California (Smith, 1944; Sparling, 1971) and from Bahía San Quintín, Pacific Baja California (Dawson, 1953a), and it was later reported from Hope Island, off the northern end of Vancouver Island, British Columbia (Norris and Abbott, 1972).

Acrochaetium secundatum (Lyngbye) Nägeli

FIGURE 21D–F

Callithamnion daviesii (Dillwyn) Nägeli β [var.] *secundatum* Lyngbye, 1819:129, pl. 41: figs. β4–β6 [note figs. β4–β6 chosen as lectotype by Woelkerling, 1983a:65].

Acrochaetium secundatum (Lyngbye) Nägeli in Nägeli et Cramer, 1858:532 [footnote]; Nägeli, 1862:405; Collins, 1906b:194; Kylin, 1944:19, fig. 11; Tokida, 1960:92; Stegenga, 1985b:305, figs. 10, 11; Y.-P. Lee, 1987:36, fig. 18; Perestenko, 1996:46, pl. 6: figs. 8, 9; Nielsen et al., 1995:4; González-González et al., 1996:167.

Ceramium secundatum (Lyngbye) C. Agardh, 1824:132.

Callithamnion secundatum (Lyngbye) C. Agardh, 1828:187.

Chantransia secundata (Lyngbye) Thuret in Le Jolis, 1863b:106.

Chromastrum secundatum (Lyngbye) Papenfuss, 1945:323.

Kylinia secundata (Lyngbye) Papenfuss, 1947a:437; Dawson, 1953a:32, pl. 1: fig. 3; 1957b:112, figs. c, d; Taylor, 1957:214, pl. 31: figs. 1–3; Dawson, 1961b:405; González-González et al., 1996:231.

Colaconema secundatum (Lyngbye) Woelkerling, 1973a:94, figs. 7, 8.

Audouinella secundata (Lyngbye) P. S. Dixon in Parke et Dixon, 1976:590; Dixon and Irvine, 1977a:114, fig. 39A–C; Woelkerling, 1973b:575, figs. 77–83; Garbary, 1978:218, figs. 33, 34; 1979a:952; 1979c:479; Woelkerling, 1983a:65, 81, figs. 5, 6; Garbary, 1987:166; González-González, 1993:441; Yoshida, 1998:469.

Algae epiphytic, erect filaments, arising from a prostrate, monostromatic base developed from an initial monospore and forming a layer of compacted cells on (and sometimes between) the host cells. Filaments up to 1.5 mm long, 5–8 µm in diameter; branching sparse or absent in lower portions; more abundant above; hair-like cells often extending from upper branches. Cells (5–)8–24 µm long, with a stellate plastid, and a single large pyrenoid located distally.

Monospores ovoid, to 6 µm diameter, usually pedicellate or occasionally sessile. Tetrasporangia and sexual reproduction unknown in Gulf material.

HABITAT. Rocky reef, epiphytic on *Sargassum*, also often found growing with *Colaconema punctatum*; intertidal.

DISTRIBUTION. Gulf of California: Bahía Bocochibampo (vicinity of Guaymas); Nayarit. Western Pacific: Russia; Korea; Japan; Vietnam; Enewetak Atoll (Eniwetok), Marshall Islands (Micronesia).

TYPE LOCALITY. Kvivig (Kvívík), Streymoy Island, Faroe Islands (Faeroe; Føroyar), Farö County, Denmark.

REMARKS. *Acrochaetium secundatum* is known only in the northern Gulf by the report of a single collection from Sonora (Dawson, 1953a). A cold water species, its presence in the Gulf of California requires more collections and further study.

Garbary (1987, as "*Audouinella secundata*") noted that specimens of *Acrochaetium secundatum* from the northeast Pacific are probably misidentified and represent other species. Although Woelkerling (1973b:575, as "*Colaconema secundata*") had suggested that this taxon "will be transferred to *Audouinella*," he later designated *Acrochaetium secundatum* as the lectotype species for the genus *Acrochaetium* (Woelkerling, 1983a). (See also Remarks under *Colaconema tenuissimum*.)

Acrochaetium seriaspora (E. Y. Dawson) J. N. Norris, *comb. nov.*

FIGURE 21G–J

Kylinia seriaspora E. Y. Dawson, 1953a:32, pl. 2: figs. 2–5; 1961b:405; González-González et al., 1996:231.

Audouinella seriaspora (E. Y. Dawson) Garbary, 1987:170.

Chromastrum seriasporum (E. Y. Dawson) Stegenga et Mulder, 1979:305.

Algae epiphytic; of erect, branched filaments, arising from a monostromatic base of several to many cells, with some penetrating between the host's cells. Filaments branching mostly secund, sometime alternate; erect filaments 600–800 µm long by 5–7 µm in diameter; cells 10–28 µm long, with a stellate chloroplast and a single, large pyrenoid.

Monosporangia ovoid, to 6 µm in diameter, usually borne on 1-celled pedicels in secund series. Tetrasporangia ovoid, 7–8 µm in diameter; sessile, borne lateral on branch or terminal or lateral on 1- to 2-celled pedicels on branches (Figure 21G). Sexual reproduction unknown.

HABITAT. Epiphytic on *Sargassum*; intertidal.

DISTRIBUTION. Gulf of California: Isla Turner (off SE end of Isla Tiburón).

TYPE LOCALITY. Epiphytic on *Sargassum* from intertidal rock reef; Isla Turner (Turners), off SE end of Isla Tiburón, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. Described from the northern Gulf of California, *Acrochaetium seriaspora* is known only from the type collection. Dawson (1953a), in his original description of *Kylinia seriaspora,* noted that occasionally one or both of the pedicel cells became tetrasporangia. Primarily on the basis of the stellate chloroplast with single pyrenoid of *K. seriaspora*, a new combination is proposed. Further collections and DNA analyses are needed to test the specific and generic status of this taxon.

COLACONEMATALES

Colaconematales J. Harper et G. W. Saunders, 2002:471.

Algae are marine, composed of uniseriate, simple, or branched filaments. Cells contain one or more parietal plastids of various shapes, lobed, spiral, or irregular (but never stellate) and are with or without pyrenoids.

Asexual reproduction is mainly by monosporangia. Life histories, where known, are biphasic or triphasic. Sexual phases are monoecious or dioecious.

Currently a monotypic order, the Colaconematales is represented by the single family in the northern Gulf of California.

COLACONEMATACEAE

Colaconemataceae J. Harper et G. W. Saunders, 2002:471.

The Colaconemataceae is apparently a monotypic family, with the characteristics of the order.

Life histories, where known, are biphasic, involving two free-living isomorphic or slightly heteromorphic phases (rarely with a markedly distinct heteromorphic generations). Tetrasporophytes have a nonpersistent spore that develops a prostrate multicellular filamentous portion that gives rise to erect axes. Gametophytes of most species usually have a persistent spore that upon bipolar germination remains unicellular in a few species or in most develops a basal system of multicellular, prostrate filaments, from which the erect filaments arise.

REMARKS. Harper and Saunders (2002) noted that although the Colaconemataceae includes only one genus, it is likely that future research will add other genera to the family on the basis of their morphological, life history, and molecular features. The family is worldwide in distribution, and all of the species are exclusively marine, with the highest diversity in warm temperate to tropical seas.

Currently, the family contains a single genus, *Colaconema*, which is known to occur in the Gulf of California.

Colaconema Batters

Colaconema Batters, 1896:8; Harper and Saunders, 2002:473.

Algae are microscopic to minute, usually epiphytic, and composed of simple to branched, uniseriate filaments. Branching of the erect axes may be irregular, secund, or opposite. Occasionally, the branches may have multicellular pseudohairs. Cells usually contain one parietal plastid, but a few species may have several lobed, parietal plastids. Chloroplasts are lobed, spiral, or irregular in shape and with or without pyrenoids.

Monosporangia are the predominant mode of reproduction, found in both generations, and borne terminal on the axes or on short lateral branches. In many species of *Colaconema*, monosporangia are the only known mode of reproduction. Tetrasporangia are cruciately divided, single or in clusters, and are borne lateral or terminal on axes and lateral branches. Gametophytes, where known, are monoecious or dioecious. Carpogonia are sessile or pedicellate and lack a distinct carpogonial filament. The fertilized carpogonium divides transversely to produce short, filamentous gonimoblasts with terminal carposporangia. Spermatangia are borne in clusters of various shapes.

REMARKS. Species of *Colaconema* are usually epiphytic, but some are also reported to be endo-epiphytic or epizoic or endo-epizoic. One species, *Colaconema pectinatum* (Kylin) J. T. Harper et G. W. Saunders (2002) is reported in the southern Gulf from La Paz (Huerta-Múzquiz and Mendoza-González, 1985, as *Acrochaetium pectinatum* (Kylin) G. Hamel, 1927).

Nine species of *Colaconema* are now reported in the northern Gulf of California.

KEY TO THE SPECIES OF *COLACONEMA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Filaments exclusively endo-epiphytic (i.e., within and on outer cells) on species of *Scinaia* . . . . **C. scinaiae**
1b. Filaments growing on other algal species (not *Scinaia*) 2
2a. Thalli less than 300 µm tall . . . . **C. punctatum**
2b. Thalli more than 300 µm tall 3
3a. Erect filaments 8.0–12.0 µm in diameter; above a basal system of free filaments or of filaments coalescing into pseudoparenchymatous disc 4
3b. Erect filaments narrower, 4.0–8.0 µm in diameter; basal attachment either a single cell or prostrate basal filaments (not coalescing or discoid) 5
4a. Filaments arising above by a basal pseudoparenchymatous disc of coalescing basal filaments or entangled mass of basal filaments; monosporangia in clusters of 3 or more on branched stalks . . . . **C. daviesii**
4b. Filaments attached by prostrate system of basal filaments (not coalescing); monosporangia single or in pairs (not in clusters) on unbranched stalks . . . . **C. savianum**
5a. Filaments attached by a single basal cell (either enlarged and conspicuous or similar in size to filament cells) 6
5b. Filaments attached by a basal system of basal filaments (not coalescing) creeping on host's surface 7
6a. Single basal cell enlarged (much larger in diameter than filament cells); filaments 4.0–6.0 µm in diameter . . . . **C. sinicola**

6b. Single basal cell not enlarged or modified (same diameter and shape as filament cells); filaments 5.0–7.0 µm in diameter . . . . *C. hancockii*
7a. Erect filaments 4.0–6.0 µm in diameter; upper portions usually branched; monosporangia terminal or sometimes lateral on short secund branchlets . . . . *C. pacificum*
7b. Erect filaments mostly larger than 6 µm in diameter; upper portions unbranched or branched 8
8a. Erect filaments 8.0–9.5 µm in diameter; upper portions branched or unbranched; attached by a basal disc of coalesced filaments, 1–2 cell layers thick; monosporangia terminal or lateral . . . . *C. variabile*
8b. Erect filaments 6.0–8.0 µm in diameter; upper portions unbranched; attached by basal system of creeping filaments (not coalescing); monosporangia lateral on branchlets . . . . *C. tenuissimum*

Colaconema daviesii (Dillwyn) Stegenga

Conferva daviesii Dillwyn, 1809:73, suppl. pl. F.

Colaconema daviesii (Dillwyn) Stegenga, 1985b:317, 320, fig. 20; Perestenko, 1996:47; Harper and Saunders, 2002:473; Serviere-Zaragoza et al., 2007:9.

Ceramium daviesii (Dillwyn) C. Agardh, 1817:XXVII.

Callithamnion daviesii (Dillwyn) Lyngbye, 1819:129, pl. 41: figs. B1–B3; Harvey, 1853:243.

Acrochaetium daviesii (Dillwyn) Nägeli, 1862:405, figs. 26, 27; Collins, 1906b:194; Papenfuss, 1945:308; Taylor, 1945:134; Papenfuss, 1947a:435; Dawson, 1953a:28; Dawson et al., 1960b:15; Tokida, 1960:92; Dawson, 1961b:403; Dawson and Neushul, 1966:175; Hollenberg and Abbott, 1966:41, fig. 14; Abbott and Hollenberg, 1976:313, fig. 254; Silva, 1979:316; Stegenga and van Erp, 1979:443, figs. 11–14; Stewart and Stewart, 1984:142; González-González et al., 1996:166; Y.-P. Lee and Yoshida, 1997:162, fig. 1A–F; Yoshida, 1998:463, fig. 3-4C.

Chantransia daviesii (Dillwyn) Thuret (in Le Jolis, 1863b:106.

Rhodochorton daviesii (Dillwyn) K. M. Drew, 1928:172; Setchell and Gardner, 1930:166; Smith, 1944:184; Nakamura, 1944:106, fig. 5; I. K. Lee and Lee, 1974:41, fig. 4a–f; González-González et al., 1996:264.

Audouinella daviesii (Dillwyn) Woelkerling, 1971:28, figs. 7, 22; Woelkerling, 1973b:550, figs. 32–43; Dixon and Irvine, 1977b:90, fig. 22; Garbary, 1979a:952; 1979c:478; Garbary et al., 1983:19, fig. 6; Stegenga, 1985b:317, fig. 20; Garbary, 1987:54; Y.-P. Lee, 1987:10, fig. 3A–E; Scagel et al., 1989:145; Ramírez and Santelices, 1991:179; Mateo-Cid and Mendoza-González, 1991:19; 1992:19; Mendoza-González and Mateo-Cid, 1992:16; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:38; Mendoza-González et al., 1994:105; Y.-P. Lee and Yoshida, 1997:162, fig. 1A–F; Yoshida, 1998:463, fig. 3, 4C; Y.-P. Lee, 2008:175, figs. A–D.

Algae often in tufts, usually epiphytic, or sometimes partially endo-epiphytic; erect, branched, uniseriate filaments, up to 4 mm tall; arising from a base of creeping, entangled filaments, some of which may penetrate host cells. Erect filaments sparsely to more or less densely branched, mostly irregular, sometimes alternate or secund, up to several orders; filaments sometimes tapering upward, ending with multicellular, almost colorless extensions. Cell of axes and branches, 14–40 µm long by 9–15 µm in diameter (2–3 times longer than wide); cells of upper portions, narrower, 3–10 µm in diameter and 20–50 µm in length; cells of basal filaments 12–25 µm long and 6–14 µm in diameter. Plastids parietal, with a single prominent pyrenoid.

Monosporangia ovoid to ellipsoid, 12–14 µm long, 8–10 µm wide; in clusters of 4–8 on short branchlets; borne on lowermost cells of branches. Sexual reproduction not yet observed in Gulf of California specimens; reported to be dioecious elsewhere. Carposporophyte with branched gonimoblast filaments with terminal carposporangia, 16–20 µm long by 8–10 µm in diameter. Spermatangia 2–4 µm in diameter, terminal or lateral in few to many, sometimes dense, clusters on branched stalks (see Womersley, 1994:51, fig. 9F,G).

HABITAT. Epiphytic or partially endo-epiphytic on *Padina* and various other algae; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Punta Robinson (east of Puerto Libertad); Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Alaska to Todos Santos (Baja California Sur); Isla Guadalupe; Isla Clarión (Islas Revillagigedo); Colima; Chile. Western Pacific: Russia; Korea; Japan.

LECTOTYPE LOCALITY. Probably north Wales, United Kingdom (Dixon and Irvine, 1977b; Silva et al., 1996b).

REMARKS. *Colaconema daviesii* is widely reported in temperate to tropical seas and now in the northern Gulf of California. Garbary (1987, as *Audouinella daviesii*) noted that many of the published accounts and records using this taxon name may be misidentified.

Colaconema hancockii (E. Y. Dawson) J. N. Norris, _comb. nov._

FIGURE 23A,B

Rhodochorton hancockii E. Y. Dawson, 1944a:255, pl. 41: figs. 4–6; González-González et al., 1996:264.

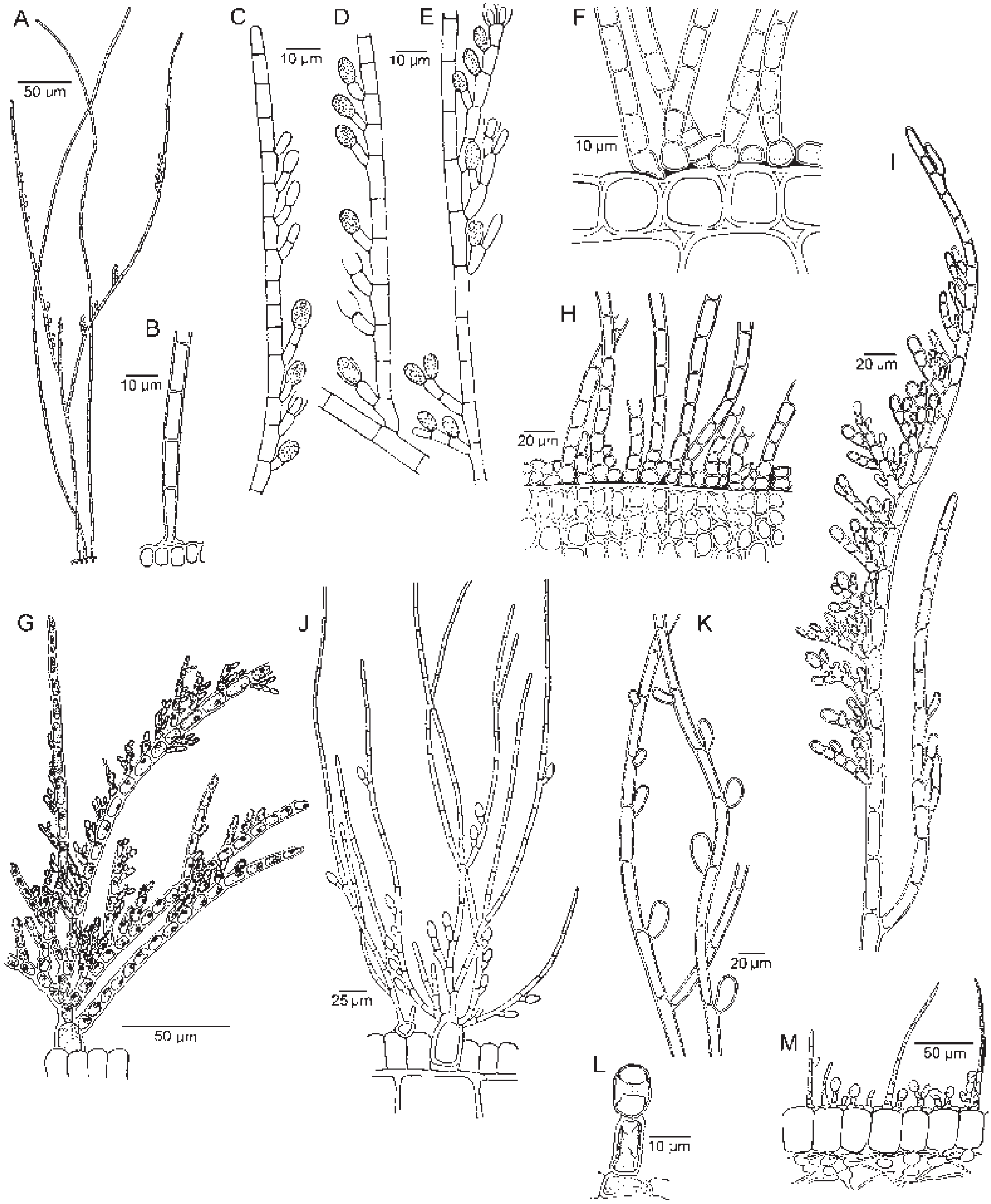
Acrochaetium hancockii (E. Y. Dawson) Papenfuss, 1945:306; Dawson, 1953a:25, pl. 12: fig. 2; 1961b:403; Huerta-Múzquiz and Mendoza-González, 1985:48; Garbary, 1987:83.

Algae epiphytic, of cylindrical, narrow, erect filaments; attached to host alga by a single unmodified, rectangular basal cell. Erect filaments 0.5–1.5 mm long, simple or sparsely branched, up to 3 orders, becoming slightly attenuated upward; ultimate branchlets in more or less secund series on branches, very short, up to 4 µm in diameter, 3–4 µm long. Cells of filaments rectangular, 15–28 µm long, 5–7 µm in diameter; plastids not in original description, but noted to be "parietal" in the taxonomic key of Dawson (1953a:19).

Monospores ovoid, 10–11 µm long, 6–7 µm wide, borne on short lateral branchlets or sessile. Sexual reproduction unknown.

HABITAT. Epiphytic on *Gelidium*; intertidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; La Paz.


A
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L
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M
50 µm

Type Locality. On *Gelidium*, rocky shore along west side of Puerto Refugio, Isla Ángel de la Guarda, Islas de la Cintura, Gulf of California, Mexico.

Remarks. Described from the northern Gulf of California, *Colaconema hancockii* is a apparently known only from a few collections in the Gulf. It has also been reported in the Philippines (Silva et al., 1987). More Gulf collections for comparative molecular and life history culture studies will help to evaluate its taxonomic status.

Colaconema pacificum (Kylin) Woelkerling

FIGURE 23C–F

Acrochaetium pacificum Kylin, 1925:11, fig. 4g–i; Papenfuss, 1945:310; Doty, 1947:162; Papenfuss, 1947a:435; Dawson, 1953a:29; Dawson et al., 1960a:15; Tokida, 1960:92; Dawson, 1961b:404; Dawson et al., 1964:33, pl. 30: fig. B; Dawson and Neushul, 1966:175; Abbott and Hollenberg, 1976:315 [in part; excluding *Rhodochorton variabile* and *R. plumosa*]; Pacheco-Ruíz and Aguilar-Rosas, 1984:76; Stewart and Stewart, 1984:142; Huerta-Múzquiz and Mendoza-González, 1985:48; R. Aguilar-Rosas and Aguilar-Rosas, 1994:519; González-González et al., 1996:166; L. Aguilar-Rosas et al., 2002:234; Mateo-Cid et al., 2006:55, 62.

Colaconema pacificum (Kylin) Woelkerling, 1971:9, 47, figs. 17A–D, 26A.

Rhodochorton pacificum (Kylin) K. M. Drew, 1928:169, pl. 38: fig. 25.

Chantransia pacifica (Kylin) Levring, 1941:631.

Audouinella pacifica (Kylin) Garbary, 1979a:490; Garbary et al., 1983:37; Garbary, 1987:131; Scagel et al., 1989:147; Ramirez and Santelices, 1991:180.

Algae epiphytic; tufts of erect, uniseriate filaments, 4.0–6.0 µm in diameter, up to 1 mm tall; sometimes unbranched or with a few, lateral branches, mostly in upper portion; laterals with numerous, short, secund, or sometimes opposite branchlets of 1–3 cells in length; erect filaments arising from a prostrate system of creeping, branched, basal free filaments (not coalescing) on surface of host. Cells 2–3(–4) times longer than wide, (8–)10–21(–28) µm in length, 4.0–7.0 µm in diameter; with parietal plastid and a large pyrenoid in distal potion of cell.

Monosporangia ellipsoidal, 8.0–10(–12) µm long, 6.0–9.0 µm in diameter; terminal or sometimes lateral on short, secund branchlets. Sexual reproduction unknown.

Habitat. Epiphytic on *Scinaia latifrons, Tricleocarpa,* and probably other algae; low intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Ensenada de San Francisco (vicinity of San Carlos-Guaymas); Bahía de La Paz. Eastern Pacific: Alaska to Islas San Benito (off Isla Cedros), Baja California; Peru.

Type Locality. Syntype localities: Brown Island, Shaw Island, and Peavine Pass, vicinity of Friday Harbor, Washington (Kylin, 1925). Lectotype locality: Epizoic on *Sertularia* (Hydrozoan); Brown Island, east-northeast of Friday Harbor, San Juan Island, San Juan County, Puget Sound, Washington, USA (Abbott and Hollenberg, 1976).

Remarks. More collections are needed to elucidate the taxonomic status of the Gulf of California *Colaconema pacificum* and its phylogenetic relationship with type locality *C. pacificum* from the the northeastern Pacific.

Although recognizing that *Colaconema pacificum* and *C. plumosum* shared some features, Woelkerling (1971) separated the two by filament diameter, branch arrangement, and arrangement of sporangia. Drew (1928) and Nakamura (1944) had earlier noted that specimens of *Rhodochorton plumosum* K. M. Drew (1928) were not easy to separate from *R. variabile* K. M. Drew (1928), and later these two northeastern Pacific species were considered conspecifc with *C. pacificum* by Abbott and Hollenberg (1976, as *Acrochaetium pacificum*). Stegenga (1985b), in part supporting Abbott and Hollenberg (1976), observed that these two (as *Acrochaetium plumosum* and *A. variabile*) were likely conspecific but that *A. pacificum* was a species different from both of them on the basis of the distinctions as noted by Woelkerling (1971) and Garbary et al. (1983). Pueschel (1989, as *Audouinella* species) supported separation of *C. pacificum* and *C. plumosum* on the basis of ultrastructural evidence of different outer caps in the pit plugs and suggested

FIGURE 23. (Opposite) Species of *Colaconema*. A, B. *Colaconema hancockii*: A. Habit. B. Basal portion showing unenlarged attachment cell on host (type collection) (A, B after Dawson, 1944a, pl. 41, figs. 4, 6, as *Rhodochorton hancockii*). C–F. *Colaconema pacificum:* C–E. Erect filaments with monospores (after Kylin, 1925: figs. 4g–i, as *Acrochaetium pacificum*). F. Base of a group of erect filaments and cells of the creeping filaments, showing the parietal chloroplasts (after Drew, 1928: pl. 38, fig. 25, as *Rhodochorton pacificum*). G. *Colaconema punctatum:* Erect filaments with numerous short, secund branchlets, attached superficially to host by a slightly enlarged basal cell (after Dawson, 1953a, pl. 2, fig. 1, as *Acrochaetium punctatum*). H, I. *Colaconema variabile:* H. Multistromatic layer of horizontally growing filaments of epiphyte on host. I. Secund arrangement of branchlets on erect filament (H, I after Drew, 1928: pl. 39, figs. 30, 31, as *Rhodochorton variabile*). J. *Colaconema sinicola:* Habit of type collection showing enlarged basal cell embedded in host and filaments bearing monosporangia (after Dawson, 1944a, pl. 41, fig. 1, as *Rhodochorton sinicola*). K. *Colaconema tenuissimum:* Part of two erect filaments enlarged (after Drew, 1928: pl. 38, fig. 27, as *Rhodochorton tenuissimum*). L, M. *Colaconema scinaiae:* L. Detail of an upright filament bearing a monospore. M. Habit of creeping filaments endophytic among utricles and cortical cells of host, *Scinaia* (L, M after Dawson, 1949b: pl. 2, figs. 11, 12, as *Acrochaetium scinaiae*).

that *C. pacificum* may have affinities with *C. variabile* (see also Remarks under *Colaconema variabile*).

Colaconema punctatum (E. Y. Dawson) J. N. Norris, *comb. nov.*

FIGURE 23G

Acrochaetium punctatum E. Y. Dawson, 1953a:25, pl. 2: fig. 1; 1961b:404; Garbary, 1987:145; Espinoza-Avalos, 1993:332; González-González et al., 1996:167.

Thalli erect and epiphytic; of several curved filaments, 100–300 µm tall; attached to algal host by a single, slightly enlarged, basal cell, 9–12 µm in diameter. Filaments 6–7 µm in diameter, with numerous short, secund branchlets on convex side. Cells 12–14 µm long, 6–7 µm in diameter, with a parietal chloroplast and single pyrenoid.

Asexual reproduction unknown. Female gametophytes not found. Spermatangia borne on short, secund lateral branchlets.

Habitat. Epiphytic on leaf-like blades of *Sargassum*; intertidal.

Distribution. Gulf of California: Puerto Peñasco; Bahía Bocochibampo.

Type Locality. Southern shore, Bahía Bocochibampo, Sonora, Gulf of California, Mexico.

Remarks. Generally considered a Gulf of California endemic, *Colaconema punctatum* has also been recorded from Michoacán (Stout and Dreckmann, 1993, as "*Acrochaetium punctatum*").

Colaconema savianum (Meneghini) R. Nielsen

Callithamnion savianum Meneghini, 1840a:[3]; Meneghini, 1840b:511; J. Agardh, 1842:74; Kützing, 1849:641; J. Agardh, 1851:14.

Colaconema savianum (Meneghini) R. Nielsen, 1994:715; Nielsen et al., 1995:5.

Colaconema savianum (Meneghini) Perestenko, 1996:47.

Acrochaetium savianum (Meneghini) Nägeli, 1862:405, 414; Papenfuss, 1945:311; Papenfuss, 1947a:435; L. Aguilar-Rosas et al., 2000:130, 137; Mateo-Cid et al., 2000:63.

Chantransia saviana (Meneghini) Ardissone, 1883:276.

Audouinella saviana (Meneghini) Woelkerling, 1973b:560, figs. 56–60; Garbary, 1979c:479; 1987:163; Schneider and Searles, 1991:207, figs. 247–249; Mendoza-González and Mateo-Cid, 1996b:65, 83, pl. 2: figs. 7–9; Mateo-Cid and Mendoza-González, 1997:56, pl. 1: figs. 3, 4; Dreckmann et al., 2006:140,154.

Algae epiphytic or partly endo-epiphytic; up to 4 mm in length; attached by a prostrate basal system of short, simple to branched filaments that remain free or partly coalesce into an irregularly shaped disc (initial spore not always evident). Erect filaments mostly irregularly branched or sometimes alternate to secund. Cells in axes and branches, 20–60 µm long, 8–12(–14) µm in diameter; cells narrower in ultimate branchlets, 4–6 µm in diameter. Cells with a single parietal plastid and 1 pyrenoid.

Reproduction not reported in Gulf of California specimens. The following description is as reported for this species elsewhere (Woelkerling, 1973b; Schneider, 1983). Monosporangia ovoid to ellipsoid, single or in pairs, either sessile or on 1- to 3-celled pedicels; 18–27 µm long by 10–15 µm in diameter. Tetrasporangia cruciate, 26–34 µm long by 17–24 µm in diameter. Carpogonia singular, near base of branches in lower portion of thallus; carpospores, 18–21 µm long by 9–13 µm in diameter. Spermatangia sparse, on short branchlets near base of branches.

Habitat. Epiphytic on *Ulva intestinalis*, *Chaetomorpha*, *Bryopsis,* and *Sargassum* and epizoic on *Aglaophenia* (Hydrozoa); intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Pelícano, Puerto Peñasco; Puertecitos; Punta Arenas. Eastern Pacific: Oaxaca to Chiapas. Western Pacific: Russia.

Type Locality. Epiphytic on *Zostera*; Genoa, Ligurian Sea, province of Genoa, Italy.

Remarks. A collection, epizoic on the feather-like hydrozoan *Aglaophenia* from the rocky low intertidal on the southwest shore of Punta Pelícano, Puerto Peñasco, is tentatively referred to *Colaconema savianum* (*JN-5058*, US Alg. Coll. microscope slide 4263). It has numerous monosporangia, as well as the empty spore walls left after their release, and is a northern extension of the Gulf distribution.

A Mediterranean species, *Colaconema savianum* has been reported from the coastal eastern United States (Woelkerling, 1973b; Schneider and Searles, 1991, as *Audouinella saviana*), western Atlantic (Taylor, 1960; Wynne, 2005), Europe (Guiry and Guiry, 2010), and northwestern Pacific (Perestenko, 1996). It was reported in the northern Gulf of California by Aguilar-Rosas et al. (2000, as *Acrochaetium savianum*).

There are two taxonomic combinations of *Colaconema savianum,* and some confusion as to which is the earliest valid publication. Regarding the publication of Nielsen (1994), the index to the *Nordic Journal of Botany* (1994, volume 14) gives the "effective date of publication" of issue number 6 as "28 Dec. 1994." The back page of the book by Perestenko ("1994"; in Russian) notes date accepted for publication as "29.12.92," and that the "date authorized for printing" was "29.12.94" (indicating it was published on or after that date). Although they may have been published one day apart, the Perestenko work was apparently published much later, in 1996.

Colaconema scinaiae (E. Y. Dawson) J. N. Norris, *comb. nov.*

FIGURE 23L,M

Acrochaetium scinaiae E. Y. Dawson, 1949b:3, pl. 2: figs. 11, 12; 1953a:26; 1961b:404; Garbary, 1987:166; Kajimura, 1987a:131, figs. 1–8; Stout and Dreckmann, 1993:9; González-González et al., 1996:167; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Yoshida, 1998:458; CONANP, 2002:136; Riosmena-Rodríguez et al., 2005b:102.

Acrochaetium desmarestiae sensu Abbott and Hollenberg, 1976:314 [in part; only *A. scinaiae*; non *Acrochaetium desmarestiae* Kylin, 1925:10].

Algae minute; in patches, 1–2(–3) mm in diameter; some entirely epiphytic, others partially endo-epiphytic; attached by creeping filaments on and between utricles and cortical cells of their host, species of *Scinaia*. Endophytic filaments cylindrical; irregular in shape, of variously curved, narrow elongate cells among the cortical cells of alga host. Erect filaments, (18–)30–100 μm tall and 3.5–5.0 μm in diameter, of (2–)5–10 cells; unbranched or irregularly and sparsely branched; apical cells rounded. A few cells of the filaments may (sparsely) bear long, simple hairs. Cells mostly 5.0–20 μm long; with a parietal, band-shaped plastid.

Monosporangia terminal on 1- to 2-celled pedicel; 10–15 μm long by 5–10 μm in diameter. Sexual reproduction not known.

Habitat. Endo-epiphytic on *Scinaia johnstonii*, *S. latifrons*, or *S. confusa*; low intertidal to 9 m depths.

Distribution. Gulf of California: Puerto Peñasco to Ensenada de San Francisco; Punta Los Frailes. Eastern Pacific: Santa Barbara Island (California Channel Islands); Michoacán. Western Pacific: Oki Islands, Japan.

Type Locality. Epiphytic on *Scinaia articulata* Setchell; dredged to 30–41 m depths, off north end of Santa Barbara Island (33°30′58″N, 119°50′W), California Channel Islands, southern California, USA.

Remarks. The distribution range of *Colaconema scinaiae* is extended to the northern Gulf by the collection from Puerto Peñasco (endo-epiphytic on *Scinaia confusa* (*JN-5024b*, US Alg. Coll. microscope slide 4247). Dawson (1953a) noted the species probably occurs throughout the range of the species of *Scinaia* in Pacific Mexico. Although noting its resemblance to *A. desmarestiae* Kylin (1925; =*Colaconema desmarestiae* (Kylin) P. W. Gabrielson (in Gabrielson et al., 2004:95), Dawson (1949b, as *A. scinaiae*) stated *C. scinaiae* differed in generally forming smaller colonies on the host alga and in having much longer, distinctly attenuated, filaments of 6–10 cells, up to 100 μm in length, with some of the filaments possibly also having short branchlets and some of the cells possibly also bearing multicellular hairs. Although Abbott and Hollenberg (1976) considered *C. scinaiae* to be conspecific with *A. desmarestiae*, Kajimura (1987a, as *A. scinaiae*) retained it as a distinct taxon. I too recognize them as a separate species, and primarily on the basis of their chloroplast characteristics (see also Dawson, 1949b: fig. 11), I propose the new combination. Culture, cytological, and DNA studies on Gulf *C. scinaiae* and comparison to type locality material will allow testing of their taxonomic status.

Colaconema sinicola (E. Y. Dawson) J. N. Norris, *comb. nov.*

FIGURE 23J

Rhodochorton sinicola E. Y. Dawson, 1944a:256, pl. 41: figs. 1, 2; González-González et al., 1996:264.

Acrochaetium sinicolum (E. Y. Dawson) Papenfuss, 1945:317; Dawson, 1953a:26, pl. 12: fig. 1; 1961b:404; Garbary, 1987:173; Dreckmann et al., 1990:27, pl. 4: fig. 3; Espinoza-Avalos, 1993:332; González-González et al., 1996:167, 381.

Algae epiphytic; composed of 1 to several erect filaments, up to 500 μm tall; branched abundantly basally; branching sparse above, but with longer branches; branches not markedly attenuated; arising from an enlarged basal cell embedded between cells of alga host. Cells 12–33.6 μm long, 4.0–5.6 μm wide, with a parietal plastid.

Monosporangia ovoid, 11–14 μm long, borne terminally on, usually 2-celled, lateral secund branchlets. Carposporangia unknown. Spermatangia borne in clusters terminally on short lateral branchlets.

Habitat. Epiphytic on *Dictyota*; intertidal to shallow subtidal.

Distribution. Gulf of California: Isla Turner. Eastern Pacific: Michoacán.

Type Locality. Isla Turner (Turners), off SE end of Isla Tiburón, Islas de la Cintura, Gulf of California, Mexico.

Colaconema tenuissimum (Collins) Woelkerling

FIGURE 23K

Chantransia virgatula (Harvey) Bornet f. *tenuissima* Collins in Collins, Holden and Setchell, 1900: Exsiccate *P.B.-A.* No. 714.

Colaconema tenuissimum (Collins) Woelkerling, 1971:9, 51, fig. 21.

Acrochaetium virgatulum (Harvey) Bornet f. *tenuissimum* (Collins) Collins, 1906b:194.

Acrochaetium tenuissimum (Collins) Papenfuss, 1945:319; Dawson, 1961b:404; Abbott and Hollenberg, 1976:319, fig. 262; Stegenga, 1985b:305, fig. 12.

Rhodochorton tenuissimum (Collins) K. M. Drew, 1928:170, pl. 38: figs. 26, 27.

Chantransia tenuissima (Collins) Kylin, 1941:5, figs. 1e,f.

Audouinella tenuissima (Collins) Garbary, 1979c:479, 490; 1987:182.

Chromastrum tenuissimum (Collins) Stegenga et Kemperman, 1983:72.

Algae epiphytic, erect filaments unbranched or sparingly and irregularly branched, attached by a prostrate basal system of creeping filaments. Branches tapering slightly toward the apices. Cells cylindrical, 6–8 μm in diameter by 25–48 μm long, with a single parietal plastid and 1 pyrenoid.

Monosporangia sessile, ovoid, 12–15 μm in diameter by 21–23.5 μm long, scattered along main axis and branches. Other reproductive structures unknown.

Habitat. Epiphytic on *Ceramium caudatum,* which was growing on *Dictyopteris*; mid to low intertidal.

Distribution. Gulf of California: Punta Pelícano, vicinity of Puerto Peñasco. Eastern Pacific: San Pedro, southern California.

Type Locality. Epiphytic on *Phyllospadix*; San Pedro harbor entrance, San Pedro, Los Angeles County, southern California, USA.

Remarks. A single collection from the upper Gulf seems closest to *Colaconema tenuissimum*. New to the Gulf, *C. tenuissimum* was originally only known from southern California (Kylin, 1941; Abbott and Hollenberg, 1976) and has been subsequently reported in Australia (Woelkerling, 1971), Atlantic Costa Rica (Stegenga and Kemperman, 1983), and South Africa (Stegenga, 1985b).

Woelkerling (1973b), studying specimens of *Colaconema tenuissimum* from the northeastern United States, considered it to be a synonym of *Colaconema secundatum* (Lyngbye) Woelkerling (1973a). However, Stegenga and Kemperman (1983, as *Chromastrum tenuissimum* (Collins) Stegenga et Kemperman) and Stegenga (1985b) did not follow Woelkering (1973b) and commented on their distinction, primarily the larger monosporangia of *C. tenuissimum*, and its very different initial development. The basal portion of *C. tenuissimum* has a conspicuous angular, 3-celled septate spore and short prostrate filaments, and *A. secundatum* has a discoid base in which the initial spore divides into a 4- to 6-celled pattern. Herein these two are considered separate until life history studies and molecular comparisons have been undertaken on Gulf of California specimens.

Colaconema variabile* (K. M. Drew) J. N. Norris, *comb. nov.

FIGURE 23H,I

Rhodochorton variabile K. M. Drew, 1928:174, pl. 38: fig. 28, pl. 39: figs. 30, 31; Garbary, 1987:138; González-González et al., 1996:264.

Acrochaetium variabile (K. M. Drew) G. M. Smith, 1944:179; Dawson, 1949c:222; 1953a:29; 1954a:4; 1961b:405; 1962d:394; Dawson et al., 1964:37, pl. 30: fig. A; Stewart and Stewart, 1984:142; Ramírez and Santelices, 1991:179; González-González et al., 1996:168, 381; Serviere-Zaragoza et al., 2007:9; Fernández-García et al., 2011:59.

Audouinella variabilis (K. M. Drew) Garbary in Garbary et al., 1980a:322; Garbary, 1987:138, 192.

Audouinella plumosa var. *variabilis* (K. M. Drew) Garbary, G. I. Hansen et Scagel, 1983:42; Garbary, 1987:138; Scagel et al., 1989:148.

Colaconema plumosum (K. M. Drew) Woelkerling var. *variabile* (K. M. Drew) P. W. Gabrielson in Gabrielson et al., 2000:40.

Acrochaetium pacificum sensu Abbott and Hollenberg, 1976:315 [in part; only in reference to *A. variable*]; Stewart and Stewart, 1984:142 [non *Acrochaetium pacificum* Kylin, 1925:11, which is now *Colaconema pacificum* (Kylin) Woelkerling, 1971:9].

Algae minute, of several erect filaments, 0.5–1.0 mm tall; arising above a basal system of prostrate filaments that have coalesced to form a layer 1–2 cells thick. Erect filaments, 8.0–9.5 µm in diameter; lower portions unbranched or with long branches; upper portions with short, unbranched or branched, branchlets in secund series. Cells elongated, 2–3(–4) times longer than wide, 16–29(–38) µm in length by 8–9.5 µm in diameter; with a parietal plastid and a single large pyrenoid.

Monosporangia terminal or lateral on secund branchlets; monosporangia ovoid, 5.0–7.0 µm wide.

HABITAT. Epiphytic on various algae; low intertidal.

DISTRIBUTION. Gulf of California: Mazatlán. Eastern Pacific: British Columbia to Punta Baja, Baja California; Isla Guadalupe; Isla San Martín; Isla San Benedicto (Islas Revillagigedo); Nicaragua; Peru; Chile.

TYPE LOCALITY. Epiphytic on *Laminaria andersonii*; Cypress Point, Monterey County, central California, USA.

REMARKS. Difficulties in separating *Colaconema variabile* from *C. plumosa* were discussed by Drew (1928), Nakamura, (1944), Woelkerling (1971), and Stegenga (1985b) (see also Remarks under *C. pacificum*). Although *Rhodochorton variabile* has been recognized at a varietal rank, first as *Auduoinella plumosa* var. *variabile* (Garbary et al., 1983) and later as *C. plumosa* var. *variabile* P. W. Gabrielson (in Gabrielson et al., 2000), Pueschel (1989, as a species of *Audouinella*) provided ultrastructural data of pit plugs that *C. plumosa* and *C. variabile* were not related, and that *C. variabile* showed possible affinities with *C. pacificum*.

Dawson (1953a, as *Acrochaetium variabile*) observed that Pacific Mexico *C. variabile* were comparatively slender forms of the species and mostly unbranched in lower portions. Although thus far known only in the southern Gulf, *C. variabile* is included here to call attention to the fact that the Gulf material is in need of critical study.

NEMALIALES

Nemaliales F. Schmitz, 1892:17 [as "Nemalionales"; see Nicolson and Norris, 1983:286].

Members of the Nemaliales include algae that are terete, compressed or flattened thalli, that are mostly erect, or some may be decumbent, and subdichotomously or variously to irregularly branched. Members have a triphasic life history with isomorphic, dimorphic, or heteromorphic phases. Gametophytic thalli are multiaxial in structure, with a central medulla of diffuse to compact filaments that bear anticlinal filaments that ultimately form the cortex. The Nemaliales presently includes three families, the Liagoraceae, Galaxauraceae, and Scinaiaceae (Huisman, 2006). In some families the cortex is composed of loose filaments; in others the filaments may be more compact, laterally adjoined, or with cells fused to form a pseudoparenchymatous cortex. Members of some families are noncalcified (i.e., Scinaiaceae), and other members are calcified with calcium carbonate in the aragonite form of the mineral (e.g., Galaxauraceae and most of the Liagoraceae). Some taxa are gelatinous or mucilaginous, with external mucilage (some Liagoraceae) and mucilage-filled axes contained by cortical layers (Scinaiaceae), whereas members of the Galaxauraceae are not mucilaginous. Cells are uninucleate and have one or more plastids with pyrenoids. Secondary cell fusions occur in some taxa, but secondary pit connections are absent in all members.

Life histories, where known, are triphasic, involving haploid, monoecious or dioecious gametophytes, a postfertilization diploid carposporophyte that develops on or within the female gametophyte, and diploid tetrasporophytes. Tetrasporophytic thalli are (1) isomorphic (similar morphology to the gametophytes) or almost isomorphic (similar external morphology but with differences in cortical structure; e.g., Howe, 1917, 1918), (2) dimorphic (similar in size but with some differences in external morphology and cortical anatomy), or (3) markedly heteromorphic, with relatively larger gametophytes and smaller to minute tetrasporophytes of a different form, either uniseriate filaments or prostrate crusts (e.g., Feldmann and Feldmann, 1943; von Stosch, 1965; Ramus, 1969; Couté, 1971, 1976; Delépine et al., 1979; Magruder, 1984; Guiry, 1990a; Brodie and Norris, 1996). Tetrasporangia are typically cruciately divided.

Sexual reproduction in the Nemaliales is characterized by the absence of an auxiliary cell; the gonimoblast develops directly from the fertilized carpogonium. In the Galaxauraceae and Scinaiaceae, the carpogonial branches are three-celled, composed of a basal cell, a hypogynous cell, and a terminal carpogonium, with the hypogynous cell bearing nutritive branches (or cells). The gonimoblasts can be compact, and the carposporophyte has a surrounding distinct pericarp and ostiole. In the Liagoraceae, the carpogonial branch is extremely variable, from (2–)3 to many celled, and the hypogynous cell is usually naked. The gonimoblasts can be compact or diffuse, and the carposporophyte can be naked or with a loose involucre of filaments. Spermatangia of the Nemaliales are borne superficially on the thallus surface or in clusters on cortical filaments or in cavities.

REMARKS. Although the order has often been referred to as the "Nemalionales" (e.g., Kylin, 1956), Nicolson and Norris (1983) pointed out that the correct name is the Nemaliales.

All three families of the Nemaliales are represented in the northern Gulf of California.

KEY TO THE FAMILIES OF NEMALIALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Algae noncalcified; gametophytes terete or compressed to somewhat flattened; life histories heteromorphic, tetrasporophytes either crusts or uniseriate filaments . . . . **Scinaiaceae**

1b. Thalli lightly to heavily calcified; gametophytes terete, compressed, or flattened; life histories isomorphic, dimorphic, or heteromorphic 2

2a. Axes terete to compressed (not flattened); cortex of loosely arranged filaments, easily disassociated from each other; spermatangia are borne in clusters at or near the tips of assimilatory filaments or in whorls on midcortical cells; life histories heteromorphic, tetrasporophytes uniseriate filaments . . . . **Liagoraceae**

2b. Axes terete to distinctly flattened; cortex not easily disassociated, cortical filaments tightly packed, somewhat laterally coherent or with fusions between some adjacent inner cortical cells; spermatangia in conceptacle-like cavities; life histories either isomorphic, dimorphic, or heteromorphic (tetrasporophytes either uniseriate filaments or crusts) . . . . **Galaxauraceae**

GALAXAURACEAE

Galaxauraceae P. G. Parkinson, 1983:606.

Chaetangiaceae Kützing, 1843:389, 391 [as "Chaetangieae"]; Silva, 1980:81 [see Parkinson, 1983].

Gametophytes of this family are erect and calcified, with terete, compressed, or flattened axes. Most members are dichotomously to subdichotomously, or rarely irregularly, branched. Anatomically, all are multiaxial, with an axial core of longitudinal medullary filaments, from which subdichotomously branched filaments grow anticlinally outward and ultimately form the cortex. The cortex either remains filamentous or develops a pseudoparenchymatous layer of laterally coherent cells, with some having fusions between adjacent cortical cells. The surface is partially to entirely smooth or has spinulose cells or short to long pigmented assimilatory filaments ("hair-like") extending from the cortex of various species.

Life histories involve tetrasporophytes and gametophytes that are (1) isomorphic (i.e., externally similar in habit, differing only in cortical structure), (2) dimorphic (i.e., similar in size but differing in both habit and cortical structure), or (3) heteromorphic with macroscopic gametophytes and either a much smaller filamentous or crustose tetrasporophyte. Tetrasporophytes, where known, produce cruciately divided tetrasporangia. The carpogonial branch of the female gametophyte is borne on inner cells of a cortical filament and is three-celled with nutritive cells or filaments issued from the hypogynous cell and sterile filaments derived from the basal cell. Gonimoblast filaments develop directly from the zygote. At maturity, the carposporophyte has produced branched gonimoblast filaments with terminal carposporangia, either solitary or in chains, within a conceptacle formed from filaments developed from the basal cell of the carpogonial branch or from gonimoblast filaments. Cystocarps are immersed in the axes (outer medulla) and are ostiolate. Spermatangia are scattered over the outer cortical cell layer or on hypodermal cells (inner cortical cells) or within conceptacle-like cavities.

REMARKS. Dimorphism of life history phases (gametophytes and tetrasporophytes) was proposed for species of *Galaxaura* by Howe over 98 years ago (1916, 1918); however, a single entity may have received two different species names, one for the tetrasporophyte and another for the gametophyte, because of their morphological dissimilarity. This has complicated *Galaxaura* taxonomy (Chou, 1945; Zhou and Chen, 1983) and subsequently resulted in many synonyms (e.g., Papenfuss et al., 1982). The correlation of the presumed alternate generations cannot be resolved solely by studying herbarium material. Direct seasonal observations of field populations may reveal associations of asexual and sexual species, which may be involved in a single life cycle. These associations could then be tested in the laboratory with life history studies and verified by phylogenetic analyses using instructive genetic markers to correlate haploid and diploid phases to the correct species names (e.g., Huisman et al., 2004c; Kurihara et al., 2005).

Currently, there are four genera recognized in the Galaxauraceae, three of which are recorded in the northern Gulf of California.

KEY TO THE GENERA OF GALAXAURACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes flattened, nonsegmented (in Gulf species); gametophytes and sporophytes macroscopically isomorphic, differing mainly in cortical anatomy; surfaces of both gametophytes and sporophyte glabrous (cortex without extended assimilatory filaments, "hairs") . . . . ***Dichotomaria***

1b. Axes terete, nonsegmented (some may appear "segmented" because of breaks in calcification, usually at branching points); gametophytes and sporophytes either (1) dimorphic (differing in both habit and cortical anatomy) only gametophyte surface glabrous (without "hairs") and sporophytes with hirsute ("hairy") surface (cortex with extended assimilatory filaments) or (2) phases markedly heteromorphic, sporophytes are branched uniseriate filaments 2

2a. Gametophytes and sporophytes heteromorphic; gametophytes surface glabrous (smooth), without extended assimilatory filaments; cortical cells not firmly laterally attached to each other (fusions lacking); sporophytes uniseriate, branched filaments . . . . ***Tricleocarpa***

2b. Gametophytes and sporophytes dimorphic, differing in habit and cortical cell structure; sporophyte surface entirely or partially covered in extended assimilatory filaments; gametophytes surface mostly glabrous; inner cortex of firmly, laterally cohering cells (fused in some species) . . . . ***Galaxaura***

KEY TO THE SPECIES OF *DICHOTOMARIA, GALAXAURA,* AND *TRICLEOCARPA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli distinctly flattened or strongly compressed 2

1b. Thalli terete throughout or partially terete with upper portions slightly compressed 3

2a. Lateral margins thicken and raised on drying; cortex of sporophytes with stalk-like cells bearing subspherical outer cortical cells that occasionally have an apiculate apex (more common near margins); cortex of gametophytes with outer spinulose cells mostly along axes margins . . . . ***Dichotomaria marginata***

2b. Lateral margins usually not raised on drying; cortex of sporophytes with stalk-like cells bearing ellipsoid or slightly flattened outermost cortical cells, cell apices not apiculate; cortex of gametophytes with outer spinulose cells covering thallus surface . . . . ***Dichotomaria spathulata***

3a. Thallus surface partially or entirely hirsute (hairy); cortical layer with some extending assimilatory filaments (not completely smooth) 4

3b. Thallus surface glabrous throughout (without hairs/assimilatory filaments) 6

4a. Thallus mostly terete (upper portions may be slightly compressed); surface either glabrous, often annulate (calcification interrupted by clear transverse bands), or with lower portions hairy and upper portions with occasional assimilatory filaments on outer cortical cells; some fusions present between adjacent inner cortical cells (gametophyte) . . . . ***Galaxaura rugosa* (in part)**

4b. Thallus terete; surface not smooth, hirsute (hairy), with both long and short assimilatory filaments; adjacent inner cortical cells not fused 5

5a. Cortex of tumid basal cells, 50–60 µm long, 30–40 µm in diameter, that bear assimilatory filaments that are either (a) short, of 2 or 3 subglobose cells, or (b) long filaments of elongated cells, 28–54 µm long, 14–16 µm in diameter basally, slightly wider upward, 16–18 µm in diameter (sporophyte) . . . . ***Galaxaura rugosa* (in part)**

5b. Cortex of tumid basal cells, 40–65 µm long by 20–40 in diameter, that bear assimilatory filaments that are either (a) short, of 2(–3) cells and a subglobose terminal cell, 20–32 µm in diameter), or (b) short to long filaments, 0.8–1.2 mm in length, of elongated cells, 18–60 µm long, 12–15 µm in diameter basally, widening upward to 18–20 µm in diameter (sporophyte) . . . . ***Galaxaura ramulosa***

6a. Branches narrow, 0.5–1.5 mm in diameter; gonimoblast filaments lining all sides of pericarp, mixed with numerous, well-developed paraphyses . . . . ***Tricleocarpa cylindrica***

6b. Branches broader, 1.5–2.0 mm in diameter; gonimoblast filaments growing laterally only along base of pericarp, mixed with poorly developed paraphyses . . . . ***Tricleocarpa fragilis***

***Dichotomaria* Lamarck**

Dichotomaria Lamarck, 1816:143; J. Agardh, 1876:529.

Alysium C. Agardh, 1823:433; Wynne, 2008:323, figs.1–3.

Algae are calcified, terete or flattened and subdichotomously branched thalli with axes that are smooth, or some have basal portions that are hirsute (hairy). Branches sometimes have proliferations, with or without distinct segments depending on the species. Medulla is filamentous. Gametophytes and tetrasporophytes are isomorphic, and although these life history phases are similar in habit, their cortical anatomy differs. Gametophytes have a closely packed cortex, usually of 3 layers: inner 2 cortical layers of large, nearly hyaline cells that frequently fuse laterally, and an outer cortical layer of smaller pigmented cells. Carpogonial branches are borne in place of a normal vegetative filament. The carpogonial branch is 3-celled, composed of a basal cell, a hypogynous cell, and carpogonium. Before fertilization the hypogynous cell has 3–4 nutritive branches, and the basal cell has up to 4(–5) small-celled sterile filaments (Huisman, 2006). After fertilization, gonimoblast initials develop from the carpogonium and radiate outward. Cystocarps have a central fusion cell. Surrounding the carposporophyte is a pericarp formed by both gonimoblast filaments and involucral filaments derived from the basal cell of the carpogonial branch. Carposporangia are terminal on gonimoblast filaments that project toward center of the cystocarp cavity; pericarp filaments never extend into the cystocarp cavity. Spermatangia are borne in conceptacle-like cavities.

Sporophytes have a cortex of 3–6 layers: inner 1–3 cortical layers of large hyaline cells and an outermost layer of pigmented ellipsoid, subglobose, or wedge-shaped cells borne on loosely spaced stalk-like cells. Tetrasporangia are cruciately divided, borne laterally on stalk cells of cortex or terminally from outermost cortical cells.

REMARKS. Huisman et al. (2004b), on the basis of genetic, life history, and morphological characters, resurrected the genus *Dichotomaria* and transferred some *Galaxaura* species to the genus.

Two species of *Dichotomaria*, both flattened, occur in the northern Gulf of California.

KEY TO THE SPECIES OF *DICHOTOMARIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes flattened, with thickened margins (raised on drying); Gulf gametophytes surface mostly smooth, but with spinulose cells (often dense) protruding along axes margins; sporophyte (not known in Gulf) cortex with pairs of subspherical cells on stalk cells; subspherical cells occasionally with apiculate apices, notably along axes margins . . . . ***D. marginata***

1b. Axes flattened, margins even or only slightly raised (on drying); gametophytes (not known in Gulf) with spinulose cells over entire thallus surface; Gulf sporophytes with stalk cells bearing subspherical, nonapiculate cells that form outermost cortical layer . . . . ***D. spathulata***

Dichotomaria marginata (J. Ellis et Solander) Lamarck

FIGURE 24

Corallina marginata J. Ellis et Solander, 1786:115, pl. 22: fig. 6 [fig. 6 selected as lectotype by Papenfuss et al., 1982:411].

Dichotomaria marginata (J. Ellis et Solander) Lamarck, 1816:146; Huisman et al., 2004b:230; Huisman et al., 2004c:344, fig. 10; Huisman and Kurihara, 2006:17, figs. 5A,B, 6A; Fernández-García et al., 2011:61; Wiriyadamrikul et al., 2014:34, fig. 6A–I.

Galaxaura marginata (J. Ellis et Solander) J. V. Lamouroux, 1816:264; Dawson, 1944a:258; 1961b:407; Papenfuss et al., 1982:411, figs. 7–9, 24, 36–37; Huisman and Borowitzka, 1990:157, figs. 14–27; Dreckmann, 1991:33; González-González et al., 1996:311; Abbott, 1999:67, fig. 7G,H; Mateo-Cid et al., 2000:63; Cruz-Ayala et al., 2001:191; CONANP, 2002:141; Y.-P. Lee, 2008:218, figs. A–C; Bernecker, 2009:CD-Rom p. 61.

Zanardinia marginata (J. Ellis et Solander) J. Agardh, 1876:534.

Galaxaura veprecula Kjellman, 1900:80, pl. 16, figs. 17–33, pl. 20: fig. 20; Tanaka, 1936:169, figs. 36, 37, pl. 43: fig. 1; Taylor, 1945:143; Chou, 1947:16, pl. 6: figs. 1–8, pl. 12: fig. 2; Dawson, 1953a:53, pl. 18: fig. 2; 1957c:14; 1959a:20; 1961b:407; 1962b:229; Zhou and Chen, 1983:84, pl. 2: figs. 9, 10; Huerta-Múzquiz and Mendoza-González, 1985:48; González-González et al., 1996:203: Riosmena-Rodríguez et al., 1998:28.

Galaxaura ventricosa sensu Taylor, 1945:143 [in part; Nayarit specimen]; Chou, 1947:18, pl.6: figs. 9–12, pl. 12: fig.2; Zhou and Chen, 1983:85, pl. 1: fig. 11; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:202 [non *Galaxaura ventricosa* Kjellman, 1900:81].

Algae erect, bushy, calcified, pale pink to grayish red, of flattened smooth and regularly subdichotomously branched axes, up to 8 cm high, axes 1.0–2.5(–4.0) mm in diameter, of more or less uniform width throughout; branch dichotomies 3–10(–15) mm apart; attached below by a broad flattened or discoid holdfast. Branches glabrous above, often with distinct transverse bands (striations where calcification interrupted), margins often thickened; basal portions subterete, often hirsute (hairy). Medullary filaments of elongated cells, 8–16 µm in diameter. Gametophyte cortex pseudoparenchymatous, of 3 closely packed cell layers, inner 2 layers of large colorless subglobose cells, and single outer layer of pigmented smaller cells (15–)20–30(–35) µm in diameter, polygonal in surface view (4–6 sided). Surface cortical cells commonly bearing spinulose (apiculate) epidermal cells along the axes margins and occasional in patches elsewhere; spinulose cells 30–40 µm long by 10–15 µm in diameter, with a rounded or mucronate apex. Sporophytes not found in our collections; as reported from elsewhere (Wang et al., 2005): cortex of 4–5 layers; inner layers of large, colorless, globose cells; outermost layer of pigmented subspherical cells borne singly or in pairs on elongate, loosely spaced stalk-like cells; subspherical cells sometimes apiculate (see Huisman, 2006: fig. 5b), with a short simple spine on their external surface, particularly on cells near axes margins (Wiriyadamrikul et al., 2014: fig. 6-I).

Tetrasporangia cruciately divided; borne laterally on subepidermal stalk cells or terminally on outermost cortical cells. Gametophytes usually dioecious. Spermatangia in conceptacle-like cavities (Figure 24B, C).

HABITAT. On rocks; low intertidal to shallow subtidal; dredged to 40 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Punta Cirio to Guaymas; Caleta Santa María (about 11.3 km [7 miles] north of Santa Rosalía) to Bahía Agua Verde; Bahía de

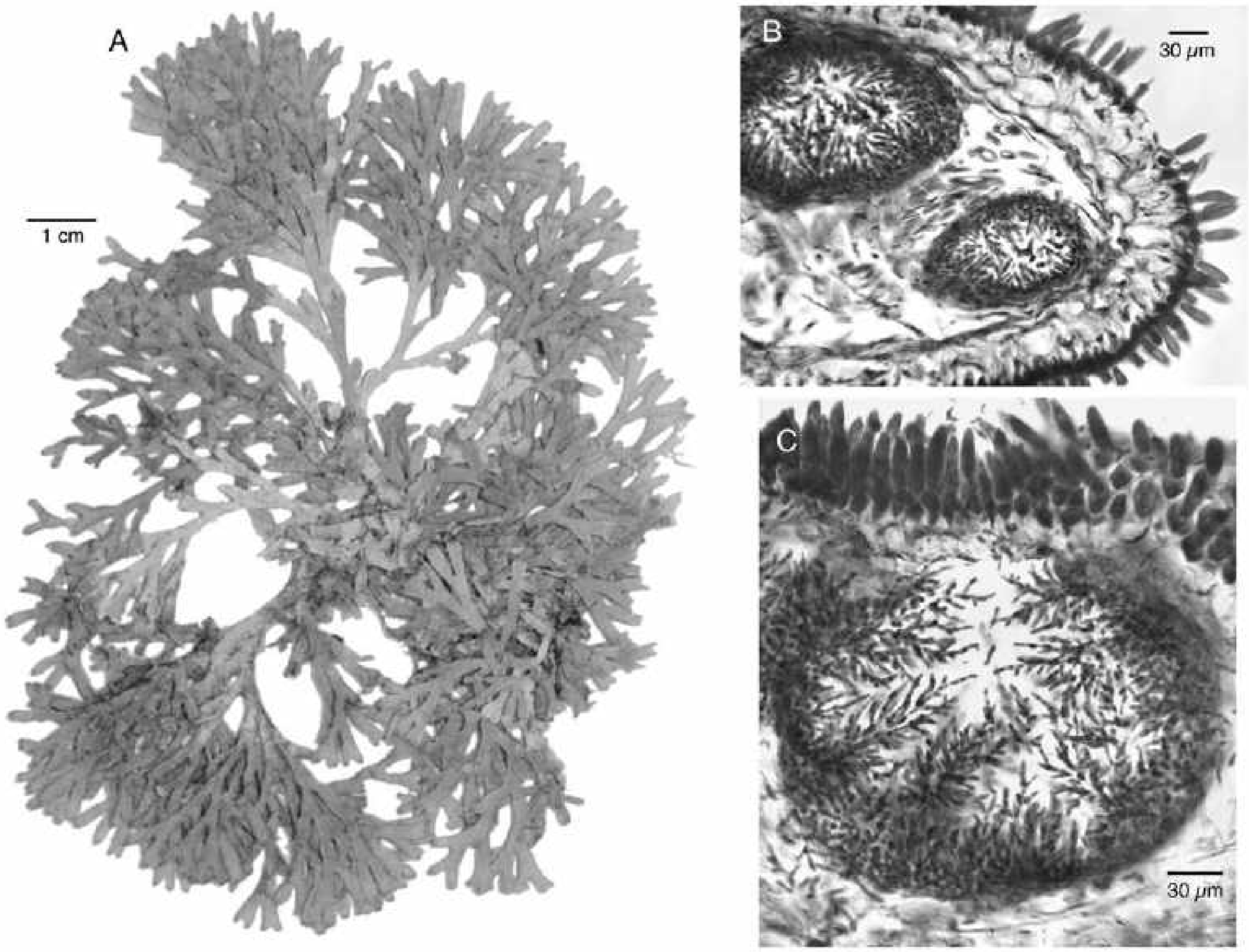

FIGURE 24. A–C. *Dichotomaria marginata*: A. Habit of gametophyte (*JN-3400a*, US Alg. Coll.-159143). B. Transection of male gametophyte showing two embedded spermatangial cavities and tightly arranged outer cortical cells (epidermis) bearing spinulose cells. C. Transection showing densely branched spermatangial filaments projecting into cavity of male conceptacle (B, C *JN-4891a*, US Alg. Coll. microscope slide 8707).

La Paz to Punta Los Frailes; Nayarit to Jalisco; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: Costa Rica; Galápagos Islands. Central Pacific: Hawaiian Islands. Western Pacific: China; Taiwan; Korea; Japan.

Type Locality. "On the shore of one of the Bahama Islands" (Ellis and Solander, 1786:115).

Remarks. Molecular phylogenies based on *rbc*L sequence data (Wang et al., 2005; Wiriyadamrikul et al., 2014: fig. 1) indicate specimens identified as *D. marginata* from around the world are not monophyletic but instead diverge into several clades. *Dichotomaria marginata* is currently a species complex in need of taxonomic revision (Wang et al., 2005; Huisman et al., 2004b; Huisman, 2006). Northern Gulf specimens from Guaymas identified as *D. marginata* grouped in a clade near specimens of *D. tenera* from South Africa (Wang et al., 2005: figs. 8, 9; Liu et al., 2013: fig. 1). Gulf of California *D. marginata* and South African *D. tenera* (De Clerck et al., 2005a) are similar in morphology, and both have small axes diameters of 1–2(–3) mm. The sporophytes of these two species have been separated on the presence or absence of apiculate ends on their ultimate epidermal cells. They are often present on those of *D. marginata,* particularly on cells along the axes margins (Huisman et al., 2004b), and they are absent from ultimate epidermal cells of *D. tenera.* However, apiculate epidermal cells have since been occasionally observed on *D. tenera* sporophytes, so this feature is apparently not entirely consistent (De Clerck et al., 2005a).

Only gametophytic thalli of *Dichotomaria marginata* were found in our northern Gulf collections. The specimens generally agree in external morphology and internal anatomy with Australian *D. marginata* (see Huisman and Kurihara, 2006:17), although size measurements of Gulf specimens are smaller. Branches of Gulf of California specimens of *D. marginata* (*JN-4891a*, US Alg. Coll.-159149; and *JN-3400a*, US Alg. Coll-159142), when viewed under a dissection scope, reveal tiny brown spinulose cells bristling along their axes margins, whereas in the middle, the branches are pink and shiny, with a reflective sparkle off the cortical surface.

Detailed comparative morphological studies and phylogenetic analyses of DNA sequences of Gulf of California *D. marginata* are needed to determine if they are in agreement with type locality material (Bahamas Islands) or are possibly a separate entity. The Gulf *D. marginata* should also be studied to understand its relationship to Gulf specimens identified with *D. spathulata*.

Dichotomaria spathulata (Kjellman) A. Kurihara et Huisman

FIGURE 25

Galaxaura spathulata Kjellman, 1900:74, pl. 12: figs. 5–12, pl. 20: fig. 35; Taylor, 1945:142; Dawson, 1961b:407; Fernández-García et al., 2011:61.

Dichotomaria spathulata (Kjellman) A. Kurihara et Huisman in Huisman and Kurihara, 2006:21, 135, figs. 5C, 6B.

Galaxaura arborea Kjellman, 1900:72, pl. 11: figs. 1–11, pl. 20: fig. 39; Tanaka, 1936:161, figs. 24, 25, pl. 40; Tseng, 1941:94, fig. 6; Chou, 1945:50, pl. 5: figs. 2–5, pl. 10: figs. 1, 2; Dawson, 1953a:49, pl. 17: fig. 2; 1959a:5, 6, 19; 1961b:407; 1962d:394; 1966a:15; Zhou and Chen, 1983:87, pl. 1: fig. 6; Tseng, 1983:58, pl. 32: fig. 2; Norris, 1985d:211; Huerta-Múzquiz and Mendoza-González, 1985:48; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:28; CONANP, 2002:141; Fernández-García et al., 2011:61.

Galaxaura marginata sensu Dawson, 1944a:258 [non *Galaxaura marginata* (J. Ellis et Solander) J. V. Lamouroux, 1816:264, which is now *Dichotomaria marginata* (J. Ellis et Solander) Lamarck, 1816:146].

Algae erect, bushy, composed of flattened calcified axes, grayish green to reddish brown, up to 12 cm tall; above a terete to compressed stipe, 1–4 mm long; attached below by a small holdfast of compacted rhizoidal cells. Axes 1–3 mm wide and 250–400 µm thick. Surfaces of axes with transverse bands or

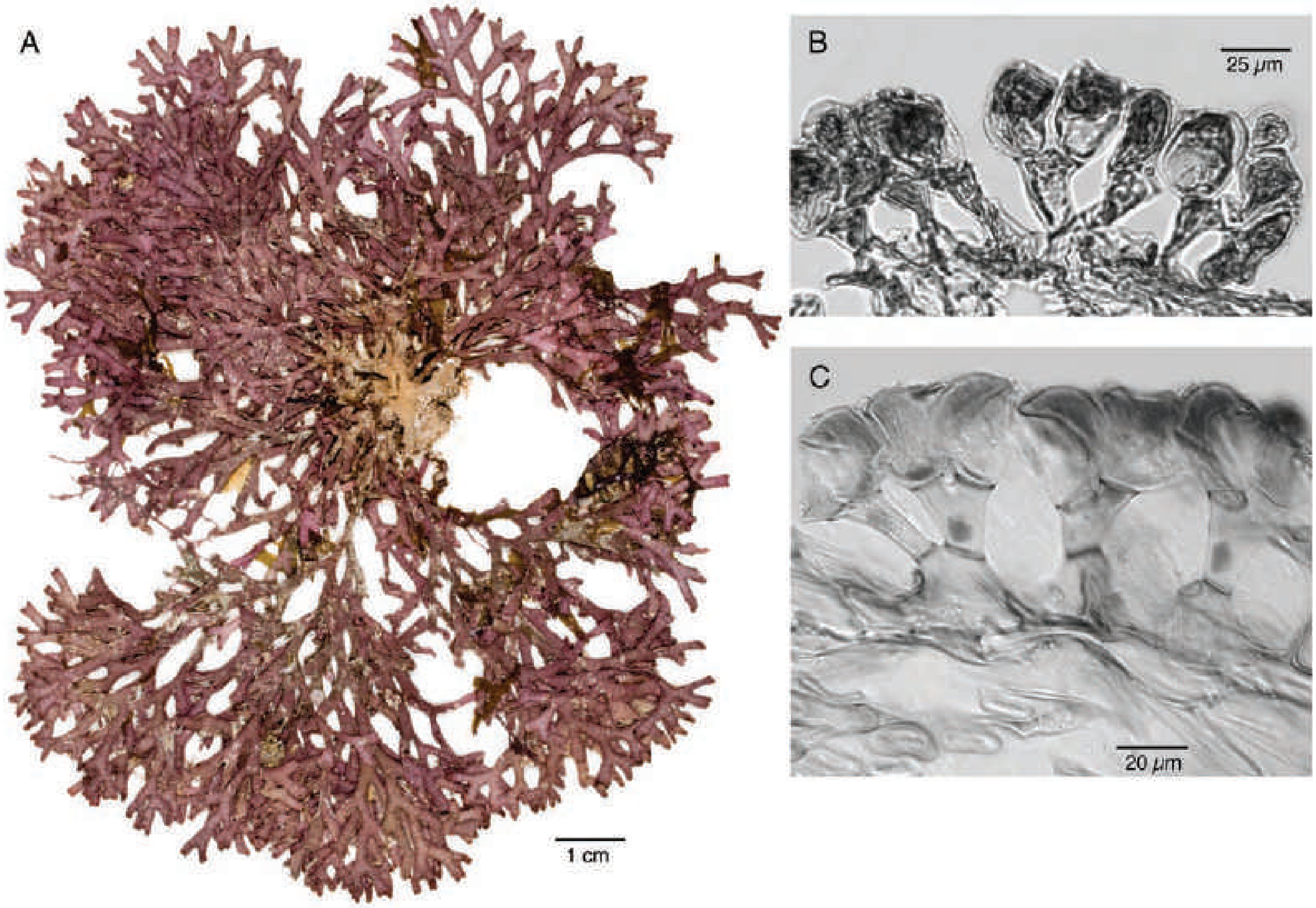

FIGURE 25. *Dichotomaria spathulata:* A. Habit, tetrasporophyte (*JN-5859*, US Alg. Coll.-159150). B, C. Portion of transections through sporophyte cortex showing loosely arranged stalk-like cells bearing 1–2 subspherical, nonapiculate ultimate cortical cells (B, *JN-4891b*, US Alg. Coll. microscope slide 8708; C, *JN-2941*, US Alg. Coll. microscope slide 5366).

striations where calcification has been interrupted; axes repeatedly subdichotomously branched, up to 6 orders. Medulla filamentous. Sporophyte cortex of 4–5 layers; inner 2–3 layers of globose colorless cells and borne singly or in pairs above a short (about 20 μm long) stalk-like cell, the outermost layer of oval to obovoid cells, 30–45 μm tall, 25–35 μm in diameter. Gametophytes (not known in the northern Gulf); elsewhere reported with pseudoparenchymatous cortex, of 3–4 compact layers; inner 2 layers of colorless, laterally cohering cells, 24–60 μm tall, 60–80 μm wide; outer layer of smaller, pigmented cells, many with spinulose cells at the thallus surface.

HABITAT. On intertidal platforms, on rocks, and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Punta Cirio; Bahía de Loreto to Cabo San Lucas. Eastern Pacific: Costa Rica; Nicaragua; Galápagos Islands. Central Pacific: Hawaiian Islands. Western Pacific: China; Japan.

TYPE LOCALITY. Fremantle, Western Australia, Australia.

REMARKS. Only sporophytes of *Dichotomaria spathulata* were found in our northern Gulf collections as well as those of Dawson (1966a, as "*Galaxaura arborea*"). *Galaxaura arborea* was considered to be conspecific with *D. spathulata* by Huisman and Kurihara (2006). Morphologically, the Gulf of California specimens referred to *D. spathulata* are on the small end of the size range for the species, with branches up to 3 mm in width. Sporophytes of Australian *D. spathulata* (Huisman and Kurihara, 2006:21) can have wider axes (up to 5 mm) and also differ in being more sparingly branched, with longer intervals between dichotomies. Structures, possibly immature tetrasporangia (not yet divided), were observed to be terminal on some epidermal cells of northern Gulf *D. spathulata* (*JN-4833*, US Alg. Coll. microscope slide 5250). If they are sporangia, then the Gulf tetrasporangia differ in position from tetrasporangia reported for Australian *D. spathulata,* which are borne laterally from the subepidermal cells (stalk cells).

Outside the Gulf of California, sporophytes of *D. spathulata* from Pacific Mexico and Costa Rica (Chou, 1945; Dawson, 1953a, both as "*Galaxaura arborea*") were found growing sympatrically among gametophytes identified as "*Galaxaura veprecula.*" The ecological association of the two suggested they might be life history phases of a single species, and they were later treated as being conspecific (Papenfuss et al., 1982). However, more recently, Huisman and Kurihara (2006) considered *G. veprecula* Kjellman (1900; type locality: Madagascar) to be a synonym of *Dichotomaria marginata* (J. Ellis et Solander) Lamouroux.

Dichotomaria spathulata is currently reported as being widespread in distribution. Phylogenetic analyses of DNA sequences are needed to assess whether Gulf of California algae referred to *D. spathulata,* as well as those from around the world, are identical with type or type locality material (Western Australia) or are perhaps separate species.

Galaxaura J. V. Lamouroux

Galaxaura J. V. Lamouroux, 1812:185.

Algae of erect, calcified, subdichotomously branched terete axes of multiaxial construction. Gametophytes and tetrasporophytes are dimorphic, both having a filamentous medulla, but differ in external morphology and in cortical anatomy. Gametophytes have smooth surfaces (glabrous) or partly smooth in the upper portions and with hairy surfaces in lower portions. The cortex of gametophytes is typically 3 layers thick: inner 2 layers of large colorless cells that are often laterally adjoined (fused) and an outer layer of smaller tightly arranged pigmented cells. The cortex of sporophytes is composed of supporting cells bearing short and long assimilatory filaments, giving the surface a hairy appearance. The assimilatory filaments/hairs are supported on inflated or noninflated basal cells.

Sporophytes produce cruciately divided tetrasporangia. Tetrasporangia develop laterally or terminally on the assimilatory filaments that extend beyond the thallus surface.

Gametophytes are usually dioecious, although some are monoecious. Carpogonial branches are 3-celled, developing in place of a vegetative filament. Before fertilization the hypogynous cell of the carpogonial branch bears 3–4 nutritive filaments, and the basal cell has 3–4 sterile filaments of 3–4 small cells. The filaments derived from the basal cell do not form a pericarp but remain at the base of the cystocarp in *Galaxaura* (Wang et al., 2005). The primary gonimoblast filaments are initiated from the fertilized carpogonium and form most of the cystocarpic conceptacle wall. A fusion cell is formed from the carpogonium, hypogynous cell, basal cell, and part of conceptacle wall filaments (i.e., inner gonimoblast cells). Cystocarps are immersed within the axes, with carposporangia terminal on gonimoblast filaments that arise from the conceptacle wall and grow toward the center of the cystocarpic cavity (Huisman, 2006). Spermatangia are formed in conceptacle-like cavities.

REMARKS. The generic name, *Galaxaura* (Greek: *Galaxaurh*), is after one of the Okeanides (Oceanides), the three thousand goddess nymphs who were daughters of Okeanos (Oceanus) and Tethys (Huisman, 2006).

Two species of *Galaxaura* occur in the northern Gulf of California.

KEY TO THE SPECIES OF *GALAXAURA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus pinkish to peach colored, generally wider and with smooth branch surfaces in upper parts; cortex of lower portions of thallus often with sparse to dense assimilatory filaments/hairs (gametophyte) . . . . ***G. rugosa* (in part)**

1b. Thallus usually dark reddish; surface hairy (hirsute) throughout, cortex with short and long extended assimilatory filaments/hairs (in whorls or not in whorls) 2

2a. Short assimilatory filaments commonly composed of 3 cells (occasionally 2) (sporophyte) .... **G. *rugosa* (in part)**
2b. Short assimilatory filaments mostly of 2-cells (infrequently of 3 cells) (sporophyte) .... ***G. ramulosa***

Galaxaura ramulosa Kjellman

FIGURE 26

Galaxaura ramulosa Kjellman, 1900:50, pl. 3: figs. 24–26, pl. 4: figs. 1–3, pl. 20: fig. 18; Chou, 1945:44, pl. 2: figs. 3–5, pl. 7: fig. 1; Taylor, 1945:140; Dawson, 1957c:13; 1961b:407; 1962b:229; 1966a:15; 1966b:59; González-González et al., 1996:202; Bernecker, 2009:CD-Rom p. 61.

Tetrasporophytes up to 6(–10) cm tall; axes terete, 0.5–1.2 mm in diameter; dichotomously to subdichotomously branched, heavily calcified. Dichotomies 2–15 mm apart; surface mostly hairy (hirsute), but may become denuded in lower portions. Assimilatory filaments/hairs occasionally in whorls. Medullary filament cells elongate, 6–20 µm in diameter. Cortex of cortical supporting cells, 30–35 µm tall by 20–40 µm wide; each support cell often with both a short and a long extended assimilatory filament on a tumid basal cell. Short assimilatory filament, usually of 2 cells (infrequently 3): a tumid basal cell, 40–65 µm long by 20–40 µm in diameter, and a subglobose terminal cell, 20–32 µm in diameter (usually nearly the same diameter as basal cell). Long assimilatory filaments (also on a tumid basal cell) 0.8–1.2 mm long, of cells 18–60 µm in length, 12–15 µm in diameter basally, cells wider above to 18–20 µm in diameter.

Gametophytes unknown in Gulf of California collections.

HABITAT. On rocks and tidal platforms and in tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía de San Carlos (“Nuevo Guaymas”), north of Guaymas. Eastern Pacific: Costa Rica; Panama.

TYPE LOCALITY. [Probably Recifie], Pernambuco, Brazil.

REMARKS. Only the sporophyte of *Galaxaura ramulosa* is thus far reported in the northern Gulf of California. It has extended assimilatory filaments that resemble those described for sporophytes of other species (see Tanaka, 1936: Chou, 1945; Wang et al., 2005), e.g., *G. delabida* Kjellman (1900) and *G. lapidescens*, that have been considered conspecific with *G. rugosa*. Dawes and Mathieson (2008) list *G. ramulosa* in synonyms of *G. rugosa,* but without comment. Northern Gulf specimens referred to *G. ramulosa* and Brazilian *G. ramulosa* (type and type locality) need to be comparatively tested with DNA sequence analyses to clarify their phylogenetic relationship, and then compared to *G. rugosa*.

Galaxaura rugosa (J. Ellis et Solander) J. V. Lamouroux

FIGURE 27

Corallina rugosa J. Ellis et Solander, 1786:115, pl. 22: fig. 3.

Galaxaura rugosa (J. Ellis et Solander) J. V. Lamouroux, 1816:263; Papenfuss et al., 1982:421, figs. 17–19, 29, 40, 41, 45; Huisman and Borowitzka, 1990:153, figs. 1–13; Dreckmann, 1991:33; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:47; León-Tejera and González-González, 1993:496; González-González et al., 1996:390; Yoshida, 1998:502; Abbott, 1999:68, fig. 8A–E; Cruz-Ayala et al., 2001:191; CONANP, 2002:141; Huisman et al., 2004c:344, figs. 1–6; Wang et al., 2005:693, figs. 3d–g, 4a–i, 6c–f, 7a–e; Mateo-Cid et al., 2006:55; Huisman, 2006:22, fig. 7A–G; Serviere-Zaragoza et al., 2007:9; Y.-P. Lee, 2008:220, figs. A–D; Bernecker and Wehrtmann, 2009:226; Fernández-García et al., 2011:61.

Corallina lapidescens J. Ellis et Solander, 1786:112, pl. 22: fig. 9.

Galaxaura lapidescens (J. Ellis et Solander) Lamouroux, 1816:264; Taylor, 1960:337; Papenfuss et al., 1982:407, figs. 4, 5, 22, 23, 34, 44.

Galaxaura squalida Kjellman, 1900:55, pl. 6: figs. 1–12, pl. 20: fig. 9; Svedelius, 1945:3, figs. 1–7, pl. 1; Taylor, 1945:142; Chou, 1947:9, pl. 4: figs. 1–11, pl. 8: fig. 2; Dawson, 1953a:52, pl. 19: fig. 1; 1961b:407; 1962b:198, 229, fig. 73; 1966a:15; Zhou and Chen, 1983:83, pl. 2: figs. 6, 7; Huerta-Múzquiz and Mendoza-González, 1985:48; González-González et al., 1996:311; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:28.

Galaxaura subfruticulosa R. Chou in Taylor, 1945:140; Chou, 1945:41, pl. 2: fig. 6, pl. 8: fig. 2; Dawson, 1953a:52, pl. 20: fig.1; 1961b:407; Itono, 1977b:6, fig. 4; Papenfuss et al., 1982:409; Tseng, 1983:60, pl. 33, fig. 4; Zhou and Chen, 1983:87, pl. 1: fig. 5; González-González et al., 1996:202.

Galaxaura subverticillata Kjellman, 1900:48, pl. 3: figs. 12–14, pl. 20: fig. 17; Tanaka, 1936:146, figs. 3, 4, pl. 34: fig. 2; Dreckmann, 1991:33; Yoshida, 1998:503.

Gametophytic and tetrasporophytic thalli are dimorphic, differing in external morphology and cortical anatomy. Gametophytes erect, forming clumps 4–8(–10) cm tall, branches terete, glabrous (without hairs) in upper parts, with assimilatory filaments/hairs on outer cortical cells of lower portions. Thalli light pink, yellowish green, or peach colored, with rosy orange apices; branches mostly (2.0–)5–12 mm long, 1–2 mm in diameter; slightly segmented (not constricted) and repeatedly dichotomously to subdichotomously branched; attached by a discoid, expanding holdfast. Heavily calcified throughout, with evident annulations (transverse striations) interrupting calcification in upper portions. Cortex 3(–4) cell layers thick, inner two cortical layers of large, subglobose cells, 20–40 µm tall by 25–40 µm in diameter; innermost cells often fuse with adjacent cortical cell becoming larger, much wider than tall, 20–30 µm tall, 25–80 µm in width, and sometimes fused with 2–3 lobes (in longitudinal section); middle layer of globose to ovate cells, 15–30 µm tall, 15–25(–30) µm in diameter. Outer layer of flat-topped pigmented angular cells (4–7 sided); in surface view 14–22 µm wide, with a single stellate chloroplast and central pyrenoid; surface cells in cross section 8–12(–15) µm tall by 18–25 µm wide.

Gametophytes apparently dioecious. Cystocarps spherical, embedded in medulla, with ostiole opening through cortical layer to thallus surface; mature carposporangia about 50 µm long by 30 µm in diameter. Spermatangial reproduction unknown in Gulf material (reported from elsewhere: spermatangial cavities 230–450 µm in diameter; inner parent cells cutoff

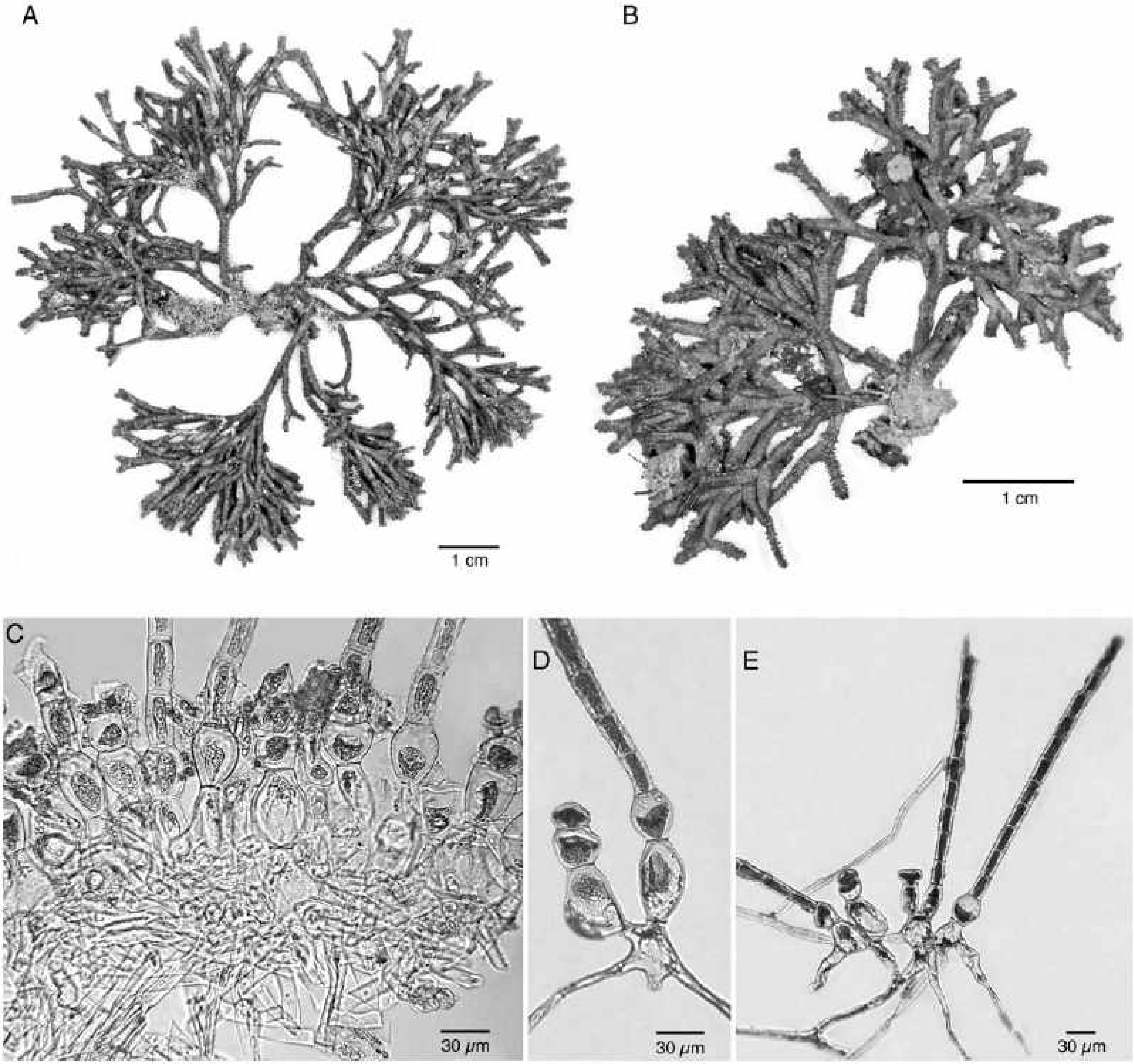

FIGURE 26. *Galaxaura ramulosa*: A. Habit of sporophyte (*JN-3563*, US Alg. Coll.-159169). B. Sporophytic specimen with dark reddish extended assimilatory filaments in whorls (*EYD-27457*, US Alg. Coll.-40824). C. Transection of branch showing cortex of tangled filaments and supporting cells that bear inflated basal cells with long or short assimilatory filaments (*JN-3080*, US Alg. Coll.-159167). D, E. Separated cortical filaments showing supporting cell bearing one or two tumid cells each with a single short or long assimilatory filament. Short filaments consist of a tumid cell and a terminal cell (occasionally one additional cell), with the terminal cell subglobose or sometimes flat topped (D, E, *JN-4280*, US Alg. Coll. microscope slide 8697).

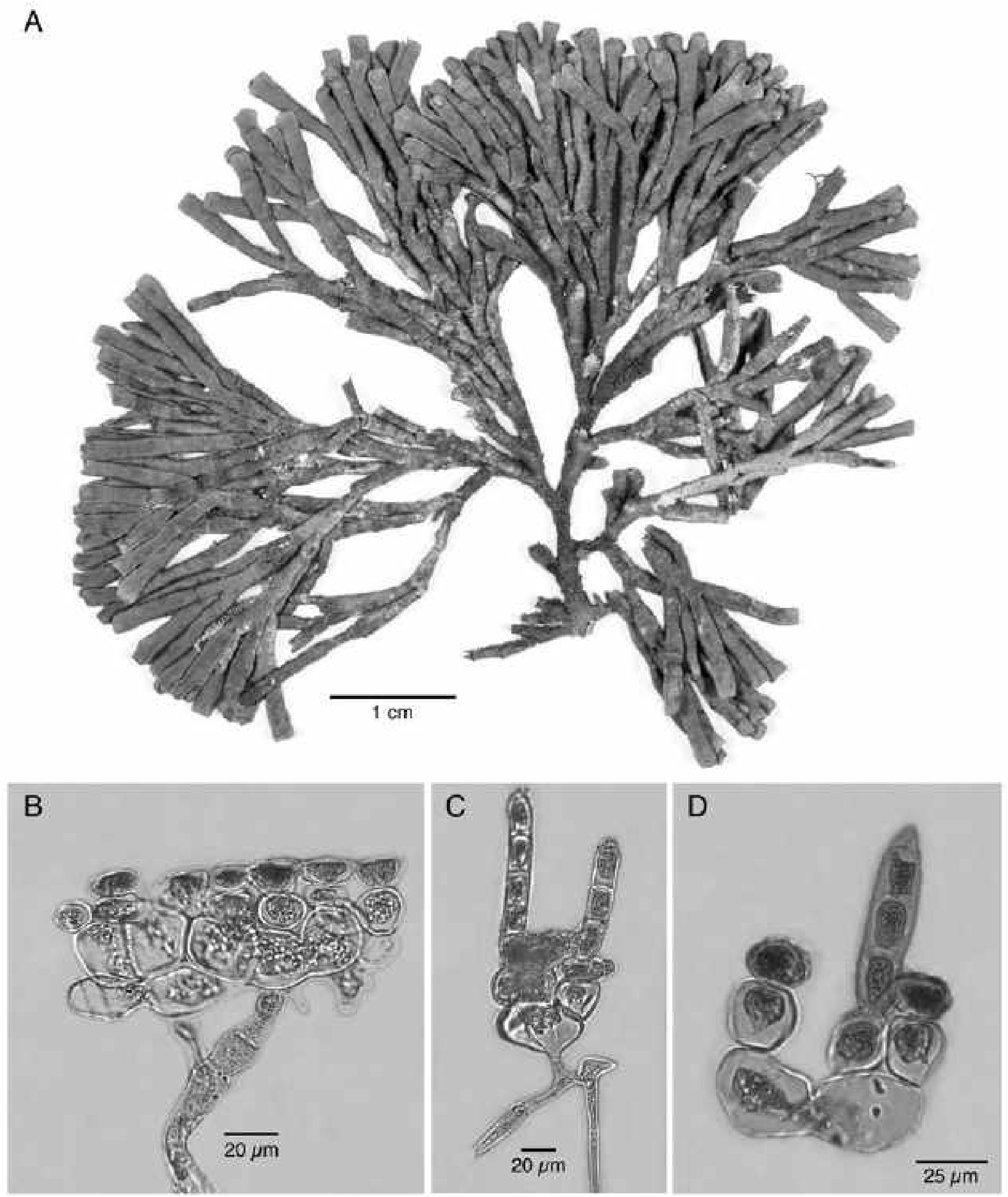

FIGURE 27. *Galaxaura rugosa*: A. Habit of gametophyte (*JN-3634*, US Alg. Coll.-159199). B. Transection of gametophyte cortex showing lateral fusion of colorless cortical cells and outermost layer of smaller pigmented cells. C, D. Small portion of gametophyte cortex showing lateral fusions of inner cells and the occasional extended assimilatory filaments (B–D, *JN-3077*, US Alg. Coll. microscope slide 8698).

highly branched, spermatangial filaments that develop terminal and subterminal spermatangia, 7–10 µm in diameter [after Wang et al., 2005]).

Tetrasporophytes, dark red in color, up to 8 cm tall (generally shorter in height with axes thinner in diameter than gametophytes); subdichotomously branched; branch segments 3–7 mm long; surface characteristically furry or hairy; with simple or sometimes branched, extended assimilatory filaments, up to 1.0 mm in length, arising from inflated basal cells of cortical layer; intermixed long (5- to 12-celled or more) and short (2- to

3-celled) assimilatory filaments of elongated cells, 22–30(–54) µm in length and 14–18 µm in diameter, slightly narrower proximally. Medullary filaments 6–18 µm in diameter. Cortical layer of tumid, oval to pyriform, basal cells, 45–65 long by 28–40 in diameter; with a subglobose terminal cell 20–35 µm in diameter (similar or smaller in diameter than subterminal and basal cells).

Tetrasporangia globose to ovoid, 27–33 µm in diameter; terminal on long and short assimilatory filaments (after Huisman, 2006).

HABITAT. On rocks; low intertidal to shallow subtidal, down to 10 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena. Eastern Pacific: Punta Palmilla (Baja California Sur); Isla Clarión (Islas Revillagigedo); Costa Rica; Panama. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Taiwan; China; Korea.

TYPE LOCALITY. Jamaica, Greater Antilles, Caribbean Sea.

REMARKS. Gametophytes of *Galaxaura rugosa* are generally wider, pinkish to peach in color, with smooth branch surfaces, distinguishing them from the other terete species of *Galaxaura* in the northern Gulf. Gulf of California tetrasporophytes are reddish, often dark red, with hirsute (hairy) branch surfaces covered in dark red extended assimilatory filaments.

Wang et al. (2005), comparing molecular analyses from specimens of Taiwan *G. rugosa* with those from other Pacific and Atlantic locales, demonstrated the species was polyphyletic. Analysis of *rbc*L sequence data revealed that three clades separated out in their phylogenetic trees, with each clade correlated to morphological differences of the sporophytes—i.e., the absence or presence and numbers and density of long and short assimilatory filaments borne on tumid basal cells. The *G. rugosa* complex is in need of taxonomic revision (Wang et al.. 2005), and may possibly include overlooked species as well as some of the species currently considered to be conspecific. Testing of gametophytes and tetrasporophytes of Gulf of California *G. rugosa* will help elucidate their relationship to Caribbean *G. rugosa* (type locality: Jamaica) and the western Pacific *G. rugosa* of Wang et al. (2005).

Tricleocarpa Huisman et Borowitzka

Tricleocarpa Huisman et Borowitzka, 1990:164.

The gametophyte and tetrasporophyte phases of *Tricleocarpa* species are heteromorphic. Tetrasporophytes are minute, branched, *Acrochaetium*-like filaments (not yet discovered in the Gulf of California), and gametophytes are macroscopic, erect, calcified, subdichotomously branched fronds (proliferations rare). Axes of gametophytes are terete with a smooth surface devoid of hairs (glabrous) or hirsute only in the basal portion, attached by discoid holdfasts. The medulla is composed of branched longitudinal filaments. The cortex is of 3 or 4 cell layers, with cortical filament cells that remain separate (i.e., not fusing with adjacent cells). Cortical filaments are dichotomously branched, with inner layers of large, nearly colorless cells, and outer layers of progressively smaller pigmented cells.

Gametophytes may be dioecious or monoecious. Carpogonial branches are 3-celled and are borne in the position of normal vegetative filaments; prior to fertilization the basal cell of the carpogonial branch produces 4–5 branches that contribute to the pericarp of the immersed cystocarp, whereas the hypogynous cell cuts off 3–4 nutritive branches. The gonimoblast initials originate directly from the fertilized carpogonium and grow laterally along the base of the pericarp, or in some species also contribute to the walls of the pericarp as they intermingle with filaments of the pericarp (Huisman, 2006). Carposporangia are borne terminally on gonimoblast filaments that extend toward the center of the cystocarpic cavity. Pericarp filaments can extend from the cystocarp wall to produce paraphyses that may or may not intermingle with the gonimoblast filaments. Cystocarps are immersed within the outer medulla of axes and are ostiolate. Spermatangia are formed in cavities within the axes.

Tetrasporophytes produce cruciately divided tetrasporangia that are borne laterally or terminally on *Acrochaetium*-like filaments (Magruder, 1984, as *Galaxaura oblongata*; Huisman and Borowitzka, 1990).

Two species of *Tricleocarpa* occur in the northern Gulf of California.

KEY TO THE SPECIES OF *TRICLEOCARPA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes 0.8–1.3 mm in diameter; cystocarp cavity with well-developed sterile paraphyses that intermingle with gonimoblast; gonimoblast filaments line the pericarp and protrude into the cystocarpic cavity from all around the pericarp . . . . *T. cylindrica*

1b. Axes 1.5–2.0 mm in diameter; cystocarp cavity with poorly developed sterile paraphyses that do not intermingling with gonimoblast; gonimoblast filaments grow laterally along the base of the cystocarp cavity . . . . *T. fragilis*

Tricleocarpa cylindrica (J. Ellis et Solander) Huisman et Borowitzka

FIGURE 28

Corallina cylindrica J. Ellis et Solander, 1786:114, pl. 22: fig. 4.

Tricleocarpa cylindrica (J. Ellis et Solander) Huisman et Borowitzka, 1990:164, figs. 40–45, 50–52; Dreckmann, 1991:33; Yoshida, 1998: 508, fig. 3-91I–K; Mendoza-González and Mateo-Cid, 1999:40, figs. 2–5; Abbott, 1999:73, fig. 10A; Huisman, 2006:25, fig. 9A–E; Mateo-Cid et al., 2006:55; Y.-P. Lee, 2008:221, figs. A–E; Bernecker and Wehrtmann, 2009:226; Fernández-García et al., 2011:65.

Galaxaura cylindrica (J. Ellis et Solander) J. V. Lamouroux, 1821:22, pl. 22: fig. 4; Itono, 1977b:14, figs. 17, 19, 37; Salcedo-Martínez et al., 1988:83.

Galaxaura fastigiata Decaisne, 1842b:116; Tanaka, 1936:157, figs. 20, 21, pl. 37: fig. 2; Dawson, 1944a:258; Svedelius, 1945:28, figs. 14–16, pls. 4, 5, pl. 6: fig. 2; Dawson, 1953a:50, pl. 20: fig. 2; 1959a:20; 1961b:407; 1966a:15; Itono, 1977b:12, figs. 15, 34; Pedroche and González-González, 1981:66; Stewart and Stewart, 1984:142; Norris, 1985d:212; León-Tejera et al., 1993:200; González-González et al., 1996:202.

Galaxaura oblongata sensu Taylor, 1945:143; Chou, 1947:7 [both in part, with reference to Pacific Mexico material; non *Galaxaura oblongata* (Ellis et Solander) Lamouroux, 1816:262, which is *Tricleocarpa fragilis* (Linnaeus) Huisman et R. A.Townsend, 1993:100].

Thalli forming clumps of erect, terete, subdichotomously branched fronds; up to 6 cm tall, axes 0.8–1.3 mm in diameter; pale pink to purple-gray, surface glabrous, sometimes with faint annulations; attached below by a small discoid holdfast. Calcification heavy, restricted to cortical layers; usually fractured at nodes/branching points (thus not truly segmented), causing internodes to assume tubular appearance. Medulla composed of longitudinal filaments (mostly 5–20 µm in diameter), giving rise to dichotomously branched cortical filaments. Cortex 3–4 layers thick; inner layers of large rotund cells, slightly longer than wide (18–35 µm in diameter), fusions absent between adjacent cells; outer layers of progressively smaller pigmented round cells; outer cells in surface view 5–6 sided, 9–20 µm wide

Reproduction as for genus. Gametophytes usually dioecious. Gonimoblast filaments lining the pericarp and projecting into the cystocarpic cavity from all directions; sterile paraphyses well developed and projecting into the cavity as well, intermingling with gonimoblast filaments (Huisman, 2006).

HABITAT. On rocks, mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena; Nayarit to Jalisco; Isla María Madre (Islas Marías; Islas Tres Marías). Eastern Pacific: Isla Guadalupe; Bahía Sebastián Vizcaíno, Baja California Sur; Guererro to Oaxaca; El Salvador; Nicaragua; Costa Rica; Peru.

TYPE LOCALITY. West Indies (Ellis and Solander, 1786); type lost, lectotype illustration of Ellis and Solander (1786: pl. 22: fig. 4) selected by Papenfuss et al. (1982:416, fig. 26).

REMARKS. Gulf of California specimens are tentatively referred to *Tricleocarpa cylindrica*, and their identification requires more investigation. In their phylogenetic study,

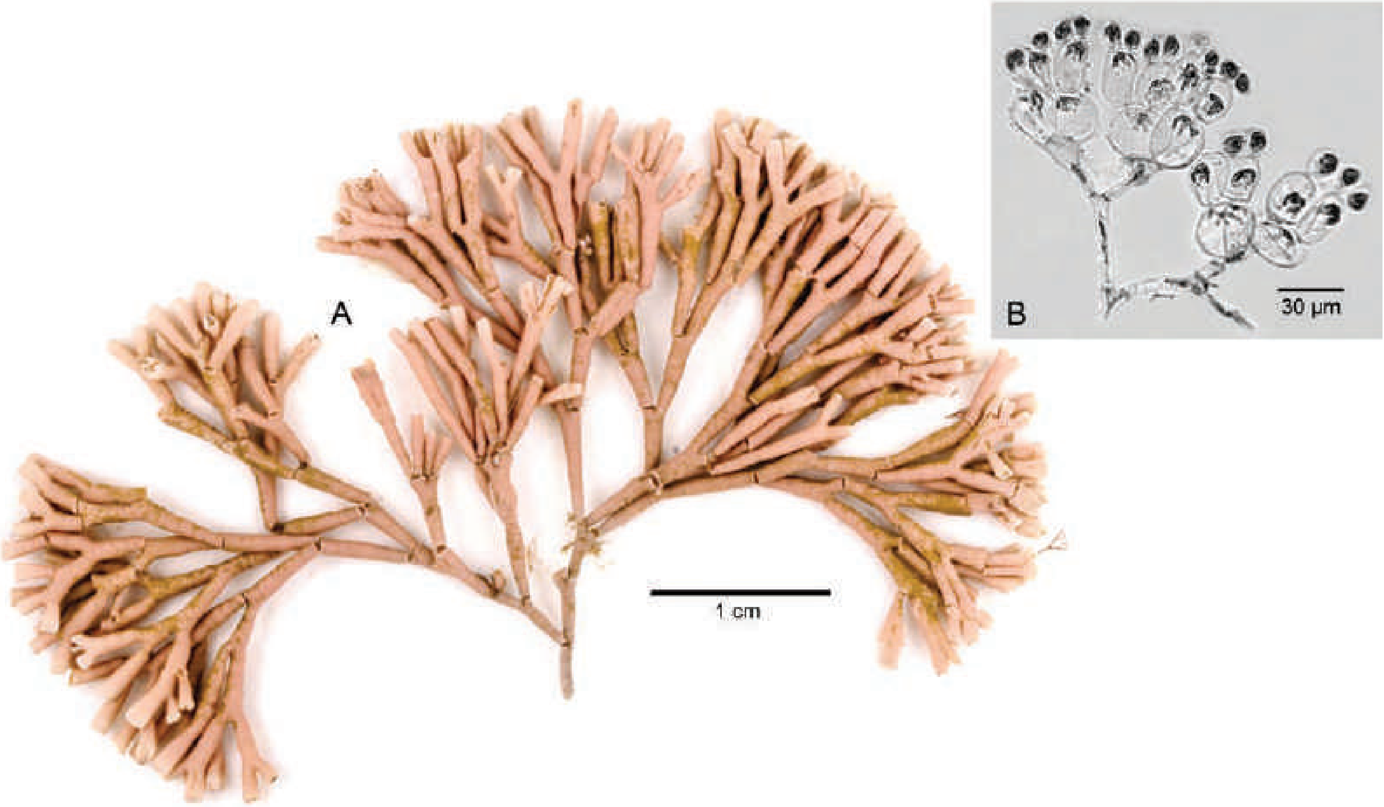

FIGURE 28. Gametophytes of *Tricleocarpa cylindrica*: A. One frond from a clump, surface smooth and heavily calcified (*JN-5955*, US Alg. Coll.-159165). B. Cortical filaments separated out from the cortex, showing adjacent large inner cortical cells not fusing, and outer layer of smaller pigmented cells (*JN-3078*, US Alg. Coll.-8699).

Wiriyadamrikul et al. (2013: fig. 1) found those from the Caribbean Sea (Western Atlantic) and some from southeast Asia and Hawaii (Western and Central Pacific) to be *T. cylindrica*. However a northern Gulf of California "*T. cylindrica*" from Guaymas, Sonora (AY688015; Wang et al., 2005) was revealed to be different from *T. cylindrica* and *T. fragilis*. Wiriyadamrikul et al. (2013) suggested the Guaymas specimen might be "*Galaxaura constipata* Kjellman," a Western Atlantic species described from Veracruz (Gulf of Mexico), and one of several members of *Galaxaura* sect. *Eugalaxaura* Descaine (1842b) recognized by Kjellmann (1900). Wiriyadamrikul et al. (2014: fig. 1), however, later referred to the Guaymas specimen (AY688015) as "*T. cylindrica.*"

***Tricleocarpa fragilis* (Linnaeus) Huisman et R. A. Townsend**

Eschara fragilis Linnaeus, 1758:805.

Tricleocarpa fragilis (Linnaeus) Huisman et R. A. Townsend, 1993:100, fig. 1 [lectotype]; Yoshida, 1998:508; Abbott, 1999:74, fig. 10B–G; L. Aguilar-Rosas et al., 2000:130; Huisman, 2006:28, figs. 8B, 9F–H; Fernández-García et al., 2011:65.

Dichotomaria fragilis Lamarck, 1816:145.

Galaxaura fragilis (Linnaeus) Lamouroux ex Decaisne, 1842b:116.

Corallina oblongata J. Ellis et Solander, 1786:114, pl. 22: fig. 1.

Galaxaura oblongata (J. Ellis et Solander) J. V. Lamouroux, 1816:262; Tseng, 1941:93; Chou, 1947:7, pl. 2: figs. 1–16, pl. 3: figs. 1–14, pl. 10: figs. 1, 2; Itono, 1977b:13, figs. 18, 36; Papenfuss et al., 1982:416; Zhou and Chen, 1983:80, pl. 1: fig.1; Tseng, 1983:60, pl. 33: fig. 1; Mateo-Cid and Mendoza-González, 1992:19; Mateo-Cid et al., 1993:47; Mendoza-González et al., 1994:105; Mateo-Cid et al., 2000:63.

Tricleocarpa oblongata (J. Ellis et Solander) Huisman et Borowitzka, 1990:168, figs. 46–49, 53–56; Dreckmann, 1991:33; Bula-Meyer, 1995:33; Cruz-Ayala et al., 2001:191.

Gametophytes forming clumps, up to 6 cm tall; branches terete, 1.5–2.0 mm in diameter; calcified, pale pink to gray, subdichotomously branched; attached by discoid holdfast. Axes segmented, segments mostly 6–10 mm long, slightly rounded on upper and lower ends; surface glabrous (without hairs). Medulla of slender filaments, mostly 6–8 µm in diameter, giving rise to cortical filaments. Cortex of 3–4 layers of cells; inner cortical cells large, colorless, 20–30 µm in diameter; outer surface cells, pigmented, more or less globose, 8–15 µm in diameter.

Tetrasporophytes not known in the Gulf of California. Gametophytes dioecious or monoecious. Basal cell of the carpogonial branch with 4–5 branches; hypogynous cell with 3–4 nutritive branches. Cystocarps globose to subglobose, 400–500 µm in diameter; cystocarp cavity with gonimoblast filaments lining base of pericarp; and paraphyses poorly developed, 3- to 4-celled, on inner side of pericarp (after Huisman, 2006). Carposporangia 45–65 µm long and 25–40 µm in diameter. Spermatangia borne in spherical cavities.

HABITAT. On rocks, tidal platforms, and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: El Faro de San Felipe to Bahía Concepción; Punta Arena to Bahía de La Paz; Mazatlán, Sinaloa.

TYPE LOCALITY. "Oceano Americano" (Linnaeus, 1758); Jamaica (see Huisman and Townsend, 1993).

REMARKS. Presence of *Tricleocarpa fragilis* in the Eastern Pacific of North America, including the Gulf of California, requires confirmation (Wynne, 2011;Wiriyadamrikul et al., 2013). Culture studies by Magruder (1984, as "*Galaxaura oblongata*") showed the tetrasporophyte in the life history of Hawaiian *T. fragilis* was heteromorphic, a minute "*Acrochaetium*-like" thallus that produced cruciately divided tetrasporangia, borne laterally and terminally on the uniseriate filaments.

LIAGORACEAE

Liagoraceae Kützing, 1843:321

Gametophytes of this family are usually erect, with axes that are terete or slightly compressed, and sparingly to abundantly branched. Thalli are dichotomously, pinnately to irregularly branched; or with a percurrent axes and lateral branches. The thalli can be tough and chalky to gelatinous or mucilaginous in texture, and most are calcified to some degree, with calcium carbonate in the mineral form aragonite or uncalcified. All are multiaxial in structure. The medulla is a core of longitudinally aligned colorless filaments of similar or assorted diameters, from which the anticlinal assimilatory filaments radiate outward to form a loosely arranged cortex, not forming a continuous surface layer. Assimilatory filaments are dichotomously to polychotomously branched and are composed of pigmented cells that can vary in shape and size throughout the length of the filament.

Life history, where known, is a alternation of heteromorphic generations. The tetrasporophytes are microscopic filaments that bear cruciately divided tetrasporangia (known only from culture studies). Asexual reproduction is by monosporangia in some genera but is unknown in most genera. Gametophytes are typically dioecious, but some are monoecious, or occasionally, both types occur in a species. The carpogonial branch is three to many celled, straight or curved, and usually borne on an assimilatory filament. Carpogonial branches may be compound. The hypogynous cell is typically naked (i.e., nutritive or sterile branches or cells are absent). Gonimoblast filaments develop from the fertilized carpogonium (zygote) and are branched and compact in some or somewhat diffuse to loose in others, intermingling with assimilatory filaments. Terminal cells of the gonimoblast filaments produce carposporangia, or nearly all cells become carposporangia. Carposporophytes develop within the cortex among the assimilatory filaments, either with associated sterile filaments in various arrangements or without sterile filaments. Carposporangia are undivided or quadripartite ("carpotetrasporangia"). Spermatangia are borne in clusters at or near the tips of the assimilatory filaments or in whorls on midcortical cells.

REMARKS. One genus, *Dermonema* Harvey ex Heydrich (1894), is reported in the southern Gulf, with *D. virens* (J. Agardh) Pedroche et Ávila-Ortiz (1996; basionym: *Nemalion virens* J. Agardh, 1847) from Isla San Ildefonso, Bahía de La Paz to Cabeza Ballena, and Mazatlán (Dawson, 1953b, as *N. virens*;

Huerta-Múzquiz and Mendoza-González, 1985, as *D. frappieri* (Montagne et Millardet) Børgesen; Pedroche and Ávila-Ortiz, 1996). Originally described from Oaxaca, *D. virens* is also recorded elsewhere in Pacific Mexico from Islas Revillagigedo (Serviere-Zaragoza et al., 2007) and Jalisco to Oaxaca. A second species, the Japanese *D. pulvinatum* (Grunow et Holmes) K.-C. Fan (1962; basionym: *Nemalion pulvinatum* Grunow et Holmes in Holmes, 1896) was reported from Bahía Agua Verde (Dawson, 1953b, as *N. pulvinatum*) and later listed without comment from Bahía de Loreto (CONANP, 2002, as *N. pulvinatum*).

Three genera of the Liagoraceae are known in the northern Gulf of California.

KEY TO THE GENERA OF LIAGORACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Gulf thalli moderately to heavily calcified throughout, coarse grained (mealy, ropy) in texture; medullary filaments relatively few, of large cells, 25–150 (most >40) µm in diameter; spermatangia forming dense, cap-like heads at ends of assimilatory filaments . . . . *Ganonema*

1b. Thalli lightly to moderately calcified, not mealy in texture; medullary filaments of cells, 5.0–50 µm in diameter, with thinner cells more numerous; spermatangia not as cap-like 2

2a. Assimilatory filaments dichotomously branched; cystocarp borne on distinct elongated stalk cell (fusion cell including cells of carpogonial branch and many cells of the bearing cortical filament); 2 discrete clusters of filaments associated with cystocarp, a distal cluster of gonimoblasts, and below a subtending cluster of sterile filaments . . . . *Izziella*

2b. Assimilatory filaments di-, tri- or polychotomously branched; cystocarp not borne on an elongated stalk (fusion cell may be present but does not include numerous cells of the bearing cortical filament); cystocarp a single cluster that includes both gonimoblast and involucral filaments, without a separate cluster beneath it . . . . *Liagora*

Ganonema K.-C. Fan et Y.-C. Wang

Ganonema K.-C. Fan et Y.-C. Wang, 1974:492; Huisman and Kraft, 1994:76 [emended description].

Algae are erect, calcified or uncalcified, with a texture ranging from solid and chalky to soft and mucilaginous, and attach to the substratum by a discoid holdfast. Axes are terete, and dichotomously to irregularly branched or with percurrent axes and frequent short lateral branches. Construction is multiaxial, with a central core of longitudinally aligned medullary filaments that bear lateral radiating assimilatory filaments to form cortical fascicles on distinctive isodiametric basal cells. Mature medullary filaments are relatively wide, usually >40 µm in diameter. Assimilatory filaments of cylindrical, barrel-shaped or ovoid cells are sparingly or much branched, generally dichotomous, but are often unbranched for a number of cells near thallus surface. Adventitious rhizoid-like filaments, commonly issued by lower cells of the assimilatory filaments and basal cells, descend to join the medulla and then produce additional cortical laterals; these are generally simple or less robust than original cortical fascicles. Outer cortical cells are occasionally with terminal hairs or glandular cells.

Life histories are heteromorphic but not known in all species. Tetrasporangia (where known) are developed on a filamentous tetrasporophyte. Gametophytes are monoecious or dioecious. Carpogonial branches are 3- to 6-celled, straight to slightly curved, and borne in positions of vegetative cortical laterals and on subsidiary cortical and rhizoid-like filaments. Gonimoblast develops directly from the fertilized carpogonium, initially by a transverse division, eventually forming a compact cluster of gonimoblast filaments with terminal carposporangia. Cell fusions are typically lacking. Carposporangia either undivided or quadripartite. Postfertilization filaments arise from cells in the vicinity of the carpogonial branch, including those of nearby branches and those above and below the supporting cell (rarely the supporting cell itself) subtending or forming a partial involucre around the gonimoblast. Spermatangia are in dense, dendroid clusters, arising on short specialized branches issued from apical and subapical cells of the assimilatory filaments.

Ganonema is represented by one species that is apparently restricted to the warmer waters of the Gulf of California.

Ganonema farinosum (J. V. Lamouroux) K.-C. Fan et Y.-C. Wang

FIGURE 29

Liagora farinosa J. V. Lamouroux, 1816:240; Yamada, 1938a:23, figs. 15, 16, pls. 8–10; Dawson, 1953a:42, pl. 2: figs. 9–12, pl. 14: fig. 1; 1954b:415, figs. 25d, 26; 1959a:5, 20; 1961b:406; Stewart and Stewart, 1984:142; Huerta-Múzquiz and Mendoza-González, 1985:48; Mendoza-González and Mateo-Cid, 1985:30; Sánchez-Rodríguez et al., 1989:41; Abbott, 1990a:122, fig. 23 [type specimen]; Dreckmann, 1991:31; González-González et al., 1996:322; Silva et al., 1996b:232 [as "*L. farinosa* f. *pinnatiramosa* Yamada"]; Cruz-Ayala et al., 2001:191.

Ganonema farinosum (J. V. Lamouroux) K.-C. Fan et Y.-C. Wang, 1974:492, pl. 94: figs. 1–3, 6, 7, pl. 95: figs. 1–6; Tseng, 1983:53, pl. 29: fig. 2; Huisman and Kraft, 1994:83; Yoshida, 1998:511; Abbott, 1999:77, fig. 11A–G; Huisman, 2000:30; Abbott et al., 2002:310, fig. 21; Huisman, 2002:821, figs. 118–123; Huisman et al., 2004a:299, figs. 1–12; Huisman, 2006:38, figs. 13E–H, pl. 10.

Thalli erect to 18(–25) cm tall, of terete axes and branches, mostly 1.0–1.6(–2.5) mm in diameter, moderately to heavily calcified, whitish purple to whitish reddish brown in color, coarse grained, mealy in texture; branching variable, generally dichotomous but may be pinnately to irregularly branched and frequently with lateral proliferations; attached by a small discoid holdfast. Multiaxial in construction; medullary filaments longitudinally aligned, broad (up to 150 µm in diameter). Anticlinal assimilatory (cortical) filaments extend to 450 µm long, outer

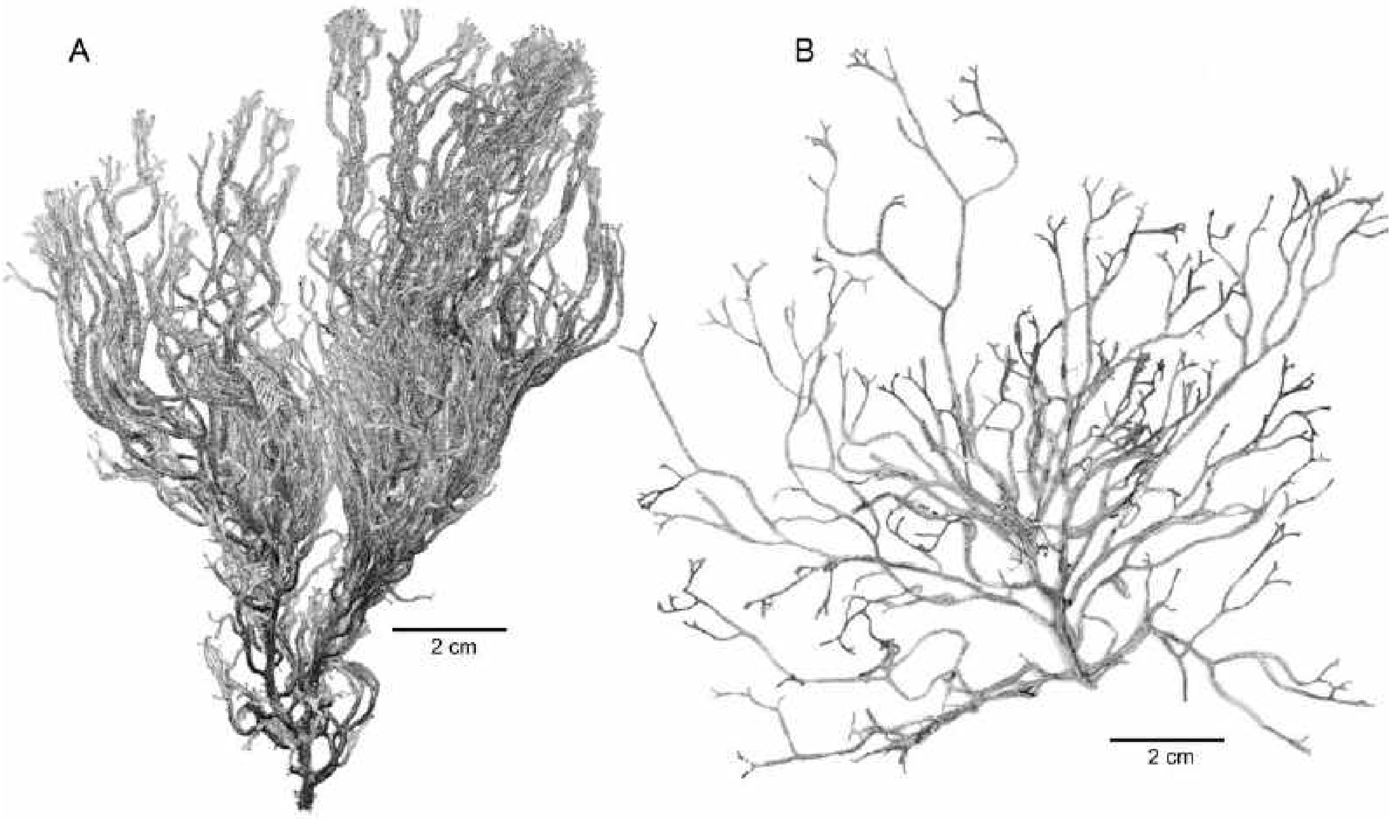

FIGURE 29. *Ganonema farinosum*: A, B. Habit of gametophytes (A, *EYD-18914*, US Alg. Coll.-8101; B, *JN-7173*, US Alg. Coll.-160431).

filament cells cylindrical, 19–22 µm in diameter, cell walls not indented at joints. Cortical fascicles with isodiametric basal cells. Adventitious rhizoidal-like filaments, issued by lower and basal cells of cortical fascicles, join and form part of the medulla and produce additional assimilatory filaments.

Tetrasporophyte unknown in the Gulf of California. Gametophytes usually dioecious. Carpogonial branches 4- to 5-celled; straight to slightly curved, borne laterally on proximal portions of assimilatory filaments. After fertilization, the zygote divides transversely, and gonimoblasts develop from the distal cell of the initial division. No fusion of carpogonial branch cells occurs. Gonimoblast compact with branched radiating filaments, carposporangia terminal on gonimoblast filaments. Some involucral filaments loosely surround the gonimoblasts; carposporangia elongate, in a compact cluster on short, branched gonimoblast filaments. Spermatangia forming dense capitate heads near tips of assimilatory filaments.

HABITAT. On rocks; shallow subtidal, down to 14 m depths.

DISTRIBUTION. Gulf of California: Isla San Diego to Punta San Evaristo; Bahía de La Paz to Punta Los Frailes, Baja California Sur. Eastern Pacific: Isla Guadalupe (off Baja California); Bahía San Sebastian Vizcaíno (northern Baja California) to Bahía Magdalena (Baja California Sur); Rocas Alijos. Central Pacific: Hawaiian Islands. Western Pacific: China; Taiwan; Vietnam; Japan.

TYPE LOCALITY. near Suez, Egypt, Red Sea.

REMARKS. Thus far, *Ganonema farinosum* has been collected in the southern Gulf of California but is likely to be found in the northern Gulf as well. The mealy, coarse-grained (farinose) texture, cylindrical outer cells of its assimilatory filaments, and compound cap-like spermatangial branches are diagnostic features of this species.

***Izziella* Doty**

Izziella Doty, 1978:34; Huisman and Schils, 2002:244, tbl. 1.

Thalli are mucilaginous, lightly to moderately calcified, and variable in color (typically a whitish green-gray tinged pink). Percurrent primary axes bear indeterminate lateral branches, and both the axes and lateral branches in turn bear further orders of short lateral branches or become irregularly branched. Thalli are multiaxial, with center medulla of colorless, longitudinally aligned filaments (15–50 µm in diameter), bearing anticlinal, pigmented, assimilatory filaments. Assimilatory filaments are sparsely, dichotomously branched. Basal cells of the assimilatory filaments issue rhizoidal filaments that add to the core of medullary filaments; these also adventitiously produce additional assimilatory filaments, although those produced are simple or less robust. Cells of assimilatory filaments have a central pyrenoid.

Carpogonial branches are 3–4(–5)-celled, curved, and borne laterally off an assimilatory filament cell. A mature cystocarp has two clusters of filaments: the distal cluster of gonimoblast filaments with the carposporangia, forming a compact whorl around a short longitudinal core of cells that arise from the divided zygote, and, below that, a separate, subtending cluster of sterile filaments arising from cells to both sides of the carpogonial branch's supporting cell. An extensive fusion cell is formed that includes cells of the carpogonial branch and many cells of the assimilatory filament bearing the carpogonial branch. The fusion cell is part of the long stalk that bears the gonimoblast. Spermatangia are borne on spermatangial parent cells on terminal and subterminal cells of the assimilatory filaments.

REMARKS. The reproductive characteristics differentiating *Izziella* are its cystocarp borne on an elongated stalk, which is composed of a fusion cell incorporating carpogonial branch cells and many cells of the bearing assimilatory filament, and the cystocarp having two distinct clusters of filaments, an upper fertile cluster of gonimoblast filaments and carposporangia and a second cluster of sterile filaments below.

Izziella is represented in the northern Gulf of California by one of its four species.

Izziella orientalis (J. Agardh) Huisman et Schils

Liagora orientalis J. Agardh, 1896:99; Yamada, 1938a:4 [in part], fig. 1A–C [only], pl. 1; 1944:18; Dawson, 1953a:40, pl. 17: fig. 1; 1954b:415, fig. 27b; 1961b:406; Abbott, 1990b:314, figs. 7 (lectotype), 8–11; Rocha-Ramírez and Siqueiros-Beltrones, 1991:32; González-González et al., 1996:237; Riosmena-Rodríguez and Paul-Chávez, 1997:70; Abbott, 1999:87, figs. 14F–J.

Izziella orientalis (J. Agardh) Huisman et Schils, 2002:247, figs. 1–9, 17, 18; Mateo-Cid and Mendoza-González, 2004:78, figs. 1–19.

Izziella abbottiae Doty, 1978:34 [as "*abbottae*"], fig. 10.

Liagora tanakae I. A. Abbott, 1976:33 [as "*L. tanakai*"], figs. 1–5.

Algae of 1 to a few terete branched axes, soft and lubricous, lightly to moderately calcified, whitish in color, up to 15 cm tall; attached by a small discoid holdfast. Axes 3–5 mm in diameter, branching more or less pinnate to irregularly pinnate, multifariously arranged; branches mostly 2–3 mm in diameter, branched; upper branches about 1.0 mm in diameter. Medullary filaments of elongated cells, 10–35(–45) μm in diameter. Rhizoidal-like filaments, produced by basal portions of assimilatory filaments, become part of the medulla. Assimilatory filaments moniliform, dichotomously branched up to 5 orders, 250–350 μm long; basal cells narrow, cylindrical, elongated, 21–35(–60) μm long, 6–11 μm in diameter; outer cells clavate to ovate, 25–30 μm long, 20–25 μm in diameter; terminal cells to 15 μm in diameter, often with terminal hyaline hairs. Cells of assimilatory filaments with lobed plastids containing a large central pyrenoid.

Asexual reproduction is not known. Gametophytes dioecious. Carpogonial branch 3- to 5-celled, somewhat curved, and borne laterally off a proximal cell of assimilatory filament. After fertilization, zygote divides transversely and the distal cell undergoes further divisions that develop gonimoblast filaments, while the proximal cell of the initial division remains undivided. Gonimoblast compact, subglobose cluster, 110–150 μm in diameter, gonimoblast filaments bearing terminal carposporangia. Gonimoblast without a surrounding involucre; on cells distal and proximal to the the supporting cell below, a smaller cluster of short, sterile filaments develops. An extensive fusion cell is formed from cells of the carpogonial branch and many cells of the bearing assimilatory filament. The fusion cell lengthens, becomes hyaline, and appears as an elongated stalk bearing the gonimoblast. Spermatangia in small clusters of 2–4; developed from spermatangial parent cells on apical and subapical cells of assimilatory filaments; spermatia, 2–3 μm in diameter.

HABITAT. On rocks and in tide pools; mid to low intertidal.

TYPE LOCALITY. "Ceylon" (Sri Lanka) (J. Agardh, 1896).

DISTRIBUTION. Gulf of California: Ensenada Lalo, Sonora; Bahía de La Paz; Nayarit to Jalisco. Eastern Pacific: Punta Malarrimo (Bahía Sebastian Vizcaino) to Punta Conejo, Baja California Sur; Michoacán to Guerrero; Ecuador. Central Pacific: Hawaiian Islands. Western Pacific: Taiwan; China; Japan; Vietnam.

REMARKS. Thalli of *Izziella orientalis* from mainland Pacific Mexico have been reported up to 51 cm tall (Mateo-Cid and Mendoza-González, 2004), much larger than those found in the Gulf of California.

Liagora J. V. Lamouroux

Liagora J. V. Lamouroux, 1812:185.

Gametangial algae are erect above a discoid holdfast, and lightly to heavily calcified, with a texture from firm to soft and mucilaginous. Axes and branches are terete to somewhat compressed and regularly dichotomous, pinnate, or irregularly branched. Thalli are multiaxial in construction, with a medulla composed of colorless, longitudinally aligned filaments that bear pigmented, anticlinal assimilatory filaments that form a loose cortex. Assimilatory filaments are dichotomously to trichotomously branched. Narrow rhizoid-like filaments often develop from the lower cells of the assimilatory filaments and function as medullary filaments and may issue additional assimilatory filaments. Photosynthetic cells of the assimilatory filaments (cortical fascicles) contain a single large parietal plastid and usually 1 pyrenoid. Outer cortical cells sometimes may bear terminal hairs or glandular cells.

The tetrasporic phase in the life history is heteromorphic, where known, consisting of uniseriate filaments that develop tetrasporangia. Monosporangia are reported in some species, borne on the tips of assimilatory filaments. Gametophytes of most species are dioecious, but some species are monoecious, and other species may be both monoecious and dioecious. Carpogonial branches are generally 3- to 6-celled, with only one species issuing (post-fertilization) short sterile filaments from the basal cell (i.e., *L. tsengii* Husiman et M. J. Wynne, 1999). Carpogonial branches are borne laterally on lower to middle cortical cells. Fusing cells, although lacking or unknown in many species, are reported in some, with fusion cells formed from the cells of the carpogonial branch and rarely include the supporting or adjacent cells. Gonimoblasts develop directly from the distal cell of the initial transverse division of the fertilized carpogonium and form a diffuse or compact cluster of gonimoblast filaments that terminate in a single carposporangium or a short chain of carposporangia. Involucral filaments develop from the cells in the vicinity of the carpogonial branch, and either remain separate or become entwined with the gonimoblast filaments. Carposporangia in most species produce a simple, undivided carpospore, but some divide and produce carpotetraspores (4 carpospores). Spermatangia develop either singularly or in clusters on the spermatangial parent cells on the outer cortical cells.

REMARKS. Two species have been reported in the southern Gulf from Bahía de La Paz: *Liagora abbottiae* E. Y. Dawson (1953b:41, pl. 2: figs. 6–8, pl. 15: fig. 2) by Huerta-Múzquiz and Mendoza-González (1985), a Pacific Baja California species described from Punta Santa Rosaliita (note that the locality was incorrectly given as “Punta Santa Rosalía” by Dawson, 1953b), and *L. californica* Zeh (1912) by Riosmena-Rodríguez et al. (1998) and Cruz-Ayala et al. (2001), a species described from Santa Catalina Island (California Channel Islands) and known from southern California to Baja California Sur (Dawson, 1953a; Abbott and Hollenberg, 1976; Castañeda-Fernández de Lara et al., 2010).

Two species of *Liagora* are found in the northern Gulf of California.

KEY TO THE SPECIES OF *LIAGORA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli irregularly dichotomously branched, branches with short lateral branchlets; dioecious; gonimoblast surrounded by prominent, long, slender involucral filaments . . . . **L. magniinvolucra**

1b. Thalli regularly dichotomously branched, branches sometimes with proliferous short lateral branchlets; monoecious; gonimoblast surrounded by involucral filaments but not long and prominent . . . . **L. ceranoides**

Liagora ceranoides J. V. Lamouroux

FIGURE 30

Liagora ceranoides J. V. Lamouroux, 1816:239; Yamada, 1938a:20, pl. 6; Abbott, 1945:156, figs. 8, 9; Taylor, 1945:135; Dawson, 1957c:13 [tentatively]; 1961b:406; Abbott, 1990a:118; Dreckmann, 1991:31; González-González et al., 1996:322; Abbott, 1999:84, fig. 13I–M; Cruz-Ayala et al., 2001:191; Mateo-Cid et al., 2006:55; Bernecker, 2009:CD-Rom p. 61; Fernández-García et al., 2011:62.

Thalli of 1 to a few cylindrical axes, calcification moderate (more or less even throughout), whitish to pale rose in color, firm with a gelatinous texture, to 4 cm tall, attached by a small discoid holdfast. Axes repeatedly, subdichotomously branched from near base; main axes to 1 mm diameter; with or without proliferous short lateral branchlets. Assimilatory filaments moniliform, branching at wide angles, dichotomously to trichotomously branched; outer cells to about 10 μm diameter.

Asexual reproduction unknown. Gametophytes monoecious. Carpogonial branch curved, of 3–5 cells. Gonimoblast a cluster of branched filaments bearing carposporangia terminally and surrounded by a filamentous involucre. Involucral filaments mostly unbranched and slender. Spermatangia in small clusters on outer cortical cells; borne terminally on spermatangial parent cells.

HABITAT. On sides of rocks and crevices and in tide pools; low intertidal and also collected in drift.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía de La Paz. Eastern Pacific: Costa Rica. Central Pacific: Hawaiian Islands. Western Pacific: Japan; China; Taiwan; Vietnam.

TYPE LOCALITY. St. Thomas, U.S. Virgin Islands, Caribbean Sea.

REMARKS. Previously unknown in the northern Gulf, drift collections from Playa Las Conchas (Playa Estación), Puerto Peñasco (*JN-3195,* US Alg. Coll.), establish *Liagora ceranoides* in the northern Gulf of California. The branches of the Gulf specimens have short lateral branchlets and seem closest

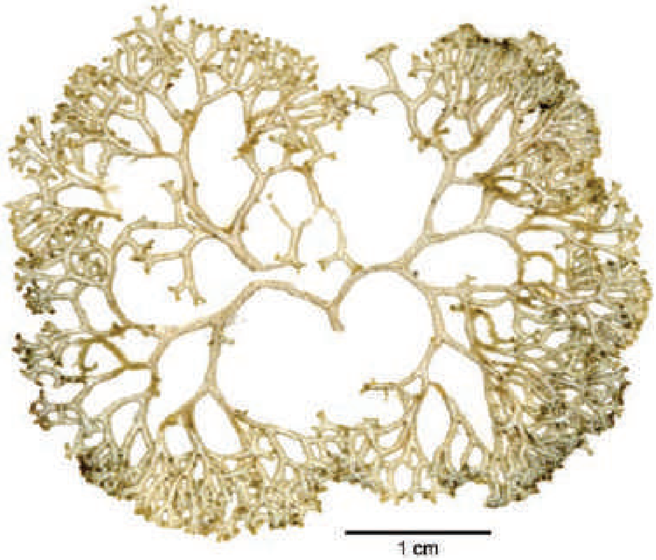

FIGURE 30. *Liagora ceranoides:* Habit of a gametophyte (*JN-3195*, US Alg. Coll.-160430).

to *L. ceranoides* f. *pulverulenta* (C. Agardh) Yamada (1938a; =*Liagora ceranoides* var. *pulverulenta* (C. Agardh) Børgesen, 1942; basionym: *Liagora pulverulenta* C. Agardh, 1822. Another form, *L. ceranoides* f. *leprosa* (J. Agardh) Yamada (1938a; basionym: *Liagora leprosa* J. Agardh, 1847) has been recorded from Pacific Baja California from Punta Malarrimo, Bahía San Sebastián Vizcaino and Isla Guadalupe (Dawson, 1953a; Stewart and Stewart, 1984). *Liagora ceranoides* is reportedly widespread in tropical to subtropical seas (Abbott, 1990a, 1999), including Australia (Huisman, 2006).

Liagora magniinvolucra E. Y. Dawson

FIGURE 31

Liagora magniinvolucra E. Y. Dawson, 1953a:39, pl. 3: figs. 1–11, pl. 16: fig. 2; 1959a:20; 1961b:406; 1966a:14; 1966b:59; Huerta-Múzquiz and Mendoza-González, 1985:48; González-González et al., 1996:237; CONANP, 2002:141; Mateo-Cid et al., 2006:50.

Thalli of 1 to a few cylindrical axes, chalky whitish in color, up to 15 cm tall, arising from a small discoid holdfast. Axes dichotomously branched, with irregularly alternate, short branchlets, to 3 mm long. Thalli soft, the calcification mainly on surface. Assimilatory filaments, more or less moniliform; inner portions with long fusiform cells; outer portions with ovate to subclavate cells, 7–12 µm diameter.

Asexual reproduction unknown. Gametophytes dioecious. Cystocarp a hemispherical cluster of branched filaments, with carposporangia borne terminally, and surrounded by an involucre of long, slender ascending filaments. Spermatangia in clusters at ends of assimilatory filaments.

Habitat. On sides of rocks; mid to low intertidal.

Distribution. Gulf of California: Playa Arenosa, Puerto Peñasco; Isla de San Diego to Cabo Pulmo.

Type Locality. Cabeza Ballena, Baja California Sur, Gulf of California, Mexico.

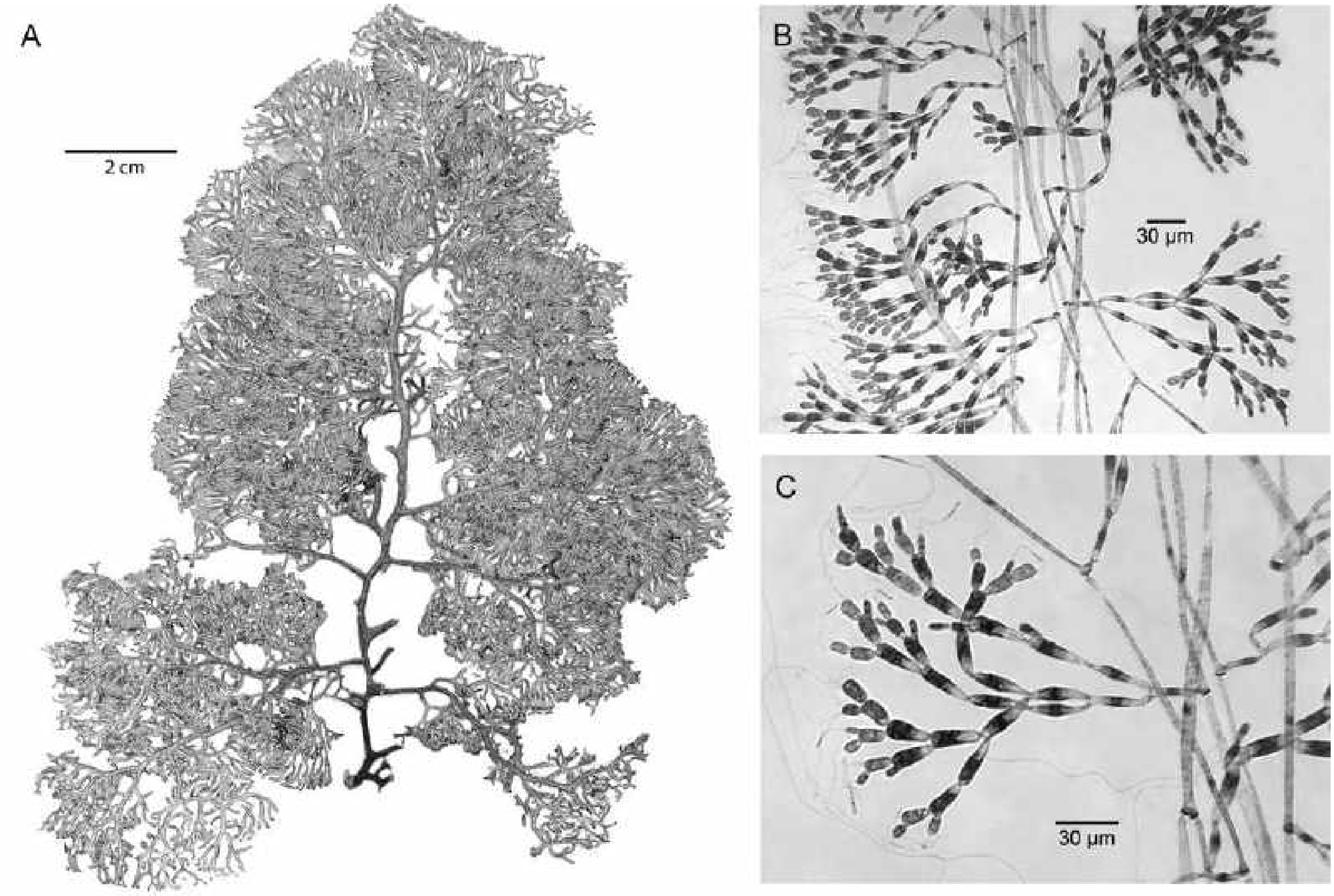

FIGURE 31. *Liagora magniinvolucra*: A. Habit of gametophyte (*R.D. Staker, s.n.*, US Alg. Coll.-204280). B, C. Slender longitudinal medullary filaments bearing subdichotomously branched anticlinal assimilatory filaments that form the cortex (*JN-4046*, US Alg. Coll. microscope slide 4283).

SCINAIACEAE

Scinaiaceae Huisman, J. T. Harper et G. W. Saunders, 2004b:228.

Family members are uncalcified, with markedly heteromorphic life history phases (where known). Sporophytes can be minute, uniseriate branched filaments, as discovered in the life cycles of *Scinaia* and *Gloiophloea* J. Agardh (1872), or crustose thalli, as found in *Nothogenia* Montagne (1843); both kinds of sporophytes produce tetrasporangia. Gametophytes are erect, macrothalli with axes ranging from terete to compressed or somewhat flattened, that are usually dichotomously or subdichotomously branched, rarely trichotomously or irregularly branched. Gametophytic thalli are multiaxial in structure, with longitudinally aligned medullary filaments that issue anticlinal, subdichotomously branched filaments that ultimately form the cortex. The cortex remains filamentous (composed of free filaments) or can become pseudoparenchymatous when ultimate cortical cells (at times colorless utricles) cohere laterally, forming a continuous surface layer as in species of *Scinaia*.

Gametophytes develop three-celled carpogonial branches on inner cortical filaments composed of a basal cell, a hypogynous cell, and a carpogonium. The hypogynous cell bears nutritive branches, and branched gonimoblast filaments develop directly from the fertilized carpogonium (and/or hypogynous cell in some species). Cystocarps are immersed in the outer medulla and are composed of branched gonimoblast filaments with terminal carposporangia, surrounded by a distinct pericarp of sterile filaments arising from the basal cell of the carpogonial branch. Carpospores are released through an ostiole at the thallus surface. Spermatangia are borne terminally on pigmented cortical filaments, scattered or in sori (i.e., *Scinaia* and *Gloiophloea*), or within small surface cavities in species of *Nothogenia*.

One genus of the family, *Scinaia*, is known from the northern Gulf of California.

Scinaia Bivona-Bernardi

Scinaia Bivona-Bernardi, 1822:232.

Ginannia Montagne, 1841:162, 200; Montagne, 1842a:257 [non *Ginannia* Scopoli, 1777: 300].

Pseudoscinaia Setchell, 1914:119.

Pseudogloiophloea Levring, 1956:420.

Scinaia has a alternation of heteromorphic generations, a multiaxial gametophyte, and a sporophyte that is a tuft of uniseriate "*Acrochaetium*-like" filaments. The sporophytic phase is known only from culture studies on several species, one of them *Scinaia confusa* (Ramus, 1969, as *Pseudogloiophloea confusa*; specimens cultured were from California). Thalli of gametophytes are erect, dichotomously to subdichotomously branched, rarely trichotomous or irregular, and attached to substratum by a small discoid holdfast. Gametophytes are multiaxial in structure and may be cartilaginous or soft but more or less turgid. Axes and branches may be terete to markedly compressed. Some species have regular or irregular constrictions at the nodes, whereas others are unconstricted. Internally, the medulla is loosely filamentous, with a central axis of longitudinally arranged filaments, which radiate dichotomously branched slender filaments that give rise to a cortex of several layers. The cortical filaments are slender, dichotomously branched, and composed of pigmented cells (hypodermal cells) many of which terminally bear larger, nearly colorless cells (utricles), a characteristic feature of this genus. The outermost cortical layer either is almost entirely composed of closely packed, laterally coherent inflated utricles that become pseudoparenchymatous (forming a continuous surface layer) or is a less consolidated mixture of inflated utricles or smaller utricles, with small pigmented cells interspersed around them, forming a rosette pattern in surface view. Slender rhizoidal-like filaments are periclinally aligned among and below the hypodermal cells.

Culture studies revealed monosporangia can be formed by both gametophytic and filamentous sporophytic phases for asexual reproduction (Ramus, 1969; Yoshizaki, 1993). Tetrasporophytes are branched uniseriate filaments, with irregularly zonate, cruciately, or decussately divided tetrasporangia terminal on branched filaments or sometimes displaced laterally by sympodial branching. Sometimes new sporangia proliferate within old sporangia. A crust presumed to be a sporophytic phase of *Scinaia* has also been reported (Le Gall and Saunders, 2010, as *S. interrupta*).

Gametophytes are monoecious or dioecious. Carpogonial branches are three-celled, developing in the inner cortex. Prior to fertilization, the hypogynous cell produces two to four sterile branches (nutritive cells), and the basal cell initiates pericarp filaments. After presumed fertilization, gonimoblast filaments develop from the carpogonium (or from the hypogynous cell in some species; see Leon-Cisneros et al., 2009), and fusion cells are formed from the carpogonium, hypogynous cell, with or without the carpogonial branch basal cell, and basal cells of the gonimoblasts, and sterile branches on the hypogynous cell may also be incorporated. Cystocarps are immersed and have a dense, filamentous pericarp with a small pore at the thallus surface. Carposporangia are single and in opposite pairs or in chains on gonimoblast filaments. Spermatangial parent cells are elongate, on pigmented filaments interspersed among the utricles (in most species) or on the cortex. Clusters of terminal spermatangia form continuous or scattered superficial sori. The spermatangial sori of *S. johnstoniae* cover the branch apices, giving them a cap-like appearance, and the utricles are absent from the cortex beneath the spermatangia.

REMARKS. Regarding the generic relationship of *Scinaia* to *Pseudoscinaia* Setchell (1914), Huisman (1985) noted that Ramus' (1969, as *Pseudogloiophloea confusa*) illustration of a cystocarp showed a loosely arranged gonimoblast similar to that of *Pseudoscinaia snyderae* (generitype) and concluded that their cystocarps were basically identical to those of the generitype of *Scinaia* (i.e., *S. forcellata* Bivona-Bernardi, 1822; =*S. furcellata* (Turner) J. Agardh, 1851; basionym: *Ulva furcellata* Turner, 1801); therefore considering them to be congeneric. Although not known in Gulf of California, "*Pseudoscinaia snyderiae*" has been reported in Pacific Baja California from Bocana de Santo Tomas (R. Aguilar-Rosas and Aguilar-Rosas, 1986).

Four species of *Scinaia* are known in the Gulf of California, including *Scinaia interrupta* (A. P. de Candolle) M. J. Wynne (1989), which was recently reported in the southern Gulf (León-Cisneros et al., 2009). Three of these occur in the northern Gulf. Most often they are found in the cooler months of winter through spring.

KEY TO THE SPECIES OF *SCINAIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Branches somewhat flattened, wide (5–10 mm in diameter); thalli branched in 1 plane; cystocarps primarily along margins (some may be scattered over thallus) . . . . ***S. latifrons***

1b. Branches terete (or sometimes slightly compressed), slender (mostly 2–5 mm in diameter); thalli branched in two planes; cystocarps scattered over thallus (not predominantly on margins) 2

2a. Outer cortical layer in cross section of nearly colorless, obovoid utricles interspersed with numerous filaments of 2–3 smaller pigmented cells; in surface view forming a rosette pattern; spermatangial branches scattered over branches, overtopping colorless utricles . . . . ***S. confusa***

2b. Outer cortical layer in cross section of nearly uninterrupted, colorless, square to oblong utricles (not interspersed with numerous filaments of pigmented cells); utricles polygonal in surface view, with an isolated pigmented cell occasionally among them; spermatangial branches forming cap-like sori over apices, without utricles beneath them . . . . ***S. johnstoniae***

Scinaia confusa (Setchell) Huisman

FIGURE 32

Gloiophloea confusa Setchell, 1914:118, pl. 14: figs. 44–47; Kylin, 1941:6; Smith, 1944:190, pl. 42: fig. 1; Dawson, 1945d:37; Taylor, 1945:145; Dawson, 1953a:48, pl. 4: fig. 2; 1960a:36; Dawson et al., 1960a:64, pl. 16: fig. 5, pl. 17: fig. 4; Dawson, 1961b:406; 1962b:199, 229, figs. 79, 80.

Scinaia confusa (Setchell) Huisman, 1985:417, tbl. 1; Scagel et al., 1989:258; Stewart, 1991:67; Ramírez and Santelices, 1991:184; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Pacheco-Ruíz and Zertuche-González, 2002:467; Y.-P. Lee and Ko, 2006:278, fig. 6; Y.-P. Lee, 2008:222, figs. A–C; León-Cisneros et al., 2009:195, figs. 2–14, tbls. 1–3; Bernecker, 2009:CD-Rom p. 61; Fernández-García et al., 2011:64.

Pseudogloiophloea confusa (Setchell) Levring in Svedelius, 1956:13, fig. 8; Ramus, 1969:1–25, figs. 1–10, pls. 1–12; Norris and Abbott, 1972:90; Norris, 1973:9; Acleto O., 1973:20, figs. 43, 50; Abbott and Hollenberg, 1976:335, fig. 277; González-González et al., 1996:261; CONANP, 2002:141.

Pseudogloiophloea confusa (Setchell) Hollenberg et I. A. Abbott, 1965:1178; Dawson, 1965:23; 1966a:14; Mateo-Cid et al., 2006:50.

Scinaia furcellata var. *undulata* sensu Farlow, 1875:367 [non *Scinaia furcellata* var. *undulata* (Montagne) J. Agardh, 1851:422, which is now *Scinaia undulata* (Montagne) Huisman, 1985:417].

Algae forming clumps, up to 15 cm tall, of several (rarely single) erect, semi-turgid, terete axes repeatedly dichotomously to subdichotomously branched, (4–)6–15 orders in 2 planes; branch dichotomies mostly at 2–7 mm intervals; rose red to dark red; attached by a small discoid holdfast. Branches slender, (1.0–)1.5–3.5(–5) mm in diameter; more or less uniform diameter throughout, without constrictions; branch apices narrowed, more or less acute or blunt tips. Medulla of loose filaments surrounding a more compact axial strand; medullary filaments radiate anticlinal branched slender filaments outward to the cortical layers. Inner cortex of 2–3 more or less ovoid cells, 9–12 µm in diameter (hypodermal cells); outward continuing with shorter filaments of 2–3 pigmented cells, 6–7 µm in diameter, that become interspersed among the larger, nearly colorless utricles of the outer layer. Rhizoid-like filaments aligned periclinally among and beneath hypodermal cell layer. Utricles in transverse section, spherical to obovate, mostly 20–30 µm tall, (15–)25–35 µm in diameter. In surface view, the rotund colorless utricles of various sizes surrounded by smaller pigmented cells gives a rosette appearance to the cortex.

Tetrasporophytes were found on "*Acrochaetium*-like" filaments in culture studies; sporophytes not yet identified in field. Gametophytes dioecious, sexual reproductive structures generally in the central portions of thalli. Cystocarps ovoid to pyriform, 200–300 µm long and 200–250 µm wide, embedded in outer medulla (see León-Cisneros et al., 2009, for cystocarp development). Spermatangial branches composed of 2–4 elongate pigmented cells, arising from hypodermal cells, intermingled among the utricles, with clusters of spermatangia on thallus surface.

HABITAT. On rocks; low intertidal to subtidal, down to 15 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Nayarit to Jalisco. Eastern Pacific: southern Alaska to Punta María, Baja California; Costa Rica; Peru; Galápagos Islands. Western Pacific: Korea.

TYPE LOCALITY. Monterey, Monterey County, central California, USA (Smith, 1944:191).

REMARKS. Tetrasporophytes were discovered to be "*Acrochaetium*-like" filaments in culture studies of *S. confusa* from California (see Ramus, 1969, as *Pseudogloiophloea confusa*), but this phase has not been found in nature. The central California *Scinaia confusa* and the southern California *S. snyderae* (Setchell) Huisman (1986; basionym: *Pseudoscinaia snyderae* Setchell, 1914) may be the same species (Abbott and Hollenberg, 1976; Huisman, 1985, 1986). Although *S. snyderae* was noted to be occasionally collected (Dawson, 1945d, as "*P. snyderae*") or apparently rare (Abbott and Hollenberg, 1976), according to Stewart (1991) it is known only from the original collection at Pacific Beach in San Diego. The taxonomic

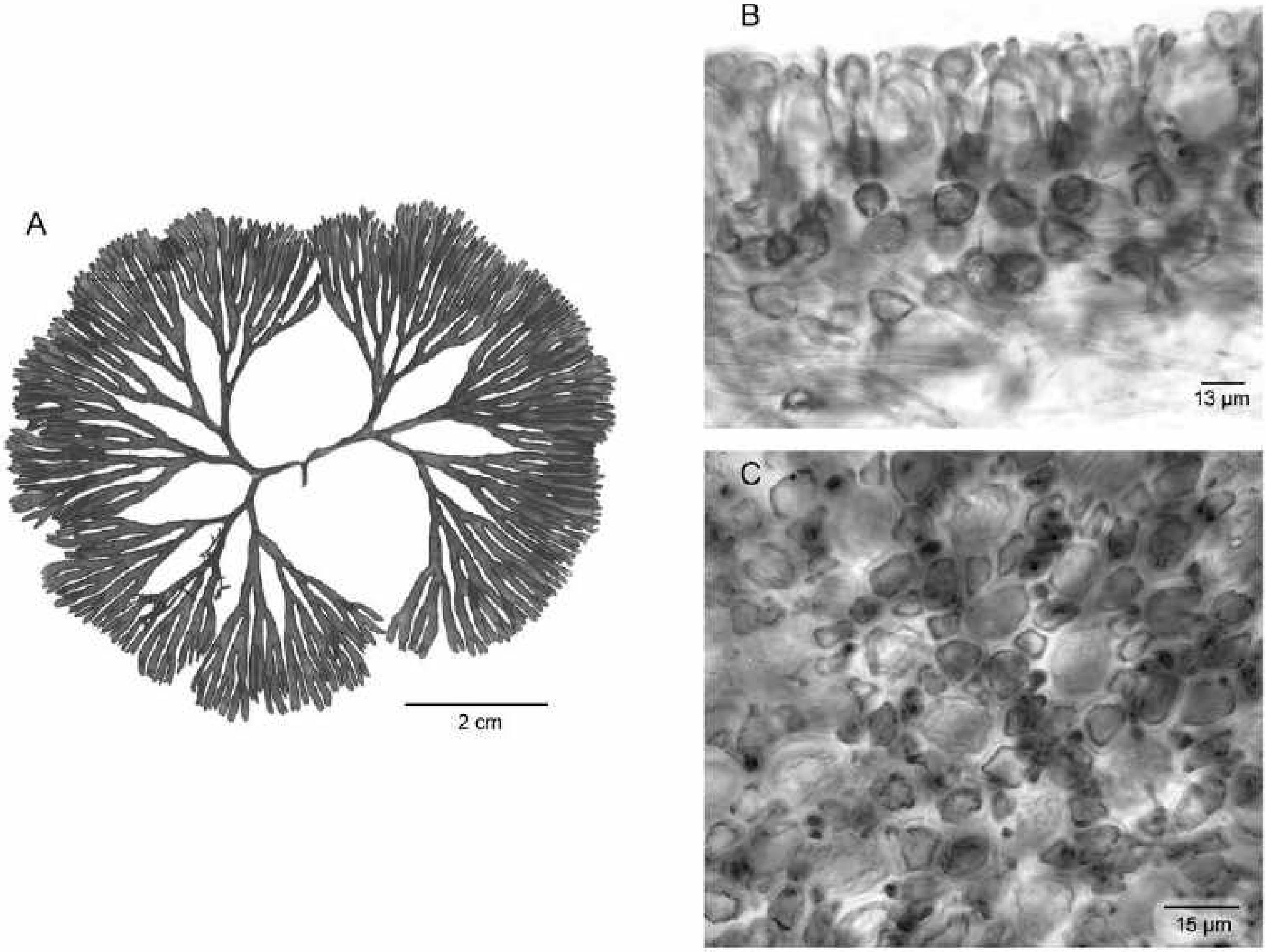

FIGURE 32. A–C. *Scinaia confusa*: A. Thin, terete, subdichotomously branched female gametophyte (*JN-5302 A*, US Alg. Coll.-217350). B. Transection of cortex with outermost layer of a mixture of pigmented filaments among colorless, somewhat round utricles. C. Surface view of cortex with rosette pattern of nearly colorless utricles encircled by rosette pattern of pigmented cells of various sizes and shapes (B, C, *JN-5024*, US Alg. Coll. microscope slide 4247).

status and relationship of northern Gulf of California *S. confusa* to type locality material of *S. confusa* and *S. snyderae* should be further investigated and genetically tested.

Scinaia johnstoniae Setchell

FIGURES 33, 34

Scinaia johnstoniae Setchell, 1914:97, pl. 11: figs. 14, 15; Setchell and Gardner, 1924:742; Dawson, 1944a:257; Taylor, 1945:147; Dawson, 1945d:37; 1949b:237, 243; 1953a:44, pl. 3: fig. 12, pl. 21: fig. 1; Dawson et al., 1960a:80, pl. 17: fig. 5; Dawson, 1961b:406; 1962b:199, 229, fig. 78; Norris, 1973:8; Acleto O., 1973:19, figs. 19, 48, 49; Abbott and Hollenberg, 1976:332, fig. 274; Ramírez and Santelices, 1991:184; Stewart, 1991:68; Serviere-Zaragoza et al., 1993a:484; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; González-González et al., 1996:269; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; L. Aguilar-Rosas et al., 2000:130; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:467; Riosmena-Rodríguez et al., 2005b:34; R. Aguilar-Rosas et al., 2009:6, fig. 2d; León-Cisneros et al., 2009:200, figs. 28–43, tbls. 4–6; Bernecker, 2009:CD-Rom p. 61; Fernández-García et al., 2011:64.

Scinaia complanata sensu Taylor, 1945:146 [in part; non *Scinaia complanata* (Collins) Cotton, 1907:260; basionym: *Scinaia furcellata* f. *complanata* Collins in Collins, Holden and Setchell, 1901a: *P.B.-A.* No. 836].

Scinaia furcellata var. *undulata* sensu Howe, 1911:502 [non *Scinaia furcellata* var. *undulata* (Montagne) J. Agardh, 1851:422; basionym: *Ginnania undulata* Montagne (1841) which is now *Scinaia undulata* (Montagne) Huisman, 1985:417].

Algae of 1 to a few erect, terete fronds, 6.0–23 cm tall, and dichotomously to subdichotomously branched in 2 planes,

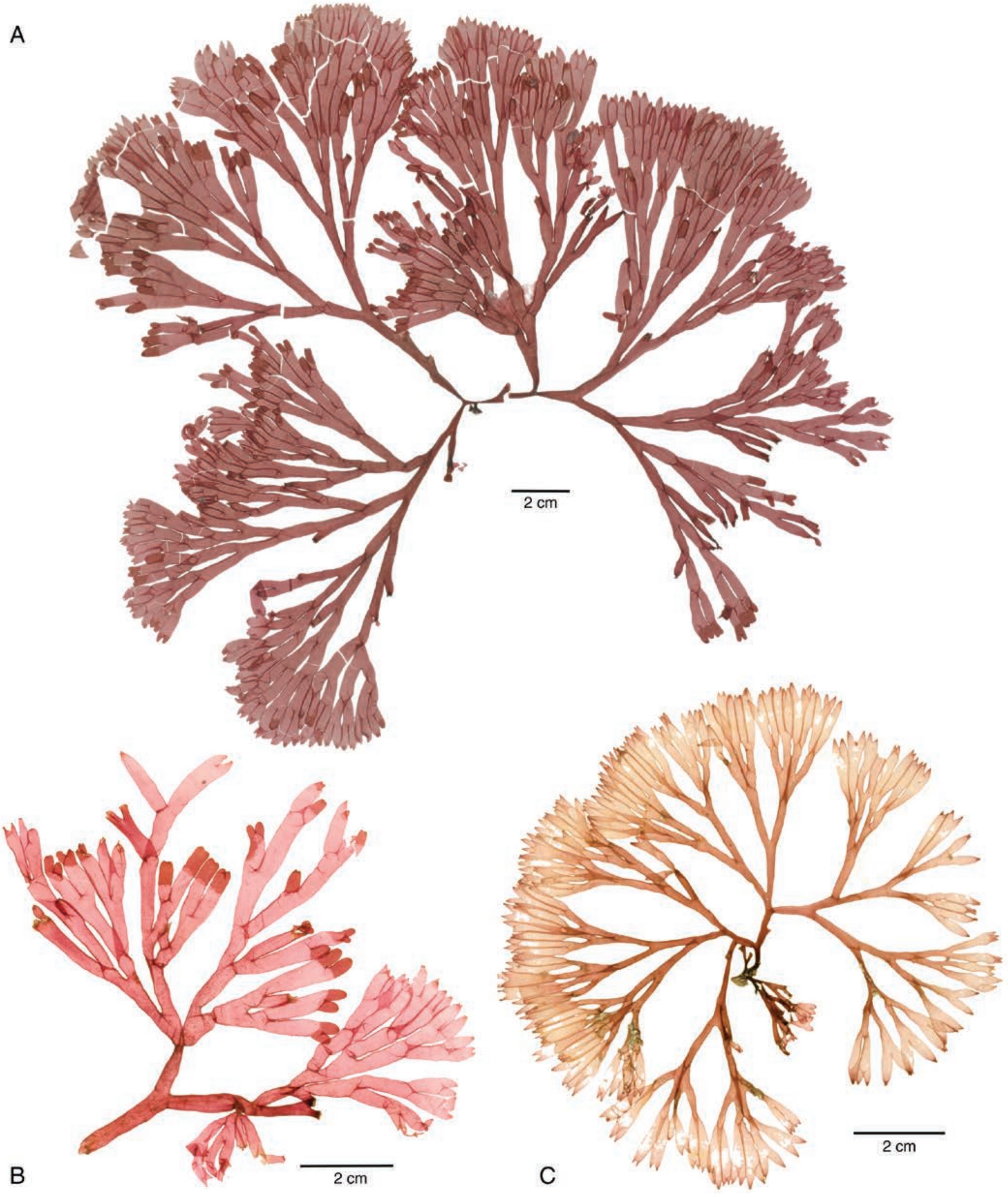

FIGURE 33. *Scinaia johnstoniae*: A. Habit of male gametophyte with dense spermatangia covering some apices forming darker cap-like sori (*JN-5670*, US Alg. Coll.-217351). B. Branch with darker cap-like spermatangial sori on some apices (*JN-5670*, US Alg. Coll.-160916). C. Smaller thallus to show morphological variation (*JN-5023*, US Alg. Coll.-160907).

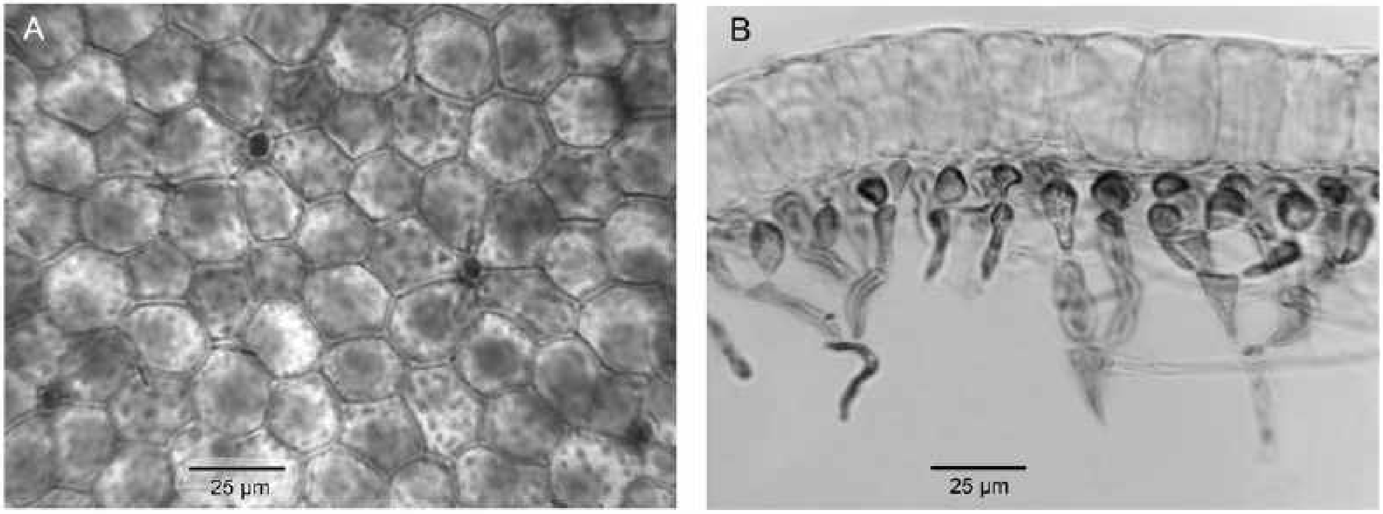

FIGURE 34. *Scinaia johnstoniae*: A. Surface view of cortex with laterally cohering utricles forming polygonal pattern with isolated pigmented cells. B. Transection with outermost cortical layer of nearly colorless abutting utricles above a layer of pigmented hypodermal cells that are connected to medullary filaments, and rhizoidal filaments (A, B, *JN-5023*, US Alg. Coll. microscope slide 4301).

6–8(–10) orders at 2.0–12 mm intervals; attached by a small discoid holdfast. Branches without constrictions; 3.5–5.0 mm in diameter in upper portions, with acute to blunt apices; becoming narrower proximally (downward), to 1.0–2.0 mm in diameter. Internally composed of a thin central axis of compact longitudinal aligned filaments that radiate out into loose dichotomously branched medullary filaments that ultimately produce the cortical filaments. Cortex differentiated into two sections; inner cortical layers of pigmented spherical to pear-shaped cells (hypodermal cells, 10–18 μm in diameter) and an outer layer of larger, nearly colorless utricles forming a continuous surface layer. Utricles in transection, squarish to oblong and slightly taller than wide, 18–30 μm length, 17–25 μm wide; in surface view, utricles polygonal, of similar size, with an occasional, small pigmented cell interspersed among them.

Tetrasporophytes not known. Gametophytes monoecious or dioecious. Cystocarps embedded in outer medulla, about (140–)160–220 μm in diameter; scattered throughout central portion of thallus. The cap-like spermatangial sori (“apical cap type” of Kajimura, 1988) densely cover the surface of branch apices and are easily noticed because of the difference in color. Cortical utricles are absent beneath the sori. Spermatangial branches a mixture of smaller cells arising from hypodermal cells (similar to those of the California *S. articulata* Setchell (1914; cf. Dawson, 1949b:23, pl.7: figs. 44, 45).

HABITAT. Growing on rocks and various other substrata, often in shell and sand bottoms and sometimes partially sand covered; subtidal, down to 20 m depths.

DISTRIBUTION. Gulf of California: El Coloradito to Punta Los Frailes; laguna, Santa María-La Reforma; Sinaloa to Jalisco; Islas Marías (Islas Tres Marías). Eastern Pacific: southern California to Bahía de Ballenas, Baja California Sur; Islas Los Coronados (off northern Baja California); Costa Rica; Peru; Galápagos Islands.

TYPE LOCALITY. San Pedro, Los Angeles County, southern California, USA.

REMARKS. *Scinaia johnstoniae* is a cylindrical species, with an outer cortex of utricles that tend to flatten on their outer (distal) end. Dawson (1953a:48) suggested *Scinaia minima* E. Y. Dawson (1945a:103; type locality: off Isla Cedros, Pacific Baja California) may prove to be a dwarfed form of *S. johnstoniae*. Similar cap-like spermatangial sori are found in the southern California *S. articulata* Setchell (1914; cf. Dawson, 1949b:23, pl.7: figs. 44, 45; type locality: Santa Barbara), but *S. johnstoniae* does not have the characteristic constricted segments of *S. articulata*. Known from the type locality and Santa Barbara Island (California Channel Islands; Dawson, 1949b, 1961b), *S. articulata* has also been reported to the south from Cabo Colonet (Colnett), Pacific Baja California (R. Aguilar-Rosas and Aguilar-Rosas, 1986). Although León-Cisneros et al. (2009) recently considered *S. articulata* conspecific with *S. johnstoniae*, their relationship should additionally be elucidated by molecular testing.

Gulf *Scinaia johnstoniae* is also similar to the Japanese *S. tokidae* Kajimura (1988, type locality: off Tsudo, Oki Islands). *Scinaia tokidae* has branches that are not constricted, but it branches in three planes, with 5–11 branch dichotomies, and has slightly pigmented, larger rounded to oval utricles. Gulf *S. johnstoniae* somewhat resembles *S. japonica* Setchell (1914; type locality: Misaki, Kanagawa Prefecture), but it differs primarily in being smaller, lacks constricted segments, has fewer branch dichotomies (mostly 6–8), branches in two planes, and, in transection, utricles are squarish to oblong (only slightly taller than wide), whereas *S. japonica* has constricted segments, 9–11 branch dichotomies, and elongated utricles (in transection) [note: see comments of Y.-P. Lee and Ko, 2006:280 on taxonomic status of *S. japonica*]. The taxonomic distinction and molecular phylogenetic relationship of the nonconstricted *S. johnstoniae*, *S. japonica* (Kaneko, 1975:9, figs. 2–11), *S. minima*, and *S. tokidae,* and the constricted *S. articulata* needs to be further investigated.

Scinaia latifrons M. Howe

FIGURE 35

Scinaia latifrons M. Howe, 1911:500, fig. 1, pl. 28 (type); Setchell, 1914:102, pl. 11: fig. 23; Setchell and Gardner, 1924:742; Dawson, 1944a:258; Taylor, 1945:148; Dawson, 1945d:37; 1949c:237; 1953a:46, pl. 4: fig. 1; 1960a:36; 1961b:406; 1962b:229; Norris, 1973:9; Acleto O., 1973:18, figs. 41, 44–47; Abbott and Hollenberg, 1976:332, fig. 275; Ramírez and Santelices, 1991:184; Kajimura, 1995:540, fig. 19; González-González et al., 1996:270; Yoshida, 1998:506; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:467; León-Cisneros and Riosmena-Rodriguez, 2005:31, fig.1; Riosmena-Rodríguez et al., 2005b:34; Bernecker and Wehrtmann, 2009:226; León-Cisneros et al., 2009:203, figs. 44–60, tbls. 7–9; Fernández-García et al., 2011:64.

Gametophytes erect, flattened, unconstricted, subdichotomously branched in 1 plane, and up to 22 cm tall; above a short, terete stipe (2–5 mm long); attached by a small discoid holdfast. Branch segments 5–10(–12) mm wide, 1.3–3.0 cm long. Internally, a distinct central axial strand is absent, medullary filaments branch outward, ultimately forming cortical layers of 1–2 small, globose, pigmented cells, 18–20 µm in diameter, beneath an outer surface layer of larger, nearly colorless, closely abutting oblong to square utricles, 33–45 µm tall by 18–30 µm wide in transverse view. In surface view, utricles polygonal, with a minute pigmented cell occasionally among them.

Tetrasporophyte not known. Gametophytes dioecious (Kajimura, 1995). Cystocarps, spherical to pyriform, (200–)320–375 µm in diameter; embedded within the outer medulla and scattered but aggregated most abundantly along thallus margins. Spermatangia in elongate sori continuous along margins from base to upper thallus, except the apices and axils ("marginal belt type" of Kajimura, 1995). Spermatangial branches 2–3 elongated

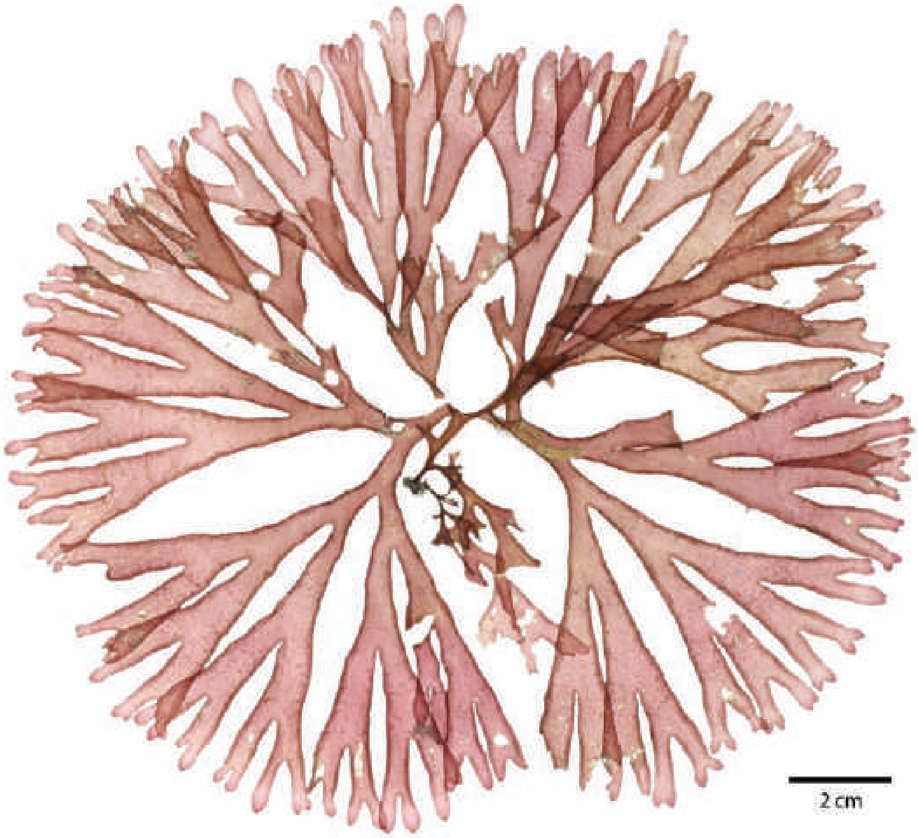

FIGURE 35. *Scinaia latifrons:* Habit of female *gametophyte* showing flattened wide axes with the majority of cystocarps along lateral margins, some scattered (*JN-5049*, US Alg. Coll.-160925).

cells arising from hypodermal cells, inserted among the utricles, with terminal spermatangia at frond surface.

HABITAT. Growing on rocks or hard substratum, which are often partially sand covered, or on shell and sand bottoms; subtidal, from 5 to 22.7 m depths.

DISTRIBUTION. Gulf of California: Punta Pelicano (vicinity of Puerto Peñasco) to Guaymas; Isla Willard (Bahía San Luis Gonzága) to Punta Períco (Baja California Sur); Puerto Refugio, Isla Ángel de la Guarda. Eastern Pacific: California Channel Islands to Oaxaca; Costa Rica; Peru; Galápagos Islands.

TYPE LOCALITY. Near La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Scinaia latifrons* is similar to the western Pacific *S. cottonii* Setchell (1914) (Okamura, 1921; Tseng, 1941; Dawson, 1953a). Although Yoshida (1998, as *S. latifrons*) considered them conspecific, León-Cisneros and Riosmena-Rodríguez (2005) suggested this synonymy not be followed, and others have also kept them separate (e.g., Tseng, 1983; Kajimura, 1995; Y.-P. Lee and Ko, 2006; Y.-P. Lee, 2008).

Kajimura (1995) supported Dawson's (1953a) observation that the most apparent distinction between these two may be the location of the spermatangial sori. Gulf *S. latifrons* had spermatangial sori along the entire margin from base to top except for the apices and axils (marginal-belt-type of Kajimura, 1995:540, fig. 19), and the Japanese *S. cottonii* had spermatangia in small, scattered, irregularly shaped sori on the frond surface ("irregular-type" of Kajimura, 1988; 1995:536, fig. 18). Kajimura (1995) further characterized *S. latifrons* to be dioecious, with cystocarps (320–375 µm in diameter), utricles elongated in tranverse view (33–45 µm tall by 18–29 µm in diameter), and 1–2 cortical layers of cells (18–20 µm in diameter); and *S. cottonii* to be monoecious, have larger cystocarps (up to 482 µm in diameter), utricles square, roundish, or elongate (26–40 µm by 21–40 µm), and a thicker cortex of 2–3(–4) layers of smaller cells (5–10 µm in diameter). In an expanded definition, León-Cisneros et al. (2009) reported *S. latifrons* to be monoecious, described cystocarp development with a new pattern of fusion cell development involving adjacent cells of the basal cell, observed spermatangia in marginal belts, and added they were also scattered throughout the thallus. Gulf specimens exhibiting these characters should be tested by molecular analyses and compared to *S. latifrons* sensu stricto as well as *S. cottonii*.

PALMARIALES

Palmariales Guiry et D. E. G. Irvine in Guiry, 1978b:138.

Algae are of various forms, including filamentous, thin prostrate crusts of laterally fused filaments and narrow to wide fronds. Gametangial thalli are monoecious or dioecious. Some species have spermatangial and tetrasporangial thalli of similar morphologies. Some have both carpogonia and spermatia on the same thallus.

Life history is diphasic. There is an absence of a carposporophyte in the life history. A single-cell carpogonium is developed in much smaller carpogonial thalli, and a tetrasporangial thallus is developed directly from a fertilized carpogonium, overgrowing the carpogonial thallus. Tetrasporangia are repeatedly regenerated from a basal generative stalk cell (unique to the order). Monosporangia are not known. Pit plug ultrastructure shows a two-cap membrane.

REMARKS. Ragan et al. (1994), on the basis of their molecular analysis, found that rDNA SSU (small-subunit ribosomal DNA) data of some morphologically different taxa of the Acrochaetiales were related to members of the Palmariales.

At present the Palmariales is composed of four families, one of which is reported in the northern Gulf of California.

RHODOPHYSEMATACEAE

Rhodophysemataceae G. W. Saunders et J. McLachlan. 1990:20; Saunders and McLachlan, 1991:272.

Filamentous algae, composed of erect and prostrate uniseriate filaments that attach to substratum or algal host by laterally fused cells that form a compact monostratic base. Erect filaments develop individually or in clusters and may become adherent and pseudoparenchymatous, resulting from cell fusions or mucilaginous envelopes or a combination of both. Cells contain either a parietal or ribbon-shaped chloroplast or numerous discoid chloroplasts and lack pyrenoids. The pigment B-phycoerythrin is present. Ultrastructure reveals a two-cap layer (Pueschel and Cole, 1982).

Gametophytes are monoecious with sessile carpogonia and paired spermatangia. After presumed fertilization, the carpogonium gives rise directly to a tetrasporangium that is subtended by a stalk cell.

REMARKS. Pueschel and Cole (1982) reported that *Rhodophysema* Batters (1900) had the same kind of pit plugs as members of the Palmariales. DeCew and West (1982) found the *Rhodophysema* crusts to be a gametangial, with both carpogonia and spermatangia, and its sexual life history was anomalus. The fertilized carpogonium divides into a stalk cell and a tetrasporangium (the stalk cell can produce successive tetrasporangia), and DeCew and West (1982) suggested the genus belongs in the Palmariales.

The Rhodophysemataceae, on the basis of *Rhodophysema*, was described by Saunders and McLachlan (1990). Saunders et al. (1995) and Clayden and Saunders (2010) confirmed the earlier suggestion of Saunders and McLachlan (1990, 1991) that the family belongs in the Palmariales. Members of the family do not produce monosporangia, lack a carposporophyte phase in their life histories, and are characterized by the presence of the pigment B-phycoerythrin. These characters separate Rhodophysemataceae from the Palmariaceae Guiry (1974), which has tetrasporophyte and carposporophyte phases and the pigment R-phycoerythrin.

Currently, five genera are recognized in the family. One—the recently described genus *Rhodonematella*—was tentatively placed in the family (Clayden and Saunders, 2010) and is now reported in the northern Gulf of California.

Rhodonematella Clayden et G. W. Saunders

Rhodonematella Clayden et G. W. Saunders, 2010:297, figs. 7–11.

Algae are microscopic to minute gametophytes; composed of uniseriate, simple to branched erect filaments and prostrate, sometimes branched, basal filaments. Cells of basal and erect filaments usually have one parietal chloroplast and are without pyrenoids. The filamentous gametophytes are composed of a basal system of endophytic cells that are "immersed" in the host cortex (but apparently not penetrating host cortical cells) and an erect system of free one- to three-celled filaments that arise directly from the basal cells.

Monoecious filaments have both sessile carpogonia and spermatangia on one- to two-celled erect filaments. Following presumed syngamy, the carpogonia directly gives rise to diminutive, moderately branched, filamentous tetrasporophyte. Tetrasporangia, produced directly from the fertilized carpogonium, are cruciately divided, borne terminally on the filaments, and surrounded by presumed gametophytic, multicelled filaments (paraphyses) (reproduction after Clayden and Saunders, 2010).

Remarks. *Rhodonematella* is most easily confused with some members of *Rhodochorton* Nägeli (1862). Although both genera lack pyrenoids and monosporangia, the marine species of *Rhodochorton* reproduce asexually by tetrasporangia and have stellate plastids (Y.-P. Lee and Lee, 1988; Harper and Saunders, 2002). In contrast, *Rhodonematella* has gametangial thalli in which the carpogonia directly produces a terminal cruciate tetrasporangium and has cells with a single parietal plastid (Y.-P. Lee and Kurogi, 1978; Garbary et al., 1983).

Although both genera are found in the intertidal to shallow subtidal of temperate to subtropical seas, *Rhodonematella subimmersa* is an endo-epiphyte on its foliose red algal hosts, e.g., species of *Halymenia*, *Grateloupia,* and *Kallymenia*, whereas most species of *Rhodochorton* grow on rocks or other hard substratum. The life histories of *Rhodochorton subimmersum* and *R. floridulum* (Dillwyn) Feldmann (in Christensen, 1978; basionym: *Conferva floridula* Dillwyn, 1809; generitype of *Rhodonematella*) (Y.-P. Lee and Kurogi, 1978; Stegenga, 1978, 1979) were reinterpreted by Clayden and Saunders (2010), who recognized *Rhodonematella* and tentatively placed it in the Rhodophysemataceae.

Rhodonematella is represented by a single species in the northern Gulf of California.

Rhodonematella subimmersa (Setchell et N. L. Gardner) Clayden et G. W. Saunders

Rhodochorton subimmersum Setchell et N. L. Gardner, 1903:347, pl. 17: fig. 12; Kylin, 1925:45; Drew, 1928:191, pl. 47: fig. 81; Nakamura, 1941:290, fig. 17; Smith, 1944:185; Y.-P. Lee and Kurogi, 1978:115, figs. 1–10; Y.-P. Lee, 1987:45, fig. 22A–H; Y.-P. Lee and Yoshida, 1997:206; Yoshida, 1998:472; Y.-P. Lee, 2008:178, figs. A–C.

Rhodonematella subimmersa (Setchell et N. L. Gardner) Clayden et G. W. Saunders, 2010:297, figs. 7–11.

Acrochaetium subimmersum (Setchell et N. L. Gardner) Papenfuss, 1945:318; Dawson, 1961b:404; Hollenberg and Abbott, 1966:42; Abbott and Hollenberg, 1976:319, fig. 261; Silva, 1979:317; Josselyn and West, 1985:143; González-González et al., 1996:167; Pacheco-Ruíz et al., 2008:206.

Audouinella subimmersa (Setchell et N. L. Gardner) Garbary et Rueness, 1980:22; Garbary et al., 1983:56, fig. 23; Garbary, 1987:178; Scagel et al., 1989:151; Hansen, 1997:5.

Colaconema subimmersum (Setchell et N. L. Gardner) P. W. Gabrielson in Gabrielson et al., 2004:95.

Algae filamentous; endo-epiphytic, forming dark red to reddish patches on algal host; of short, erect filaments protruding above surface, attached by basal filaments on host surface with endophytic filaments immersed between cortical cells of host. Basal endophytic filaments, unbranched or sometimes branched; of irregularly shaped elongated cells, (15–)25–40(–50) μm long and 4.0–6.0 μm wide. Erect filaments (above host surface), short, simple, or occasionally branched above, usually not more than 2–6(–10) cells tall; of cells mostly about as long as wide to oblong, 4.0–7.0 μm long, 3.0–6.0 μm in diameter. Cells with a single parietal chloroplast and without pyrenoids.

Tetrasporangial thalli filamentous, developed directly from fertilized carpogonium; tetrasporangium on a stalk cell, borne lateral and terminal on erect filaments, cruciately divided, ellipsoid, 15–21 μm long, 10–13 μm wide. Carpogonial and spermatangial thalli filamentous, monoecious (as reported elsewhere). Carpogonium "flask shaped," 5–10 μm long and 3–4 μm wide, with a terminal trichogyne, up to 8.0 μm long, 2.0–3.0 μm in diameter; sessile on a single basal cell, on 1- to 3-celled, erect filaments. Presumably fertilized carpogonium divides transversely and develops simple to branched gonimoblast filaments that bear a terminal, cruciate tetrasporangia. Spermatangial parent cell develops a single, globose spermatangium lateral on cells of creeping prostrate filaments and terminal on short erect filaments; spermatia 3–4 μm in diameter (reproduction after Y.-P. Lee and Kurogi, 1978; Y.-P. Lee and Yoshida, 1997; Clayden and Saunders, 2010).

Habitat. An endo-epiphyte found growing within the cortical layer and partially on the surface of *Halymenia californica* and *Kallymenia pertusa*; shallow subtidal, down to 10 m depths.

Distribution. Gulf of California: Isla San Esteban. Eastern Pacific: southern British Columbia to California Channel Islands (off southern California). Western Pacific: Japan; Korea.

Type Locality. Endo-epiphyte on *Grateloupia doryphora*; Whidbey Island (Whidby), Island County, Puget Sound, Washington, USA.

Remarks. A new record for the Gulf of California, *Rhodonematella subimmersa* was found growing in *Halymenia californica* (*JN-5540*, US Alg. Coll. microscope slide 4243) and *Kallymenia pertusa* (*JN-5538,* US Alg. Coll. microscope slide 4262), off the southern end of Isla San Esteban. The Gulf specimens referred to *R. subimmersa* mostly closely resemble those of Abbott and Hollenberg (1976: fig. 261, as *Acrochaetium subimmersum*). Previously known on the Pacific coast of North America, *R. subimmersa* has been found growing, in addition to *Halymenia*, on *Grateloupia, Prionitis,* and *Schizymenia* (Abbott and Hollenberg, 1976) and should be looked for on the Gulf species of these genera as well.

CORALLINOPHYCIDAE

Corallinophycidae L. Le Gall et G. W. Saunders, 2007:1129.

A large group of articulated and nonarticulated calcified algae, with calcification in the form of calcite. Members are characterized by pit plugs that have two cap layers, and the outer pit plug is dome shaped. Tetrasporophytes, where known, produce zonately or cruciately divided tetrasporangia. Carpogonial branches are two-celled.

REMARKS. Coralline algae are ecologically important and widespread in distribution from polar regions to the tropics. They are critical, often predominant components of intertidal to deep subtidal marine ecosystems and are the deepest known plants on earth (Littler et al., 1985, 1986). Studies of global and climate changes have shown coralline algae to be vulnerable to environmental changes such as warming and ocean acidification (Nelson, 2009; Díaz-Pulido et al. 2012; Nash et al., 2012; Teichert et al., 2012). Coralline algae and their habitats will require further studies and long-term ecological monitoring.

There are three orders currently recognized in the subclass Corallinophycidae: the Corallinales; Rhodogorgonales Fredericq, J. N. Norris, et Pueschel (in Fredericq and Norris, 1995); and the Sporolithales L. Le Gall, Payri, Bittner et G. W. Saunders (2010).

One order, the Corallinales, is well represented in the northern Gulf of California.

CORALLINALES*

Corallinales P. C. Silva et Johansen, 1986:250.

The Corallinales are considerably varied in shape and size and include pink to purple calcified algae that may be growing attached to various substrates, unattached and free-living, or partly endophytic in other corallines. Members are either (1) nonarticulated, crustose, and prostrate, (2) articulated (jointed) and erect, or (3) partially endophytic. The nonarticulated, crustose corallines are smooth, warty, or with protuberances and usually spreading. Some apparently may break away from the rocky or hard substrata, with the crustose fragments continuing to grow or possibly attaching to calcium carbonate particles or mollusk shell fragments, eventually surrounding them to form rhodoliths (e.g., Foster et al., 1997; Riosmena-Rodríguez et al., 2010) or maërl (e.g., Blunden et al., 1997; Foster, 2001; Hinojosa-Arango et al., 2009). Rhodoliths remain unattached as free-living, subspherical to irregular-shaped nodules that may be smooth or with protuberances or branches. The other major group, the articulated or jointed species have erect parts or fronds consisting of calcified segments (intergenicula) that are separated by flexible, uncalcified joints (genicula). These articulated fronds are attached to rocks, shells, or other algae by holdfasts of thin crusts or of entangled, segmented rhizomes.

Living rhodolith or maerl (maërl) beds are unique marine ecosystems worldwide. An individual rhodolith may be a single species, but sometimes a rhodolith may be composed of multiple species. Rhodolith beds, although disjunct in distribution, are particularly abundant in the Pacific from the Gulf of California and southern Japan; the Eastern Atlantic coasts of Norway, Ireland, and Scotland; the Mediterranean Sea and Red Sea; the Western Atlantic coasts of northeast Canada, Caribbean Sea, and Brazil; and the Indian Ocean and southern ocean coasts of western Australia (Foster, 2001; Amado-Filho et al., 2012). Rhodoliths were known as "chicaron" on the former pearl-fishing banks around La Paz (Dawson, 1944a). In the Gulf of California, rhodolith beds are often extensive, occuring from Puerto Peñasco to Islas Marietas off Nayarit (Foster et al., 1997; Yabur-Pacheco and Riosmena-Rodriguez, 2006; Riosmena-Rodríguez et al., 2010: fig. 3.1). With their high ecological and economic value they are now recognized as critical habitats in need of monitoring and conservation (Ávila and Riosmena-Rodríguez, 2010; Riosmena-Rodríguez et al., 2010).

The internal structure of most coralline algae is pseudoparenchymatous, composed of delicate filaments cemented together by cell walls impregnated with calcium carbonate in the mineral form of calcite. Meristematic cells are intercalary and produce epithallial cells outward and other vegetative cells inward. Cells of the contiguous vegetative filaments can be united by fusions or by direct secondary pit connections, and trichocytes may be either present or absent. Ultrastructure of those studied thus far shows the primary pit plugs have two cap layers, with the outer cap layer dome-shaped (Pueschel and Cole, 1982; Pueschel, 1987, 1989). Internally the fronds of articulated coralline algae are composed of a central core of filaments, the medulla, and the surrounding pigmented tissue of the cortex. The crustose corallines are composed of three tissue layers of filaments: (1) a hypothallium, in which the filaments are close to the substrate and more or less parallel to it; (2) a perithallium, in which the filaments are above the hypothallium and more or less perpendicular to the substratum; and (3) an epithallium, the upper or superficial layer of cells that in many may regularly slough off. In some species epithallial cells are rarely seen, in others they can build up to several layers, and in a few they give rise to a significant photosynthetic tissue.

Although vegetative reproduction by fragmentation has been assumed in rhodolith species, Schaeffer et al. (2002) found no genetic evidence of cloning among Gulf of California species they investigated.Tetrasporangia or bisporangia are borne

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* Contributed by James N. Norris and H. William Johansen. H. W. Johansen: Department of Biology, Clark University, Worcester, Massachusetts 01610, USA.

within conceptacles with large red bisporangia or zonately divided tetrasporangia (Corallinaceae). In some genera, conceptacles are developed with a uniporate opening. In others, sporangia develop thick cap walls ("beak") that eventually break out, giving rise to conceptacles that are multiporate (Hapalidiaceae subfam. Melobesioideae, e.g., *Lithothamnion*) with one pore for each sporangium. For some, asexual reproduction may also be by means of thallus fragmentation, apomeiotic bispores, or propagules. Gametangial thalli may be monoecious or dioecious, with gametangia always produced within uniporate conceptacles located on the surfaces of crustose (nonarticulated) species and either in the surface or apices of the calcified segments (intergenicula) of the articulated species. Carpogonial conceptacles bear supporting (auxiliary) cells on the floor, each with one to two two-celled carpogonial filaments in which the trichogynes project through the pore at maturity. After fertilization the auxiliary and associated cells irregularly or sometimes completely fuse to form a more or less flat fusion cell. Short gonimoblast filaments grow from the margins or upper surface of a fusion cell, forming large red carposporangia, each containing a single carpospore. Spermatangial conceptacles contain simple to dendroid spermatangial filaments either on the conceptacle floor and/or sometimes along the conceptacle walls and roof that produce spermatangia.

The Corallinales as currently interpreted comprise two families, the Corallinaceae J. V. Lamouroux (1812) and Hapalidiaceae J. E. Gray (1865). The family Sporolithaceae Verheij (1993), previously considered to belong to the Corallinales, has been recognized to be a new order, the Sporolithales L. Le Gall, Payri, Bittner et G. W. Saunders (Le Gall et al., 2010), supported by molecular evidence and the morphological studies of Townsend et al. (1995) of *Sporolithon* Heydrich (1897b).

Terminology and characters, along with illustrations, unique to members of the Corallinales are elucidated in Johansen (1981), Woelkerling (1988), Irvine and Chamberlain (1994), Womersley (1996), Keats (n.d. [accessed 2010]), and Rasser (2010).

The two families of the Corallinales are represented in the northern Gulf of California.

KEY TO THE FAMILIES OF THE CORALLINALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Sporangial conceptacles uniporate; bisporangia and tetrasporangia do not produce apical plugs .... **Corallinaceae**
1b. Sporangial conceptacles multiporate; bisporangia and tetrasporangia produce apical plugs at pore .... **Hapalidiaceae**

CORALLINACEAE

Corallinaceae J. V. Lamouroux, 1812:185.

The Corallinaceae is separated from the other families primarily by the manner of sori development and characters of tetrasporangia and bisporangia. In the Corallinaceae, tetrasporangia and bisporangia are borne in conceptacles (interpreted as modified sori) with calcified roofs and may be somewhat sunken, more or less level, or protruding from the thallus surface. The tetrasporangia are simultaneously cleaved and zonately divided and are not developed below multiporate plates, and they are not individually within calcified compartments (see Townsend et al., 1995; A. Harvey et al., 2003b).

REMARKS. Articulated and crustose coralline algal species of the Corallinaceae are prominent in the Gulf of California and include species from seven of the subfamilies. The articulated species reported from the northern Gulf are members are in two subfamilies: C. subfam. Corallinoideae, which includes *Corallina*, *Haliptilon*, and *Jania*, and C. subfam. Amphiroideae, with *Amphiroa*.

The Corallinaceae are widespread and ecologically important in the Gulf of California, with 55 species; 31 nonarticulated (crustose) coralline species in 17 genera, 23 articulated species in 4 genera, and 1 parasitic genus.

KEY TO THE SUBFAMILIES OF THE CORALLINACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli geniculate; branches composed of uncalcified genicula (joints) and calcified intergenicula (calcified segments between uncalcified joints) (articulated corallines) 2
1b. Thalli nongeniculate; either without branches or with solid calcified branches not composed of genicula and intergenicula (nonarticulated corallines) 3
2a. Articulated branches with uncalcified genicula of 1 to several tiers of cells; secondary pit connections present; cell fusions absent .... **C. subfam. Amphiroideae**
2b. Articulated branches with genicula of 1 tier of cells; secondary pit connections absent; cell fusions present .... **C. subfam. Corallinoideae**
3a. Some cells of vegetative filaments linked by secondary pit connections; cell fusions absent or very rare .... **C. subfam. Lithophylloideae**
3b. Some cells of vegetative filaments linked by cell fusions; secondary pit connections absent or very rare 4
4a. Spermatangial filaments develop on conceptacle chamber floor, walls, and roof ...... **C. subfam. Neogoniolithoideae**
4b. Spermatangial filaments developed only on conceptacle chamber floor 5

5a. Trichocytes present in large tightly packed horizontal rows without vegetative filaments between them . . . . . **C. subfam. Porolithoideae**
5b. Trichocytes absent or present; if present, solitary, in pairs, or in small groups or rows with vegetative filaments between them (not in large tightly packed horizontal rows) 6
6a. Gulf of California members primarily dimerous in thallus construction; sporangial conceptacle pore canal lined by cells oriented more or less perpendicular to conceptacle roof and that do not protrude into pore canal . . . . . **C. subfam. Hydrolithoideae**
6b. Gulf of California members monomerous or dimerous in thallus construction; sporangial conceptacle pore canal lined by cells oriented more or less parallel to conceptacle roof and that protrude laterally into pore canal . . . . . **C. subfam. Mastophoroideae**

KEY TO THE GENERA OF CORALLINACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Nonarticulated calcified crustose algae, consisting of crusts or nodules (rhodoliths); with protuberances or branches without flexible noncalcified joints, or without protuberances; nonarticulated Corallinaceae 2
1b. Articulated calcified algae, composed of flexible fronds of calcified segments (intergenicula) that are separated by noncalcified joints (genicula); articulated Corallinaceae 18
2a. Semiendophytic minute, parasite on articulated corallines; lateral cells of adjacent filaments not linked (no secondary pit connections nor cell fusions) . . . . . ***Choreonema***
2b. Not semiendophytic or parasitic, larger; with some form of lateral cell linkage (secondary pit connections and/or cell fusions) between cells of adjacent filaments 3
3a. Secondary pit connections link some cells of adjacent filaments; cell fusions absent or rare 4
3b. Cell fusions link some cells of adjacent filaments; secondary pit connections absent or rare 6
4a. Primigenous (basal) filaments of palisade cells (vertically elongated cells) 5
4b. Primigenous (basal) filaments of nonpalisade cells (quadrate or squarish cells) . . . . . ***Lithophyllum***
5a. Crusts very thin, usually a single cell layer; overgrowing each other (up to 4 layers) . . . . . ***Litholepis***
5b. Crusts thicker, of 2 or more cells layers thick . . . . . ***Titanoderma***
6a. Tetrasporangial and bisporangial conceptacles uniporate 7
6b. Tetrasporangial and bisporangial conceptacles multiporate 16
7a. Thallus construction either dimerous or monomerous; or both monomerous and dimerous 8
7b. Thallus construction primarily dimerous (protuberances, if present, may be radially arranged and monomerous) 11
8a. Thallus construction primarily monomerous 9
8b. Thallus construction both monomerous and dimerous . . . . . ***Spongites* (in part)**
9a. Spermatangial filaments arise from spermatangial chamber floor, walls, and roof . . . . . ***Neogoniolithon***
9b. Spermatangial filaments arise only from spermatangial chamber floor 10
10a. Trichocytes tightly packed in large horizontal fields . . . . . ***Porolithon***
10b. Trichocytes, if present not as above, not tightly packed, usually with vegetative cells between trichocytes; if trichocytes in horizontal rows, in smaller groups (rows shorter) . . . . . ***Spongites* (in part)**
11a. Crusts thin, usually less than 200 µm thick, without protuberances; often epiphytic, not forming free living rhodoliths 13
11b. Crusts thicker, usually greater than 200 µm thick, may have protuberances; on rocks, epiphytic or may form free living rhodoliths 12
12a. Sporangial conceptacle pore canal in vertical section lined with cells parallel to roof that protrude into pore canal; trichocytes not observed in primigenous (basal) filaments . . . . . ***Spongites* (in part)**
12b. Sporangial conceptacle pore canal in vertical section lined with cells perpendicular to roof surface that do not protrude into pore canal; trichocytes terminal on primigenous filaments . . . . . ***Hydrolithon* (in part)**
13a. Trichocytes absent ; crusts epiphytic . . . . . ***Heteroderma***
13b. Trichocytes present or absent; on rocks or epiphytic 14
14a. Trichocytes when present, intercalary within primigenous (basal) filaments or terminal on postigenous (erect) filaments; pore canal of sporangial conceptacles (in vertical section) lined, at least initially, by horizontally oriented cells (parallel to conceptacle roof surface); germination disc with 8-celled center . . . . . ***Pneophyllum***
14b. Trichocytes, when present, terminal on primigenous filaments or intercalary on postigenous filaments; pore canal of sporangial conceptacles (in vertical section) lined by enlarged, vertically oriented cells (perpendicular to conceptacle roof); germination disc with 4-celled center 15

15a. Crusts not extensively overlapping each other; sporangial conceptacles 200–225 μm in diameter . . . . . ***Fosliella*? *paschalis***
15b. Crusts often overlapping each other; sporangial conceptacles smaller, 100–160 μm in diameter . . . . ***Hydrolithon* (in part)**
16a. Thallus construction dimerous . . . . ***Melobesia***
16b. Thallus construction monomerous 17
17a. Epithallial cells flattened and flared at corners; monomerous core of filaments noncoaxial . . . . ***Lithothamnion***
17b. Epithallial cells not flared; monomerous core of filaments coaxial . . . . ***Mesophyllum***
18a. Genicula of 2 or more medullary cell tiers (one species, *A. valonioides,* has 1 tier); medullary cell tiers in the intergenicular segments of differing heights; conceptacles on surfaces of segments; secondary pit connections present between some cells of adjacent filaments; cell fusions absent . . . . ***Amphiroa***
18b. Genicula a single tier of thick-walled medullary cells; medullary cell tiers in the intergenicular segments all the same height; conceptacles mostly in the apices of fertile segments; secondary pit connections absent; cell fusions present between some cells of adjacent filaments 19
19a. Primarily dichotomously branched; terete to subterete segments (intergenicula) less than 300 μm in diameter; intergenicula mostly of 3–6 tiers of cells holdfast crustose or stoloniferous . . . . ***Jania***
19b. Pinnately branched; compressed segments (intergenicula) more than 300 μm wide; medulla of intergenicula mostly of 3–25 tiers of cells; crustose holdfast (stolons absent, rare or sometimes along with crustose base) 20
20a. Axes and branches mostly greater than 500 μm wide; intergenicula of 10–25 tiers of medullary cells; holdfast crustose (stolons absent or rare); reproductive conceptacles without or occasionally with short branchlets; fusion cells thin and broad; spermatangia conceptacles with low ceiling and short beaks . . . . ***Corallina***
20b. Axes mostly less than 500 μm in diameter; intergenicula usually with 2 or more subcylindrical branchlets; intergenicula of 3–6 tiers of medullary cells; holdfast crustose (some also with stolons); tetrasporangial and carposporangial conceptacles with branchlets; fusion cells thick and compact; spermatangial conceptacles with high ceiling and without beaks or branchlets . . . . ***Haliptilon***

CORALLINACEAE SUBFAM. CORALLINOIDEAE

Corallinaceae subfam. Corallinoideae (Areschoug) Foslie, 1908:19; Womersley and Johansen, 1996:288; Bailey and Chapman, 1998:692; Bailey, 1999:208; Harvey et al., 2003a:994.

Algae usually erect, sometimes procumbent, of terete to compressed branches of genicula (joints) that alternate with longer intergenicula (segments); arising above a crustose holdfast, lowermost basal segments with basal stolons in some species. Intergenicula of medulla of laterally adjoined filaments in 1–25(–40) tiers of cells; vegetative filaments linked by lateral cell fusions; secondary pit connection absent; cortex of calcified cells. Genicula uncalcified; of a single tier of cells.

Life history of isomorphic tetrasporophytes and gametophytes. Zonate tetrasporangia and bisporangia produced in urn-shaped or embedded conceptacles. Gametophytes monoecious or dioecious, with axial or lateral conceptacles. Carpogonial filaments 2-celled, borne on conceptacle floor; carposporangia terminal on short gonimoblast filaments from basal fusion cell. Spermatangia on short filaments from floor or sides of conceptacle chamber.

REMARKS. The subfamily is represented by two genera belonging in separate tribes in the northern Gulf of California.

KEY TO THE TRIBES OF CORALLINACEAE SUBFAM. CORALLINOIDEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Fronds attached by an expansive crustose holdfast; sporangial conceptacles contain more than 30 tetrasporangia or bisporangia . . . . **Corallineae**
1b. Frond(s) attached by minute to small crustose holdfast; sporangial conceptacles contain up to 15 tetrasporangia or bisporangia . . . . **Janieae**

CORALLINOIDEAE TRIBUS CORALLINEAE

Corallineae Areschoug, 1852:509.

The articulated corallines of the tribe Corallineae are composed of calcified fronds of algae that are of pinnately, dichotomously, or irregularly branched and usually attached by spreading crustose holdfasts (lacking stolon-like attachments). Intergenicula are subcylindrical or compressed, with wings or lobes sometimes present, and more than eight cells in the medullary tiers of an intergeniculum.

Sporangial conceptacles contain more than 30 tetrasporangia or bispores. Carposporangial conceptacles have concave-convex fusion cells, up to 10 μm thick. Spermatangial conceptacles are pointed or beaked, with spermatangia lining the floor and lower inner walls of the chamber.

REMARKS. One genus, *Bossiella* P. C. Silva (1957a), was mistakenly reported in the southern Gulf from Bahía de La Paz. The record of *B. orbigniana* (Descaine) P. C. Silva (Riosmena-Rodríguez et al., 1992) was based on an incorrect locality label (see Riosmena-Rodríguez and Woelkerling, 2000). Also, the report of *Bossiella californica* (Descaine) P. C. Silva (1957a) in the upper Gulf of California (Martínez-Lozano et al., 1991) needs to be verified.

The tribe Corallineae is currently represented by one genus in the northern Gulf of California.

Corallina Linnaeus

Corallina Linnaeus, 1758:646, 805.

Algae are of articulated, calcified, pinnately branched fronds, attached by a basal crustose that can be extensive. Intergenicula calcified and composed of arching tiers of medulla cells of same length, an outer cortex of pigmented cells, and single layer of epithallial cells. Cells of the adjoining filaments often fuse, with nuclear migration occurring between cells; secondary pit connections are absent. Genicula are uncalcified, composed of single tiers of long, thick-walled cells (sometimes partly calcified by overlapping ends of the intergenicula). Trichocysts, although present, are not always evident; in surface view with a central pore and a rounded base.

If fronds are grazed or removed by storms or other physical disturbances, the species can persist vegetatively by their crustose holdfasts and later grow new erect fronds. Reproductive conceptacles are axial, one per intergeniculum, usually bulging from the surface with a central pore. Conceptacles in some may occasionally bear branches. Pseudolateral conceptacles, when present, bulge conspicuously from intergenicular surfaces. Tetrasporangial conceptacles contain more than 30 tetrasporangia prior to spore discharge; bisporangia, although reported, are apparently rare. Sporangial initials divide into stalk cells with young sporangia that develop into zonate tetrasporangia. Gametangial thalli are dioecious. Carposporangial conceptacles are rounded and sometimes may have branches. Internally, they have an extensive layer of supporting cells that bear carpogonial filaments, each with a trichogyne that extends through the pore. After fertilization, a broad, thin fusion cell develops within the conceptacle and bears carposporangial filaments along its edges and sometime on the upper surface.

Spermatangial conceptacles with a pore on the characteristic projecting point (“beaked”) on the roof and internally with an upper conceptacle canal usually more than 100 μm in length. Spermatangial parent cells produced from densely packed layer of basal cells on floor and walls of conceptacle chamber. Plastids degenerating in spermatangial parent cells as they bud off spermatangia, each spermatia has a nucleus-containing “head” and an elongate “tail.”

REMARKS. *Corallina* is widespread in temperate and boreal regions, less common in subtropical areas, and absent in the tropics. Species are found from the intertidal to shallow subtidal, usually growing on rocks or other hard substrata, but may occasionally be epiphytic or epizoic. Their fronds sometimes also provide habitat for small invertebrates, such as amphipods and worms, which can bind their fronds together. In general, among the articulated corallines in the northern Gulf, *Corallina* can be distinguished by its pinnate branching.

Currently five taxa, four species, including a single variety of one species and another with two varieties, are recorded in the northern Gulf of California.

KEY TO THE SPECIES OF *CORALLINA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Intergenicula cylindrical or only slightly compressed; main axes intergenicula with 3 or more lateral branches (appearing polystichous or verticillate); conceptacles terminal . . . . **C. polysticha**

1b. Intergenicula subcylindrical basally, compressed to flattened upward, conceptacles terminal or terminal and lateral on flattened surfaces of intergenicula 2

2a. Conceptacles predominately only terminal on flattened intergenicula; branching dichotous and pinnate, or mostly verticillate 3

2b. Conceptacles both terminal and lateral on flattened to digitate intergenicula; branching opposite, pinnate or plumose (lower portions sometimes tending toward whorled) 4

3a. Branching distichous-pinnate; intergenicula greater than 1 mm wide and 1.5–1.7 mm long; lateral branches becoming shorter upward, not appressed to main axes . . . . ***C. officinalis* var. *chilensis***

3b. Branching mostly verticillate; intergenicula mostly up to 0.75 mm (but less than 1 mm) wide and 1 mm long; lateral branches short, of more or less same length throughout, laterally appressed to main axes . . . . ***C. vancouveriensis***

4a. Ultimate intergenicula simple, lanceolate or spatulate (sometimes slightly lobed) . . . . ***C. pinnatifolia* var. *pinnatifolia***

4b. Ultimate intergenicula pinnate, palmate, or flabellate, predominately digitately lobed . . . . ***C. pinnatifolia* var. *digitata***

Corallina officinalis var. _chilensis_ (Decaisne in Harvey) Kützing

FIGURE 36A

Corallina chilensis Decaisne in Harvey, 1849a:103; Smith, 1944:230, pl. 51: fig. 4; Taylor, 1945:45, pl. 62.

Corallina officinalis var. *chilensis* (Decaisne in Harvey) Kützing, 1858:32, pl. 66: fig.1; Yendo, 1902c:718, pl. 54: fig. 1, pl. 56: fig. 15; Dawson, 1953a:132, pl. 28: fig. 1; Dawson et al., 1960a:56, pl. 23: fig. 4; Dawson, 1961b:418; Dawson et al., 1964:45, pl. 62: figs. A, B; Dawson and Neushul, 1966:177; Abbott and North, 1972:75; Johansen, 1976a:405, fig. 354; Littler and Littler, 1981:148; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Mendoza-González and Mateo-Cid, 1985:28; 1986:423; Sánchez-Rodríguez et al., 1989:43; Scagel et al., 1989:168; R. Aguilar-Rosas et al., 1990:124; Martínez-Lozano et al., 1991:15; Stewart, 1991:84; Dreckmann,

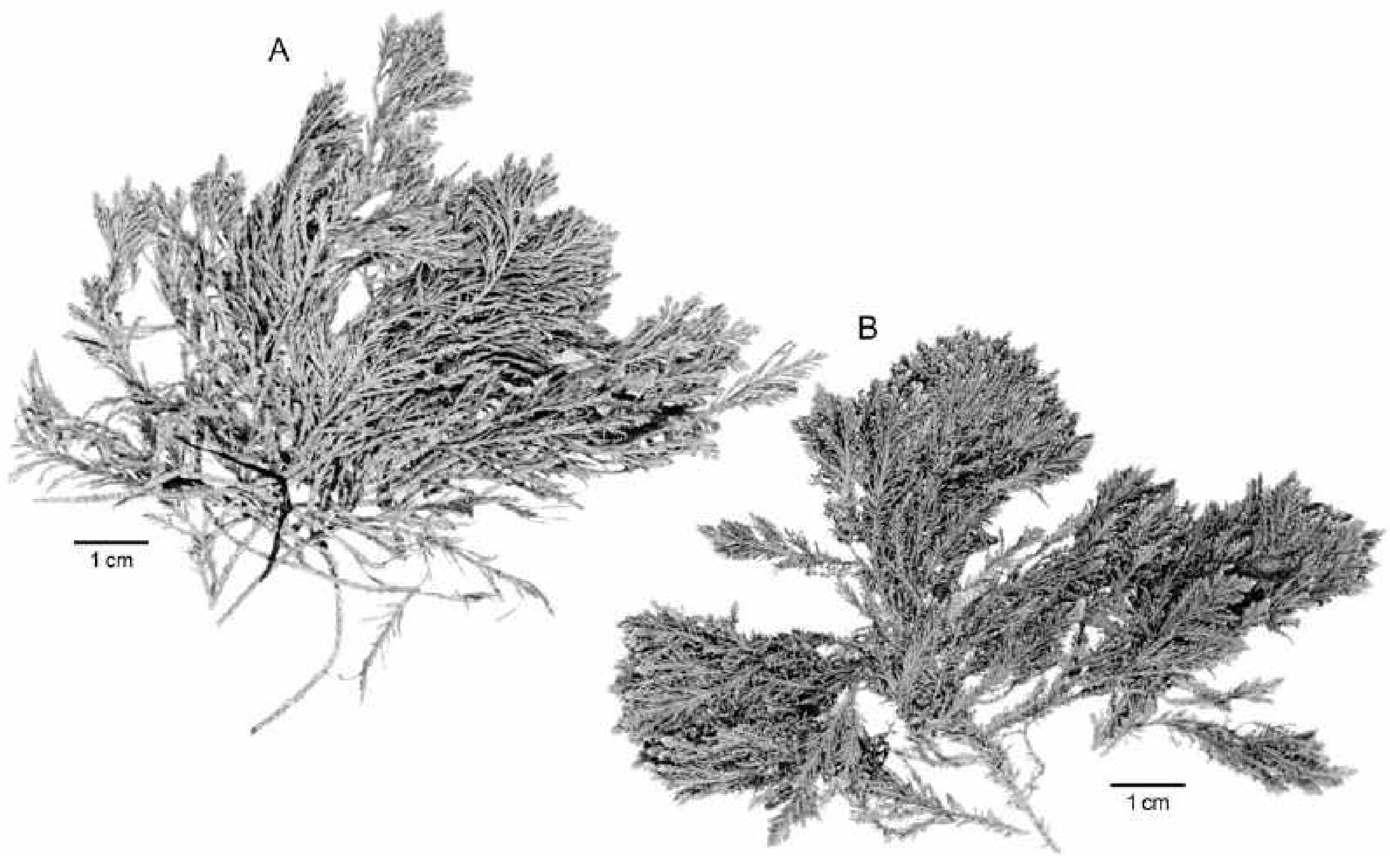

FIGURE 36. Species of *Corallina*. A. *Corallina officinalis* var. *chilensis:* Habit (*EYD-53*, AHFH, now UC). B. *Corallina vancouveriensis:* Habit (*EYD-147*, AHFH, now UC).

1991:33; Ramirez and Santelices, 1991:202; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; González-González et al., 1996:193; Riosmena-Rodríguez and Woelkerling, 2000:322; Castañeda-Fernández de Lara et al., 2010:199, tbl. 1.

Corallina officinalis f. *robusta* Setchell et N. L. Gardner, 1903:365.

Calcified articulated fronds, up to 13 cm tall; of few to several erect main axes of flat intergenicula, up to 1.5 mm long and 1–2 mm wide (at distal end); intergenicula loosely branched opposite pinnately on their upper ends, in more or less 1 plane, up to 3 orders; lateral branches subterete to flattened; ultimate branchlets lanceolate, sometimes elongated; fronds arising from a spreading crustose base.

Reproductive conceptacles mostly 500–600 µm in diameter.

Habitat. On rocks and in tide pools; low intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía Kino. Eastern Pacific: Alaska Peninsula, Alaska to Isla Magdalena (NW side of Bahía Magdalena), Baja California Sur; California Channel Islands to Islas Todos Santos (off Ensenada), Baja California; Ecuador; Peru; Chile. Western Pacific: Japan.

Type Locality. Valparaíso, Valparaíso Province, central Chile.

Remarks. *Corallina officinalis* var. *chilensis* is well known on the Pacific coast of North America (Johansen, 1976a; Scagel et al., 1989; Lindeberg and Lindstrom, 2010). The Gulf of California records of *C. officinalis* var. *chilensis* are based on the reports of Mendoza-González and Mateo-Cid (1986) and Martínez-Lozano et al. (1991); since I have not seen their specimens, the description is based on Dawson (1953a).

Corallina pinnatifolia (Manza) E. Y. Dawson var. *pinnatifolia*

FIGURE 37A

Joculator pinnatifolius Manza, 1937:47; Manza, 1940:263, pl. 1: figs. 1, 2; Taylor, 1945:198, pl. 61.

Corallina pinnatifolia (Manza) E. Y. Dawson, 1953a:124, pl. 9: figs. 7–13; 1961b:418; 1962c:278; 1966a:18; Abbott and North, 1972:75; Johansen, 1976a:405, fig. 355; Huerta-Múzquiz, 1978:336; Littler and Arnold, 1982:309; Stewart, 1982:54; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:50;

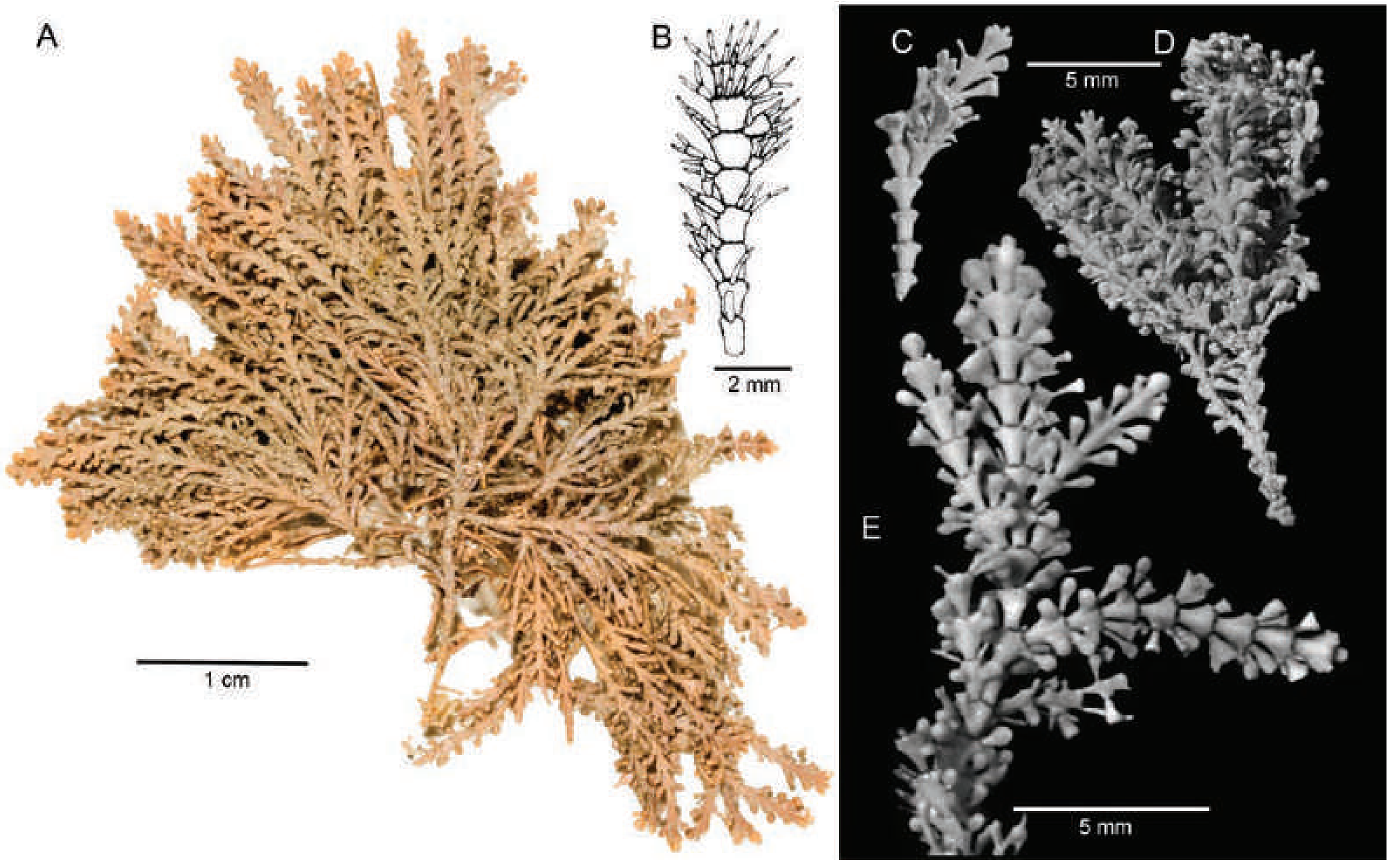

FIGURE 37. Species of *Corallina*. A. *Corallina pinnatifolia* var. *pinnatifolia:* Habit (*EYD-10673*, US Alg. Coll.-6998). B. *Corallina polysticha*: Branch of type specimen, showing the characteristic whorled, spine-like branchlets (after Dawson 1953a, pl. 9: fig. 6). C–E. *Corallina pinnatifolia* var. *digitata:* Details of intergenicula branch shapes (C, D, *JN-3687,* US Alg. Coll.; E, *JN-4593*, US Alg. Coll.).

Mendoza-González and Mateo-Cid, 1985:48; Mendoza-González and Mateo-Cid, 1986:423; Stewart, 1991:84, fig. 5 (left); Dreckmann, 1991:33; Mateo-Cid et al., 1993:46; González-González et al., 1996:193; Riosmena-Rodríguez and Woelkerling, 2000:329; R. Aguilar-Rosas et al., 2005:32.

Calcified articulated fronds mostly in compact clumps, with individual axes up to 4 cm long. Axes usually densely, pinnately to plumosely branched; axial intergenicular segments, up to 1.0(–1.5) mm long and up to 2 mm wide, with every intergenicular segment bearing mostly flattened and irregularly lobed, nonaxial indeterminate and determinate laterals. Laterals of subcylindrical to compressed segments, upward becoming flattened, usually as long as wide, up to 1.5 mm long; with a midrib and winged. Ultimate lateral branchlets usually irregularly lanceolate, sometimes spatulate or awl shaped.

Tetrasporangial conceptacles usually more abundant in lower portions of thalli; predominately terminal on modified cylindrical segments, with the tips markedly swollen (appearing to be pedicellate) or borne on flat segments or irregularly distributed and protruding on segment surfaces. Spermatangial conceptacles more or less terminal on lateral branches; appearing pedicellate with an elongated rostrum.

HABITAT. On rocks and in tide pools; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to San Felipe. Eastern Pacific: Santa Cruz Island (California Channel Islands); Santa Barbara County, California, to Punta Márquez (north of Todos Santos), Baja California Sur; Galápagos Islands.

TYPE LOCALITY. Rocky reef; Doheny State Beach, Dana Point, Orange County, southern California, USA.

REMARKS. Riosmena-Rodríguez and Siqueiros-Beltrones (1995) have questioned whether the Gulf of California specimens belong to *Corallina pinnatifolia*, suggesting all Gulf material may be *C. vancouveriensis*. The northern Gulf of California specimens referred to *Corallina pinnatifolia* or to *C. vancouveriensis* need to be compared to type locality material of each of these species using morphological and molecular DNA analyses. Until this can be done, the two species are recognized in the northern Gulf.

Corallina pinnatifolia var. *digitata* E. Y. Dawson

FIGURE 37C–E

Corallina pinnatifolia var. *digitata* E. Y. Dawson, 1953a:125, pl. 9: figs. 14–20, pl. 30: fig. 1; 1959a:20; 1961b:418; 1966a:18; Huerta-Múzquiz, 1978:337; Mendoza-González and Mateo-Cid, 1985:28; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1985:423; Stewart, 1991:84, fig. 5; Dreckmann, 1991:33; González-González et al., 1996:194; Riosmena-Rodríguez and Woelkerling, 2000:324.

Corallina pilulifera sensu Dawson, 1944a:275; Dreckmann, 1991:33 [non *Corallina pilulifera* Postels et Ruprecht, 1840:20].

Corallina frondescens sensu Johansen, 1976a:403, fig. 353 [in part; with reference to Gulf of California only]; Littler and Littler, 1981:150, 151, 153; Mendoza-González and Mateo-Cid, 1986:423; Dreckmann, 1991:33; Mateo-Cid et al., 1993:46; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:208 [non *Corallina frondescens* Postels et Ruprecht, 1840:20].

Bossiella frondescens sensu Hollenberg and Abbott, 1966:64 [in part; reference to Gulf of California only; non *Bossiella frondescens* (Postels et Ruprecht) E. Y. Dawson, 1964:540].

Calcified articulated fronds usually in compact clumps, with individual axes up to 4 cm long. Axes densely, pinnately to plumosely branched, every segment bearing lateral branches; axial intergenicular segments up to 1 mm long and up to 2 mm wide. Lateral segments flattened, characteristically flabellate to digitate, up to 2 mm long. Ultimate intergenicula larger, noticeably digitate.

Tetrasporangial conceptacles usually congested, in swollen terminal portions of modified cylindrical segments or in flattened segments; irregularly distributed on segment surfaces; primary conceptacles sometimes develop secondary conceptacles.

Habitat. On rock or other hard substrates; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Isla Turner (Turners), off SE end of Isla Tiburón); Bahía Agua Verde; Bahía Bocochibampo to Punta Colorado (vicinity of Guaymas). Eastern Pacific: Punta Santa Rosaliita (“Punta Santa Rosalía”), Baja California to Isla Magdalena (NW side of Bahía Magdalena), Baja California Sur.

Type Locality. Punta Colorado, vicinity of Guaymas, Sonora, Gulf of California, Mexico.

Remarks. Dawson (1966a) noted most of the Gulf of California specimens were *Corallina pinnatifolia* var. *digitata*. Although the variety *C. pinnatifolia* var. *digitata* was later considered to be conspecific with *C. frondescens* (Johansen, 1976a), their relationship is in need of reexamination. Northern Gulf *C. pinnatifolia* var. *digitata* should also be compared to the southern California *C. pinnatifolia* (Manza) E. Y. Dawson var. *pinnatifolia* (Dawson, 1953a). Riosmena-Rodríguez and Siqueiros-Beltrones (1995) have suggested all Gulf of California specimens identified as species of *Corallina* might be ecological variants of *C. vancouveriensis*. For now the northern Gulf *C. pinnatifolia* var. *digitata* is kept separate from the Alaskan *C. frondescens* (type locality: Unalaska Island in the Fox Islands group, eastern Aleutian Islands) and from the southern California *C. pinnatifolia* var. *pinnatifolia* and the British Columbian *C. vancouveriensis*. Studies of DNA genetic and morphological variability might spur the monographic studies needed to test the species limits and phylogenetic relationship of these taxa.

Corallina polysticha E. Y. Dawson

FIGURE 37B

Corallina polysticha E. Y. Dawson, 1953a:131, pl. 9: fig.6; pl. 29: fig. 2; 1961b:418; Abbott and North, 1972:75; Johansen, 1976a:405, fig. 356; Aguilar-Rosas, 1981:93; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Stewart and Stewart, 1984:143; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:423; Stewart, 1991:84; Anderson, 1991:22; Dreckmann, 1991:33; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:194; Riosmena-Rodríguez and Woelkerling, 2000:329; Riosmena-Rodríguez et al., 2005a:33.

Calcified articulated fronds, erect and stiff, usually clumped together above a crustose base, up to 4 cm tall; axes in lower portions often unbranched, up to 1.0 mm in diameter, gradually narrowing in diameter upward, remaining unbranched or with a few branches; axial intergenicula subcylindrical or only slightly compressed; mostly less than 1.0 mm long. Intergenicula of secondary branches with (2–)3–10 polystichous or verticillate branches.

Reproductive conceptacles ovoid, up to 500 μm in diameter; subsessile or terminal on short lateral branches (appearing verticillate). (Description is based on Dawson, 1953a).

Habitat. On rocks; intertidal.

Distribution. Gulf of California: Isla Pelícanos, Bahía Kino. Eastern Pacific: Santa Catalina Island (California Channel Islands) to Bahía de Ballenas, Baja California Sur; Isla Guadalupe.

Type Locality. About 4 km (2.5 miles) north of South Bluff, Isla Guadalupe, off Baja California, Pacific Mexico.

Remarks. Apparently rare in the Gulf of California, *Corallina polysticha* is known in the northern Gulf only from the report of Mendoza-González and Mateo-Cid (1986). It is distinguished from other species of *Corallina* by its short spine-like branchlets that are polystichous (two or more per intergenicula) or whorled on the upper ends of the intergenicula (cf.Johansen, 1976a: fig. 356). The relationship of Gulf *C. polysticha* needs to be molecularly tested with type and type locality specimens of other *Corallina* species.

Corallina vancouveriensis Yendo

FIGURE 36B

Corallina vancouveriensis Yendo, 1902c:719, pl. 54: fig. 3, pl. 55: figs. 1, 2, pl. 56: figs. 16, 17; Dawson, 1953a:126, pl. 28: fig. 2; Dawson et al., 1960a:56, pl. 21: figs. 2–4; Dawson, 1960a:43; 1961b:418; 1964:542; Hollenberg and Abbott, 1966:62; Johansen, 1976a:405, fig. 357; Littler and Littler, 1981:150; Littler and Arnold, 1982:309; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Stewart and Stewart, 1984:143; L. Aguilar-

Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:423; Scagel et al., 1989:169; Sánchez-Rodríguez et al., 1989:43; R. Aguilar-Rosas et al., 1990:124; Stewart, 1991:85, fig. 5 (right); Dreckmann, 1991:33; Mateo-Cid et al., 1993:46; Mateo-Cid and Mendoza-González, 1994b:39; R. Aguilar-Rosas and Aguilar-Rosas, 1994:521; Mendoza-González and Mateo-Cid, 1994:51; Riosmena-Rodríguez and Siqueiros-Beltrones, 1995:187; González-González et al., 1996:194; Silva et al., 1996b:232; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:129, 131; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:333; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; Riosmena-Rodríguez et al., 2005a:33; Mateo-Cid et al., 2006:56; Schubert et al., 2006:1212; Castañeda-Fernández de Lara et al., 2010:199, tbl. 1.

Corallina aculeata Yendo, 1902a:720, pl. 55: fig. 3, pl. 56: figs. 18, 19; Dawson, 1964:542.

Corallina vancouveriensis var. *aculeata* (Yendo) E. Y. Dawson, 1953a:128.

Corallina gracilis f. *densa* Collins in Collins et al., 1899: *P.B.-A.* exsiccati no. 650; Collins, 1906a:112; Smith, 1944:230, pl. 50: figs. 3–5; Dreckmann, 1991:33.

Corallina vancouveriensis var. *densa* Yendo, 1902a:719, pl. 55: fig. 1, pl. 56: fig. 17.

Corallina gracilis var. *lycopodioides* W. R. Taylor, 1945:200, pl. 65; Dreckmann, 1991:33.

Corallina vancouveriensis var. *lycopodioides* (W. R. Taylor) E. Y. Dawson, 1953a:129; Dreckmann, 1991:33.

Calcified articulated fronds violet to purplish, up to 10 cm tall; loosely tufted to mostly densely, pinnate-opposite to distichous branched, often tending toward verticillate branching. Lower axial intergenicula subcylindrical, 700–1000 µm wide and up to 1 mm long; upper intergenicula compressed, up to 1 mm long and 1 mm wide, most bearing 2–5 branches, each up to 2 mm long; branches of 1 or more intergenicula, each usually with 1 or more branchlets. Ultimate branchlets (pinnae) simple, lobed, pinnate or digitate, usually up to 1 mm long, but narrower, only 100– 500 µm in diameter.

Reproductive conceptacles up to 500 µm in outside diameter, terminal on short, thin pedicellate branchlets.

HABITAT. On rocks and in tide pools; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Puertecitos; Isla Pelícanos (Bahía Kino); Puertecitos to Bahía de La Paz. Eastern Pacific: Bering Sea and Aleutian Islands, Alaska to Punta Lobos (near Todos Santos), Baja California Sur; Islas Todos Santos (off Ensenada), Baja California; Rocas Alijos, Baja California Sur; Galápagos Islands.

TYPE LOCALITY. Port Renfrew, Vancouver Island, British Columbia, Canada.

REMARKS. The several taxonomic varieties of *Corallina vancouveriensis* recognized by Dawson (1953a) were considered to be ecological variants of a single species by Johansen (1976a). The relationship of Gulf specimens referred to *C. vancouveriensis* to the type and to other similar species is in need of further investigation. Gulf of California *C. vancouveriensis* should be critically compared to the British Columbian *C. vancouveriensis*, the Japanese *Corallina confusa* Yendo (1902a), and the Japanese "*Corallina* X" sensu Baba et al. (1988:15), which they said "appears to be identical with *C. vancouveriensis*" but which Yoshida (1998) later considered to be *C. confusa* Yendo (1902a).

CORALLINOIDEAE TRIBUS JANIEAE

Corallinoideae tribus Janieae H. W. Johansen et P. C. Silva, 1978:414; Womersley and Johansen, 1996:296.

Calcified articulated algae of the tribe Janieae are erect fronds that are primarily dichotomously branched and attached by a minute to small crustose holdfast and stolon-like holdfasts. The intergenicula are cylindrical, subcylindrical, or compressed and may be smooth, winged, or lobed.

Sporangial conceptacles contain up to 12(–15) tetrasporangia or bisporangia. Fusion cells within the carposporangial conceptacles narrow and wide, to 35 µm in height, to 130 µm wide. Spermatangial conceptacles long and narrow, lanceolate; with spermatangia along the inner walls of chamber.

REMARKS. J. H. Kim et al. (2007), using molecular analysis and morphological data, concluded that the three genera of the tribe, *Jania*, *Haliptilon*, and *Cheilosporum* (Decaisne) Zanardini (1844a, 1844b; basionym: *Amphiroa* sect. *cheilosporum* Descaine, 1842b), were congeneric, recognizing them as a single genus *Jania*. Later, Walker et al. (2009) suggested the taxonomic status and phylogenetic relationships of these three genera need further elucidation and should be based on type material. For now they are recognized as separate genera.

Two genera of tribe Janieae are represented in the northern Gulf of California.

KEY TO THE GENERA OF CORALLINACEAE SUBFAM. CORALLINOIDEAE TRIBUS JANIEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Cylindrical to subcylindrical axes primarily dichotomously branched .... ***Jania***
1b. Compressed main axes primarily pinnately branched, with cylindrical to subcylindrical branches .... ***Haliptilon***

Haliptilon **(Decaisne) Lindley**

Jania sect. *Haliptilon* Decaisne, 1842b:123, as '*Haliptylon*.'

Haliptilon (Decaisne) Lindley, 1846:26.

Articulated coralline algae, with main axes that are mostly pinnately branched, with only a few dichotomous to subdichotomous branches, arising from a crustose or stoloniferous base. Adventitious branching is present in at least one species

(*H. roseum*). Intergenicula are composed of 3–8 arching tiers of medullary cells that are often laterally fused, but without lateral pit connections. Cortex of intergenicula, composed of photosynthetic cortical cells, and an outermost single surface layer of epithallial cells. Genicula consist of a single tier of long, slender, straight, unbranched cells that are uncalcified. Trichocytes are present but not always evident; in surface view, trichocyte bases are elongate, and pores often excentric.

Reproductive conceptacles, with a central pore, are developed in medullary meristems, axial and terminal on a fertile intergeniculum. Tetrasporangial and carposporangial conceptacles usually have extended branchlets. Tetrasporangial conceptacles are swollen and develop zonately divided tetrasporangia. Sexual thalli are dioecious. Carpogonial conceptacles contain the supporting cells and 2-celled carpogonial filaments (carpogonium with an elongated trichogyne) along its base. Carposporangia develop from short gonimoblast filaments near the edges of a relatively thick fusion cell. Spermatangial conceptacles are elongate ovoid to fusiform, without branchlets, with basal cells and spermatangial parent cells along the inside of its high walls.

REMARKS. On the basis of their phylogenetic analyses of some members of the tribe Janieae, J. H. Kim et al. (2007) concluded that the genera *Jania, Haliptilon,* and *Cheilosporum* (Descaine) Zanardini (1844a) should be merged into a single genus, *Jania*, as it is the oldest validly published. Because of the uncertain generic status of the taxon of *Haliptilon* in the Gulf of California, for now it is left in that genus until its taxonomic status can be investigated.

There is one taxon of *Haliptilon* reported in the Gulf of California.

Haliptilon roseum var. *verticillatum* (E. Y. Dawson) J. N. Norris, *comb. nov.*

Corallina gracilis var. *verticillata* E. Y. Dawson, 1953a:130, pl. 25: fig. 1; 1961b:418; Stewart and Stewart, 1984:143; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1985:28; González-González et al., 1996:193.

Haliptilon gracile var. *verticillatum* (E. Y. Dawson) Garbary et H. W. Johansen, 1982:218.

Corallina subulata sensu Setchell and Gardner, 1930:179; Stewart and Stewart, 1984:143 [non *Corallina subulata* J. Ellis et Solander, 1786:119; =*Haliptilon subulatum* (J. Ellis et Solander) H. W. Johansen, 1970:79].

Algae erect, calcified, articulate, up to 4 cm tall; in clumps of several main axes, subcylindrical below, compressed above, up to 600 μm in diameter, branching to 2–3(–5) orders; lateral branching prominent, more or less irregularly verticillate, lateral branchlets densely covering main axes, mostly 4–5 cm long, slender, attenuating upward to about 70 μm in diameter (rarely larger than 200 μm in diameter at base).

Reproductive conceptacles; ovoid, 300–450 μm with long, antenna-like extensions; terminal on long pedicel of ultimate branchlets. (Description after Dawson, 1953a.)

HABITAT. On rocks; intertidal.

DISTRIBUTION. Gulf of California: Bahía de La Paz. Eastern Pacific: Santa Catalina Island (California Channel Islands); Isla Guadalupe (off Baja California).

TYPE LOCALITY. On intertidal rocks; Isla Guadalupe, Baja California, Pacific Mexico.

REMARKS. Reported in the southern Gulf, *Haliptilon roseum* var. *verticillatum* (Huerta-Múzquiz and Mendoza-González, 1985, as *Corallina gracilis* var. *verticillatum*) has coarser main axes with prominent, irregular verticillate branches. It differs from *H. roseum* (Lamarck) Garbary et H. W. Johansen (1982) var. *roseum* as known in California (Johansen, 1976a, as *H. gracile* (J. V. Lamouroux) H. W. Johansen, 1971, var. *gracile*), which has main axes that are pinnately branched in more or less distichous manner (i.e., alternately in two vertical rows on opposite sides of main axis).

Womersley and Johansen (1996; see also Johansen and Womersley, 1986), in recognizing *Haliptilon roseum* (Lamarck) Garbary et H. W. Johansen (1982), considered *Corallina gracilis* J. V. Lamouroux (1816; basionym of *H. gracilis* (J. V. Lamouroux) H. W. Johansen, 1971) to be conspecific with the Australian *Corallina rosea* Lamarck (1815). Although the latter was referred to *Jania rosea* (Lamarck) Decaisne (1842b; see J. H. Kim et al., 2007:1317), Walker et al. (2009) stated that relationship of the genera *Haliptilon* and *Jania* was in need of further study.

Herein a new combination, *H. rosea* var. *verticillata*, is proposed for the Pacific Mexico variety. Comparisons of the little-known Gulf of California material with type locality specimens of *H. roseum* var. *verticillata* need be studied to evaluate their generic placement and taxonomic status and phylogenetic relationship to the generitypes of *Haliptilon*, *Corallina*, and *Jania*.

Jania J. V. Lamouroux

Jania J. V. Lamouroux, 1812:186.

Articulated coralline thalli are erect, heavily calcified, dichotomously branched throughout, and may be attached to rocks or shells or epiphytic on other algae or sea grasses. They are primarily attached by a minute crustose base or initially by a crustose base and secondarily by stolons. Branching in most species is usually dichotomous. One species, *J. huertae*, is also trichotomously or polychotomously branched. Branchlets or pinnae are known in only a few taxa. Intergenicula (segments) are calcified and usually cylindrical or occasionally subcylindrical but in a few are compressed; they are usually considerably longer than broad and are composed of arching tiers of medullary cells, an outer cortex of pigmented cells, and an outermost single layer of epithallial cells. Medullary cells are in tiers that are all the same height. Cells are without pit connections. Trichocytes are present but are not always evident; trichocyte bases are elongate in surface view, with pores often excentric. Genicula (joints) are uncalcified and consist of a single tier of long, straight cells (sometimes partially covered by overlapping calcification of intergenicula).

Vegetative propagation can occur when a thallus or portions of the fronds become unattached and then entangled in other algae or may settle and continue to grow, reattaching by production of stolons. Reproductive structures begin development from the uppermost medullary cells. The conceptacles, with a central pore, are terminal on the intergenicula of branch apices. Tetrasporangial conceptacles contain fewer than 15 zonately divided sporangia that develop from an initial stalk and immature sporangium. Gametangial thalli are usually dioecious, although at least one species is monoecious. Carpogonial conceptacles have supporting cells and carpogonial filaments, each with a single carpogonium and an elongate trichogyne. After fertilization, gonimoblast filaments arise from the margins of narrow thick fusion cells and bear carpospores. Spermatangial conceptacles are long and narrow, more or less lanceolate (Johansen, 1972); inside chambers are 90–250 µm in diameter, with their upper walls lined with basal cells and spermatangial parent cells and a canal up to 120 µm long.

REMARKS. Two species are reported to occur in the southern Gulf (Dawson, 1953a, 1959a, 1961b; Huerta-Múzquiz and Mendoza-González, 1985; Riosmena-Rodríguez and Woelkerling, 2000): *Jania subpinnata* E. Y. Dawson (1953a), described from La Paz, Baja California Sur, and *J. pacifica* Areschoug (1852; type locality: Huatulco, Oaxaca) from Bahía de La Paz (Cruz-Ayala et al., 2001) and Bahía de Banderas, Nayarit-Jalisco (Serviere-Zaragoza et al., 1993a, 1998), and in Pacific Mexico from Michoacán to Oaxaca (León-Tejera et al., 1993).

Eight taxa, including seven species, one with a unique variety, are reported in the northern Gulf of California.

KEY TO THE SPECIES OF *JANIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli of markedly compressed intergenicula throughout . . . . **J. tenella** **var.** ***zacae***
1b. Thalli of cylindrical intergenicula throughout or to only slightly compressed 2
2a. Thalli dichotomously, subdichotomously, and trichotomously branched and sometimes polychotomously branched (giving a whorled appearance) . . . . ***J. huertae***
2b. Thalli dichotomously branched throughout 3
3a. Thalli decussately dichotomously branched; branch angles wide, mostly greater than 45°; branch intergenicula (segments) 60–180 µm in diameter 4
3b. Thalli not decussately branched; branch angles narrower, mostly less than 45°, but up to about 30°; branch intergenicula (segments) mostly 120–200 µm in diameter 5
4a. Branch angles wide, 60°–90º; branch intergenicula (segments) mostly 60–100 µm in diameter; mostly 5–6 times longer than wide, 300–600 µm in length . . . . ***J. capillacea***
4b. Branch angles also wide, up to or often greater than 45°; branch intergenicula wider in diameter, mostly 120–180 µm; about 2.5–5.0 times longer than wide, 300–900 µm in length . . . . ***J. decussato-dichotoma***
5a. Branch angles mostly less than 30°; branch intergenicula 120–200 µm in diameter; 2–5 times longer than wide, 240–700(–1000) in length . . . . ***J. adhaerens***
5b. Branch angles usually narrow; intergenicula 60–200 µm in diameter, 2.5–11 times longer than wide 6
6a. Branching not densely dichotomous; branch intergenicula very long, 6–11 times longer than wide, 720–1650 µm in length; mostly wider in diameter, 120–150 (–210) µm in diameter . . . . ***J. longiarthra***
6b. Branching more or less densely subdichotomous in upper portions; branch intergenicula shorter in length, 1–5 times longer than wide, about 100–600(–800) µm in length; usually narrower in diameter, 60–150 µm in diameter 7
7a. Branch intergenicula narrow, 60–120 µm in diameter; mostly 2.5–5.0 times longer than wide, 150–600 µm in length; tetrasporangial conceptacles terminal (not conspicuously or predominately seriate) . . . . ***J. tenella*** **var.** ***tenella***
7b. Branch intergenicula 120–150(–200) µm in diameter; mostly 1–2 times longer than wide, 120–150 in diameter in upper portions and 170–205 µm in lower portions; tetrasporangial conceptacles seriate . . . . ***J. mexicana***

Jania adhaerens J. V. Lamouroux

FIGURES 38, 39A

Jania adhaerens J. V. Lamouroux, 1816:270; Yendo, 1902a:24, pl. 3: fig. 4; pl. 7: fig. 5; Setchell and Gardner, 1930:179; Dawson, 1961b: 419; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Johansen, 1971:247; Abbott and North, 1972:76; Johansen, 1976a:418, fig. 370 [in part, excluding *J. decussato-dichotoma*]; Littler and Arnold, 1982:309; Huerta-Múzquiz and Mendoza-González, 1985:50; Stewart, 1991:86; Sánchez-Rodríguez et al., 1989:43; Mateo-Cid and Mendoza-González, 1991:20; Dreckmann, 1991:33; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:18; León-Tejera and González-González, 1993:496; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:46; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:106; González-González et al., 1996:413; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Yoshida, 1998:566; Serviere-Zaragoza et al., 1998:174; Riosmena-Rodríguez et al., 1998:28; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; Johansen, 1999:187, fig. 187; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:320; Mateo-Cid et al., 2000:64; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; Hernández-Herrera et al., 2005:148; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:208; Castañeda-Fernández de Lara et al., 2010:200; Fernández-García et al., 2011:62.

Corallina adhaerens (J. V. Lamouroux) Kützing, 1858:40, pl. 83: fig. 2a–f.

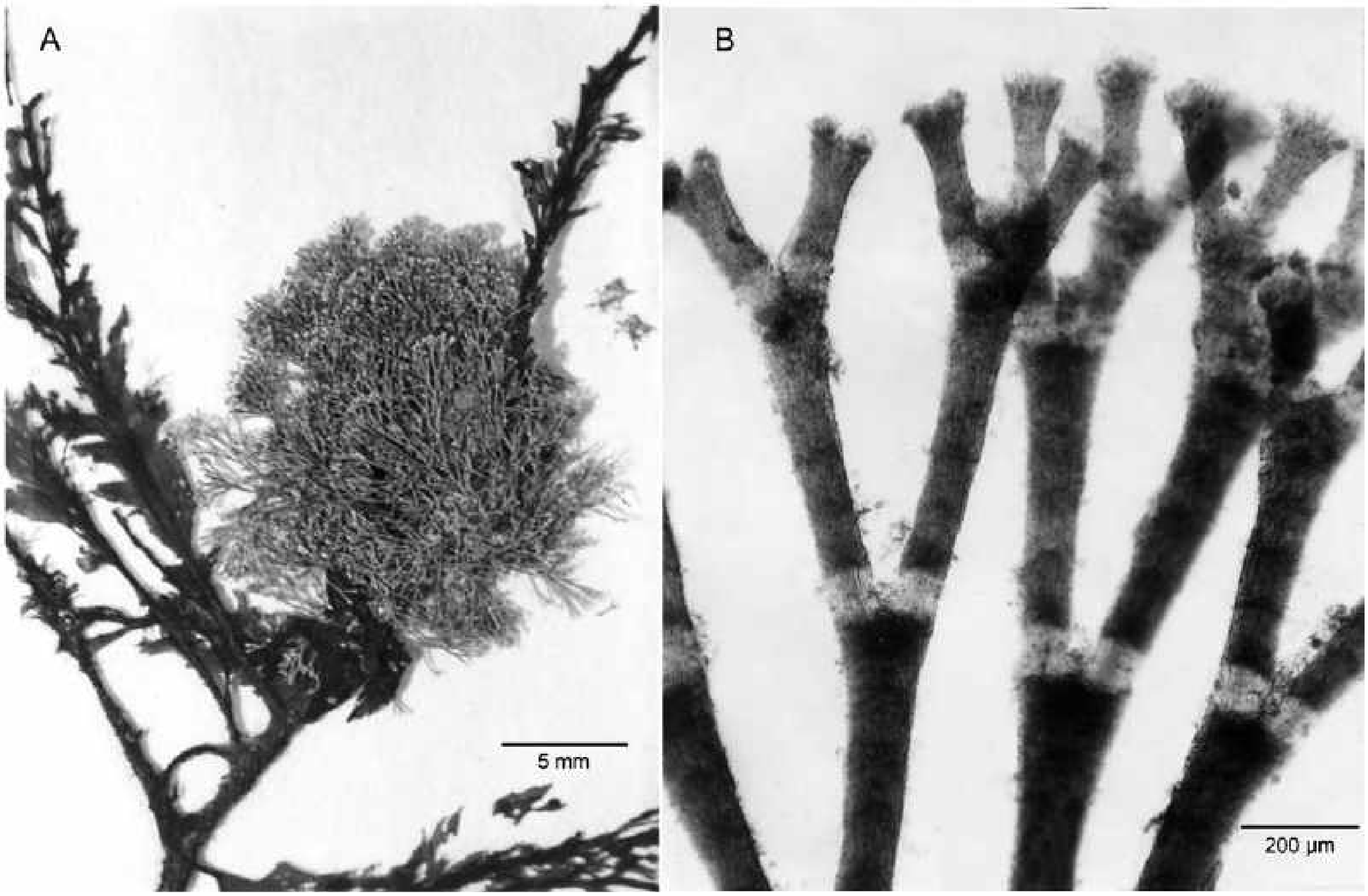

FIGURE 38. *Jania adhaerens*: A. Habit, epiphytic on *Sargassum* (*JN-3632*, US Alg. Coll.). B. Upper branches showing uncalcified genicula (joints) between intergenicula (*JN & HWJ-73-7-12*, US Alg. Coll.).

Articulated coralline algae, small and erect; forming dichotomously branched brittle turfs, usually less than 2 cm tall; above a crustose base, and secondarily attached by creeping, rhizomatous basal segments with lateral discoid holdfasts. Branch apices generally acute angles, mostly less than 30°. Intergenicula (segments) heavily calcified, cylindrical, sometimes slightly flattened at branch dichotomies; mostly 100–200 µm in diameter and (240–)300–700(–1000) µm in length.

Tetrasporangial conceptacles vase shaped, surmounted with swollen branches, 200–300 µm in outside diameter and 300–350 µm in length. Carposporangial conceptacles similar to tetrasporangial conceptacles in outer appearance. Male conceptacles different; long and narrow and not surmounted by branches.

HABITAT. Epiphytic or on hard surfaces, such as rocks, and in tide pools; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: southern California to Todos Santos, Baja California Sur; Isla Guadalupe; Isla Socorro (Islas Revillagigedo); Colima; Oaxaca; Ecuador. Central Pacific: Hawaiian Islands. Western Pacific: China; Japan; Korea; Vietnam.

TYPE LOCALITY. "Méditerranée?" (Lamouroux, 1816:270); locale was stated with doubt as "Mediterranean Sea?" (see Silva et al., 1996a; Lipkin and Silva, 2002).

REMARKS. Yendo (1902a) noted that the original description of *Jania adhaerens* J. V. Lamouroux (1816) could also apply to his *J. decussato-dichotoma* Yendo (1905) as well. Since then, the distinctiveness of these two has been questioned by some (e.g., Johansen, 1971; Yoshida, 1998), and Price and Scott (1992) have considered *J. decussato-dichotoma* conspecific with *J. adhaerens*. Others have continued to recognize them as separate species, e.g., Dawson (1953a) and Silva et al. (1987, 1996a).

Many of the Gulf specimens of *Jania adhaerens* and *J. decussato-dichotoma* are very close, making distinctions between the two in the Gulf difficult and raising the question of whether the Gulf of California has one or both species. For example, those of the upper Gulf from Puerto Peñasco (Dawson, 1966a, as *J. decussato-dichotoma*) are similar enough morphologically

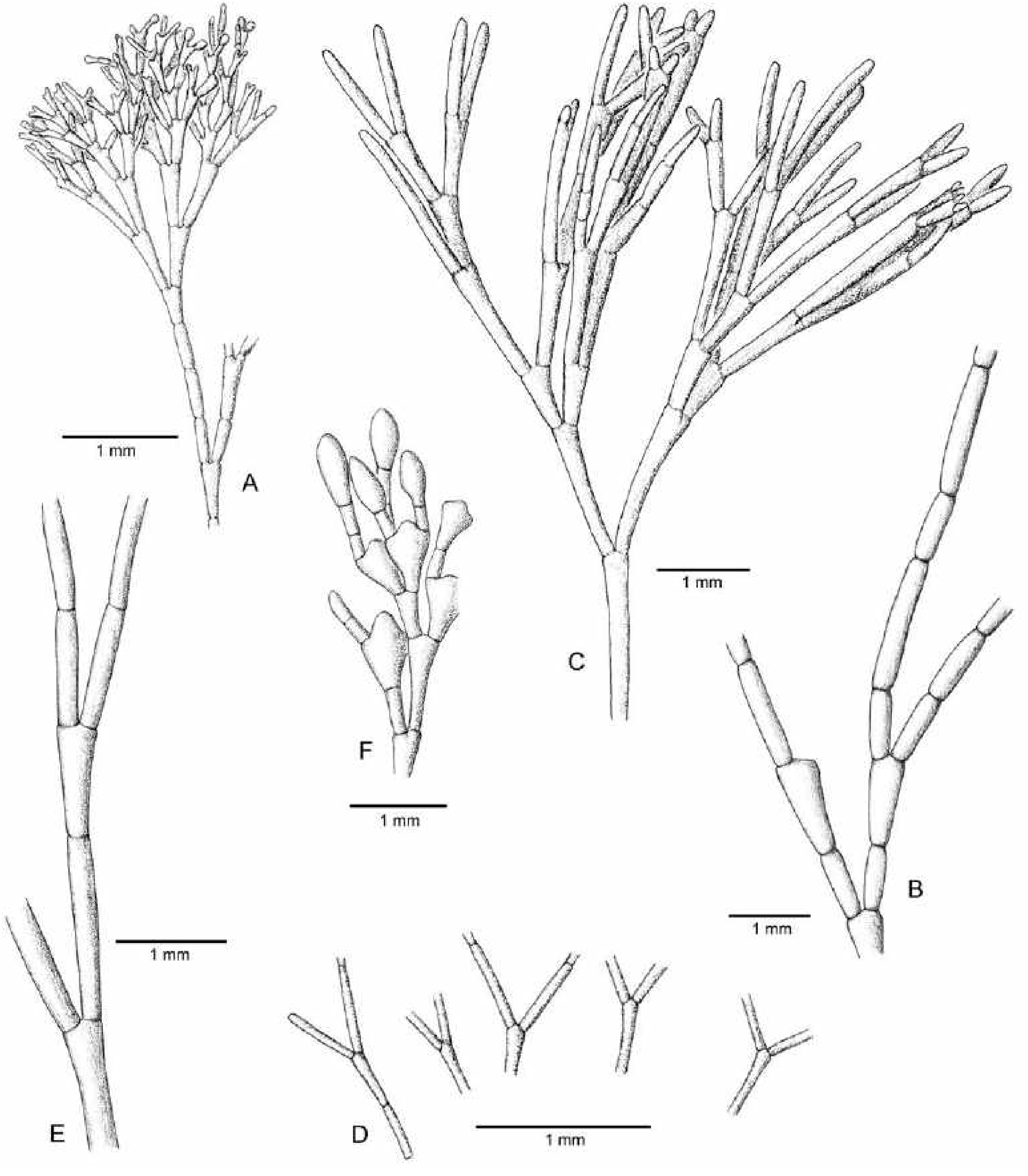

FIGURE 39. Branching pattern and branch width variation in species of *Jania*: A. *Jania adhaerens* (*JN-3529*, US Alg. Coll.). B. *Jania crassa* (drawn from type specimen, CN). C. *Jania longiarthra* (*EYD-18920,* US Alg. Coll.-8022). D. *Jania capillacea* (drawn from type specimen, TCD). E. *Jania longiarthra* (drawn from type specimen, AHFH, now UC). F. *Jania mexicana* (drawn from type specimen, MICH).

to agree with the broadly defined species concept of *J. adhaerens* sensu Johansen (1976a). However, until detailed studies of the Gulf material can be compared to the types and type locality specimens of the Mediterranean *J. adhaerens* and the Japanese *J. decussato-dichotoma,* the two are kept separate.

Jania capillacea Harvey

FIGURES 8A, 39D

Jania capillacea Harvey, 1853:84; Taylor, 1945:195; Dawson, 1953a:116, pl. 9: fig. 1; Tanaka, 1956:57, fig. 6; Dawson, 1957a:4; 1957c:20; 1959a:22; 1961b:419; 1966a:17; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:8, 11; Huerta-Múzquiz, 1978:338; Littler and Littler, 1981:151, 153; Schnetter and Bula-Meyer, 1982:130, pl. 20: fig. C, pl. 21: fig. A; Stewart and Stewart, 1984:144; Salcedo-Martínez et al., 1988:83; Dreckmann, 1991:33; León-Tejera and González-González, 1993:496; Serviere-Zaragoza et al., 1993a:484; Stout and Dreckmann, 1993:12; González-González et al., 1996:320, 398; Yoshida, 1998:567; Serviere-Zaragoza et al., 1998:174; Riosmena-Rodríguez and Woelkerling, 2000:322; Mateo-Cid et al., 2006:56; Bernecker, 2009:CD-Rom p. 59; Fernández-García et al., 2011:62.

Jania rubens sensu Dawson, 1944a:277 [in part; non *Jania rubens* (Linnaeus) J. V. Lamouroux, 1816:272; basionym: *Corallina rubens* Linnaeus, 1758:806].

Articulated coralline algae forming short tufts, mostly less than 1.0 cm tall; branching dichotomously or sometimes more or less decussate; branch angles very wide, 60°–90°; attached by a disc, secondary attachment discs often found on portion of branches in contact with substratum. Intergenicula (segments) cylindrical, 50–100 μm in diameter (ultimate branches usually more slender), (240–)300–600(–1000) μm in length.

Asexual reproduction by triangular propagules, 150–200 μm in diameter, with long antenna-like branches from each upper corner (Dawson, 1953a: pl. 9: fig. 1). Reproductive conceptacles apparently rare. Tetrasporangial conceptacles, terminal, about 300 μm wide, upper end rostrate or with 2–3 antenna-like branches.

HABITAT. Usually growing among other turf algae, sometimes on rocks or epizoic on sponges; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Isla Ángel de la Guarda to Cabo San Lucas; Nayarit to Jalisco. Eastern Pacific: Isla Guadalupe; Isla Cedros; Isla Socorro (Islas Revillagigedo); Isla Clipperton; Baja California to Guerrero; El Salvador; Costa Rica; Panama; Colombia; Ecuador; Galápagos Islands.

TYPE LOCALITY. Bahia Honda Key (Bahia Honda State Park), Florida Keys, Monroe County, Florida, USA.

REMARKS. Although *Jania capillacea* is generally recognized as a distinct species (e.g., Wynne, 2005), Cribb (1983) and Price and Scott (1992) have considered it to be conspecific with *J. adhaerens*. The relationship of Gulf of California *J. capillacea* to Gulf *J. adhaerens* and to the type material of each these species needs to be tested.

Jania decussato-dichotoma (Yendo) Yendo

Corallina decussato-dichotoma Yendo, 1902a:25, pl. 3: figs. 1–3; pl. 7: figs. 3, 4; Yendo, 1902b:194.

Jania decussato-dichotoma (Yendo) Yendo, 1905:37; Dawson, 1953a:117, pl. 27: fig. 3; 1959a:22; 1961b:419; 1966a:17; Johansen, 1971:247; Abbott and North, 1972:72; Huerta-Múzquiz, 1978:337; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:423; Dreckmann, 1991:33; González-González et al., 1996:229; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Riosmena-Rodríguez and Woelkerling, 2000:323.

Jania rubens sensu Dawson, 1944a:277 [in part; non *Jania rubens* (Linnaeus) J. V. Lamouroux, 1816:272; basionym: *Corallina rubens* Linnaeus, 1758:806].

Articulated coralline algae forming dense tufts, 1–2 cm tall, 1.0 cm or more wide; branching irregularly decussate-dichotomous; branch angles usually wide, mostly over 45°. Intergenicula cylindrical, mostly 120–180 μm in diameter, about 2.5–5.0 times longer than wide (250–900 μm long). Branch apices blunt.

Tetrasporangial conceptacles infrequent, terminal, 210–300 μm in diameter, urn shaped, slightly rostrate, with or without antenna-like extensions.

HABITAT. On rocks or other hard substratum; sometimes on sponges; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Jalisco. Eastern Pacific: San Diego, California.

TYPE LOCALITY. Three syntype localities in Japan were listed by Yendo (1902a): Miskai (Kanagawa Prefecture), Honshū Island; Province Boshū (Chiba Prefecture), Honshū Island; and Province Hiuga (Hyūga) (Miyazaki Prefecture), Kyûshû Island.

REMARKS. *Jania decussato-dichotoma* has been considered a synonym of *J. adhaerens* (Johansen, 1971), but others continue to recognize them as separate (e.g., Silva et al., 1996a; Riosmena-Rodríguez and Woelkerling, 2000; Guiry and Guiry, 2008–2010). (See also Remarks under *Jania adhaerens*.)

Jania huertae Chávez-Barrear

FIGURE 40

Jania huertae Chávez-Barrear, 1972a:133, figs. 1–5; Dreckmann, 1991:33; González-González et al., 1996:320; Riosmena-Rodríguez and Woelkerling, 2000:326.

Articulated coralline algae, 1.5–2.0 cm tall; branching dichotomous to subdichotomous, trichotomous, or sometimes polychotomous (appearing verticillate); branch angles up to 45°. Intergenicula cylindrical, 50–60 μm in diameter, 5–7 times longer than wide, 250–360 (-420) μm in length. Some branches flagelliform, of 20–22 narrow intergenicula, basally 30–40 μm in diameter, decreasing upward to 10 μm or less in diameter.

Tetrasporangia unknown. Carposporangial conceptacles 330 μm long, 170 μm wide; variable in position, sometimes terminal or at base of branches. Spermatangia unknown.

HABITAT. Growing with other turf-forming algae; intertidal.

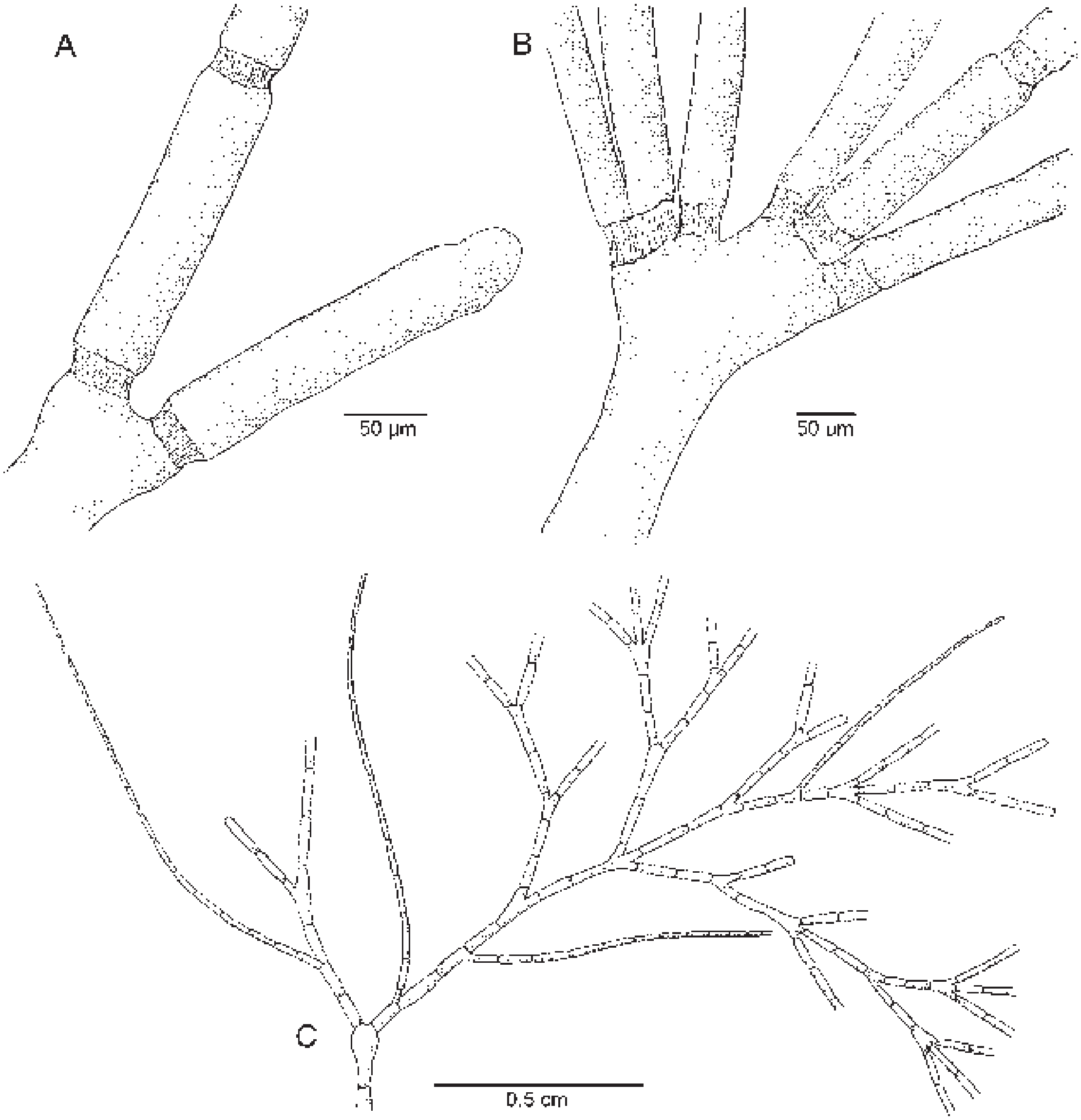

FIGURE 40. *Jania huertae* (type): A. Subdichotomous branch. B. Trichotomous branching. C. Typical branching pattern (after Chávez-Barrear, 1972a: figs. 2, 4, 5).

Distribution. Gulf of California: Isla Pelícanos, Bahía Kino.

Type Locality. Southeast of Isla Pelícanos, near Bahía Kino, Sonora, Gulf of California, Mexico.

Remarks. *Jania huertae* was described from the northern Gulf of California, where thus far it is only known from the type specimen. Chávez-Barrear (1972a) noted that some western Atlantic material from Yucatán, Gulf of Mexico, was also in agreement with the type specimen, commenting that the species has a wider distribution. Although *J. huertae* was reported from Quintana Roo (M. Aguilar-Rosas et al., 1998), Ortega et al. (2001) could not confirm its presence in Caribbean Mexico.

Jania longiarthra E. Y. Dawson

FIGURE 39C,E

Jania longiarthra E. Y. Dawson, 1953a:119, pl. 9: fig. 4, pl. 27: fig. 4; 1957c:20; 1959a:22; 1959d:4; 1961b:420; Abbott and North, 1972:76; Pedroche and González-González, 1981:66; Anderson, 1991:29; Dreckmann, 1991:33; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:229; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Paul-Chávez and Riosmena-Rodríguez, 2000:147;

Riosmena-Rodríguez and Woelkerling, 2000:326; Hernández-Herrera et al., 2005:148; Mateo-Cid et al., 2006:56; Bernecker, 2009:CD-Rom p. 59; Fernández-García et al., 2011:62.

Articulated coralline algae, erect, up to 2.5 cm tall, forming coarse tufts; usually densely dichotomously branched, sometimes irregularly decussate; branching at very narrow angles (much less than 30°); arising from a crustose base. Intergenicula cylindrical or occasionally compressed where branches arise, unconstricted, with smooth surfaces; (150–)200–500 µm in diameter, about 6–11 times longer than wide (720–5500 µm in length). Genicula 120–150(–210) µm long, about 125–260 µm in diameter.

Reproductive conceptacles not known.

Habitat. Growing among other turf algae; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas; Isla Carmén to Isla Espíritu Santo; Nayarit to Jalisco. Eastern Pacific: Punta Banda (Baja California); Clipperton Island (Île de la Passion); Costa Rica.

Type Locality. Bahía San Gabriél, Isla Espíritu Santo, Baja California Sur, Gulf of California, Mexico.

Remarks. Originally described from the southern Gulf, *Jania longiarthra* has since been reported in the upper Gulf (Mateo-Cid et al., 2006). It differs from other species of *Jania* reported in the Gulf by its characteristically very long intergenicula (segments) and narrow angles of branching (Dawson, 1953a). A single Pacific Baja California specimen, from Bahía Sebastián Vizcaíno, was tentatively referred to *J. longiarthra* by Dawson (1953a). It has also been reported in the Indian Ocean (Silva et al., 1996a). Specimens of Gulf *J. longiarthra* can resemble the California *Jania crassa* J. V. Lamouroux (sensu Johansen, 1976a; Stewart, 1991), and their relationship to each other and especially to the type of *J. crassa* (Figure 39B; type locality: Dusky Sound, New Zealand) requires further study.

Jania mexicana W. R. Taylor

FIGURE 39F

Jania mexicana W. R. Taylor, 1945:197, pl. 60 [type specimen]; Dawson, 1953a:119; 1961a:420; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Huerta-Múzquiz, 1978:339; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:423; Salcedo-Martínez et al., 1988:83; González-González et al., 1996:229; Riosmena-Rodríguez et al., 2005a:34; Serviere-Zaragoza et al., 2007:10.

Articulated coralline algae forming small, erect, dense tufts, about 1.5–2.3 cm tall; subcorymbose; axes terete, intergenicular segments cylindrical, 240–425 µm long, 170–205 µm in diameter in lower portions, narrowed in upper portions, 120–150 µm in diameter; branch apices rounded.

Tetrasporangial conceptacles ovoid, about 300 µm in diameter, with two uppermost horn-like projections, later developing into antenna-like branchlets of 1 to several segments; each can repeatedly produce additional conceptacles, forming 1–4 successive dichotomous divisions, making the reproductive branch more divergent than the vegetative branches. Cystocarpic branches not known. Spermatangial thalli of narrow branch angles; spermatangial conceptacles ellipsoidal, elongate, 450–600 µm in length, 240–280 µm in diameter, with terminal acute apices (not antenna-like); spermatia fusiform, about 5 µm long, 2 µm in diameter. (Description after Dawson, 1953a).

Habitat. Growing on rocks or sometimes attached to barnacles; intertidal.

Distribution. Gulf of California: Segundo Cerro Prieto to Roco Rojo, Bahia Kíno; Isla Tiburón and Estero Punta Perla (on Isla Tiburón); Báhia de La Paz; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Bahía de Ballenas, Baja California Sur; Colima to Oaxaca; Islas Revillagigedo.

Type Locality. Bahía de Petatlán, vicinity of Zihuatanejo, Guerrero, Pacific Mexico.

Remarks. Apparently more common on the tropical mainland coast of Pacific Mexico, *Jania mexicana* has also been reported in the northern Gulf by Mendoza-González and Mateo-Cid (1986). A densely tufted species, the successive compounding of the tetrasporangial conceptacles is apparently unique to *J. mexicana* (Dawson, 1953a). Since I have not seen their collections, the description is based on Taylor (1945) and Dawson (1953a).

Jania mexicana (Figure 39F: isotype, MICH), described from Bahía de Petatlán, Guerrero (15°34′N, 101°29′W), needs critical comparison with another Pacific Mexico species, *J. pacifica* Areschoug (1852), described from Huatulco, Oaxaca (15°78′N, 96°27′W). Silva et al. (1987) had earlier considered these two to be conspecific, and their relationship needs to be further tested.

Jania tenella (Kützing) Grunow var. *tenella*

Corallina tenella Kützing, 1858:41, pl. 85: fig. 2; Grunow, 1867:78 [as "*Corallina* (*Jania*) *tenella*"].

Jania tenella (Kützing) Grunow, 1874:42; Dawson, 1949b:25; 1953a:120, pl. 9, fig. 3 [isotype branch of *Corallina tenella* Kützing]; 1957a:6; 1959a:22; 1959d:4; Dawson et al., 1960b:7; Dawson, 1961b:420; 1966a:17; Abbott and North, 1972:76; Johansen, 1976a:418, fig. 372; Devinny, 1978:360; Huerta-Múzquiz, 1978:339; L. Aguilar-Rosas, 1981:93; Stewart and Stewart, 1984:144; Huerta-Múzquiz and Mendoza-González, 1985:50; Santelices and Abbott, 1987:8; Sánchez-Rodríguez et al., 1989:43; Dreckmann et al., 1990:30; Martínez-Lozano et al., 1991:24; Ramírez and Santelices, 1991:208; Mateo-Cid and Mendoza-González, 1991:20; Dreckmann, 1991:33; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:18; Servière-Zaragoza et al., 1993a:484; León-Tejera et al., 1993:200; Stout and Dreckmann, 1993:12; Mendoza-González et al., 1994:106; Mendoza-González and Mateo-Cid, 1994:51; León-Álvarez and González-González, 1995:363; González-González et al., 1996:229; Silva et al., 1996b:232; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Serviere-Zaragoza et al., 1998:174; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:331; Cruz-Ayala et al., 2001:191; L. Aguilar-Rosas et al., 2002:234; López et al., 2004:12; Hernández-Herrera et al., 2005:148; Silva and Chacana, 2005:110, fig. 5; Mateo-Cid et al., 2006:56; Schubert et al., 2006:1212; Serviere-Zaragoza et al., 2007:10;

Bernecker, 2009:CD-Rom p. 59; Castañeda-Fernández de Lara et al., 2010:200; Fernández-García et al., 2011:62.

Jania rubens sensu Setchell and Gardner, 1930:179 [non *Jania rubens* (Linnaeus) J. V. Lamouroux, 1816:272; basionym: *Corallina rubens* Linnaeus, 1758:806].

Articulated coralline algae forming dense tufts of congested branches, 1.0–2.0 cm tall, usually epiphytic, occasionally on rocks; branching dichotomous, at narrow angles; attached by a usually inconspicuous disc. Intergenicula cylindrical (or sometimes with lower intergenicula very slightly compressed), 60–100(–120) µm in diameter, mostly 2.5–5.0 times longer than wide, 150–600(–720) µm in length.

Tetrasporangial and carposporangial conceptacles, urn shaped, up to 250 µm in diameter, with long extensions from prominent shoulders. Spermatangial conceptacles, elongate ellipsoidal, about 300 µm in length, 150 µm in diameter.

Habitat. Epiphytic on various algae, often covering much of the host; occasionally on rocks; mid to low intertidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Puerto Peñasco; Bahía de La Paz to Cabo Pulmo; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Santa Catalina Island (California Channel Islands); southern California to Bahía Magdalena, Baja California Sur; Rocas Alijos; Isla San Benedicto (Islas Revillagigedo); Colima to Guerrero; Costa Rica; Chile; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: Japan.

Type Locality. Syntype localities: “in sinu neapolitano et ad oras mexicanas” (Kützing, 1858:41). Lectotype locality: Golfo di Napoli, Italy, given by Dawson (1953a; Silva et al., 1996a), and later Mexico, cited by South and Skelton (2003).

Remarks. *Jania tenella* is apparently restricted to the warmer subtropical waters of the Gulf of California.

Jania tenella var. *zacae* E. Y. Dawson

Jania tenella var. *zacae* E. Y. Dawson, 1953a:121, pl. 8: fig. 3, pl. 31: fig. 1; 1957c:20; 1961b:420; 1962d:394; Anderson, 1991:30; León-Álvarez and González-González, 1995:363; González-González et al., 1996:230; Serviere-Zaragoza et al., 1998:174; Riosmena-Rodríguez and Woelkerling, 2000:333; Bernecker, 2009:CD-Rom p. 59; Fernández-García et al., 2011:62.

Articulated coralline algae forming small epiphytic tufts of several erect, branched thalli, up to 1–2 cm tall; arising on a small discoid base, up to 1 mm in diameter. Dichotomously branched at very narrow angles; branch intergenicula compressed to flattened throughout, 130–160 µm wide, 2.0–2.5 times longer than wide, about 250–460 µm in length; upper branches narrower, 70–100 µm wide, about 140–250 µm long.

Tetrasporangial conceptacles urn shaped, slightly compressed, about 300 µm wide; rostrate, with a simple or forked antenna-like branch from each upper shoulder. Carpogonial conceptacles unknown. Spermatangial conceptacles, more or less cylindrical, ellipsoid, about 150 µm in diameter, 300 µm long; terminal on branches, without antenna-like branches.

Habitat. On *Padina* and possibly other algae; intertidal.

Distribution. Gulf of California: Isla San Ildefonso (off Gulf coast of Baja California Sur, northeast of Punta Púlpito). Eastern Pacific: Punta Malarrimo (Bahía Sebastián Vizcaíno), Baja California Sur; Zihuatanejo, Guerrero; Costa Rica; Nicaragua.

Type Locality. Epiphytic on *Padina*; Bahía Piedra de Blanca, Pacific Costa Rica.

Remarks. *Jania tenella* var. *zacae* is included since it may occur in the northern Gulf and to call attention to the need to investigate its taxonomic status. Its segments are markedly compressed, thus differing from those of *J. tenella* var. *tenella,* which are primarily terete.

CORALLINACEAE SUBFAM. AMPHIROIDEAE

Corallinaceae subfam. Amphiroideae H. W. Johansen, 1969a:47; Garbary and Johansen, 1987:1–10; D. S. Choi and Lee, 1988:111, figs. 1–9; Womersley and Johansen, 1996:283.

Algae are erect, of terete to compressed, usually dichotomous or subdichotomous (or occasionally whorled) articulated branches composed of genicula (uncalcified joints) that alternate with longer intergenicula (calcified segments) and arise above a crustose holdfast. Intergenicula and genicula in *Amphiroa* are similar in structure; the medulla is of laterally adjoined filaments in one or more tiers of cells; there are secondary pit connections between medullary cells, but cell fusions are absent, and the cortex of calcified intergenicula cells is a single tier of short cells separated by two to seven tiers of longer cells in *Amphiroa*.

Life histories are of isomorphic sporophytes and gametophytes. Bisporangia and zonately divided tetrasporangia are produced in urn-shaped or embedded conceptacles. Gametophytes are monoecious or dioecious, with axial or lateral conceptacles. Carpogonial filaments are two-celled, borne on the conceptacle floor. Carposporangia are terminal on short gonimoblast filaments developed from the basal fusion cell. Spermatangia are on short filaments arising the from the floor or sides of conceptacle chamber.

Remarks. Corallinaceae subfam. Amphiroideae is separated on the basis of characteristics of *Amphiroa* (Johansen, 1969b, 1981). The C. subfam. Amphiroideae may be distinguished from the C. subfam. Corallinoideae (which includes *Corallina* and *Jania*) by characteristics that are mostly evident by microscopic study (Johansen, 1969a, 1981), i.e., the presence of secondary pit connections, medullary tiers of varying heights, intergenicula that often have several tiers, a unique mode of development of tetrasporangial conceptacles (Johansen, 1968), the form of spermatangial conceptacles, and other characteristics. In addition to the macroscopic and microscopic characters of *Amphiroa*, D. S. Choi and Lee (1988) proposed that structures observed by scanning electron microscopy are also useful diagnostic characters at the subfamily level. They observed an “*Amphiroa*-type” thallus surface of epithallial concavities separated by smooth, flat calcified cell walls and observed trichocytes in the cell wall region to apparently have a simple pore and lack a differentiated base, in contrast to the distinctive trichocyte base found in *Corallina*-type and *Jania*-type (Garbary and Johansen, 1982). Recognization of the subfamily Amphiroidese is problematic. Cabioch (1972, 1988) considered this subfamily to be the same as C. subfam. Lithophylloideae, placing *Amphiroa* in Lithophylloideae tribe Amphiroeae Cabioch (1972:266), and genetic analyses of Bailey (1999) also seemingly supports their of distinctiveness.

Until further investigations can be completed, the subfamily is tentatively recognized. It is well represented by members of one genus in the Gulf of California.

Amphiroa J. V. Lamouroux

Amphiroa J. V. Lamouroux, 1812:185.

Calcified articulated algae that are erect or recumbent, composed of numerous cylindrical, compressed or flattened intergenicula (segments frequently considerably longer than broad) that are separated from one another by much shortened uncalcified genicula (joints). Thalli are branched irregularly, dichotomously or subdichotomously and arise from a base attached to rocks or other hard surfaces by a crustose holdfast or by an endophytic peglike holdfast. Medullary cells of the intergenicula are in tiers of varying heights. Trichocytes in surface view are rounded. Cortex of the medulla is made up of short, smaller cells, sharply delimited from the longer medulla cells. Cells are attached laterally to each other by secondary pit connections. The genicula consist of 1 to several medullary tiers, corticated to varying extents.

Conceptacles are usually borne on surfaces and margins of the intergenicula but are reported to be basal in at least one. Tetrasporangia and bisporangia are either developed only in the periphery or center of the sporangial conceptacle chamber, or, in some, from both the periphery and center. Sporangial pore canal of some may have large block cells, but these are not present in others. Carposporangial filaments, producing carposporangia, are developed either from the margins or the entire surface of the fusion cell in the basal region of the chamber floor. Spermatangial conceptacles are usually low and broad, with spermatangia produced on the chamber floor.

REMARKS. Emphasizing the importance of the development of reproductive conceptacles in *Amphiroa*, Rosas-Alquicira et al. (2013) found different patterns of development of the sporangial and gametangial conceptacles to be diagnostic for species within the genus. They also described the reproductive development in more detail for several of the species, including four from the Gulf of California.

Superficially, some small species of Gulf *Amphiroa*, e.g., *A. valonioides,* may sometimes resemble some members of *Jania,* but upon examination with a hand magnifying lens their distinctions become clear. Although both are dichotomously branched, the genicula (joints) and positions of the conceptacles differ. Reproductive conceptacles are on the intergenicula (segments) surfaces and margins in *Amphiroa* and at the apices in *Jania.*

Five taxa have been reported in the southern Gulf from Sinaloa to Jalisco (Mateo-Cid and Mendoza-González, 1992; Mendoza-González and Mateo-Cid, 1992, 1994; Serviere-Zaragoza et al., 1993a; Mendoza-González et al., 1994; Riosmena-Rodríguez and Woelkerling, 2000): *Amphiroa compressa* Me. Lemoine (1930), *A. compressa* var. *tenuis* W. R. Taylor (1945), *A. foliacea* J. V. Lamouroux (1824), *A. polymorpha* Me. Lemoine (1930), and *A. currae* Ganesan (1971; note that this last record is questioned by Serviere-Zaragoza et al., 1993a).

Currently nine species of *Amphiroa* are recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *AMPHIROA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Calcified intergenicula (segments) distinctly compressed (never or rarely cylindrical) 2

1b. Calcified intergenicula (segments) cylindrical to subcylindrical throughout 6

2a. Fronds recumbent, spreading, and irregularly branched; intergenicula irregularly shaped, variable in size up to 7 mm long and 3–4 mm wide . . . . **A. misakiensis**

2b. Fronds erect, clumps, regularly branched; intergenicula less than 1 mm wide 3

3a. Intergenicula cylindrical to subcylindrical or slightly compressed, mostly less than 1 mm in diameter (700–1200 µm); genicula (noncalcified joints) of 3–5 tiers of medullary cells 4

3b. Intergenicula more than 1 mm wide; genicula (noncalcified joints) of 6 or more tiers of medullary cells 5

4a. Intergenicula cylindrical to subcylindrical, 0.8–1.2 mm in diameter, of more or less similar diameter throughout, but irregular in lengths, segments (0–)1.5–4.0 times as long as wide, not often forked; genicula dark, conspicuous . . . . **A. mexicana**

4b. Intergenicula cylindrical to slightly compressed, 0.5–1.0 mm in diameter, intergenicular segments more than 4 (sometimes up to 10) times long as wide; more frequently forked; genicula apparent (but not as dark) . . . . . **A. beauvoisii (in part)**

5a. Intergenicula up to 3 mm long . . . . **A. brevianceps**

5b. Intergenicula more than 5 mm long . . . . **A. magdalenensis**

6a. Intergenicula more than 1 mm in diameter; genicula consisting of 5 or more tiers of medullary cells . . . **A. vanbosseae**

6b. Intergenicula less than 1 mm in diameter; genicula consisting of 4 or fewer tiers of medullary cells 7

7a. Intergenicula less than 0.5 mm in diameter; genicula of 1 tier of medullary cells . . . . **A. valonioides**

7b. Intergenicula 0.5–1 mm in diameter; genicula of 2 or more tiers of medullary cells 8

8a. Fronds mostly 2–12 cm tall, branched more or less in 1 plane; genicula of 3–5 tiers of medullary cells .... **A. beauvoisii** (in part)

8b. Fronds less than 2 cm tall; genicula of 2 tiers of medullary cell 9

9a. Branching alternately pinnate to irregular; rigid branches irregular placed, mostly not formed at the genicula, and usually at wide angles; genicula cells imbricated; intergenicula more or less straight, 500–1000 µm, of similar diameter throughout .... **A. rigida**

9b. Branched multifariously or pinnately to irregularly in lower portions, and unbranched to sparsely dichotomous in upper portions; genicula cells blunt (not imbricated); intergenicula 250–450 µm in diameter, usually crooked and not uniform in diameter .... **A. taylorii**

Amphiroa beauvoisii J. V. Lamouroux

FIGURE 41

Amphiroa beauvoisii J. V. Lamouroux, 1816:299; Hamel and Lemoine, 1953:42, fig. 7 [text], pl. 5: figs. 1, 7; Dawson, 1957c:18; 1961b:420; Norris and Johansen, 1981:6, figs. 1a, 2, 3, 4a–c, 5, 7b, 14b, 15b; Johansen, 1981:70, fig. 12A; Stewart and Stewart, 1984:144; Norris, 1985d:208; Lewis and Norris, 1987:18; Garbary and Johansen, 1987:3, figs. 7, 14, 15; Stewart, 1991:80; Ramírez and Santelices, 1991:195; Dreckmann, 1991:33; Mateo-Cid et al., 1993:46; León-Tejera et al., 1993:200; Serviere-Zaragoza et al., 1993a:482; Stout and Dreckmann, 1993:12; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:106; León-Álvarez and González-González, 1995;363; González-González et al., 1996:301; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137, figs. 2–5; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Serviere-Zaragoza et al., 1998:171; Abbott, 1999:177, figs. 44A,B, 45A; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:130; Mateo-Cid et al., 2000:64; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:321; Cruz-Ayala et al., 2001:190; CONANP, 2002:139; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Abbott et al., 2002:302; López et al., 2004:10; R. Aguilar-Rosas et al., 2005:32; Riosmena-Rodríguez et al., 2005a:33; Mateo-Cid et al., 2006:51, 55; Serviere-Zaragoza et al., 2007:9; Y.-P. Lee, 2008:181, figs. A–D; Mateo-Cid et al., 2008:8, figs. 1–17, 22–44; Pacheco-Ruíz et al., 2008:208; Rosas-Alquicira et al., 2008:129; Bernecker, 2009:CD-Rom p. 59; Castañeda-Fernández de Lara et al., 2010:199; Rosas-Alquicira et al., 2013:698, figs. 3–6, 8, 10, 15–19, 25–26, 28–31, 33, 39, 52, tbls. 1, 2.

Amphiroa zonata Yendo, 1902a:10, pl. 1: figs. 11–14, pl. 4: fig. 9; Dawson, 1944a:276; 1953a:146; 1959a:22; Dawson et al., 1960a:44, pl. 23: fig. 6; Dawson, 1961b:421; 1966a:18; Abbott and North, 1972:75; Johansen, 1976a:400, fig. 349; Devinny, 1978:360; Murata and Masaki, 1978:403, figs. 3–7, 18, 26, 27; Littler and Littler, 1981:151; Littler and Arnold, 1982:309; Stewart and Stewart, 1984:144; Tseng, 1983:86, pl. 46: fig. 4; Mendoza-González and Mateo-Cid, 1985:26; Mendoza-González and Mateo-Cid, 1986:422; Sánchez-Rodríguez et al., 1989:42; Martínez-Lozano et al., 1991:24; González-González et al., 1996:173; Yoshida, 1998:538, fig. 3-14C–F; Riosmena-Rodríguez and Woelkerling, 2000:333; Schubert et al., 2006:1212; Bernecker and Wehrtmann, 2009:225.

Amphiroa peninsularis W. R. Taylor, 1945:188, pl. 48: fig. 1; Norris and Johansen, 1981:6; Salcedo-Martínez et al., 1988:83; Anderson, 1991:15; Riosmena-Rodríguez and Woelkerling, 2000:328.

Amphiroa drouetii E. Y. Dawson, 1953a:140, pl. 27, figs. 5, 6; 1959a:21; 1961b:420; 1966a:18; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Huerta-Múzquiz, 1978:339; Martínez-Lozano et al., 1991:24.

Amphiroa franciscana var. *robusta* E. Y. Dawson, 1953a:150; 1961b:421; 1966b:59; Anderson, 1991:15; González-González et al., 1996:171, 383; Riosmena-Rodríguez and Woelkerling, 2000:330.

Amphiroa linearis sensu Hariot, 1895:169; León-Tejera and González-González, 1993:496; González-González et al., 1996:171, 382 [non *Amphiroa linearis* Kützing, 1858:22, pl. 46: fig. 2a–c].

Amphiroa pusilla sensu Dawson, 1944a:276 [in part; non *Amphiroa pusilla* Yendo, 1902a:13].

Amphiroa crosslandii sensu Dawson, 1953a:149; 1954d:136; 1957a:7; 1961b:420; Mendoza-González and Mateo-Cid, 1986:422; Salcedo-Martínez et al., 1988:83; Dreckmann, 1991:33; González-González et al., 1996:170 [non *Amphiroa crosslandii* Me. Lemoine, 1929a:50; Tittley et al., 1984:5].

Fronds 1.5–4.0(–6) cm high, usually more or less erect and open, sometimes in compact, pulvinate clumps; attached by a crustose disc to hard substratum. Branching dichotomous to irregular, more or less in 1 plane; branch intergenicula sometimes Y-shaped dichotomies, sometimes separated by 1 or more unbranched intergenicula. Intergenicula near base cylindrical to subcylindrical, up to 1.2(–1.7) mm in diameter and 2–3(–4) mm long. Mid to upper intergenicula cylindrical, subcylindrical, or compressed (especially near branch apices); mostly 0.5–l.0 mm broad and 3–5(–10) mm long; becoming more terete with age because of cortical thickening. Genicula between intergenicula barely visible externally because of covering calcification; becoming visible by cracking and sloughing of calcified cortical cells overlying their uncalcified 3–5 tiers of medullary cells and irregularly disposed patches of cortical cells.

Reproductive conceptacles scattered over intergenicular surfaces, protruding slightly. Tetrasporangial and bisporangial conceptacles 150–250(–300) µm inside diameter, 95–150 µm tall; tetrasporangia (40–)60–65 µm tall, 25–35 µm in diameter; bisporangia 40–80 µm tall, 22–40(–45) µm in diameter. Sporangial conceptacle canal with large block cells; sporangia only in periphery of cavity floor (Rosas-Alquicira et al., 2013: fig. 8). Carpogonial filaments develop from entire surface of fusion cell. Basal cells of spermatangial conceptacle form by basal division of cavity cells; each basal cell produces 2 spermatangial parent cells that develop simple spermatangial filaments; spermatangia release spermatia into conceptacle chamber (after Rosas-Alquicira et al., 2013).

HABITAT. On rocks and tidal platforms and in tide pools; mid intertidal to shallow subtidal.

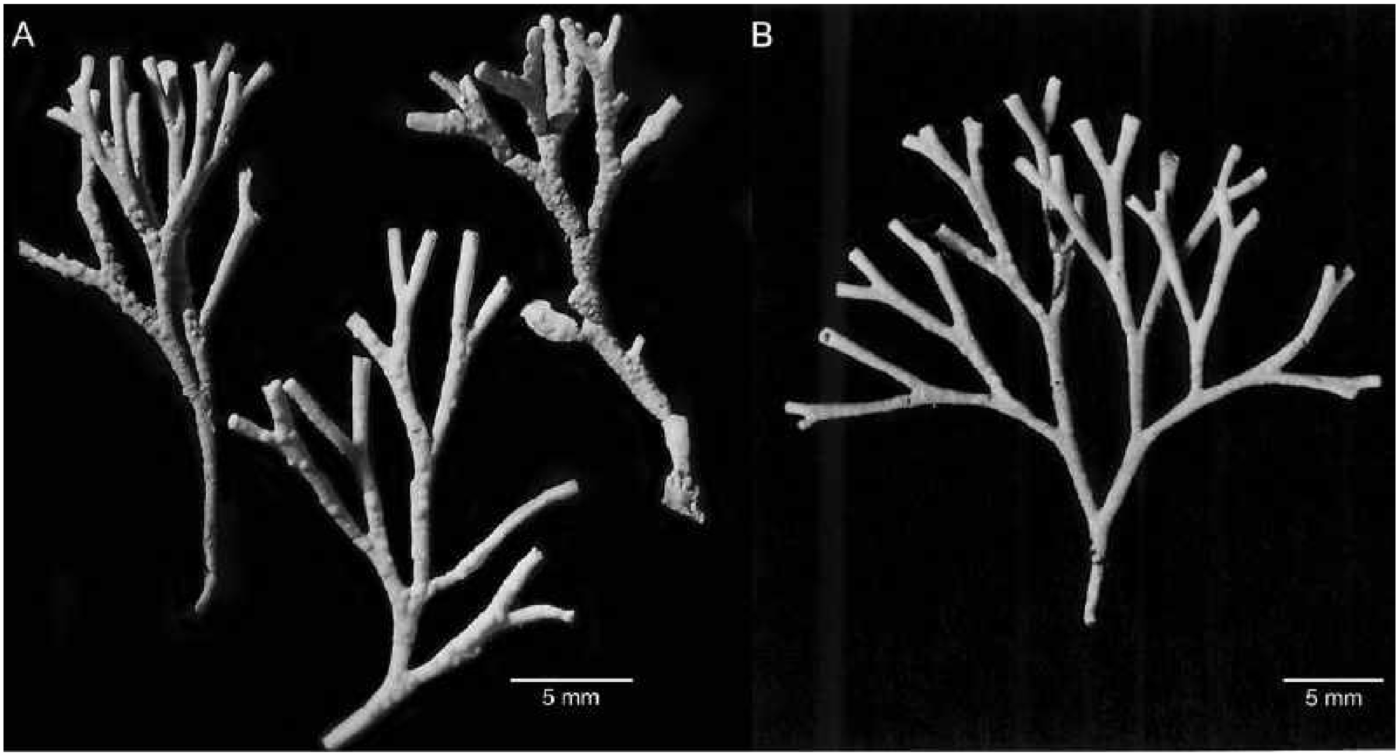

FIGURE 41. *Amphiroa beauvoisii,* branch variability: A. Fronds from a single clump. B. A single branch (A, B, *JN & HWJ-73-7-3*, US Alg. Coll.).

Distribution. Gulf of California: Piedras de la Salina (Gulfo de Santa Clara) to Cabo San Lucas; Mazatlán, Sinaloa to Jalisco. Islas Marías (Islas Tres Marías). Eastern Pacific: Santa Catalina Island (California Channel Islands) to Playa Los Cerritos, Baja California Sur; Isla Socorro (Islas Revillagigedo); Rocas Alijos; Jalisco to Oaxaca; Costa Rica to Ecuador; Galápagos Islands; Chile. Central Pacific: Hawaiian Islands. Western Pacific: China; Taiwan; Korea; Japan; Vietnam.

Type Locality. Coast of Portugal (Harvey et al., 2009).

Remarks. Primarily on the basis of similar morphologies, *Amphiroa beauvoisii*, *A. drouetii,* and *A. zonata* were considered to be conspecifc by Norris and Johansen (1981); since then, most have continued to recognize *A. beauvoisii* in the Gulf of California (Riosmena-Rodríguez and Siqueiros-Beltrones, 1996; Riosmena-Rodríguez and Woelkerling, 2000; Mateo-Cid et al., 2006, 2008; Rosas-Alquicira et al., 2013). Others have recognized the western Pacific *A. zonata* (syntype localities: Misaki, Shimoda, and Sunosaki, Japan), the eastern Atlantic *A. beauvoisii* (type locality: Portugal) (e.g., Tseng, 1983; Silva et al., 1987; Yoshida, 1998), and the northern Gulf of California *A. drouetii* (type locality: Isla Turner, off Isla Tiburón) as separate species (Mendoza-González and Mateo-Cid, 1986; Salcedo-Martínez et al., 1988; Sánchez-Rodríguez et al., 1989; Mateo-Cid and Mendoza-González, 1991; 1992; Mendoza-González and Mateo-Cid, 1992; González-González et al., 1996). Differences have been observed in sporangial conceptacles of species presumed to be the same or related. Sporangia were only on the periphery of the chamber floor in *A. beauvoisii* from the Gulf of California (Rosas-Alquicira et al., 2013) and the eastern Atlantic from the Azores (Rosas-Alquicira et al., 2011); whereas sporangia were found in the center and periphery of the chamber floor in Japanese *A. zonata* (Murata and Masaki, 1978). For now, until they can be molecularly tested using type materials, those in the Gulf of California are treated as a single species.

Upper Gulf specimens referred to "*Amphiroa franciscana* W. R. Taylor" from Bahía Kino (Mendoza-González and Mateo-Cid, 1986) should be reexamined to determine if that species is present in the northern Gulf or if they may belong here as well.

Amphiroa brevianceps E. Y. Dawson

Amphiroa brevianceps E. Y. Dawson, 1953a:142, pl. 31: fig. 2; Dawson et al., 1960b:16; Dawson, 1961b:420; Norris and Johansen, 1981:12, figs. 1b, 6, 9 [type specimen]; Mendoza-González and Mateo-Cid, 1986:422; Sánchez-Rodríguez et al., 1989:42; Anderson, 1991:14; Mateo-Cid and Mendoza-González, 1991:19; Dreckmann, 1991:33; Mendoza-González and Mateo-Cid, 1992:17; Serviere-Zaragoza et al., 1993a:482; León-Tejera et al., 1993:200; León-Tejera and González-González, 1993:496; Mendoza-González et al., 1994:106; Mateo-Cid and Mendoza-González, 1994a:51; González-González et al., 1996:169, 382; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:140; Serviere-Zaragoza et al., 1998:171; L. Aguilar-Rosas et al., 2000:130; Riosmena-Rodríguez and Woelkerling, 2000:322.

Calcified articulated fronds in small, densely branched clumps, up to 4 cm high. Branching more or less regularly dichotomous, in 1 plane. Intergenicula near base subterete or flat and up to 2 mm broad, in upper parts flat, short, and broad, up to 3 mm broad, usually less than 4 mm long, not differentiated (lack midrib and wings). Genicula externally prominent, uncalcified, dark colored, bracketed by calcified extensions of the adjacent intergenicula, 6 or more tiers of cells per geniculum.

Tetrasporangial and carposporangial conceptacles scattered over intergenicular surfaces (Dawson, 1953a); protruding above intergenicular surface, mostly 300–400 µm in diameter, with a small ostiole. Spermatangial conceptacles not reported.

HABITAT. On rocks and tidal platforms; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Coloradito to Guaymas; Punta Los Frailes; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Punta San Hipolito, Baja California to Bahía Magdalena Baja California Sur; Colima to Oaxaca.

TYPE LOCALITY. On rocky shore just east of Salina Cruz, Oaxaca, Pacific Mexico.

REMARKS. On the basis of morphological comparisons, *Amphiroa brevianceps* was considered to be conspecific with another flattened species also reported in the Gulf of California, the Japanese *A. misakiensis* (Riosmena-Rodríguez and Siqueiros-Beltrones, 1996). Although both have 5 or more tiers of medullary cells in the genicula, they can be separated by other features: *A. brevianceps* is erect and mostly regularly branched, with similar sized intergenicula throughout, 1.5–3.0 mm wide; A. *misakiensis* is recumbent, irregularly branched, and polymorphic, with irregularly shaped intergenicula that are variable in size, up to 7 mm long and mostly 3–4 mm wide. Until comparative molecular analyses are completed on Gulf specimens and the Japanese type of *A. misakiensis* to test their taxonomic status, they are herein recognized as separate taxa.

Amphiroa magdalenensis E. Y. Dawson

Amphiroa magdalenensis E. Y. Dawson, 1953a:143 [as "*magdalensis*"], pl. 30: fig. 2; 1959a:21; 1961b:421; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Norris and Johansen, 1981:13, figs. 1c, 6, 10b [type specimen]; Stewart and Stewart, 1984:144; Sánchez-Rodríguez et al., 1989:42; Anderson, 1991:15; Dreckmann, 1991:33; León-Tejera and González-González, 1993:496; González-González et al., 1996:171; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137; Riosmena-Rodríguez and Woelkerling, 2000:326.

Calcified articulated fronds forming loose tufts, up to 5 cm high. Branching sparsely, dichotomous or irregular. Intergenicula terete near base, others becoming markedly flattened, 1.0–2.5 mm broad, 3–6 times as long, (3–)7.5–15 mm in length. Genicula conspicuous because of broken out pieces of adjacent intergenicula in center of branch; up to or more than 10 cellular tiers per geniculum.

Tetrasporangial conceptacles scattered on intergenicular surfaces, usually more on one side than the other; sexual thalli not encountered in the Gulf of California.

HABITAT. Shallow subtidal.

DISTRIBUTION. Gulf of California: Isla de Tortuga (about 24.1 km or 15 mi NE of Isla San Marcos) to Isla San Ildefonso; Punta Palmilla; Mazatlán. Eastern Pacific: Isla Guadalupe; Punta Abreojos to Isla Santa Margarita (west of Bahía Almejas), Baja California Sur; Golfo de Tehuantepec, Oaxaca.

TYPE LOCALITY. Punta Entrada, Isla Magdalena (west side of Bahía Magdalena), Baja California Sur, Pacific Mexico.

REMARKS. *Amphiroa magdalenensis* is one of the compressed species with characters similar to *A. misakiensis,* and both have been considered to be conspecific by Riosmena-Rodríguez and Siqueiros-Beltrones (1996). For now the two are recognized as separate species until molecular studies are done to test the relationship of Gulf *A. magdalenensis* to Pacific Mexico (type locality) *A. magdalenensis* and Japanese *A. misakiensis*.

Amphiroa mexicana W. R. Taylor

Amphiroa mexicana W. R. Taylor, 1945:189, pl. 47; Dawson, 1961b:421; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Huerta-Múzquiz, 1978:339; Norris and Johansen, 1981:12, fig. 7a [type specimen]; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1985:26; Mendoza-González and Mateo-Cid, 1986:422; Salcedo-Martínez et al., 1988:83; Dreckmann et al., 1990:30, pl. 5: figs. 5, 6; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137; Anderson, 1991:15; Dreckmann, 1991:33; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:18; Serviere-Zaragoza et al., 1993a:483; Stout and Dreckmann, 1993:13; León-Tejera et al., 1993:200; León-Tejera and González-González, 1993:496; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:171; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137; Riosmena-Rodríguez and Woelkerling, 2000:327; Tejada, 2003:11; Hernández-Herrera et al., 2005:147.

Amphiroa peninsularis sensu Taylor, 1945:188 [in part: Guerrero specimens only; non *Amphiroa peninsularis* W. R. Taylor, 1945:188].

Calcified articulated fronds, erect, up to 7 cm tall; densely dichotomously, much branched; intergenicula cylindrical to compressed of similar diameter throughout, 800–1200 µm in diameter; branch tips truncate, 500 µm (or more) in diameter (often faint zonal banding visible); intergenicula lengths variable, 1.5–3.2 mm long, about (0–)1.5–4.0 times as long as wide; genicula dark colored (easily visible), of 4 tiers of medullary cells; branching at intervals of 1–3 segments, with branch angles usually less than 45°; arising from small crustose base. Intergenicula with relatively thick cortex of 3–5 layers of very small cells; with age, increasing up to 6–7 layers and cortical cells elongate anticlinally; multilayered medulla of 3–5 tiers of long cells alternating with a single tier of short cells.

Tetrasporangial and carposporangial conceptacles slightly elevated, about 250 µm in diameter, single pore, about 35 µm in diameter flush with conceptacle surface. Tetrasporangia, 40–60 µm long borne among paraphyses on cavity floor. Carpospores subspherical, 2528 µm in diameter. Spermatangial conceptacles not known.

HABITAT. On rocks, mostly in exposed rocky habitats; intertidal.

DISTRIBUTION. Gulf of California: Isla Pelícanos and Roca Roja, Bahía Kino; Bahía de La Paz; Sinaloa to Jalisco. Eastern Pacific: Baja California; Guerrero to Oaxaca.

TYPE LOCALITY. Bahía Petatlán, Guerrero, Pacific Mexico.

REMARKS. *Amphiroa mexicana* W. R. Taylor (1945) is included herein on the basis of its report in the northern Gulf (Mendoza-González and Mateo-Cid, 1986). Dawson (1953a) observed it to be locally abundant on the tropical mainland coasts of Pacific Mexico. Although similar to *A. zonata*, *A. mexicana* can be distinguished by its shorter intergenicula and more prominent genicula. Norris and Johansen (1981) suggested it may be conspecific with *A. beauvoisii*, and it was later treated as a synonym by Riosmena-Rodríguez and Siqueiros-Beltrones (1996). The taxonomic status of the northern Gulf *A. mexicana* and its relationships to Pacific Mexico *A. mexicana*, Eastern Atlantic *A. beauvoisii*, and Japanese *A. zonata* from their type localities need to be molecularly tested.

Amphiroa misakiensis Yendo

FIGURE 42

Amphiroa misakiensis Yendo, 1902a:14, pl. 1: figs. 24, 25, pl. 6: fig. 1; Yendo, 1902b:6; Norris and Johansen, 1981:15, figs. 1d, 6, 11, 12a, 13a, 15c [lectotype illustration]; D. S. Choi and Lee, 1988:112, figs. 4, 8; Riosmena-Rodríguez and Siqueiros-Beltrones, 1991:8; Serviere-Zaragoza et al., 1993a:483; León-Tejera et al., 1993:200; León-Tejera and González-González, 1993:496; Mateo-Cid et al., 1993:46; Stout and Dreckmann, 1993:13; Mendoza-González and Mateo-Cid, 1994:51 Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:106; León-Álvarez and González-González, 1995:363; González-González et al., 1996:171, 383; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:140, figs. 20–24 [in part]; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Yoshida, 1998:534, fig. 3-13A–F; L. Aguilar-Rosas et al., 2000:130; Mateo-Cid et al., 2000:64; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:327; Cruz-Ayala et al., 2001:190; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; López et al., 2004:10; Riosmena-Rodríguez et al., 2005a:33; Hernández-Herrera et al., 2005:147; Mateo-Cid et al., 2006:51, 55; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:208; Y.-P. Lee, 2008:187, figs. A–C; Fernández-García et al., 2011:60; Rosas-Alquicira et al., 2013:698, figs. 9, 11–13, 20–24, tbls. 1, 2.

Amphiroa pusilla sensu Dawson, 1944a:276 [in part; not *Amphiroa pusilla* Yendo, 1902a:13].

Amphiroa dimorpha sensu Taylor, 1945:192, pl. 55; Dawson, 1953a:141; 1957c:19; Dawson et al., 1960a:44 pl. 23: fig. 5; 1960b:16; Dawson, 1961b:420; 1961c:411; Dawson et al., 1964:47; Dawson, 1966a:18; Huerta-Múzquiz, 1978:337, 339; Pedroche and González-González, 1981:66; Tittley et al., 1984:5; Mendoza-González and Mateo-Cid, 1986:422; Salcedo-Martínez et al., 1988:83; Sánchez-Rodríguez et al., 1989:42; Dreckmann et al., 1990:30; Mateo-Cid and Mendoza-González, 1991:19; Dreckmann, 1991:33; Mendoza-González and Mateo-Cid, 1992:17; Mateo-Cid and Mendoza-González, 1992:20; León-Tejera et al., 1993:200; Serviere-Zaragoza et al., 1993a:482; Mendoza-González et al., 1994:106; Mateo-Cid and Mendoza-González, 1994b:39; Mateo-Cid et al., 2000:64; Riosmena-Rodríguez and Woelkerling, 2000:324; Hernández-Herrera et al., 2005:147 [non *Amphiroa dimorpha* Me. Lemoine, 1930:76].

Amphiroa dimorpha var. *digitiformis* E. Y. Dawson, 1959a:21, as "*digitiforme*"; 1961b:420; Espinoza-Avalos, 1993:333; González-González et al., 1996:170; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:140; Riosmena-Rodríguez and Woelkerling, 2000:324.

Fronds up to 4 cm tall; erect or more or less recumbent; branching dichotomous to trichotomous, but this pattern often obscure when adventitious branches arise irregularly from intergenicula; with flat and rounded apices; attached by discoid crustose holdfast. Intergenicula near base small and subcylindrical; in upper parts of fronds flat, irregularly shaped, size varying greatly but usually 3–4 mm wide and up to 7 mm long; of 2–6 rows of long cells alternating with 1 short cell; cortex of 23–25

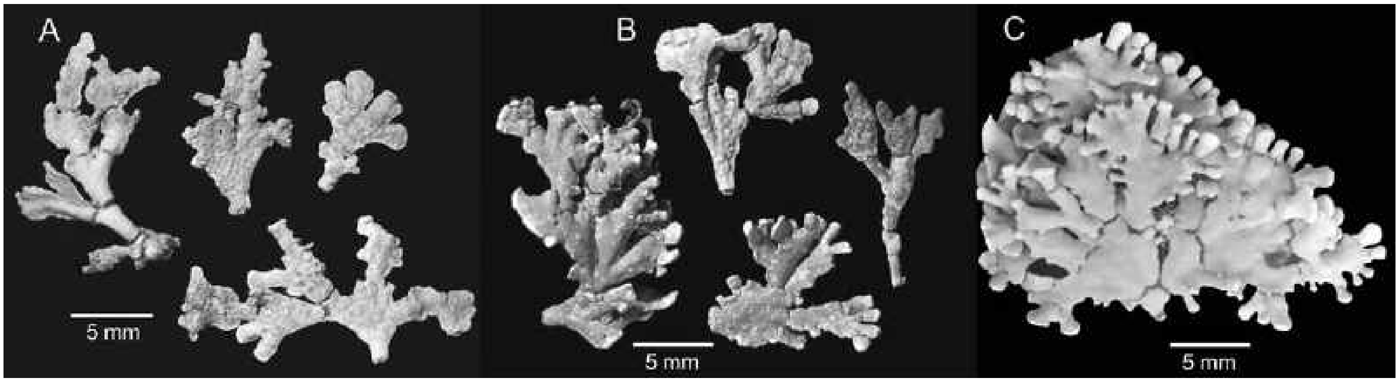

FIGURE 42. *Amphiroa misakiensis*: A. Irregular branching patterns (*JN-3674*, US Alg. Coll.). B. Branches with conceptacles (*JN-3684* US Alg. Coll.). C. Numerous small branches arising from some of the large flat intergenicula (*JN-5102*, US Alg. Coll.).

squarish cortical cells; trichocytes rare. Genicula developed by cracking and sloughing of calcified cortical tissue overlying genicular tissue; composed of 5–8 tiers of cells, with patches of uncalcified cortical tissue.

Conceptacles immersed in cortex scattered over uppermost intergenicula surfaces (or lowermost according to Dawson, 1953a:142) and protruding; verrucose appearance to branch intergenicula with gametangia; pore formed by coalition of two roof filaments. Tetrasporangial and bisporangial conceptacles oblong, (175–)200–300 μm inside diameter; with scattered paraphyses. Sporangial conceptacle canal with large block cells (Rosas-Alquicira et al., 2013); sporangia in center and periphery of cavity floor. Carposporangial conceptacles oblong to verrucose, up to 200 μm inside diameter; carpogonial filaments develop from margins of fusion cell (Riosmena-Rodríguez and Siqueiros-Beltrones, 1996) or its entire surface (Rosas-Alquicira et al., 2013). Spermatangial conceptacles verrucose, 75–125 μm inside diameter; spermatangia simple, borne on cavity floor.

HABITAT. Low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo San Lucas; Mazatlán, Sinaloa to Jalisco; Isla María Cleofa (Islas Marías; Islas Tres Marías). Eastern Pacific: Isla Cedros (Baja California); Chester Islets (NE of Punta Falsa), Bahía Sebastián Vizcaíno to Todos Santos, Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador to Costa Rica; Panama; Peru. Western Pacific: Japan; Korea.

TYPE LOCALITY. Misaki, Sagami Bay, Kanagawa Prefecture, Honshū, Japan.

REMARKS. See also Remarks under *Amphiroa brevianceps*.

Amphiroa rigida J. V. Lamouroux

Amphiroa rigida J. V. Lamouroux, 1816:297, pl. 11: fig. 1; Yendo, 1902a:6, pl. 1: figs. 5, 6, pl. 4: fig. 4; Norris and Johansen, 1981:19, figs. 1e, 6a, 14a, 14c; Garbary and Johansen, 1987:3, fig. 10; Mateo-Cid et al., 1993:46; Serviere-Zaragoza et al., 1993a:483; León-Tejera et al., 1993:200; Stout and Dreckmann, 1993:13; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:106; González-González et al., 1996:302; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137, figs. 6–9; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Yoshida, 1998:537; Abbott, 1999:178, figs. 44D, 45C; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:330; CONANP, 2002:139; López et al., 2004:10; Mateo-Cid et al., 2006:51, 55; Serviere-Zaragoza et al., 2007:9; Bernecker and Wehrtmann, 2009:225; Fernández-García et al., 2011:60; Rosas-Alquicira et al., 2013:698, fig. 48, tbl. 2.

Amphiroa rigida var. *antillana* Børgesen, 1917:182, figs. 171–173; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137; Riosmena-Rodríguez and Woelkerling, 2000:321.

Fronds up to 3 cm high, erect and isolated or sometimes in more or less erect clumps; attached by crustose holdfast. Branching alternately pinnate to irregular, sometimes dichotomous, and usually at wide angles, branch junctions usually not coinciding with genicula; branches with rounded apices. Intergenicula mostly cylindrical, occasionally subcylindrical, 0.4–1.0 mm diameter and variable in length; of 1–3 rows of long cells alternating with 1 row of short cells; cortex of 6 tiers of rounded cortical cells. Genicula often nearly invisible in young parts of fronds, becoming visible by separation of adjacent calcified segments; of 2 tiers of medullary cells, without cortication; cell wall ends mostly imbricate.

Tetrasporangial and bisporangial conceptacles embedded in cortex of the intergenicula, oblong cavities, 150–175 μm inside diameter, with scattered paraphyses; sporangia in center and periphery of chamber floor; chamber pore canal with block-shaped cells. Gametangial conceptacles embedded in the cortical cells of intergenicular margins; protruding, giving surface a verrucose appearance; with pores developed in cavity roof by repeated upward divisions of cortical cells, coalescing upward. Carpogonial conceptacles oblong to elliptical, 100–150 μm inside diameter; carpogonial filaments develop from entire surface of fusion cell. Spermatangial conceptacles oblong, 150–160 μm inside diameter; spermatangia simple, borne on cavity floor.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía Concepción to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Jalisco to Michoacán; Costa Rica; Nicaragua. Central Pacific: Hawaiian Islands. Western Pacific: Japan.

TYPE LOCALITY. Mediterranean Sea ("Mediterranee"; Lamouroux, 1816:297).

REMARKS. Some smaller specimens of Gulf *Amphiroa rigida* could be confused with *A. valonioides*. *Amphiroa rigida* may be distinguished from *A. valonioides* by its rigid branches, which are irregular placed and usually not formed at the genicula, as in other species of Gulf *Amphiroa*. Also *A. rigida* is the only species of *Amphiroa* in the Gulf with unique imbricate end walls of the genicular cells (cf. Norris and Johansen, 1981: fig. 14c). Reproductive and vegetative anatomy of Mediterranean specimens of *A. rigida* was studied by Suneson (1937). The Gulf *A. rigida* should be morphologically and molecularly tested with Mediterranean type material of *A. rigida* to resolve its phylogenetic and taxonomic status.

Amphiroa taylorii E. Y. Dawson

Amphiroa taylorii E. Y. Dawson, 1953a:138, pl. 26: fig. 1 [type specimen]; 1954b:137; 1957c:19; 1959a:22; 1961b:421; 1966a:18; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Huerta-Múzquiz and Garza-Barrientos, 1975:8, 11; Mendoza-González and Mateo-Cid, 1986:422; Sánchez-Rodríguez et al., 1989:42; Mateo-Cid and Mendoza-González, 1991:19; Anderson, 1991:15; Mendoza-González and Mateo-Cid, 1992:18; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:172; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:137; Riosmena-Rodríguez and Woelkerling, 2000:331; Bernecker, 2009:CD-Rom p. 59.

Amphiroa annulata sensu Taylor, 1945:188 [in part; Isla Socorro material only; non *Amphiroa annulata* Me. Lemoine, 1930:78].

Algae of tufts, up to 1.5 cm tall, of erect, more or less straight to curved axes; unbranched to sparsely dichotomously branched above; irregular, multifariously or pinnately branched below axes from a crustose base. Axes and branches cylindrical, 250–450 m in diameter, intergenicula usually crocked, not uniform in diameter throughout (portions irregular in diameter); cortex of 6–8 cortical cell layers. Intergenicula (2–)6–15 times longer than wide (500–)1200–5000 μm in length; prominently constricted at genicula. Genicula usually of 2 tiers of medullary cells; cell ends may be imbricated (cf. Norris and Johansen, 1981: fig. 14c).

HABITAT. On rocks; intertidal to shallow subtidal, down to 2 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Puerto Escondido; Cabeza Ballena; Nayarit to Jalisco; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: Bahía Magdalena, Baja California Sur; Isla Socorro (Islas Revillagigedo); Jalisco to Colima; Costa Rica.

TYPE LOCALITY. On intertidal rocks; Bahía Braithwaite, Isla Socorro, Islas Revillagigedo, Pacific Mexico.

REMARKS. Dawson (1959a) noted southern Gulf *Amphiroa taylorii* were more regularly dichotomously branched than the Pacific Mexico type specimen and had cylindrical branches with constricted two-tiered genicula with smooth cells wall ends.

Amphiroa taylorii has been considered a synonym of *A. rigida,* another species with two tiers of genicular cells (Norris and Johansen, 1981; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996). Although the imbricate nature of the genicula cell wall ends was used to separate *A. rigida* (Norris and Johansen, 1981), Riosmena-Rodríguez and Siqueiros-Beltrones (1996) noted their southern Gulf specimens of *A. rigida* to have both smooth and imbricate cell wall ends in the genicula. The relationship of these two species should be reconsidered. Critical morphologically and molecular studies are needed that compare Gulf specimens with type locality materials of *A. taylorii* and *A. rigida* to resolve their taxonomic status.

Amphiroa valonioides Yendo

FIGURE 43

Amphiroa valonioides Yendo, 1902a:5, pl. 1: figs. 1–3, pl. 4: fig. 1; Norris and Johansen, 1981:20, figs. 1f, 6, 12d, 13b, 15a, 16, 17 [lectotype]; Johansen, 1981:68: fig. 10C; Stewart, 1982:54; Stewart and Stewart, 1984:144; D. S. Choi and Lee, 1988:112, figs. 9A–D; Dreckmann, 1991:33; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:46; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:106; González-González et al., 1996:172, 384; D. S. Choi and Lee, 1996:269, figs. 3–4; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:136, figs. 2–5; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Yoshida, 1998:537; Serviere-Zaragoza et al., 1998:171; Abbott, 1999:180, figs. 44E, 45D; L. Aguilar-Rosas et al., 2000:130; Mateo-Cid et al., 2000:64; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:332; Cruz-Ayala et al., 2001:190; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Abbott et al., 2002:302; López et al., 2004:10; Mateo-Cid et al., 2006:51, 55; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:208; Castañeda-Fernández de Lara et al., 2010:199; Fernández-García et al., 2011:60; Rosas-Alquicira et al., 2013:698, tbl. 2.

Amphiroa annulata Me. Lemoine, 1930:78, fig. 34, pl. 4: fig. 1; Taylor, 1945:188; Dawson, 1953a:136, pl. 29: fig. 3; 1959a:20; 1961b:420; 1966a:18; Chávez-Barrear, 1972b:269; Stewart, 1982:54; Tittley et al., 1984:4; Sánchez-Rodríguez et al., 1989:42; Mateo-Cid and Mendoza-González, 1992:20; González-González et al., 1996:169, 382; Lamy and Woelkerling, 1998:140; Riosmena-Rodríguez and Woelkerling, 2000:321; Bernecker, 2009:CD-Rom p. 59.

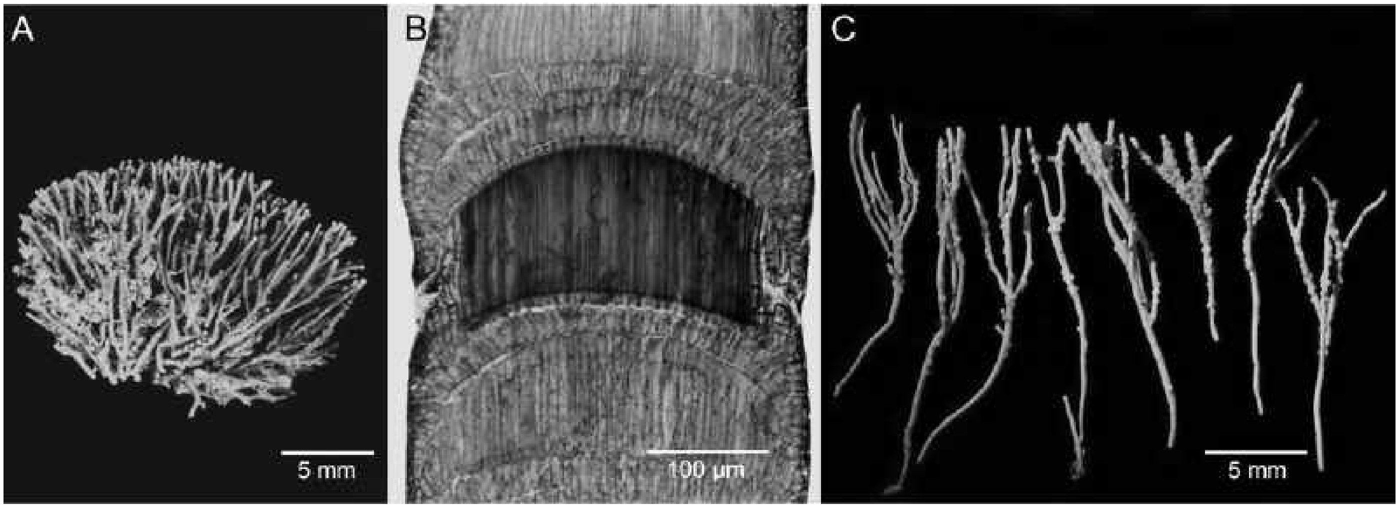

FIGURE 43. *Amphiroa valonioides:* A. Habit, tuft of fronds (*JN-3146*, US Alg. Coll.). B. Longitudinal section showing geniculum of a single tier of cells (*JN & HWJ-73-7-4*, US Alg. Coll.). C. Branches separated from the tuft; note the protruding conceptacles (*JN & HWJ-73-7-33*, US Alg. Coll.).

Amphiroa annulata var. *pinnata* E. Y. Dawson, 1953a:137; 1957:19, with query; 1959a:20; 1961b:420; Anderson, 1991:14; González-González et al., 1996:169; Riosmena-Rodríguez and Woelkerling, 2000:328.

Fronds mostly 1–2 cm high (occasionally up to 3), more or less erect clumps or turfs, branching dichotomous to oppositely pinnate; branch apices cylindrical and rounded; attached by crustose holdfast. Intergenicula cylindrical or rarely compressed, mostly less than 0.5 mm diameter (rarely more) and 1–3 mm long; of 1–3 rows of long cells that alternate with 1 row of short cells; cortex of 2–3 tiers of rectangular cells. Genicula of only 1 tier of cells; fully formed genicula barely visible in terete branches, more easily visible in compressed branches; secondary pit connections present between genicula cells.

Conceptacles often in a single row on intergenicula, protruding markedly; pore formed by degeneration of roof epithelial cells. Tetrasporangial and bisporangial conceptacles, oblong, 200–300 µm inside diameter; sporangial canal pore with block-shaped cell. Carposporangial conceptacles oblong, 150–250 µm inside diameter; carpogonial filaments develop from entire surface of fusion cell. Spermatangial conceptacles unknown.

HABITAT. Often in sand-filled turfs, on rocks and tidal platforms; high to mid intertidal, occasionally in shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo; Mazatlán. Eastern Pacific: Isla Guadalupe; Baja California to Panama. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea; Taiwan; Vietnam.

SYNTYPE LOCALITIES. Two localities in Japan were listed by Yendo (1902b:5): Province Hiuga (Hyūga) (now Miyazaki Prefecture), Kyûshû Island, and Misaki (Sagami Bay, Kanagawa Prefecture), Honshū Island.

REMARKS. *Amphiroa valonioides* is a warm temperate to tropical species. A common species of the intertidal, *A. valonioides* is most abundant in the winter and spring in the northern Gulf. It can be distinguished from similar forms of small *A. beauvoisii* by its genicula of a single row of medullary cells and its more conspicuous, protruding conceptacles.

Although considered a synonym of *A. valonioides* (Norris and Johansen, 1981), the Gulf of California *A. annulata* var. *pinnata* E. Y. Dawson (1953a; type locality: Cabeza Ballena, Baja California Sur) should be reexamined and its taxonomic status tested with molecular phylogenetic comparisons to the types and type locality specimens of *A. valonioides* (Japan) and *A. annulata* Me. Lemoine (Isla Santiago, Galápagos Islands).

Amphiroa vanbosseae Me. Lemoine

FIGURE 44

Amphiroa vanbosseae Me. Lemoine, 1930:73, fig. 30, pl. 3: fig. 7; Taylor, 1945:192; Dawson, 1961b:421; Norris and Johansen, 1981:23, figs. 1g, 4d, 6, 10a, 12b,c, 13c, 18; Littler and Littler, 1984:22; Tittley et al., 1984:5; Norris, 1985d:208; Dreckmann, 1991:33; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:385; Riosmena-Rodríguez and Siqueiros-Beltrones, 1996:138, figs. 15–19; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Lamy and Woelkerling, 1998:140; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; Mateo-Cid et al., 2000:64; Aguilar-Rosas et al., 2000:131; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:332; Cruz-Ayala et al., 2001:190; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Rivera-Campos and Riosmena-Rodríguez, 2003:59; Mateo-Cid et al., 2006:51, 56; Pacheco-Ruíz et al., 2008:208; Rosas-Alquicira et al., 2013:698, figs. 7, 14, 27, 34, 40–47, 49–51, tbls. 1, 2.

Amphiroa rigida sensu Dawson, 1944a:276 [non *Amphiroa rigida* Lamouroux, 1816:297].

Amphiroa subcylindrica E. Y. Dawson, 1953a:139, pl. 29: fig. 1; 1959a:10, 22; 1966a:18; Huerta-Múzquiz, 1978:338; Littler and Littler, 1981:151, 153–154; Johansen, 1981:68: fig. 10A; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:422; Salcedo-Martínez et al., 1988:83; Anderson, 1991:15; González-González et al., 1996:172, 383; Riosmena-Rodríguez and Woelkerling, 2000:330; Fernández-García et al., 2011:60.

Calcified articulated fronds up to 10 cm high, more or less erect, often in clumps; initially attached by a discoid holdfast, later becoming an expanding crustose holdfast. Branching dichotomous to trichotomous or sometimes polychotomous and becoming obscure and irregular; branches with rounded apices. Intergenicula cylindrical to subcylindrical, 1–2 mm diameter and variable in length, up to or more than 1.0 cm (length difficult to discern because genicula thickening with age are often barely visible); of 2–5 rows of long cells alternating with 1 row of short cells; cortex of 9 bands of oblong cortical cells. Genicula uncalcified, consisting of (4–)5–8 (–10) tiers of cells; fully formed genicula often barely visible between intergenicula near branch apices, becoming apparent by cracking and sloughing of calcified cortical tissue overlying intergenicula.

Conceptacles scattered over intergenicular surfaces, protruding only slightly, becoming buried by continuing cortical growth; pore formed by the coalescent repeated division of roof cells, oriented toward the margin. Tetrasporangial and bisporangial conceptacles 200–300 µm inside diameter. Sporangial conceptacle canal with large block cells; sporangia in center and periphery of cavity floor. Carpogonial filaments develop only on margins of fusion cell. Basal cells of spermatangial conceptacle form by basal division of cavity cells; each basal cell produces 2 spermatangial parent cells that develop simple spermatangial filaments; spermatangia release spermatia that fill conceptacle chamber (reproduction after Rosas-Alquicira et al., 2013).

HABITAT. Low intertidal to subtidal; on rocks.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Palmilla; Nayarit to Jalisco. Eastern Pacific: Panama; Galápagos Islands.

TYPE LOCALITY. "Recueillie juste audessous de la limite de la mer" (Lemoine, 1930:73); Bahía Correos (Post Office Bay), Isla Floreana (Isla Charles; Isla Santa María), Islas Galápagos, Ecuador.

REMARKS. Temporal and spatial studies of *Amphiroa vanbosseae* at El Sargento in the southern Gulf (Rivera-Campos and Riosmena-Rodríguez, 2003) showed the species occurred throughout the year, with the largest thalli found in spring. Reproduction was throughout the year. The highest proportion of

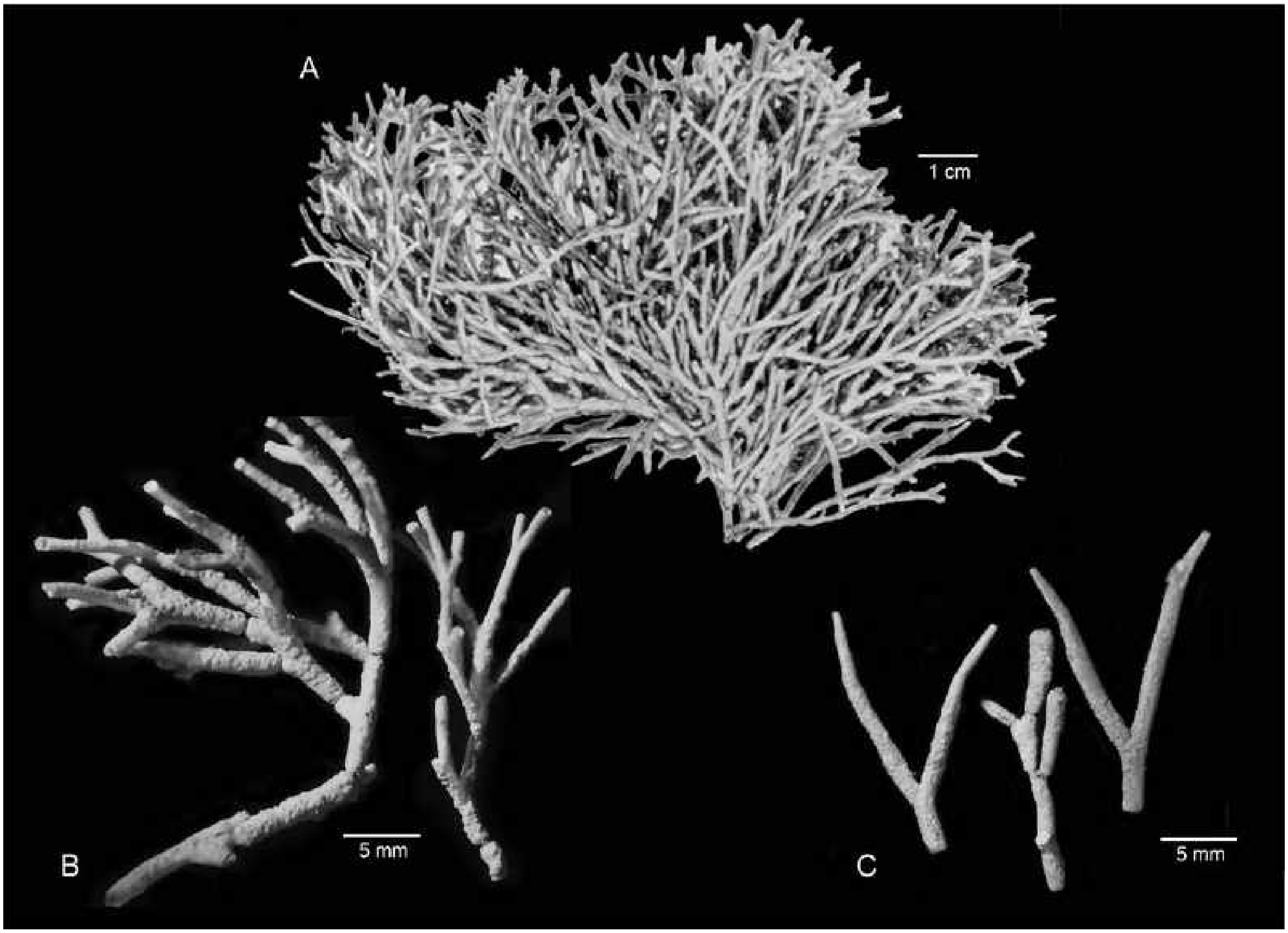

FIGURE 44. *Amphiroa vanbosseae:* A. Habit (holotype of *Amphiroa subcylindrica* E. Y. Dawson, *EYD-555,* AHFH-4277, now UC). B. Branch intergenicula with conceptacles (*JN & HWJ-73-7-1,* US Alg. Coll.). C. Coarse cylindrical intergenicula of branches (*JN-3050*, US Alg. Coll.).

reproductive thalli (mostly bisporangia and tetrasporangia) was found in summer when other algal species decreased or disappeared, presumably because of environmental stress.

Norris and Johansen (1981), on the basis of morphological comparisons, concluded the northern Gulf of California *A. subcylindrica* E. Y. Dawson (1953a; type locality: Punta Colorado, near Guaymas, Sonora) was conspecific with the Galápagos *A. vanbosseae* (see also Riosmena-Rodríguez and Siqueiros-Beltrones, 1996). It will be interesting to test if comparative molecular analyses could confirm their taxonomic status.

Corallinaceae subfam. Lithophylloideae

Corallinaceae subfam. Lithophylloideae Setchell, 1943:134, as 'Lithophylleae'; Cabioch, 1972:261, 266; Harvey et al., 2003a:994.

The subfamily Lithophylloideae is characterized by genera that have thalli without genicula and that vary in form from horizontally flattened crusts to being composed mainly of protuberances. Crustose portions internally dorsiventrally organized, protuberances, when present, more or less radially organized. Some cells of contiguous vegetative filaments with secondary pit connections adjoining them; cell fusions are absent or rare. Sporangial conceptacles produced by filaments peripheral to the fertile area and interspersed among sporangial initials. Spermatangial filaments develop from the spermatangial conceptacle floor.

Remarks. If Cabioch (1972) is followed with C. subfam. Amphiroideae treated within C. subfam. Lithophylloideae, it would include the articulated genus *Amphiroa* in addition to its nonarticulated (crustose) members. (See also Remarks under C. subfam. Amphiroideae.)

There are four genera represented in the northern Gulf of California. Two of these, tentatively placed in C. subfam. Lithophylloideae, remain problematic. *Litholepis* requires further elucidation of its generic status, and *Pseudolithophyllum*, although traditionally included, appears not to belong in this subfamily on the basis of its morphological features. It too needs testing of its generic status and taxonomic position.

KEY TO THE GENERA OF CORALLINACEAE SUBFAM. LITHOPHYLLOIDEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts thin, a single cell layer; on rocks, shells, or other corallines; individuals usually overgrowing each other to form 2–4 layers . . . . *Litholepis*

1b. Crusts thicker, of 2 or more cell layers; epiphytic, epilithic, or partly to entirely unattached and nodular (rhodoliths) . . . 2

2a. Crusts of Gulf species epiphytic (somewhat loosely surrounding algal host), with smooth to irregular surfaces; primigenous (basal) filaments composed of palisade cells (vertically elongated) . . . . *Titanoderma*

2b. Gulf crustose species epilithic or partly to entirely free living nodules (rhodoliths), with protuberances of various sizes and shapes; primigenous filaments mostly to entirely composed of nonpalisade cells 3

3a. Secondary pit connections present between some cells of contiguous filaments; intercellular fusions absent to rare, crustose portions with uni- or multistratose primigenous (basal) layer . . . . *Lithophyllum*

3b. Secondary pit connections lacking; intercellular fusions present linking some cells of contiguous filaments ; crustose portions with unistratose primigenous layer . . . . *Pseudolithophyllum*

Litholepis **Foslie**

Litholepis Foslie, 1905b:5.

Melobesia subgen. *Litholepis* (Foslie) Me. Lemoine, 1917:154, 176.

Calcified crusts are thin and delicate; composed of a single cell layer (except around the conceptacles). Monostromatic layer of thick-walled cells. Typically, overgrowth of a single crust by several other individuals results in a structure of 2–4 cell layers. Species mostly grow on rocks or shells.

Sporangial conceptacles protrude above surface and have a single pore (at least in Gulf of California *L. sonorensis*).

REMARKS. Woelkerling (1986; 1988) concluded the lectotype of the genus, *Litholepis caspica* (Foslie) Foslie (1905b; basionym: *Melobesia caspica* Foslie, 1900a), belonged in the genus *Titanoderma*, as *T. capsicum* (Foslie) Woelkerling (1986). Later *T. capsicum* was considered conspecific with *T. pustulatum* (Foslie) Nägeli (in Nägeli and Cramer, 1858; see Chamberlain, 1991), and subsequently with *Lithophyllum pustulatum* (J. V. Lamouroux) Foslie (1904; see Woelkerling and Campbell, 1992). Although Campbell and Woelkerling (1990) and Woelkerling (1996b) treated *Titanoderma* as congeneric with *Lithophyllum*, *Titanoderma* has been maintained by Chamberlain and Irvine (1994a; see Chamberlain et al., 1991). Molecular and morphological analyses are needed to elucidate species of *Litholepis*, their generic placement, and relationship to the *Lithophyllum*–*Titanoderma* complex (Bittner et al. 2011; see also Remarks under *Titanoderma*).

Currently, one species of *Litholepis* is recognized in the Gulf of California. However, its generic status is uncertain.

Litholepis sonorensis E. Y. Dawson

FIGURE 45A

Litholepis sonorensis E. Y. Dawson, 1944a:275, pl. 63: fig. 1; 1960b:59, pl. 48: fig. 1; 1961b:417; Anderson, 1991:31; Espinoza-Avalos, 1993:333; González-González et al., 1996:237, 400; Riosmena-Rodríguez and Paul-Chávez, 1997:71; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:345; Fragoso and Rodríguez, 2002:107.

Lithophyllum sonorensis (Dawson) Woelkerling ex Dreckmann, 1991:34, *comb. inval.*; León-Álvarez and González-González, 1993:462; González-González et al., 1996:401; Fragoso and Rodríguez, 2002: 105, 106, 113.

Crusts thin, delicate, gray-white, spreading; 1 cell layer in vegetative portions; thicker at conceptacle, 2–4 cell layers when thalli overgrow each other; cell layer of rectangular cells, variable in height, 11–25(–28) µm tall and 14–19 µm wide.

Sporangial conceptacles more or less conical, about 350–400 µm outside diameter; only slightly protruding, up to 60 µm above crust surface; with a single pore; conceptacle 175 µm tall, 300 µm inside diameter; with flat floor of single cell layer and roof of (1–)2–3 cell layers; tetrasporangia relatively small, approximately 50 µm long, 20 µm wide. Gametangial conceptacles unknown.

HABITAT. On old mollusk shells; subtidal, dredged.

DISTRIBUTION. Gulf of California: Canal de San Lorenzo, off Isla Espíritu Santo. Eastern Pacific: Zihuatanejo, Guerrero.

TYPE LOCALITY. Dredged from 12–25 m depths; Canal de San Lorenzo (off the southern end of Isla Espíritu Santo), Bahía de La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Litholepis sonorensis* is only known from the type and its report in tropical Pacific Mexico from Guerrero. It is included herein in the hopes that it will again be collected, reevaluated, and tested to resolve its taxonomic status.

Lithophyllum **Philippi**

Lithophyllum Philippi, 1837:387.

Calcified crustose algae, usually found growing on various-sized rocks or shells and sometimes surrounding pebbles or forming free-lying nodules (rhodoliths). Members of the genus display a variety of forms from thin crusts to stony rhodoliths

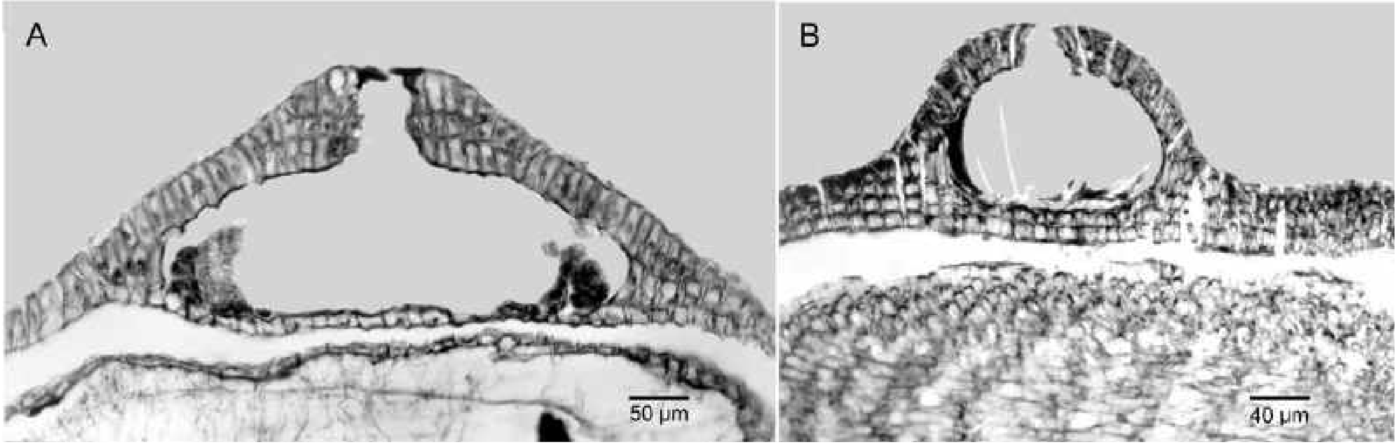

FIGURE 45. Species of *Litholepis* and *Heteroderma*. A. *Litholepis sonorensis:* Transection through a tetrasporangial conceptacle (*EYD-592x-40*, type AHFH, now UC). B. *Heteroderma corallinicola*: Transection through tetrasporangial conceptacle (*Drouet & Richards-338a*, type AHFH, now UC).

thick with protuberances of various sizes and shapes. Internal structure is pseudoparenchymatous, and construction is monomerous, dimerous, or both. A monomerous thallus consists of a single system of branched filaments that form a ventral and/or central core and a peripheral area when portions of the core filaments shift outward toward the thallus surface. A dimerous thallus consists of two groups of filaments—a single layer of primigenous filaments (hypothallium) composed of squarish (nonpalisade) cells and a second order of filaments (postigenous) produced from the dorsal side of the basal (primigenous) filament cells—which grow perpendicular to the basal/ventral layer filaments. Secondary pit connections are present between some cells of contiguous filaments. Intercellular fusions are absent, and trichocytes are absent to rare.

Sporangial conceptacles open by a single pore, internally with bisporangia or tetrasporangia scattered across conceptacle chamber floor or with a raised central columella containing a tuft of sterile filaments, with the sporangia restricted to the periphery of the chamber. Sporangial conceptacles produced by filaments peripheral to the fertile area and interspersed among sporangial initials. Gametophytes are usually dioecious; carposporangial and spermatangial conceptacles are also uniporate. Unbranched spermatangial filaments are developed from the conceptacle chamber floor.

REMARKS. Two species described from Bahía de La Paz in the southern Gulf of California have been excluded from the genus (Riosmena-Rodriguez et al., 1999). Though their generic placement was unresolved, Riosmena-Rodriguez and Woelkerling (2000) noted that *Lithophyllum californiense* Heydrich (1901b; treated as synonym of *L. pallescens* by Dawson, 1960a) belongs in Hapalidiaceae subfam. Melobesioideae; and *L. brachiatum* (Heydrich) Me. Lemoine (1930; basionym: *L. lithophylloides f. brachiatum* Heydrich, 1901b; considered a synonym of *L. lithophylloides* by Dawson, 1960a) belongs in either Corallinaceae subfam. Mastophoroideae or H. subfam. Melobesioideae.

Two other species have also been reported in the southern Gulf. *Lithophyllum corallinae* (P. Crouan et H. Crouan) Heydrich (1897b; basionym: *Melobesia corallinae* P. Crouan et H. Crouan, 1867) was reported by Dawson (1960b, as *Dermatolithon corallinae* (P. Crouan et H. Crouan) Foslie, 1909) and by Serviere-Zaragoza et al. (1993a, as *Titanoderma corallinae* (P. Crouan et H. Crouan) Woelkerling, Chamberlain et P. C. Silva, 1985), and *L. lichenare* L. R. Mason (1953), a species that Riosmena-Rodríguez and Woelkerling (2000) noted requires further study, is recorded from Bahía Concepción (Mateo-Cid et al., 1993) and Mazatlán (Mendoza-González et al., 1994) and in Pacific Mexico from Baja California (R. Aguilar-Rosas and Aguilar-Rosas, 1994), Islas Revillagigedo (Huerta-Múzquiz and Garza-Barrientos, 1975), Nayarit and Jalisco (Mendoza-González and Mateo-Cid, 1992; Serviere-Zaragoza et al., 1993a), and Michoacán (Stout and Dreckmann, 1993).

Rhodoliths were known as "chicaron" on the former pearl-fishing banks around La Paz (Dawson, 1944a). Living rhodolith or maerl (maërl) beds are unique marine ecosystems, widely distributed but particularly abundant in the Gulf of California, the Pacific off southern Japan, Atlantic waters off the coasts of Norway, Ireland, Scotland, northeast Canada, eastern Caribbean and Brazil, the Mediterranean and Red Seas, and Indian Ocean off the coast of western Australia (Foster, 2001; Amado-Filho et al., 2012). In the Gulf of California, rhodolith beds are often extensive, occurring from Puerto Peñasco, Sonora, to Islas Marietas, Jalisco (Foster et al., 1997; Riosmena-Rodríguez et al., 2010: fig. 3.1). With their high ecological and economic value they are now recognized as critical habitats in need of monitoring and conservation (Ávila and Riosmena-Rodríguez, 2010; Riosmena-Rodríguez et al., 2010).

Six species of *Lithophyllum* are recognized to occur in the northern Gulf of California.

KEY TO THE CRUSTOSE AND RHODOLITH-FORMING SPECIES OF *LITHOPHYLLUM*, *PSEUDOLITHOPHYLLUM*, AND *NEOGONIOLITHON* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts with lateral cell fusions between cells of filaments; secondary pit connections absent 2

1b. Crusts without cell fusions between cells of filaments; secondary pit connections present 3

2a. Crusts usually thin (some thicker); with low (up to 2 mm tall), short subspherical protuberances; sporangial conceptacles less than 250 µm in diameter; trichocytes absent . . . . ***Pseudolithophyllum neofarlowii***

2b. Crusts with prominent (up to 15 mm tall), subcylindrical to compressed, longer protuberances; sporangial conceptacles in apex of protuberances, large, up to 1000 µm in diameter; trichocytes present . . . . ***Neogoniolithon trichotomum***

3a. Rhodoliths either flat, broad fan-like to blade-like excrescences, with rounded edges, OR protuberant branches with broad compressed to flattened portions with angular branches that narrow to pointed apices 4

3b. Crusts or rhodoliths with slender subcylindrical branches to wart-like knobby protuberances (not flat or blade-like) . . . 5

4a. Rhodoliths predominantly fan-like to blade-like, of thin, broad flat, sometimes undulate, excrescences, some with ridges or channels and rounded edges . . . . ***L. diguetii***

4b. Rhodoliths with compressed to somewhat flattened portions; angular branches mostly narrowing upward to irregularly pointed apices . . . . ***L. margaritae***

5a. Crusts with low, irregularly undulating surface; or, surface with simple, short (mostly 2–5 mm tall), subspherical or mound-like protuberances; base subcylindrical to broad; ends broad, irregularly rounded . . . . ***L. imitans***

5b. Crusts or rhodoliths either with taller, larger, more elaborate protuberant branches, or wart-like or knob-like protuberances; ends flattened or rounded 6

6a. Crusts shrubby with clusters of irregularly branched, subcylindrical, often anastomosed branches, but free in upper parts; wider at base, upward becoming slender (1.5 mm or less in diam.) with rounded or truncate tops . . . . . . ***L. hancockii***

6b. Crust or rhodoliths with stout wart-like or knob-like protuberances with rounded or broad, flattened tops (equal to or over 2 mm diam.) 7

7a. Crusts or rhodoliths with simple or forked, compressed to knob-like protuberances (up to 3 cm tall); mostly narrow bases (to 3 mm in diameter) widened upward, with truncate, broad flattened ends (4–5 or more mm wide), often with a central depression . . . . ***L. proboscideum***

7b. Crusts and rhodoliths lumpy and knobby, with short (mostly less than 1.5 cm tall), simple, knob- to club-shaped protuberances (2–4 mm in diameter), with rounded to bulbous, slight to conspicuous swollen ends (not flattened) . . . . ***L. pallescens***

Lithophyllum diguetii (Hariot) Heydrich

FIGURE 46

Lithothamnion diguetii Hariot, 1895:167; Heydrich, 1901a:190; Woelkerling, 1984:50; Woelkerling, 1998:340; Woelkerling et al., 1998:529, figs. 240–241.

Lithophyllum diguetii (Hariot) Heydrich, 1901b:532; Foslie, 1909:26; Lemoine, 1911:120; Foslie, 1929:33, pl. 61: fig. 8; Dawson, 1944a:269, pl. 59: figs. 8, 11–16; 1960b:38, pl. 29: figs. 1–7; 1961b:416; Adey and Lebednik, 1967:45; Huerta-Múzquiz and Mendoza-González, 1985:48; Dreckmann, 1991:34; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; Steller and Foster, 1995:205, fig. 2; González-González et al., 1996:237; Foster et al., 1997:133; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Woelkerling, 1998:340; Riosmena-Rodríguez et al., 1999:403 [in part], fig. 6; Riosmena-Rodríguez and Woelkerling, 2000:337; Pacheco-Ruíz and Zertuche-González, 2002:467; Schaeffer et al., 2002: fig. 2C.

Lithothamnion dentatum sensu Foslie, 1895b:5, pl. 1: fig. 15 [non *Lithothamnion dentatum* (Kützing) Areschoug, 1852:516; =*Lithophyllum dentatum* (Kützing) Foslie, 1900a:10].

Lithothamnion dentatum f. *diguetii* (Hariot) Foslie, 1901c:21.

Lithophyllum margaritae sensu Riosmena-Rodríguez et al., 1999:403, 411 [in part: *Lithophyllum diguetii* and *L. veleroae* specimens only; non *Lithophyllum margaritae* (Hariot) Heydrich, 1901b:530].

Lithophyllum veleroae E. Y. Dawson, 1944a:270, pl. 55: fig. 5, pl. 56: figs. 1–4; 1960b:52, pl. 47: figs. 1–4(type); 1961b:417; Huerta-Múzquiz and Mendoza-González, 1985:48; Ortega et al., 1987:74, pl. 4: fig. 22, pl. 5: fig. 23; Anderson, 1991:32; Dreckmann, 1991:34; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; Steller and Foster, 1995:205, fig. 2; González-González et al., 1996:239; Foster et al., 1997:133; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Woelkerling, 1998:328; Woelkerling et al., 1998:499, fig. 211; Riosmena-Rodríguez et al., 1999:411, figs. 10–13; Riosmena-Rodríguez and Woelkerling, 2000:346.

Free-living crust, forming subspherical to irregularly shaped rhodoliths; of several thin foliose, simple to undulate or convoluted, anastomosing blade-likeextensions, up to 1–3 cm in length (seen from above), subcylindrical to compressed at their base and decreasing in thickness upward, 1.0–2.0 mm thick. Longitudinal sections of flat blade-like extensions internally with a distinct central core of filaments (medullary hypothallium) of more or

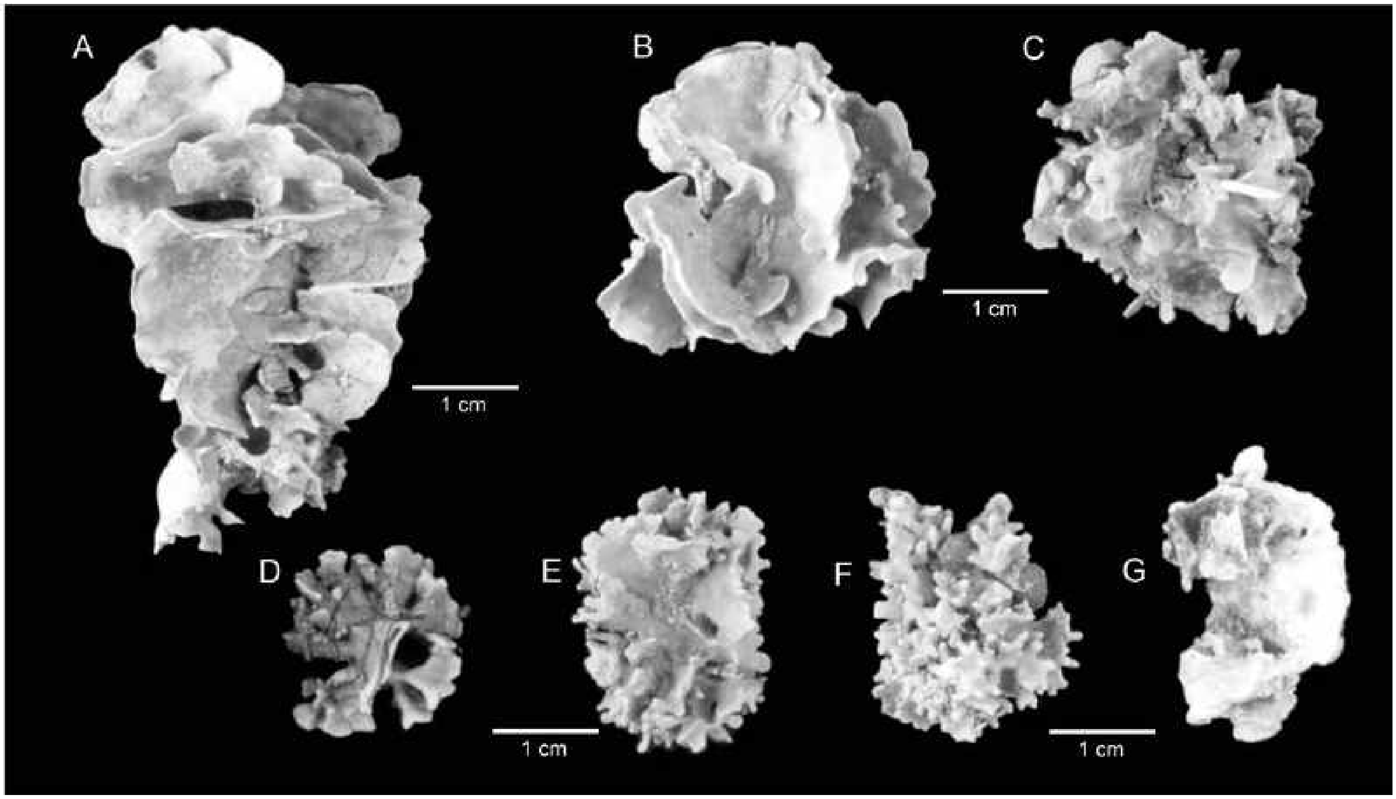

FIGURE 46. *Lithophyllum diguetii*: A, C–G. Habit variability of rhodolith morphologies (*EYD-591-40*, AHFH, now UC). B. Isotype (*L. Diguet-1894*, UC).

less rectangular cells, 14–27 µm long, 9–11µm wide; perithallium thick, of rounded cells 12–17 µm long, 7.0–10 µm wide, with prominent pit connections linking some cells of adjacent filaments; filaments terminate at thallus surface in epithallial cells (wider than tall), about 3.5 µm tall, 9–12 µm wide.

Sporangial conceptacles scattered over flat, blade-like surfaces, embedded, nearly flush with surface, up to 100–125 µm tall, with a small central pore, chamber about 100 µm deep, up to 275 µm wide, with central columella; tetrasporangia (45–) 60–70 µm long, (22–)35–45 µm in diameter. Carposporangial and spermatangial conceptacles not observed (description after Dawson, 1960b).

HABITAT. Usually on sand plains; often component of extensive rhodolith beds; occasionally cast ashore; intertidal to subtidal, 2.0–13 m depths; dredged to 26 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Bahía de La Paz; Canal de San Lorenzo, Isla Espíritu Santo; Isla Partida; Laguna Agiabampo (Sonora and Sinaloa); Sinaloa to Jalisco.

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. Dawson (1960b:44) observed *Lithophyllum diguetii* living in association with *L. margaritae* and *L. lithophylloides* (=*L. pallescens*) in the rhodolith beds in Canal de San Lorenzo, off Isla Espíritu Santo.

Dawson (1960b:52) noted some specimens showed intermediate characters of *L. diguetii*, *L. veleroae* and *L. lithophylloides* and suggested there may be hybridization between them. These species were later considered to be within a broadly circumscribed "*L. margaritae*" (Riosmena-Rodríguez et al., 1999). Schaeffer et al. (2002, as *L. margaritae*) found two genetically distinct morphological forms. They questioned the validity of treating these as forms because of their genetic differences and the apparent limited genetic exchange between them. Although reproduction by vegetative fragmentation of these rhodoliths has been generally assumed, they found no genetic evidence of clones, suggesting there is little, if any, vegetative reproduction. Of the different morphologies they tested, their "foliose forms" (Schaeffer et al., 2002: fig. 2C) match *L. diguetii*. (See also Remarks under *Lithophyllum margaritae* and *L. pallescens*.)

Lithophyllum diguetii is recognized as a separate species on the basis of morphological and genetic differences.The type collection of another species, *Lithophyllum veleroae* E. Y. Dawson (1944a: pl. 56: figs. 1–4), a rhodolith described with channeled ridges, also seems morphologically close to *L. diguetii*. It is tentatively considered conspecific until molecular comparisons of their types and type locality material can assess their phylogenetic relationship and taxonomic status.

Lithophyllum hancockii E. Y. Dawson

FIGURE 47

Lithophyllum hancockii E. Y. Dawson, 1944a:268, pl. 55: fig. 1, pl. 62: fig. 1; 1960b:40, pl. 31: fig. 1, pl. 24: fig. 2; 1961b:416; Salcedo-Martínez et al., 1988:83; Dreckmann, 1991:34; Anderson, 1991:31; Espinoza-Avalos, 1993:333; León-Álvarez and González-González, 1993:461; González-González et al., 1996:238; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:340.

Crustose corallines forminga dense shrubby, irregularly branched cluster, up to 7 cm tall and up to 10 cm wide, attached to substratum by a thin, spreading crust. Branches subcylindrical and free of each other in upper portions, about 1.5 mm in diameter, with rounded or truncate apices; lower portion of branches wart-like or irregular in shape, often coalesced. Hypothallium in longitudinal section very thick, forming most of thallus, consisting of layers of elongate-rectangular cells, about 21 µm in length, 9–12 µm wide. Perithallium generally thin, or up to 250 µm thick; of smaller rounded cells, 9–14 µm tall, 5–8 µm wide. Epithallium of cells, mostly 2.5 µm tall, 6–8 µm wide.

Sporangial conceptacles, immersed within thallus (with little to no surface bulge), 110–140 µm tall, 240–300 µm inside diameter, pore obscure; chamber floor with central columella surrounded by tetrasporangia, 50–60 µm tall, 25–30 µm in diameter; conceptacles become overgrown and deeply embedded within thallus with age. Gametangial conceptacles unknown (after Dawson, 1960b).

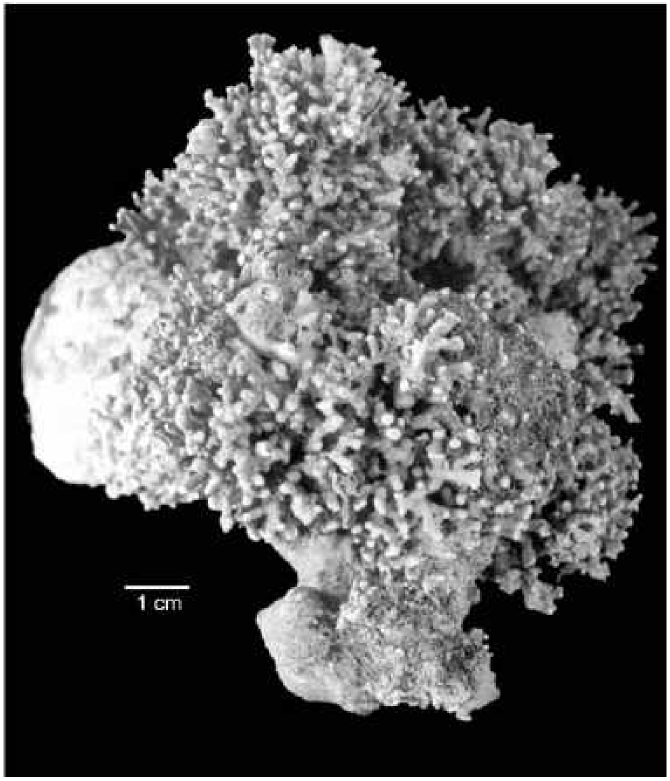

FIGURE 47. *Lithophyllum hancockii:* Habit, crust beset with protuberances (holotype, *EYD-619a-40*, UC).

HABITAT. On rocks and coral rubble; shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Espíritu Santo; Bahía de La Paz; Nayarit to Jalisco. Eastern Pacific: Guerrero.

TYPE LOCALITY. Bahía San Gabriél, Isla Espíritu Santo, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Lithophyllum hancockii* is a little-known species in the Gulf of California and is included to call attention to the need for further study. It has also been reported in Pacific Mexico from Guerrero.

Lithophyllum imitans Foslie

FIGURE 48A,B

Lithophyllum imitans Foslie, 1909:13; 1929:35, pl. 54: figs. 10, 11; Dawson, 1945d:42; Mason, 1953:340, pl. 43; Dawson, 1960b:41, pl. 32: figs. 1–4, pl. 33: figs. 1–4, pl. 34: fig. 2, pl. 35: figs. 1, 2; Dawson et al., 1960a:68, pl. 20: fig 4; 1960b:16; Dawson, 1961a:416; Dawson et al., 1964:43, pl. 38: fig. A; Hollenberg and Abbott, 1966:62; Adey and Lebednik, 1967:18; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Johansen, 1976a:393, fig. 338; Huerta-Múzquiz, 1978:335, 340; Schnetter and Bula-Meyer, 1982:125, pl. 18, fig. A; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Stewart and Stewart, 1984:143; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:423; Sánchez-Rodríguez et al., 1989:42; Stewart, 1991:78; Ramírez and Santelices, 1991:211; Dreckmann, 1991:33; Mateo-Cid and Mendoza-González, 1991:20; Mendoza-González and Mateo-Cid, 1992:18; Mateo-Cid and Mendoza-González, 1992:20; León-Álvarez and González-González, 1993:461; Woelkerling, 1993:121; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:46; Stout and Dreckmann, 1993:14; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:106; Bula-Meyer, 1995:34; González-González et al., 1996:238, 401; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:131; Mateo-Cid et al., 2000:64; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:340; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:10; Fernández-García et al., 2011:62.

Crustose thalli up to 2 mm thick, pink; firmly adherent to subtratum, rocks, and shells; surfaces in some with low irregular surface undulations, others with lumpy surfaces of protuberances of variable size and shape. Protuberances simple, subcylindrical to broad based with lumpy rounded tops, mostly short, up to 5 mm (occasionally up to 10 mm) tall, and 2–3(–6) mm in diameter. Hypothallium not well developed, 35–220 µm thick (generally about 10%–12% of overall thallus thickness), of cells 13–27 µm long, 6–11(–14) µm wide. Perithallium forming major portion of crust, usually 400–1700 µm thick, of subquadrate cells, 9–11 µm in diameter, sometimes vertically elongated up to 18 µm.

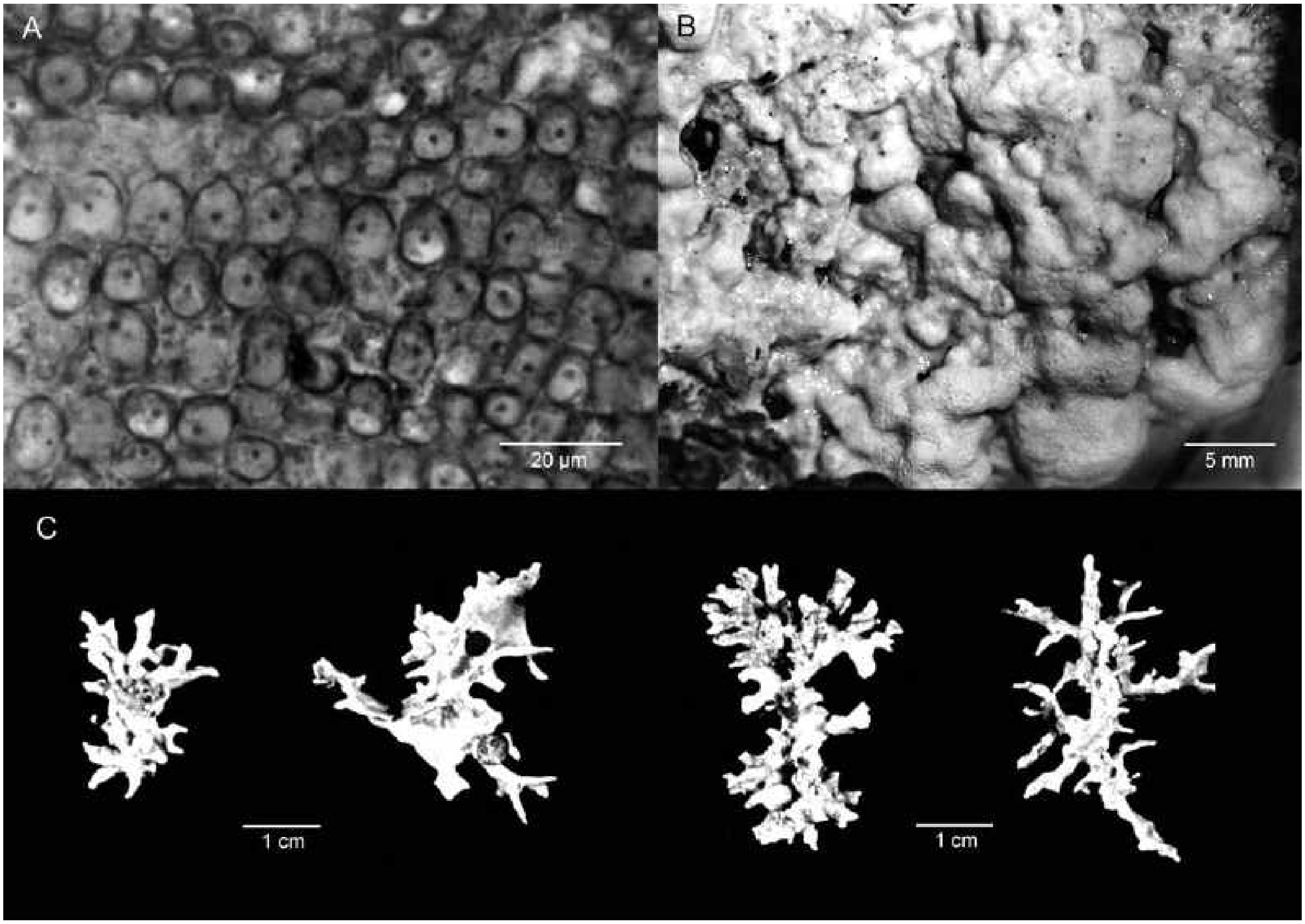

FIGURE 48. *Lithophyllum imitans:* A. Close-up of numerous conceptacles, each with a single pore (*JN & HWJ 73-7-11a*, US Alg. Coll.). B. Surface view of crust (*JN-4025*, US Alg. Coll.). C. *Lithophyllum margaritae*: habit variations of four specimens (*EYD-6942*, AHFH, now UC).

Sporangial conceptacles scattered, slightly protruding, up to 400 μm outside diameter; chamber 180–330 μm inside diameter, 51–117 μm high; tetrasporangia 40–60 μm long. Carposporangial conceptacles slightly prominent, about 200 μm inside diameter. Spermatangial conceptacles, chamber 120–167 μm inside diameter, 26–40 μm high, with flat floor. Old conceptacles becoming deeply buried in thallus.

HABITAT. On rocks and shells and in tide pools; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: southern British Columbia to Todos Santos, Baja California Sur; Isla Guadalupe; Isla Clarión and Isla Socorro (Islas Revillagigedo); Colima to Oaxaca; El Salvador; Costa Rica; Panama; Isla de Gorgona, Colombia; Peru.

TYPE LOCALITY. Pacific Beach (between La Jolla and Mission Beach, San Diego), San Diego County, southern California, USA.

REMARKS. *Lithophyllum imitans* is one of the commonest crustose coralline species throughout the Gulf. In the field, *L. imitans* can be recognized by its surfaces: some with low, irregularly undulate, somewhat shiny surfaces, and others that have lumpy surfaces of narrow to broad protuberances with irregularly shaped rounded ends. All the other species of *Lithophyllum* in the Gulf of California have more densely crowded surfaces, with more elaborate protuberances.

Lithophyllum margaritae (Hariot) Heydrich

FIGURE 48C

Lithothamnion margaritae Hariot, 1895:167; Foslie, 1900e:20; Woelkerling, 1998:354; Woelkerling et al., 1998:569, figs. 281–283; R. Aguilar-Rosas et al., 2009:7, fig. 2f.

Lithophyllum margaritae (Hariot) Heydrich, 1901b:530; Lemoine, 1911:174, fig. 100, pl. 2: fig. 2; Dawson, 1944a:266; 1960b:44, pl. 36: fig. 2; 1961b:416; Huerta-Múzquiz and Mendoza-González, 1985:48; Dreckmann, 1991:34; Mendoza-González and Mateo-Cid, 1994:51;

González-González et al., 1996:238; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Riosmena-Rodríguez et al., 1999:411 [in part; excluding *L. diguetii* and *L. pallescens*], figs. 2–5; Foster, 2001:660, fig. 1A; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:208; Riosmena-Rodríguez et al., 2010:58; Ávila and Riosmena-Rodríguez, 2011:368, fig. 2.

Pseudolithophyllum margaritae (Hariot) Me. Lemoine, 1913:46.

Lithothamnion elegans Foslie, 1895b:6; Heydrich, 1897b:64; 1897c:415; Woelkerling, 1984:52; Woelkerling, 1993:83; Riosmena-Rodríguez et al., 1999:411, fig. 8 (upper), Riosmena-Rodríguez and Woelkerling, 2000:338.

Lithothamnion elegans f. *angulata* Foslie, 1895b:6, pl. 1: fig. 9, *nom. superfl.*; Woelkerling, 1993:27.

Lithothamnion elegans f. *complanata* Foslie, 1895b:5, pl. 1: fig. 10; Heydrich, 1897b:64; 1897c:415; Adey and Lebednik, 1967:19; Adey, 1970:19; Woelkerling, 1993:83.

Lithophyllum elegans (Foslie) Foslie, 1900e:20; 1909:27; 1929:34: pl. 63, figs. 1, 2; Setchell and Mason, 1943b:95; Adey and Lebednik, 1967:44; Riosmena-Rodríguez et al., 1999:411, fig. 8 (lower).

Lithophyllum elegans f. *angulata* Foslie, 1900e:20, *nom. superfl.* [see Woelkerling, 1993:83].

Rhodoliths of compressed to flattened, variously shaped, angular plate-like portions, with irregular, subcylindrical to compressed, often elongated, branch-like extensions narrowing to pointed or sometimes truncate apices. Structurally monomerous, with a central core of filaments (=medullary hypothallium sensu Dawson, 1960b) of cells about 20 µm by 10 µm; filaments outwardly curve upward (=perithallium sensu Dawson, 1960b), with cells (about 15 µm by 8 µm) of adjacent filaments linked laterally by secondary pit connections; each filament terminating with a single (rarely 2) small flattened epithallial cell(s) at thallus surface.

Sporangial conceptacles within surfaces of branches, mostly flush or bulging very little on surface; chamber 140–200 µm inside diameter, somewhat dumbbell-shaped in vertical section with a central columella; chamber roof with a single pore. Tetrasporangia up to 50 µm long and about 25 µm in diameter. Gametangial conceptacles not known.

HABITAT. Free-living rhodoliths that may cover considerable areas, often growing with other rhodolith species; intertidal to subtidal.

DISTRIBUTION. Gulf of California: Canal de San Lorenzo, off Isla San Espíritu Santo to Isla San Juan Nepomuceno; Bahía de La Paz.

TYPE LOCALITY. Subtidal bank off Isla San Juan Nepomuceno ("Nepomezeino"), off the coast about 4 km from Pichilinque (between Punta Colorado and Punta Base) north of La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. Dawson (1960b:44) noted problems identifying some forms of Gulf rhodoliths with apparent intergrading morphologies that made it difficult to distinguish species. He suggested *Lithophyllum margaritae, L. diguetii, L. lithophylloides,* and *L. veleroae* possibly may be forms of a single polymorphic species but then concluded that those with distinct morphologies should be kept as separate species. Subsequent morphological studies of Riosmena-Rodríguez et al. (1999, as *L. margaritae*) considered these species and a few others to represent a single, broadly defined, highly variable species.

Schaeffer et al. (2002), however, found genetic differences and apparently little evidence of genetic mixing that supported separation of two morphological forms of *L. margaritae*: "fruticose forms, fig. 2A" that are closest to *L. pallescens*, and "foliose forms, fig. 2C" that agree with *L. diguetii*. They also had three "not-tested, intermediate forms, fig. 2B (upper left & two middle)" as "*L. margaritae.*" Of the several species considered conspecific by Riosmena-Rodríguez et al. (1999), *L. margaritae*, *L. diguetii,* and *L. pallescens* are recognized herein. Although these could be considered taxonomic varieties or subspecies, rather than propose new combinations, for now each is treated as a species until further molecular testing can elucidate their relationships and taxonomic status. (see also Remarks under *L. diguetii* and *L. pallescens*.)

***Lithophyllum pallescens* (Foslie) Foslie**

FIGURE 49A–E

Lithothamnion pallescens Foslie, 1895b:4, pl. 1: figs. 11–13; 1897:13; Heydrich, 1897b:60; 1897c:413; Foslie, 1901a:20; 1909:36; Lemoine, 1911:156, figs. 87–91; Foslie, 1929:37, pl. 64: figs. 15–17; Adey and Lebednik, 1967:42; Woelkerling, 1984:85; 1993:167; 1998:357; Woelkerling et al., 1998:577, figs. 289, 290; Riosmena-Rodríguez et al., 1999:411, fig. 9.

Lithophyllum pallescens (Foslie) Foslie, 1900a:20; Adey, 1970:5; Adey et al., 1982:40, figs. 23, 27; Schnetter and Bula-Meyer, 1982:126, pl. 15: figs. K, L, pl. 17: figs. D, E; Huerta-Múzquiz and Mendoza-González, 1985:48; Mendoza-González and Mateo-Cid, 1986:423; Dreckmann, 1991:34; Mendoza-González and Mateo-Cid, 1994:51; Steller and Foster, 1995:205, fig. 2; González-González et al., 1996:238; Foster et al., 1997:133; Riosmena-Rodríguez and Paul-Chávez, 1997:71; L. Aguilar-Rosas et al., 2000:131; Mateo-Cid et al., 2000:65; Schaeffer et al., 2002: fig. 2A; Fernández-García et al., 2011:62.

Lithophyllum pallescens (Foslie) Heydrich, 1901b:531; Dawson, 1944a:266, pl. 55: fig. 4; 1960a:45, pl. 31: fig. 2, pl. 38, pl. 39: figs. 1, 2; 1961b:416; 1966a:19; Schwab, 1969:189, figs. 1–14; Mendoza-González and Mateo-Cid, 1986:423; Espinoza-Avalos, 1993:334; Mateo-Cid et al., 1993:46; Bula-Meyer, 1995:34; Woelkerling et al., 1998:577, figs. 289, 290; Riosmena-Rodríguez and Woelkerling, 2000:343; Cruz-Ayala et al., 2001:191.

Goniolithon pallescens Foslie, 1898:9.

Lithophyllum lithophylloides Heydrich, 1901b:531; Dawson, 1944a:269, pl. 55: fig. 3, pl. 58: figs. 2, 3(type), 7, pl. 59: figs. 9, 10, pl. 61: fig. 1; 1960b:43, pl. 16: fig. 2, pl. 29: figs. 8, 9; 1961b:416; Adey and Lebednik, 1967:48; Huerta-Múzquiz and Mendoza-González, 1985:48; Dreckmann, 1991:34; León-Álvarez and González-González, 1993:461; León-Tejera and González-González, 1993:497; Woelkerling, 1993:138, 172; Serviere-Zaragoza et al., 1993a:484; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:238, 401; León-Tejera et al., 1996:164; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Woelkerling, 1998:354; Woelkerling et al., 1998:476, figs.188–189; Riosmena-Rodríguez et al., 1999:411, fig. 7; Riosmena-Rodríguez and Woelkerling, 2000:327; Pacheco-Ruíz and Zertuche-González, 2002:467.

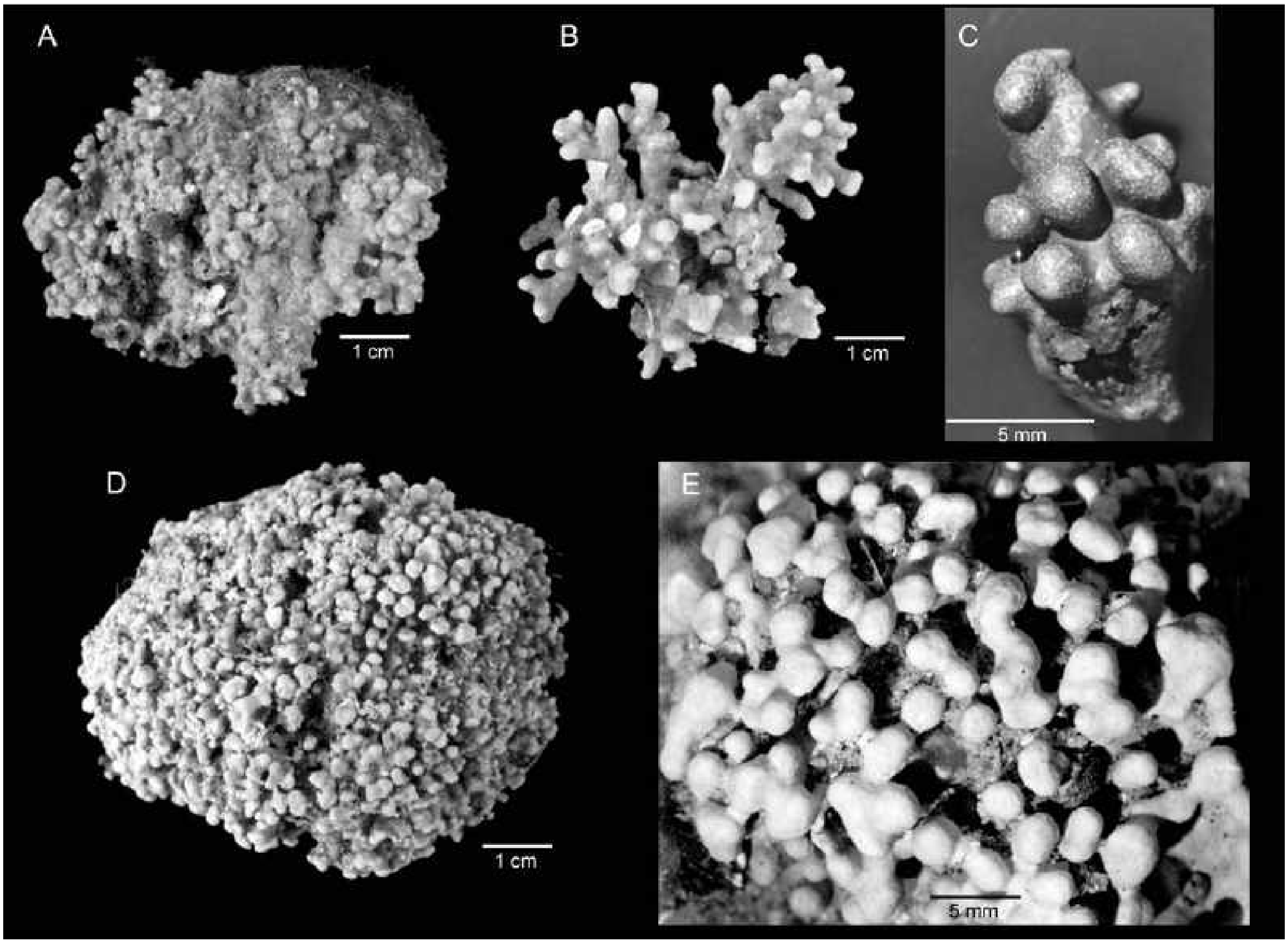

FIGURE 49. *Lithophyllum pallescens*: A, B, D. Variability of rhodolith morphologies (A, *EYD-278-40*; B, *EYD-250-40*; D, *EYD-572-50*, all AHFH, now UC). C, E. Close-up of protuberances (C, *JN-3586*; E, *JN-3503*, both US Alg. Coll.).

Lithothamnion lithophylloides (Heydrich) Foslie, 1907:11.

Crusts spreading on hard substratum, rocks, shells, or coral fragments; surfaces crowded with short, subcylindrical knob-like protuberances; or free-living subspherical-shaped, knobby rhodoliths, up to 5 cm in diameter. Protuberances simple to little branched, 2–4 mm in diameter, anastomosing in lower portions, with rounded or knob-shaped to club-shaped tops; in longitudinal sections, with a thick central core of filaments (medullary hypothallium) of elongated cells, 14–20 µm long, 9–11µm wide; perithallium layers of filaments of ovate to subspherical cells about 7.0–10 µm in diameter; some cells of adjacent perithallial filaments laterally linked by pit connections; epithallium of cells (wider than tall), about 2.4–3.5 µm tall, 7–9 µm wide.

Reproductive conceptacles scattered over surfaces of protuberances, embedded, nearly flush with surface or very low dome shaped (not prominent), with small central pore. Sporangial conceptacle chambers about 100 µm deep, 225–300 µm inside diameter; tetrasporangia 50–60 µm tall, 35–45 µm in diameter. Carposporangial conceptacles about 80–100 µm tall, 200–280 µm inside diameter, with nearly flat floor; a central fusion cell with peripheral gonimoblast filaments bearing terminal carposporangia. Spermatangial conceptacles chambers about 30–80 µm tall, 150–175 µm inside diameter, with simple spermatangial filaments along the floor (description after Dawson, 1960b).

Habitat. Crusts on hard substratum in tide pools, partially attached to small pieces of rock, shells, or coral fragments, or free-living rhodoliths that may cover considerable areas; intertidal to shallow subtidal, 1–26 m depths (Dawson, 1960b).

Distribution. Gulf of California: Puerto Peñasco to Isla Pelícanos, Bahía Kino; El Machorro, San Felipe to Puerto Escondido; Isla Mejía and NW side of Puerto Refugio, Isla Ángel de la Guarda; south of Santa Rosalía to laguna San Gabriel and Canal de San Lorenzo, Isla Espíritu Santo; Isla Carmén; Bahía de La Paz to Cabo Pulmo; Laguna Agiabampo, Sinaloa to Jalisco;

Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: Isla Clarión and Isla Socorro (Islas Revillagigedo); Jalisco to Oaxaca; Isla Brincanco and Isla Contreras, Panama; Isla de Gorgona, Colombia. Central Pacific: Hawaiian Islands.

TYPE LOCALITY. Subtidal bank of west shore, off Isla Espíritu Santo, Baja California Sur, Gulf of California, Mexico (locale information from map of M. Diguet and transcribed by Madame Marie Lemoine (PC), Paris; Dawson, 1944a:266).

REMARKS. In the field, some forms of *Lithophyllum pallescens* may be confused with *L. proboscideum*. However, *L. pallescens* lack the broad, flat-topped protuberances of *L. proboscideum*. Subsequent morphological studies of Riosmena-Rodríguez et al. (1999, as *Lithophyllum margaritae*) considered these species and a few others to represent a single, broadly defined, highly variable species.

Schaeffer et al. (2002, as *L. margaritae*) found genetic differences and little apparent evidence of genetic mixing that supported separation of two morphological forms. Their "fruticose forms" (Schaeffer et al., 2002, fig. 2A) are closest to *L. pallescens*. (See also Remarks under *L. margaritae* and *L. diguetii*.) The type collection of *L. lithophylloides* appears to be close to *L. pallescens*, and *L. lithophylloides* is tentatively treated as a synonym until molecular analyses can be done on type material.

Lithophyllum proboscideum (Foslie) Foslie

FIGURE 50

Lithothamnion proboscideum Foslie, 1897:14; Heydrich, 1897c:414; Woelkerling, 1993:176.

Lithophyllum proboscideum (Foslie) Foslie, 1900a:18; 1929:37, pl. 63: figs. 3, 4; Smith, 1944:227; Dawson, 1945d:42; Mason, 1953:342, pl. 46a, b; Dawson, 1960b:47, pl. 40: figs. 1–5, pl. 41: figs. 1, 2, pl. 42: figs. 1, 2; 1961b:416; 1966a:19; Adey and Lebednik, 1967:44; Johansen, 1976a:393, fig. 340; Adey, 1970:5; Littler and Littler, 1981:153; Lewber et al., 1983:164; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Stewart and Stewart, 1984:143; Mendoza-González and Mateo-Cid, 1986:423; Steneck and Paine, 1986:231; Ortega et al., 1987:73, pl. 5: fig. 24, pl. 6: fig. 25; R. Aguilar-Rosas et al., 1990:124; Dreckmann, 1991:33; Stewart, 1991:78; León-Álvarez and González-González, 1993:461; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; González-González et al., 1996:239, 401; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:344; Cruz-Ayala et al., 2001:191; Mateo-Cid et al., 2006:56.

Crusts on hard substratum; spreading, covering up to 17 cm or more, and to 2 mm or more thick; crowded with stout, subcylindrical flat-topped protuberances. Protuberances simple

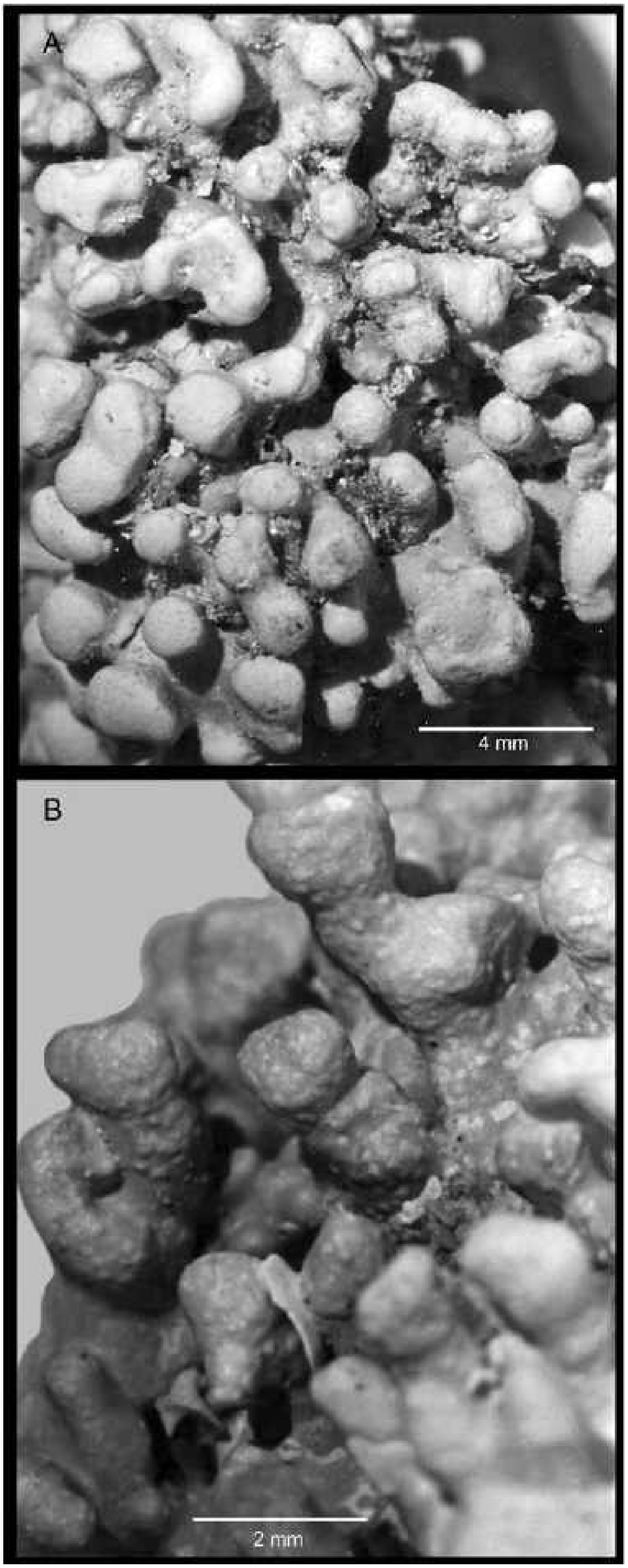

FIGURE 50. *Lithophyllum proboscideum*: A. Portion of crust showing broad-topped protuberances (*JN-3825*, US Alg. Coll.). B. Close-up of protuberances with conceptacles (*JN-3471*, US Alg. Coll.).

(undivided) to divided, frequently anastomosed; up to 3 cm high and to 3 mm in diameter at base; broadening upward, usually 4–5 mm (occasionally more) in diameter at enlarged and typically flat-topped ends, sometimes with a central apical depression. Hypothallium well developed, of elongate cells 14–36 μm long, 7–12 μm wide. Perithallium of several layers; perithallial filaments similar in both crustose portion and protuberances, of squarish cells, 6–9 μm in diameter, or slightly vertically elongated, 9–11 μm long, (6–)7–9 μm wide; perithallial cells of protuberances, 8–16 long, 6–8 μm in diameter. Epithallium of 3–4 layers of small cells (wider than tall), 2–4 μm tall, 6–8 μm wide (after Mason, 1953; Dawson, 1960b).

Sporangial conceptacles scattered over the lower surfaces of the protuberances, immersed, 190–300 μm in diameter, 95–125 μm high; tetrasporangia 50–60 μm high, 30–35 μm in diameter. Gametangial thalli not reported in the northern Gulf.

HABITAT. On rocks and in tide pools; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Playa Arenosa (Norse Beach), Puerto Peñasco to Bahía Concepción; Bahía de La Paz; Bocochibampo (near Guaymas); Laguna Agiabampo; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: southern British Columbia to Baja California; Islas Todos Santos and Isla Guadalupe, Baja California; Colima to Oaxaca.

TYPE LOCALITY. Dredged off Monterey, Monterey County, central California, USA.

REMARKS. Apparently a common crustose coralline in the Gulf, *Lithophyllum proboscideum* is conspicuous and recognized by its prominent and characteristic broad, usually flat-topped protuberances. The shape and size of these protuberances may vary considerably, sometimes even in a single specimen.

***Pseudolithophyllum* Me. Lemoine**

Pseudolithophyllum Me. Lemoine, 1913:45, fig. 13A; Adey, 1966a:480; Cabioch, 1972:144, fig. 1A, figs. 1, 2–6 (generitype); Mendoza and Cabioch, 1985:144 [non *Pseudolithophyllum* sensu Adey, 1970:12].

Pseudolithophyllum Me. Lemoine, 1912:783, *nom. illeg.*

Crustose corallines are with or without protuberances. Crustose portion varies in thickness from very thin, 50–200 μm, to 1–2 mm. The hypothallium is a single layer of cells (but at least one, *Pseudolithophyllum neofarlowii*, may have up to three weakly developed layers; Dawson, 1960b) that produces ascending rows of perithallial filaments. The perithallium is well developed, comprising almost the entire thickness of the thallus, and is weakly to strongly layered, with the cells of the perithallial filaments not laterally aligned in horizontal rows. Secondary perithallial outgrowths are also present. Subepithallial initials (meristematic cells) are intercalary and directly below the epithallium. Epithallial cells are present but may degenerate or be lacking in portions of the thallus. Lateral cell fusions are present between cells of adjacent filaments. Trichocytes and secondary pit connections are absent.

Sporangial conceptacles may be slightly sunken, flush with the surface, or in raised dome structures, and have a roof with a single pore.

REMARKS. There have been questions about the taxonomy and nomenclature of *Pseudolithophyllum* Me. Lemoine (1913). The implicit generitype is *Lithophyllum fuegianum* Heydrich (1901b), which Foslie (1901c) considered conspecific with *L. discoideum* Foslie (1900f). Lemoine (1913:46) followed Foslie's (1901c) synonomy in making the combination *P. discoideum* (Foslie) Me. Lemoine. Later, Lemoine (1978), using cytological characters, recognized that *L. fuegianum* Heydrich and *L. discoideum* Foslie were two different species, noting *L. fuegianum* Heydrich (1901b) was the type species for *Pseudolithophyllum*.

Mendoza and Cabioch (1985) also found *Lithophyllum discoideum* to comprise two species, and treated *L. discoideum* Foslie as *Hydrolithon discoideum* (Foslie) M. L. Mendoza et Cabioch (1985; later considered *Spongites discoideus* (Foslie) Penrose et Woelkerling, 1988, as '*discoidea*'). On the basis of their study of the type species, *L. fuegianum* Heydrich (1901b), Mendoza and Cabioch (1985) redescribed the genus and made the combination *Pseudolithophyllum fuegianum* (Heydrich) M. L. Mendoza et Cabioch. Silva (1986) and Silva (in Silva et al., 1996a) evaluated the confused nomenclature history of *Pseudolithophyllum* and concluded the generic name in the sense of Lemoine can be used without being conserved and is typified by *P. fuegianum*.

The generic placement of some species within the *Lithophyllum*–*Pseudolithophyllum* complex is uncertain because the distinctiveness of the genera is in question. Penrose and Woelkerling (1988) treated the generitype, *L. fuegianum* Heydrich, as a *Lithophyllum*, which would make *Pseudolithophyllum* congeneric—a conclusion supported by Woelkerling (1988), Chamberlain and Irvine (1994a), and Athanasiadis (1999). Herein *Pseudolithophyllum* is tentatively recognized on the basis of its characters (see also Guiry and Guiry, 2012), until genetic analyses can clarify its taxonomic status.

The generic status of another, "*Pseudolithophyllum* sensu Adey," is still problematic. Adey (1970) redefined *Pseudolithophyllum* based on Foslie's collection of *Lithothamnion orbiculatum* Foslie (1895a; =*Lithophyllum orbiculatum* (Foslie) Foslie, 1900e; =*Pseudolithophyllum orbiculatum* (Foslie) Me. Lemoine, 1929b). Characters used by Adey (1970) did not agree with the genus as defined by Hamel and Lemoine (1953), Adey (1966a), or Cabioch (1972). If the generic concept of *Pseudolithophyllum* sensu Adey should be accepted, it is seemingly without a type and will apparently need a new generic name.

One species of *Pseudolithophyllum* has been reported in the northern Gulf of California.

***Pseudolithophyllum neofarlowii* (Setchell et L. R. Mason) W. H. Adey**

Lithophyllum neofarlowii Setchell et L. R. Mason, 1943b:95; Smith, 1944:228; Mason, 1953:341, pl. 45a[isotype]–c; Dawson, 1960b:45, pl. 37: figs. 1–2, pl. 43: fig. 2; 1961b:416; Adey and Lebednik, 1967:17; González-González et al., 1996:238; Yoshida, 1998:576.

Pseudolithophyllum neofarlowii (Setchell et L. R. Mason) W. H. Adey, 1970:13; Johansen, 1976a:397, fig. 343; Silva, 1979:319; Steneck and Paine, 1986:227, figs. 10–12; Scagel et al., 1989:246; Stewart, 1991:79; González-González et al., 1996:261.

Lithophyllum farlowii Foslie, 1901a:12, *nom. illeg.*; 1929: pl. 54: figs. 5, 6; Woelkerling, 1993:90; 1998:310, fig. 173; Woelkerling et al., 1998:401, fig. 173 [non *Lithophyllum farlowii* Heydrich, 1901b:532; Woelkerling, 1998:311; Woelkerling et al., 1998:462, figs. 174–175; which is now *Lithophyllum decussatum* (J. Ellis et Solander) Philippi, 1837:389; basionym: *Millepora decussata* J. Ellis et Solander, 1786:131, pl. 23: fig. 9].

Crustose coralline, initially discoid, later becoming irregular in outline, spreading up to 10 cm wide; 300–500(–1000) µm thick, with rough surface of low hemispherical to subspherical protuberances, mostly 1–2 mm in diameter, usually densely congested, sometimes growing together. Hypothallium either apparently lacking or weakly developed, of 1–3 cell layers; cells mostly 7–10 µm long by 3–6 µm wide. Perithallium of several ascending layers; cells squarish but can be slightly wider than tall, 5–15 µm tall by 6–12 µm wide. Epithallium usually a single layer, occasionally of 2 layers; upper surface of rounded and relatively thick-walled cells, 2–4 µm tall, 4–8 µm wide. Cell fusions abundant; trichocytes absent.

Reproductive conceptacles on crust surface and at base of protuberances up to 250 µm in outside diameter, with a single pore opening. Sporangial conceptacles hemispherical, 180–225 µm inside diameter, 50–100 µm deep; tetrasporangia 90–100 µm tall, 50–60 µm in diameter. Carposporangial conceptacles 190–215 µm outside diameter (80–100 µm inside diameter; about 65 µm deep). Spermatangial conceptacles 100–200 µm outside diameter (90–110 µm inside diameter; 40–50 µm deep).

HABITAT. On rocks and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: San Felipe to Punta Palmilla. Eastern Pacific: southern Alaska to Bahía Asunción, Baja California. Western Pacific: Japan.

TYPE LOCALITY. Monterey, Monterey County, California, USA.

Titanoderma Nägeli

Titanoderma Nägeli in Nägeli and Cramer, 1858:532; Chamberlain, 1991:13, 22, figs. 1–48, 50, 51; Irvine and Chamberlain, 1994:89.

Dermatolithon Foslie, 1898:11.

Crustose thalli that are irregular in outline (surface view), mostly with smooth to irregular surfaces, and some may have protuberances; attached loosely or tightly adherent on other algae, sometimes surrounding host branches, or some attached to hard substratum such as rocks. Crustose portions are dorsiventrally organized and dimerous or dimerous and monomerous; protuberances, if present, are radially organized and monomerous. In dimerous crusts, filaments of the first order (hypothallium) are composed of 1 layer of palisade cells (elongated cells) oriented obliquely to vertically to the substratum or host. Second-order filaments (perithallium) grow at right angles from the first-order filaments. In some species these filaments are unicellular (i.e., only an epithallial cell), while in others the filaments are multicellular with a subepithallial initial that issues epithallial cells outward toward the crust surface, and additional vegetative cells inward. Terminal epithallial cells are rounded or flattened. Secondary pit connections are present between some cells of adjoining filaments. Cell fusions are absent or rare. Trichocytes are absent in most members.

Sporangial conceptacles have a single pore, tetrasporangia and bisporangia are without apical plugs. The conceptacles may be with or without a central columella. Tetrasporangia and bisporangia develop around the chamber periphery if a columella is present; if absent, they are scattered across the conceptacle floor. Gametangial thalli are poorly known.

REMARKS. Although some recognized *Titanoderma* as a distinct genus (e.g., Woelkerling, 1988; Chamberlain, 1991; Irvine and Chamberlain, 1994), others have questioned its generic status (e.g., Woelkerling et al., 1985; Bittner et al., 2011) or have considered it to be congeneric with *Lithophyllum* (e.g., Campbell and Woelkerling, 1990, Woelkerling and Campbell, 1992). *Titanoderma* is morphologically close to *Lithophyllum* in that both genera lack haustoria (specialized cells that are presumed to absorb nutrients from host) and are dorsiventrally (distinct dorsal and ventral sides) or radially organized. Perithallial cells of *Titanoderma* are frequently laterally connected to neighboring cells by secondary pit connections, a character also seen in *Lithophyllum*. Unlike *Lithophyllum,* the cells of primigenous filaments of *Titanoderma* are palisade (vertically elongated), forming a unistratose ventral cell layer; but use of this character to separate these genera has been questioned by Woelkerling et al. (1985, 2012).

Campbell and Woelkerling (1990), Woelkerling and Campbell (1992), and Woelkerling (1996a) considered the type of the genus, *Titanoderma pustulatum* (J. V. Lamouroux) Nägeli (in Nägeli and Cramer, 1858; basionym: *Melobesia pustulata* J. V. Lamouroux, 1816), to be conspecific with *Lithophyllum pustulatum* (J. V. Lamouroux) Foslie (1904). Thus the genus *Titanoderma* would be congeneric with *Lithophyllum*. Others have kept the genera separate (e.g., Adey, 1970; Irvine and Johansen, 1994; Silva et al., 1996a), and on the basis of the molecular analyses of *T. pustulata* (generitype), Bailey (1999) concluded *Titanoderma* was genetically distinct from *Lithophyllum* but that the two genera were difficult to separate solely on morphology. Bittner et al. (2011) noted that while limited molecular data supported their separation, anatomical characters alone could not distinguish *Titanoderma* and *Lithophyllym*, and they similarly concluded that additional morphological, anatomical, and molecular studies were needed to better circumscribe these two genera.

Some species of *Titanoderma* have been referred to *Dermatolithon* Foslie (1898). However, the generitype, *D. pustulatum* (J. V. Lamouroux) Foslie (1898; basionym: *Melobesia pustulata* J. V. Lamouroux, 1816), is currently considered to be either *Lithophyllum pustulatum* (J. V. Lamouroux) Foslie (1904; see Campbell and Woelkerling, 1990) or *Titanoderma pustulatum* (see Chamberlain, 1991). For now, *Titanoderma* is herein recognized until critical studies, including molecular analyses, can be carried out on the generitypes and type locality material.

The generic placement of *Dermatolithon veleroae* E. Y. Dawson (1944a: 274), described from Bahía Agua Verde, Baja California Sur, also needs to be reevaluated. Other southern Gulf reports of *D. veleroae* are in Dawson (1960b, 1961b), Espinoza-Avalos (1993), Riosmena-Rodríguez and Woelkerling (2000), and Dreckmann (1991, as *Lithophyllum veleroae* (E. Y. Dawson) Woelkerling ex Dreckmann, *comb. invalid*.; non *Lithophyllum veleroae* E. Y. Dawson, 1944a: 270).

Three species of *Titanoderma,* including one with two varieties, are known to occur in the northern Gulf of California.

KEY TO THE SPECIES OF *TITANODERMA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts in transsections of 3 different types of cell layers 2
1b. Crusts in cross sections of 2 different types of cell layers 3
2a. Crusts thin, less than 120 µm thick; sporangial conceptacles 300–350(–500) µm in outside diameter . . . . . ***T. canescens***
2b. Crusts much thicker, up to 1(–2) mm thick; sporangial conceptacles 200–350 µm in diameter . . . . ***T. dispar***
3a. Sporangial conceptacle roof 3 cells thick throughout, cells in each layer of more or less consistent size and regular arrangement; top (epithallial) layer and bottom layer of small cells, middle layer of vertically elongated cells . . . . ***T. pustulatum*** var. ***pustulatum***
3b. Sporangial conceptacle roof 3–5 (or more) cells near pore; cells somewhat variable in size and irregular arrangement . . . . ***T. pustulatum*** var. ***confine***

Titanoderma canescens (Foslie) Woelkerling, Y. M. Chamberlain et P. C. Silva

Melobesia canescens Foslie, 1900d:6 [as "*Melobesia* (*Heteroderma*) *canescens*"]; Adey and Lebednik, 1967:37; Woelkerling, 1993:47.

Titanoderma canescens (Foslie) Woelkerling, Y. M. Chamberlain et P. C. Silva, 1985:333; Yoshida, 1998:333.

Lithophyllum canescens (Foslie) Foslie, 1905b:8; Foslie, 1929:32, pl. 72: fig. 3 [type]; Dreckmann, 1991:34; Bernecker, 2009:CD-Rom p. 59; Fernández-García et al., 2011:62.

Dermatolithon canescens (Foslie) Foslie, 1909d:58; Dawson, 1955:274; 1960b:33, pl. 21: fig. 3; Masaki and Tokida, 1960:38, pl. 1: figs. 2–3, pl. 2: figs. 4–7, pl. 5; Masaki, 1968:49.

Tenarea canescens (Foslie) W. H. Adey, 1970:7; Stewart and Stewart, 1984:143; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:18; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:107; Riosmena-Rodríguez and Woelkerling, 2000:335.

Crusts pink, epiphytic, orbicular on flat surfaces of algal host, up to 2 cm wide, or encircling host branches; mostly less than 120 µm thick; hypothallium of palisade cells 25–60(–100) µm tall; perithallium little developed; epithallium of small triangular cells (in cross section).

Tetrasporangial conceptacles protruding, more or less hemispherical, 300–350(–500) µm in outside diameter. Carposporangial and spermatangial conceptacles not observed.

Habitat. Epiphytic on *Dictyota* and *Padina* and probably on various other red and brown algae; intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Colorado (Sonora); Isla Turner off SE end of Isla Tiburón; Mazatlán, Sinaloa. Eastern Pacific: Isla Guadalupe; El Salvador; Costa Rica. Western Pacific: Japan.

Type Locality. On *Padina arborescens*, [Manazuru] Marine Laboratory, Sagami Province (now Kanagawa Prefecture), Honshū, Japan.

Remarks. Dawson (1960b, as "*Dermatolithon canescens*") noted *Titanoderma canescens* seems to be more characteristic of warmer waters. Johansen (1976a, as *Tenarea canescens*; see also Stewart, 1991) said the records of Dawson (1960b: Santa Cruz Island and Cardiff, San Diego) required further study to verify the presence of *T. canescens* in southern California.

Titanoderma dispar (Foslie) Woelkerling, Y. M. Chamberlain et P. C. Silva

FIGURE 51

Lithophyllum tumidulum Foslie f. *dispar* Foslie, 1907:29; Nichols, 1909:357, pl. 10: fig. 6, pl. 11: figs. 11, 13, 14, pl. 13: figs. 26, 27; Mason, 1953:344 (lectotype).

Titanoderma dispar (Foslie) Woelkerling, Y. M. Chamberlain et P. C. Silva, 1985:333; Scagel et al., 1989:262; Mateo-Cid and Mendoza-González, 1994b:40; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; Mateo-Cid and Mendoza-González, 1997:57, pl. 1: fig. 5; Yoshida, 1998:619; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:338; Y.-P. Lee, 2008:211, figs. A–E.

Lithophyllum dispar (Foslie) Foslie, 1909:50; 1929:33, pl. 72: fig. 14 (type); Adey and Lebednik, 1967:39; Woelkerling, 1993:77.

Dermatolithon dispar (Foslie) Foslie, 1909:58; Mason, 1953:343; Dawson, 1960b:34, pl. 23: fig. 1, pl. 25: figs. 4, 5; Dawson et al., 1960a:16; Masaki and Tokida, 1960:37, pl. 1: fig. 1, pl. 2: figs. 1–3, pls. 3, 4; Dawson, 1961b:415; Masaki, 1968:52; Mendoza-González and Mateo-Cid, 1985:28; González-González et al., 1996:198.

Fosliella dispar (Foslie) G. M. Smith, 1944:225, pl. 50: fig. 6.

Tenarea dispar (Foslie) W. H. Adey, 1970:7; Johansen, 1976a:395, fig. 342; Stewart, 1991:80; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Mateo-Cid et al., 1993:47; Serviere-Zaragoza et al., 1993a:484; Mendoza-González et al., 1994:107; González-González et al., 1996:272.

Thalli epiphytic, forming orbicular to irregularly shaped crusts, up to 1.0 cm in diameter, mostly less than 1 mm (occasionally up to 2 mm) thick; often partly to completely encircling host. Polystromatic: hypothallial filaments of obliquely elongated cells, 15–100 µm long by 2–11 µm diameter; perithallium of 2–7 cell layers, erect filaments of elongated cells, 12–120 µm

FIGURE 51. *Titanoderma dispar*: Epiphytic irregularly shaped crusts, some completely surrounding host branches (*JN-4112,* US Alg. Coll.).

long by 3–11 µm diameter; epithallium of rectangular cells, periclinally flattened, 2–10 µm wide by 2–3 µm tall.

Tetrasporangial and bisporangial conceptacles slightly convex, 120–210 µm tall and up to 375 µm outside diameter, with central columella; tetrasporangia 100–150 µm long by 50–70 µm diameter. Carposporangial conceptacles slightly convex to slightly protruding, 225–260 µm inside diameter and 300–350 µm outside diameter (after Dawson, 1960b). Spermatangial conceptacles 35–45 µm tall and 90–120 µm outside diameter (after Mason, 1953, as *Dermatolithon dispar*).

Habitat. Epiphytic on various algae, including *Gelidium*, *Gracilaria*, *Laurencia,* and *Digenea*; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco; Bahía Concepción to Guaymas; Cabeza Ballena; Mazatlán; Sinaloa to Nayarit. Eastern Pacific: Alaska to Todos Santos, Baja California Sur; Oaxaca. Western Pacific: Japan; Korea.

Type Locality. In drift, epiphytic on *Ahnfeltia gigartinoides* (=*Ahnfeltiopsis gigartinoides* (J. Agardh) P. C. Silva et DeCew); Whidbey (Whidby) Island, Island County, Puget Sound, Washington, USA.

Remarks. Relatively rare in the Gulf of California, specimens of *Titanoderma dispar* are more delicate than those from the colder waters of northern California and northward to Alaska. However, like many other crustose corallines on the Pacific coast of North America, the species limits of *T. dispar* are in need of elucidation.

Titanoderma pustulatum* (J. V. Lamouroux) Nägeli var. *pustulatum

Melobesia pustulata J. V. Lamouroux, 1816:315, pl. XII: fig. 2; Adey and Lebednik, 1967:39.

Titanoderma pustulatum (J. V. Lamouroux) Nägeli in Nägeli and C. E. Cramer, 1858:532; Woelkerling et al., 1985:329, figs. 29 [lectotype], 30–39; Chamberlain, 1991:26, figs. 2, 4, 7–15, 19–48, 52a–I, 53, 55–81; Chamberlain and Irvine, 1994a:96, figs. 39–49; Yoshida, 1998:620, fig. 3-36C–G.

Lithophyllum pustulatum (J. V. Lamouroux) Foslie, 1904:8; Campbell and Woelkerling, 1990:115, figs. 1, 4; Ramírez and Santelices, 1991:211; Dreckmann, 1991:34; Woelkerling and Campbell, 1992:80, fig. 50A; Woelkerling, 1996b:227, figs. 100, 101; Riosmena-Rodríguez et al., 2005b:34.

Dermatolithon pustulatum (J. V. Lamouroux) Foslie, 1898:11; Fernández-García et al., 2011:61.

Lithophyllum pustulatum f. *ascripticium* Foslie, 1907:34; Foslie, 1909:47; Nichols, 1909:354, pl. 10: figs. 2, 3, pl. 11: fig. 10, pl. 12: figs. 18–20, pl. 13: fig. 28; Woelkerling, 1993:31; Riosmena-Rodríguez and Woelkerling, 2000:327.

Titanoderma ascripticium (Foslie) Woelkerling, Y. M. Chamberlain et P. C. Silva, 1985:333; Scagel et al., 1989:262; Stout and Dreckmann, 1993:14.

Dermatolithon pustulatum f. *ascripticium* (Foslie) Foslie ex De Toni, 1924:665; Dawson, 1960b:32, pl. 25: figs. 8, 9; León-Álvarez and González-González, 1993:461; Serviere-Zaragoza et al., 1993a:483.

Dermatolithon ascripticium (Foslie) Setchell et L. R. Mason, 1943b:96; Mason, 1953:344; Dawson, 1955:275; León-Álvarez and González-González, 1993:461; Serviere-Zaragoza et al., 2007:9.

Fosliella ascriptica (Foslie) G. M. Smith, 1944:224, pl. 50: fig. 7.

Tenarea ascriptica (Foslie) W. H. Adey, 1970:6; Johansen, 1976a:395, fig. 341; Schnetter and Bula-Meyer, 1982:127, pl. 18: figs. B,C; Stewart and Stewart, 1984:143; Dreckmann, 1991:34 [as "*Lithophyllum ascripticum*"]; Mateo-Cid and Mendoza-González, 1991:20; Bula-Meyer, 1995:34.

Crusts epiphytic, adherent to and sometimes surrounding host; up to 200 µm thick and to 1.2 cm in diameter. Hypothallium of a single layer of obliquely elongated, palisade cells, 20–80(–115) µm tall and 4–15 µm wide; perithallium weakly developed, also of elongated cells of similar size, 28–60 µm long by 4–15 µm wide. Epithallial cells small, 5–7 µm tall, 4–7 µm wide.

Tetrasporangial and bisporangial conceptacles protruding, 200–350(–500) µm outside diameter. Sporangial conceptacle roof 3 cell layers thick; top (epithallial) and bottom layer of small cells, and a middle layer of vertically elongated cells (cf. Dawson, 1960b: pl. 25: fig. 9; Johansen, 1976a: fig. 341).

Habitat. On *Corallina*, *Gelidium,* and *Pterocladia*, and probably on other macroalgae; intertidal.

Distribution. Gulf of California: Puerto Peñasco; Jalisco. Eastern Pacific: Oregon to California; Isla Guadalupe to

Bahía de Ballenas (Baja California Sur); Isla San Benedicto (Islas Revillagigedo); Colima to Michoacán; Costa Rica; Chile. Western Pacific: Japan.

TYPE LOCALITY. France.

Titanoderma pustulatum var. *confine* (P. Crouan et H. Crouan) Y. M. Chamberlain

Melobesia confinis P. Crouan et H. Crouan, 1867:150; Chamberlain, 1991:50, figs. 155–158 [lectotype]; Woelkerling, 1998:369; Woelkerling et al., 1998:606, fig. 318.

Titanoderma pustulatum var. *confine* (P. Crouan et H. Crouan) Y. M. Chamberlain, 1991:50, figs. 59–204; Chamberlain and Irvine, 1994a:102, figs. 43–46; Mendoza-González and Mateo-Cid, 1996a:24, figs. 8–12; Babbini and Bressan, 1997:181; Mateo-Cid et al., 2006:56.

Lithophyllum hapalidiodides f. *confine* (P. Crouan et H. Crouan) Foslie, 1909:12 [as "*confinis*"]; Lemoine, 1913:137, fig. 3; Foslie, 1929: pl. 72: fig. 7.

Tenarea confinis (P. Crouan et H. Crouan) W. H. Adey et P. J. Adey, 1973:393.

Titanoderma confine (P. Crouan et H. Crouan) J. H. Price, D. M. John et G. W. Lawson, 1986:86.

Crusts epiphytic; initially discoid, becoming orbicular to confluent, surface flat to imbricate; expanding up to 1 cm or more, sometimes overlapping other thalli; up to 600(–900) µm thick; margins entire; loosely to moderately attached to host algae. Basal (hypothallium) filaments a single layer of oblique palisade cells, 25–125 µm long and 11–22 µm wide. Erect filaments (perithallium) either absent or, in some, up to 14 cells in length. Epithallial cells more or less triangular, rectangular, or domed. Trichocytes present, occasional in basal and erect filaments.

Sporangial conceptacles not seen in Gulf (as reported from Pacific Mexico [Mendoza-González and Mateo-Cid, 1996a]: 320–360 µm in outside diameter; tetrasporangia 66–75 µm tall, 27–45 µm in diameter). Bisporangial conceptacles widely spaced to dense, rounded-conical, protruding over surface, distinct periphery or sometimes a rim at base; 400–500 µm in diameter; chamber floor 2–3 cell layers below crust surface; chambers hemispherical to elliptical, 90–230 µm tall, 240–420 µm wide; roof of 3–5 (or more) cell layers, cells not in consistent arrangement by size; chamber with up to 60 bisporangia per conceptacle; bisporangia 62–104 µm long, 25–52 µm in diameter. Gametangial conceptacles not observed.

HABITAT. Epiphytic on various algae, notably corallines, and rocks, stones, or shells; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Jalisco. Eastern Pacific: northern Washington to Baja California Sur; Isla Guadalupe; Isla San Benedicto (Islas Revillagigedo); Colima; Oaxaca; Colombia; Chile. Western Pacific: Japan.

TYPE LOCALITY. Presumably near Brest, Finistère, France (Chamberlain, 1991).

REMARKS. *Titanoderma pustulatum* var. *confine* is one of the taxonomic varieties of *T. pustulatum* recognized by Irvine and Chamberlain (1994). The northern Gulf specimens (Mateo-Cid et al., 2006) should be molecularly compared with type locality material.

CORALLINACEAE SUBFAM. HYDROLITHOIDEAE

Corallinaceae subfam. Hydrolithoideae A. Kato et M. Baba, in Kato, Baba and Suda, 2011:669.

Calcified crusts have lateral cell fusions joining cells of contiguous filaments. Trichocytes are present, but not in large, tightly packed horizontal fields. Secondary pit connections are absent, and the basal layer is without palisade cells. Sporangial conceptacles are produced both by filaments that are peripheral to the fertile area and interspersed among tetrasporangia and bisporangial initials. Spermatangial filaments develop on the chamber floor of the spermatangial conceptacle.

The C. subfam. Hydrolithoideae is represented by *Hydrolithon* in the northern Gulf of California (included in the Key with C. subfam. Mastophoroideae).

Hydrolithon (Foslie) Foslie

Goniolithon subgen. *Hydrolithon* Foslie, 1905b:7.

Hydrolithon (Foslie) Foslie, 1909:55; Bittner at al., 2011:710.

Crustose calcified thalli, which form thin crusts mostly on other algae, and are two or more cell layers thick, or may be thicker crusts with some becoming unattached rhodoliths. Thalli are primarily dimerous in construction, with a single layer (hypothallium) of nonpalisade basal filaments which may be with or without unicellular or multicellular filaments arising perpendicularly from this basal layer, forming the perithallium. Epithallial cells terminate the filaments at the thallus surface, usually a single layer with distal walls rounded or flattened (not flared). Trichocytes are present and may be singular, in pairs, and/or in small horizontal fields, trichocytes usually separated from each other by vegetative filaments. Secondary pit connections are absent. Intercellular fusions are present linking cells of adjacent filaments.

Sporangial and gametangial conceptacles are uniporate. The pore canals of tetrasporangial and bisporangial conceptacles are lined by elongate cells that do not protrude into the pore canal and are oriented somewhat perpendicularly to the roof surface. Each zonate tetrasporangium or bisporangium is without an apical plug. Gametophytes monoecious or dioecious. Gonimoblast filaments develop from the peripheral surface (margins) of the central fusion cell in the carposporangial conceptacles. Spermatangial filaments are unbranched and develop from the conceptacle chamber floor.

REMARKS. *Hydrolithon* is distinguished from *Heteroderma* by the presence of large trichocytes. Penrose and Woelkerling (1988) merged the genera *Hydrolithon* (Foslie) Foslie (1909) and *Porolithon* Foslie (1909) with *Spongites* Kützing (1841). Later, Penrose and Woelkerling (1992) recognized *Spongites* but concluded that *Hydrolithon* was a discrete genus. Many recent treatments recognize the three to be distinct genera (cf.

Guiry and Guiry, 2008–2010). Woelkerling et al. (2012) concluded that anatomical characters alone could not separate two of the genera, referring to them as the "*Hydrolithon–Porolithon* complex," and stated that more morphological, anatomical, and molecular data were needed to better delineate this complex. In finding molecular support for its generic separation, Bittner et al. (2011) restricted *Hydrolithon* to include species having dimerous thallus construction and trichocytes that are singular, in pairs, and/or in small horizontal fields and usually interspersed with normal vegetative filaments. Bittner et al. (2011) also recognized *Porolithon* for species with a primarily monomerous thallus construction and trichocytes in large horizontal rows without any normal vegetative filaments between individual trichocytes. On the basis of these generic boundaries, Bittner et al. (2011) also suggested that some species of *Hydrolithon* should be reassigned to the genus *Porolithon.*

Two species have been reported in the southern Gulf of California from Bahía de La Paz: *Hydrolithon chamaedoris* (Foslie et M. Howe) M. J. Wynne (2005; basionym: *Lithophyllum chamaedoris* Foslie et M. Howe, 1906; =*Heteroderma chamaedoris* (Foslie et M. Howe) E. Y. Dawson, 1960a) by Riosmena-Rodríguez and Paul-Chávez (1997, as *Fosliella chamaedoris* (Foslie et M. Howe) M. Howe, 1920); and *H. reinboldii* (Weber-van Bosse et Foslie) Foslie (1909; basionym: *Lithophyllum reinboldii* Weber-van Bosse et Foslie in Foslie, 1901b; Verheij and Woelkerling, 1992) by Cruz-Ayala et al. (2001).

Two species of *Hydrolithon* are recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *HYDROLITHON* AND "*FOSLIELLA*" IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts thicker; of multiple cell layers, typically 400–800 µm thick (sometimes up to 1 mm thick) . . . . *Hydrolithon samoënse*
1b. Crusts much thinner; of 1–3 cell layers in vegetative portions, less than 25 µm thick 2
2a. Crusts usually overgrowing or overlapping each other; sporangial conceptacles, 200–225 µm in outside diameter . . . . *Hydrolithon farinosum*
2b. Crusts not usually overgrowing each other; sporangial conceptacles smaller, 100–160 µm in diameter . . . . *Fosliella*? *paschalis*

Hydrolithon farinosum (J. V. Lamouroux) D. Penrose et Y. M. Chamberlain

FIGURE 52

Melobesia farinosa J. V. Lamouroux, 1816:315, pl. 12: fig. 3; Okamura, 1936:506; Hamel and Lemoine, 1953:102, fig. 64, pl. 21: figs. 1, 2; Masaki and Tokida, 1960:39, pl. 1: figs. 4, 5, pl. 2: figs. 8–12, pls. 6, 7; Adey and Lebednik, 1967:32; Chamberlain, 1983:343, fig. 19.

Hydrolithon farinosum (J. V. Lamouroux) D. Penrose et Y. M. Chamberlain, 1993:295, figs. 2–19; Irvine and Chamberlain, 1994:123, figs. 3A, 54, 55; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Yoshida, 1998:559; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:339; CONANP, 2002:139; Fragoso and Rodríguez, 2002:119, figs. 20, 21; L. Aguilar-Rosas et al., 2002:234; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:9; Y.-P. Lee, 2008:194, figs. A–D; Mendoza-González et al., 2009:223, figs. 3, 4.

Fosliella farinosa (J. V. Lamouroux) M. Howe, 1920:587; Hamel and Lemoine, 1953:102, fig. 64, pl. 21, figs. 1, 2; Dawson, 1960b:30, pl. 21: fig. 1, pl. 22: fig. 1; Masaki, 1968:21; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:8, 11; Chamberlain, 1977:343; Coppejans, 1978:55; Johansen, 1981:34: figs. 19A,B, 45: fig. 4A; Chamberlain, 1983:343, fig. 19 [lectotype]; Tseng, 1983:76, pl. 41: fig. 4; Stewart and Stewart, 1984:143; Mendoza-González and Mateo-Cid, 1986:423; Salcedo-Martínez et al., 1988:83; Ramírez and Santelices, 1991:205; Dreckmann, 1991:34; León-Álvarez and González-González, 1993:461; Serviere-Zaragoza et al., 1993a:483; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:397.

Crusts epiphytic, very delicate, thin, of 2–3 cell layers, flat with a smooth surface; initially suborbicular, up to 4 mm broad, up to 20 µm thick, crust margins rounded, lobed; later expanding, up to 1–2 cm (or more), often overlapping or overgrowing each other, up to 90 µm thick. Single basal layer of branched filaments with quadrangular cells, in surface view 15–30 µm long by 5.0–15 µm in diameter; cell fusions present. Epithallium a single layer of rounded cells. Trichocytes frequent throughout crust, often terminating a basal filament; single, 20–30 µm tall by 13–16 µm in diameter (Figure 52B).

Reproductive conceptacles uniporate; protruding above surface. Sporangial conceptacles 85–100 µm tall, 180–250 µm outside diameter; chamber 140–165 µm inside diameter; roof of 2–3 cell layers, about 15 µm thick; pore canal about 30 µm long and to 12 µm in diameter, lined with nonprotruding and more or less vertically oriented cells; tetrasporangia usually peripheral to central columella; zonately divided, (35–)70–80 µm tall, (20–)40–50 µm in diameter. Gametangial conceptacles smaller; monoecious; carpogonia and spermatangia in separate conceptacles. Carposporangial conceptacles chambers 40–105 µm tall, 75–205 µm inside diameter; conceptacle roof of 3–6 cell layers, 10–21 µm thick; gonimoblast filaments develop from fusion cell margins (peripheral surfaces); carposporangia 25–50 µm long, 24–40 µm in diameter. Spermatangial conceptacle chamber 11–40 µm tall, 45–75 µm inside diameter; conceptacle roof of 3 cell layers, roof pore about 6–12 µm in diameter, with mucilaginous spout extending to about 12 µm in length; spermatangial filaments produced only from chamber floor (gametangia not known in Gulf; after Mendoza-González et al., 2009, for Atlantic and Caribbean Mexico).

HABITAT. Epiphytic on other algae, especially *Padina, Dictyota, Dictyopteris,* and *Sargassum*, and should be looked for

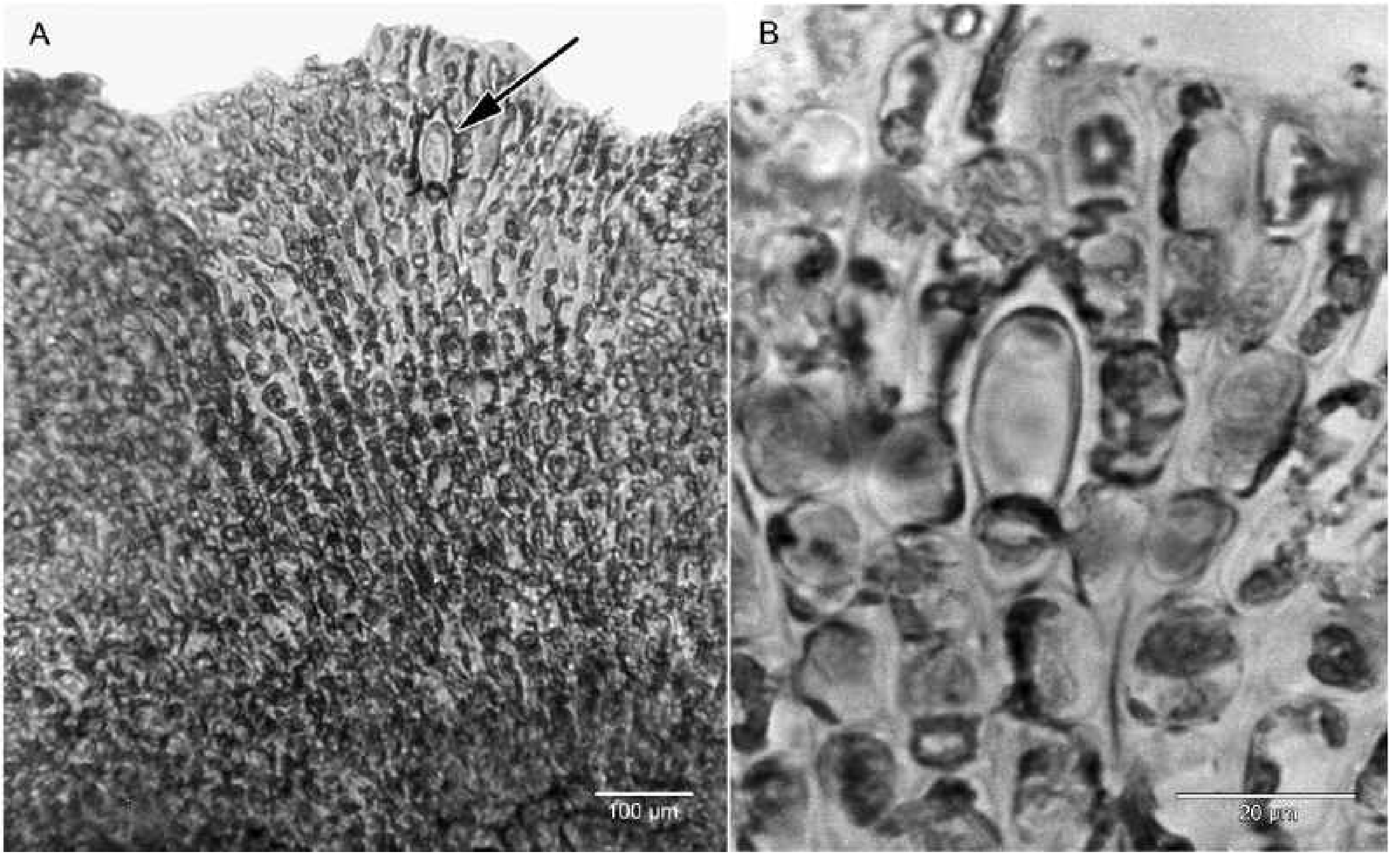

FIGURE 52. *Hydrolithon farinosum*: A. Surface view of decalcified crust showing prominent trichocytes (arrow). B. Surface view of decalcified crust showing cells of adjacent filaments conjoined by fusions and trichocytes at ends of filaments (*JN-3169*, US Alg. Coll.).

on sea grasses as well; mid intertidal to shallow subtidal, down to 5 m depths.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Isla Tiburón; Bahía de Loreto; Punta Palmilla to Cabeza Ballena; Isla María Cleofa (Islas Marías; Islas Tres Marías); Nayarit to Jalisco. Eastern Pacific: Isla Guadalupe; Punta Santa Rosaliita ("Punta Santa Rosalía") to Desembarcadero de Miller (Miller's Landing), Baja California; Isla Socorro (Islas Revillagigedo); Jalisco to Oaxaca; Chile. Western Pacific: China; Vietnam; Japan; Korea.

Type Locality. "On *Sargassum linifolium*, Mediterranean" (Chamberlain, 1994:123); "probably from Adriatic Sea" (Dawson, 1960b:30; Chamberlain, 1983:341).

Remarks. *Hydrolithon farinosum* is presumed to be a cosmopolitan species found growing on various benthic algae and sea grasses. In the northern Gulf, *H. farinosum* is often associated with another epiphytic crustose coralline, *Heteroderma gibbsii*; both are sometimes found growing on species of *Padina* and *Dictyota*.

Melobesia farinosa J. V. Lamouroux (1816) is the type species of the generic name *Fosliella* M. Howe (1920). Studies by Penrose and Chamberlain (1993) determined that the type of *M. farinosa* belonged to the genus *Hydrolithon,* thus making *Fosliella* M. Howe a heterotypic synonym of *Hydrolithon*.

Hydrolithon samoënse (Foslie) Keats et Y. M. Chamberlain

Lithophyllum samoënse Foslie, 1906b:20; 1929:38, pl. 53: fig. 19 (lectotype); Adey and Lebednik, 1967:17; Masaki, 1968:37, pl. 20: figs. 3, 4, pl. 23: figs. 1–4, pl. 61: figs. 3–6, pl. 62: figs. 1–5; Guzmán del Próo et al., 1972:259; Mendoza-González and Mateo-Cid, 1985:30; 1986:423; Ramírez and Santelices, 1991:212; Serviere-Zaragoza et al., 1993a:484; Woelkerling, 1993:193; González-González et al., 1996:239; Woelkerling, 1998:324; Woelkerling et al., 1998:493, fig. 205 (paratype).

Hydrolithon samoënse (Foslie) Keats et Y. M. Chamberlain, 1994:15, figs. 31–54; Chamberlain, 1994:126, figs. 56, 57; Yoshida, 1998:563; Riosmena-Rodríguez and Woelkerling, 2000:344; Fragoso and Rodríguez, 2002:123, figs. 27, 28; Bittner et al., 2011:710.

Pseudolithophyllum samoënse (Foslie) W. H. Adey, 1970:13; Tseng, 1983:84, pl. 45: fig. 1.

Crusts pink, prostrate and spreading, with a relatively smooth surface (sometimes surface appearance somewhat irregular, resulting from uneven surface of substratum), 400–800(–1100) µm thick; attached to rocks or mollusk shells. In vertical section: hypothallium of several layers of rectangular cells, (12–)15–20 µm tall and 5–7(–10) µm wide; perithallium forming largest portion of thallus, of small, squarish to rounded cells, 4–7 µm in diameter. Cell fusions frequent between cells in both hypothallial and perithallial filaments. Epithallium a single layer of rectangular cells, 2.5–4 µm tall and 4–7 µm wide. Trichocytes occasional, terminal on erect (perithallial) filaments at thallus surface sometimes singular or forming short, loose horizontal rows (Fragoso and Rodríguez, 2002).

Sporangial conceptacles in crust surface, convex and slightly protruding, each with a single pore; in vertical section, ovoid, 93–102 µm in diameter, 37–66 µm tall; with zonately divided tetrasporangia. Conceptacle roof composed of an epithallial cell layer and an inner cell layer of tall thin elongated cells. Enlarged pore cells occur at base of conceptacle pore (Fragoso and Rodríguez, 2002). Spermatangial conceptacles in vertical section, 50–80 µm in diameter.

Habitat. On rocks and shells; mid to low intertidal.

Type Locality. Sataua, Savai'i Island, Samoa (formerly Western Samoa).

Distribution. Gulf of California: Isla Pelícanos (Bahía Kino); Nayarit. Eastern Pacific: Isla Cedros (Baja California) to Bahía Tortugas, inside southeast Bahía San Bartolomé (Baja California Sur); Colima; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: China; Korea; Japan; Vietnam. Central Pacific: Samoa.

Remarks. *Hydrolithon samoënse*, recorded by Mendoza-González and Mateo-Cid (1986), is poorly known in the northern Gulf of California. Dawson (1960b, 1961b, as *Lithophyllum samoënse*) noted that his identification of this species from Isla Cedros (Pacific Mexico) was questionable and that more collections and critical comparisons were needed. A similar conclusion was made by Masaki (1968, as *L. samoënse*) who observed Japanese specimens were twice as thick as those of Dawson (1960b), and Keats and Chamberlain (1994) also suggested some of the specimens may not be this species. In their description of *Hydrolithon samoënse* from tropical Pacific Mexico, Fragoso and Rodríguez (2002) also noted that Dawson's (1960b) specimens need to be reexamined. In another study, Bittner et al. (2011) suggested *H. samoënse* belongs in the genus *Porolithon*, but Kato et al. (2011) noted that its relationship to *Porolithon* was unresolved. All Gulf of California specimens identified as *H. samoënse* should be critically compared with type material.

CORALLINACEAE SUBFAM. MASTOPHOROIDEAE

Corallinaceae subfam. Mastophoroideae Setchell, 1943:134 [as "Mastophoreae"]; Woelkerling, 1996c:237.

Members include crustose corallines that are prostrate to partially erect and may be discoid or spreading with more or less smooth to warty surfaces, or with short unbranched to branched protuberances. They grow on rocks or other hard substratum, some are free-living rhodoliths, and a few are reported to be endophytic. Thalli are dimerous (first-order filaments making a single layer and second-order filaments arising at right angle from the dorsal side of first-order filaments) or monomerous (single order of filaments) in construction or both. Some cells of adjacent filaments linked by cell fusions. Secondary pit connections are absent in most, or rare (known in one genus, *Metamastophora* Setchell, 1943). Sporangial conceptacles are uniporate, tetrasporangia and bisporangia are without apical plugs. Gametangial thalli, where known, are monoecious or dioecious. Carpogonial and spermatangial conceptacles are uniporate.

Remarks. Gene sequence analyses of Bailey et al. (2004) revealed C. subfam. Mastophoroideae to be polyphylectic, belonging to four distinct lineages. Kato et al. (2011) restricted the subfamily to include only *Mastophora* Decaisne (1842a; see Keats et al., 2009:417, for summary of genus characters) and *Metamastophora* Setchell (neither of which have been found in the Gulf of California), and left the placement of *Spongites* and *Pneophyllum* unresolved until their generitypes could be studied. Until the needed studies are completed, for convenience the other genera are treated in C. subfam. Mastophoroideae (following Woelkerling, 1996c). Much work remains to clarify the molecular systematics and phylogenetic relationships of the genera and species of *Pneophyllum, Spongites,* and *Heteroderma*, as well as the generic placement of one species of "*Fosliella*."

The five genera reported in the northern Gulf of California are provisionally retained in the C. subfam. Mastophoroideae.

KEY TO THE GENERA IN C. SUBFAM. HYDROLITHOIDEAE AND THOSE TENTATIVELY IN C. SUBFAM. MASTOPHOROIDEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts thin, usually less than 200 µm thick, without protuberances; often epiphytic, not forming free-living rhodoliths 3
1b. Crusts thicker, generally greater than 200 µm thick, may have protuberances; on rocks, epiphytic, or may form free-living rhodoliths 2
2a. Sporangial conceptacle pore canal in vertical section lined with cells parallel to roof that protrude into pore canal; thallus construction either monomerous or dimerous, although in some may be both; trichocytes not observed in primigenous (first order; basal) filaments . . . . . ***Spongites***
2b. Sporangial conceptacle pore canal in vertical section lined with cells perpendicular to roof surface that do not protrude into pore canal; thallus construction primarily dimerous (can be monomerous and radially arranged in protuberances); trichocytes terminal on primigenous filaments . . . . . ***Hydrolithon* (in part)**
3a. Trichocytes absent . . . . . ***Heteroderma***
3b. Trichocytes present or absent 4

4a. Trichocytes when present, intercalary within primigenous filaments or terminal on postigenous (second order; erect) filaments; pore canal of sporangial conceptacles (in vertical section) lined, at least initially, by horizontally oriented cells (parallel to conceptacle roof surface); germination disc with 8-celled center . . . . ***Pneophyllum***

4b. Trichocytes when present, terminal on primigenous filaments or intercalary on postigenous filaments; pore canal of sporangial conceptacles (in vertical section) lined by enlarged vertically oriented cells (perpendicular to conceptacle roof); germination disc with 4-celled center 5

5a. Thalli not extensively overlapping each other; sporangial conceptacles 200–225 µm in diameter . . . **"*Fosliella*?" *paschalis***

5b. Thalli often overlapping each other; sporangial conceptacles smaller, 100–160 µm in diameter . . . . ***Hydrolithon* (in part)**

Heteroderma Foslie

Heteroderma Foslie, 1909:56.

Crustose corallines are thin, 2–5 cells layers thick, and found growing as epiphytes on other macroalgae. Thallus construction is dimerous, composed of basal, first-order (primigenous) filaments, and second-order (postigenous) filaments. Trichocytes and secondary pit connections are absent. Intercellular fusions are present.

Sporangial and gametangial conceptacles open by a single pore. In some species a gelatinous spout extends outward from pore of the spermatangial conceptacles.

REMARKS. *Heteroderma* is tentatively recognized until the genus can be further clarified. The use of a single diagnostic character—the absence of trichocytes in *Heteroderma* versus their presence in *Hydrolithon*—for their generic separation has been questioned by some. It has been suggested that presence or absence of trichocytes may reflect an environmental response. Others, however, contend that trichocytes represent a fundamental phylogenetic difference between these groups (e.g., Masaki, 1968:56). In recognizing *Heteroderma* as a genus, Foslie (1909) did not designate a type species (generitype). Setchell and Mason (1943b) later chose *H. subtilissimum* (Foslie) Foslie (1909; basionym: *Melobesia subtilissima* Foslie, in Weber-van Bosse and Foslie, 1904) to lectotypify the genus. Chamberlain (1983) examined the type collection of *H. subtilissimum* (Foslie) Foslie and considered it to be a minute *Pneophyllum* Kützing (1843) but did not transfer the species (Woelkerling, 1988).

For now, the species from the Gulf of California are tentatively referred to *Heteroderma* until their generic status and phylogenetic relationships can be further elucidated, including genetic comparisons to the type from the reef at Atjatuning, off the west coast of New Guinea.

Three species of *Heteroderma*, including two described from the Gulf of California, are known to occur in the northern Gulf.

KEY TO THE SPECIES OF *HETERODERMA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts mostly a single cell layer; very thin, 7–10 µm thick; sporangial and carpogonial conceptacles small, 70–100 µm outside diameter; spermatangial conceptacles conical, small, base 45 µm in diameter, upward narrowed to 25–28 µm in diameter, pore often with extending gelatinous spout . . . . ***H. subtilissimum***

1b. Crusts initially only 1 cell layer, later developing more cell layers; thicker, 10–50 µm thick; sporangial and carpogonial conceptacles slightly larger (mostly more than 90 µm outside diameter); spermatangial conceptacles not conical, pore without extending gelatinous spout 2

2a. Crusts 25–50 µm thick, of 2–4 vegetative cell layers; reproductive portions of 10–12 cell layers and up to 100 µm thick; sporangial conceptacles up to 200 µm outside diameter, chamber about 100 µm inside diameter,70 µm tall; carposporangial conceptacle chambers 90 µm inside diameter, 80 µm tall . . . . ***H. corallinicola***

2b. Crusts mostly thinner, 10–30 µm thick, of 1–2 vegetative cell layers, reproductive and older portions of 3–5 cell layers; sporangial conceptacles larger, 250–300 µm outside diameter, chamber 210 µm inside diameter, 105 µm tall; carposporangial conceptacles larger, 225–275 µm outside diameter, chambers 140–200 µm inside diameter . . . . . . ***H. gibbsii***

Heteroderma corallinicola E. Y. Dawson

FIGURE 45B

Heteroderma corallinicola E. Y. Dawson, 1944a:273, pl. 63: fig. 2; 1960b: 53, pl. 48: fig. 2; 1961b:417; González-González et al., 1996:224; Riosmena-Rodríguez and Woelkerling, 2000:327.

Crusts epiphytic, minute, closely adherent on surfaces of host; monostromatic only in marginal portions; centrally, 25–50 µm thick, usually of 2–4 layers of quadrangular cells, 9–14 µm in diameter; reproductive portions up to 100 µm thick, up to 10–12 cell layers. Hypothallium of slightly horizontally broadened cells, up to 14 µm wide. Perithallium layers of squarish to slightly vertically elongated cells. Trichocytes absent.

Sporangial conceptacles dome shaped, up to 200 µm outside diameter; chamber about 100 µm inside diameter and 70–90 µm tall, with concave floor of 2 or more cell layers; tetrasporangia faintly divided or appearing undivided (possibly immature), up to 70 µm long, 30 µm in diameter. Carposporangial conceptacles more or less hemispherical; chambers about 90 µm in diameter, about 80–90 µm tall, with concave floor of 3 or more cell layers. Spermatangial conceptacles prominent, chamber 50–60 µm inside diameter, 40–50 µm tall, with a flat to slightly concave floor.

HABITAT. Epiphytic on *Corallina* on rocks and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Guaymas.

Type Locality. On *Corallina* in tide pools; cove north of Cabo Arco, Guaymas, Sonora, Gulf of California, Mexico.

Remarks. Dawson (1960b) commented the Gulf endemic *Heteroderma corallinicola* grows on *Corallina*, has tetrasporangia, and is morphologically very similar to the western Atlantic *H. chamaedoris* (Foslie et M. Howe) E. Y. Dawson (1960b; basionym: *Lithophyllum chamaedoris* Foslie et M. Howe, 1906). *Heteroderma chamaedoris*, described from the Bahama Islands, is epiphytic on the green alga *Chamaedoris peniculum* (J. Ellis et Solander) Kuntze (1898) and has bisporangia. Apparently the type of sporangia, different algal hosts, and geographical separation are the primary differences between these two species.

Heteroderma gibbsii (Setchell et Foslie) Foslie

FIGURES 53, 54

Melobesia gibbsii Setchell et Foslie in Foslie 1907:26; Woelkerling 1993:106.

Heteroderma gibbsii (Setchell et Foslie) Foslie, 1909:56; Dawson, 1944a:272; 1959a:20; 1960b:54, pl. 21: figs. 4–6, pl. 23: fig. 2; 1961b:417; 1966a:19; Adey 1970:16; González-González et al., 1996:224; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Riosmena-Rodríguez and Woelkerling, 2000:339; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:208.

Coralline crusts, initially suborbicular in surface view, with lobed margins; basically monostromatic in young crusts and margins, thin, up to 30 µm thick; later becoming irregular in outline and increasing to 3–4 cell layers in reproductive and older portions; epiphytic on various brown and red algae; numerous individuals can cover extensive portions of host alga, usually with little overlap of one another. Hypothallium parallel to substratum, a single layer of filaments of horizontal elongated cells (11–16 µm long, 6–12 µm wide). Perithallium of 2–4 cell layers of squarish cells (about 7–12 µm in diameter); the uppermost layer of vertically elongated cells, 11–16 µm long, 6–12 µm in diameter. Epithallium irregularly developed, a single layer of small cells 2–4 µm high and 6–10 µm wide. Trichocytes absent.

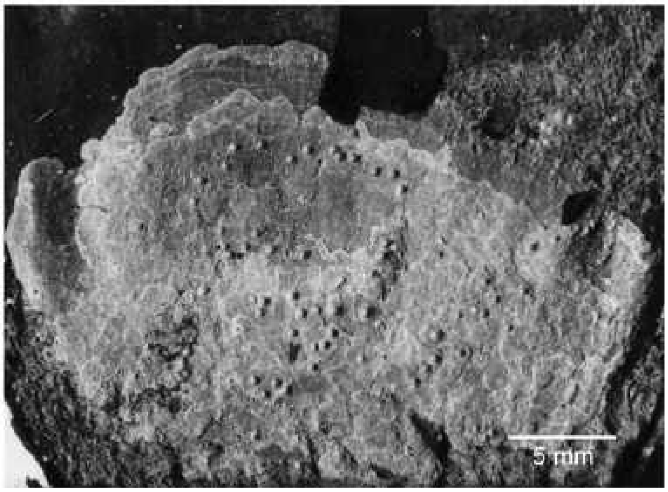

FIGURE 53. *Heteroderma gibbsii:* Habit of irregularly shaped crust epiphytic on *Padina,* mostly monostromatic, except for conceptacles (*EYD-457*, AHFH, now UC).

Sporangial conceptacles dome-shaped above crust surface, 250–300 µm outside diameter; chamber 210 µm inside diameter and 105 µm tall, with floor of 1–2 cell layers; zonate tetrasporangia about 50 µm long. Carposporangial conceptacles 225–275 µm outside diameter; chambers 140–160(–200) µm inside diameter, 40–70 µm tall, with floor of 1–2 cell layers. Spermatangial conceptacles only slightly prominent; chambers 40–50 µm inside diameter, (12–) 16–30 µm tall.

Habitat. Epiphytic on various red and brown algae, including *Dictyota*, *Padina*, *Sargassum*, *Gracilaria,* and *Laurencia*; often found growing along with other epiphytic species of crustose corallines on same host; intertidal (although probably restricted to the intertidal zone, it has also been dredged from 40 m depth; Dawson, 1944a).

Distribution. Gulf of California: Puerto Peñasco to Guaymas; Puerto Refugio, Isla Angel de la Guarda and Isla Turner (Islas de la Cintura); Isla San José to San José del Cabo.

Syntype Localities. Epiphytic on *Sargassum*: Isla San José (25°00’N; 110°38’W), and Isla Espíritu Santo (east of Bahía de La Paz: 24°30’N; 110°22’W), Baja California Sur, Gulf of California, Mexico.

Remarks. Dawson (1960b) observed that Gulf of California endemic *Heteroderma gibbsii* could resemble some *Pneophyllum nicholsii.* The most apparent differences are that *H. gibbsii* has larger sporangial conceptacles and smaller spermatangial conceptacles than those of *P. nicholsii*. Dawson (1960b) suggested the La Paz specimen identified by Mason (1953) as “*H. nicholsii*” [*non H. nicholsii* Setchell et L. Mason, 1943b; now *P. nicholsii* (Setchell et L.R. Mason) P. C. Silva et P. W. Gabrielson, in Gabrielson et al., 2004] was in all probability also *H. gibbsii*.

Heteroderma subtilissimum (Foslie) Foslie

FIGURE 55

Melobesia subtilissima Foslie in Weber-van Bosse and Foslie, 1904:55; Foslie, 1905b:8; Chamberlain, 1983:312; Woelkerling, 1993:218.

Heteroderma substilissimum (Foslie) Foslie, 1909:56; Dawson, 1956:48, fig. 41; 1960b:58, pl. 49: figs. 5, 6; 1961b:417; 1966a:20; Adey, 1970:17; Stewart and Stewart, 1984:143; Dreckmann 1991:34, as “*Pneophyllum subtilissima*”; González-González et al., 1996:225; Riosmena-Rodríguez and Woelkerling, 2000:345; Fernández-García et al., 2011:62.

Crusts minute, epiphytic on various algae; initially more or less discoid, later forming lobed crusts up to 2 mm wide, very thin, 7–9 µm thick. Vegetative portion of crust essentially monostromatic; in vertical section, quadrangular cells squarish to rounded to slightly horizontally elongated, 7–12 µm in diameter; cells in surface view 11–17 µm long, 7–12 µm wide, arranged in radiating rows. Crust thicker near conceptacles.

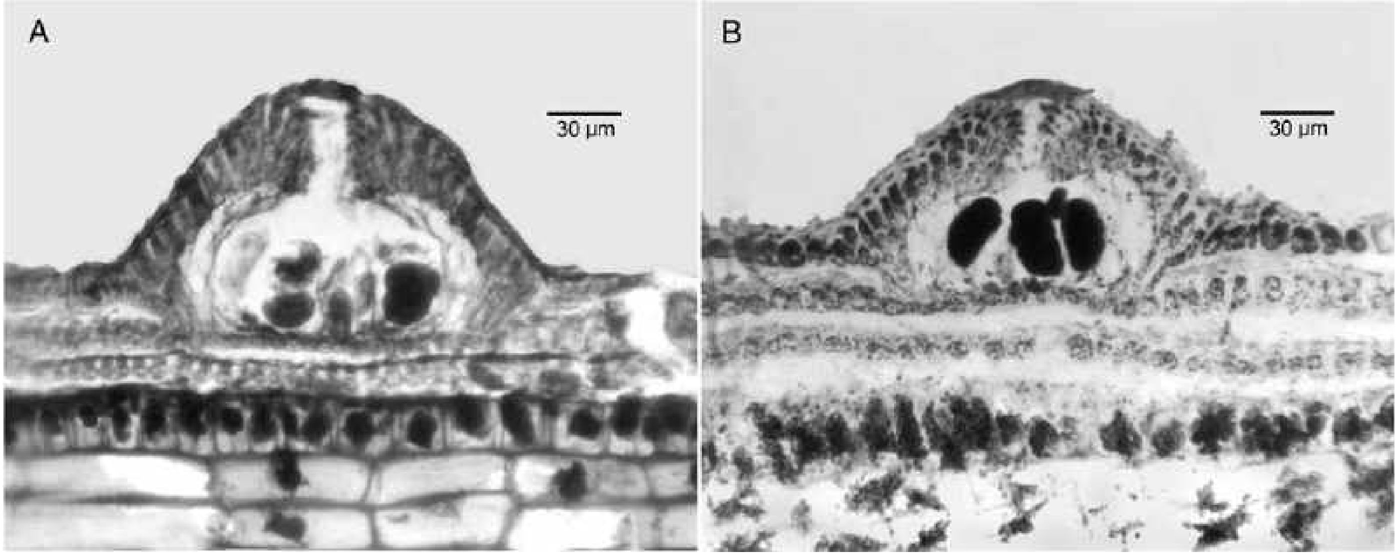

FIGURE 54. *Heteroderma gibbsii*: A. Transection through algal host and decalcified crust with tetrasporangial conceptacle (*JN & HWJ-73-7-22c*, US Alg. Coll.). B. Transection through algal host and decalcified crust with tetrasporangial conceptacle (*JN & HWJ-73-7-15*, US Alg. Coll.).

Erect filaments (perithallial and epithallial cells) mostly absent. Trichocytes absent.

Sporangial conceptacles dome-shaped, 70–100 µm in outside diameter; chamber 45–60 µm in diameter, with flat floor of one cell layer; tetrasporangia zonate, about 25 µm tall, 14–17 µm in diameter. Carposporangial conceptacles also dome-shaped, 60–90 µm in outside diameter, nonrostrate to slightly rostrate. Spermatangial conceptacles small, conical, about 45 µm wide at base, narrowing upward to 25–28 µm in diameter; ostiolate with a gelatinous spout, up to 25 µm long (after Dawson 1960b).

Habitat. Epiphytic on *Cladophoropsis*, *Halimeda*, leaf-like blades of *Sargassum*, *Jania*, and probably other algae as well; intertidal to shallow subtidal.

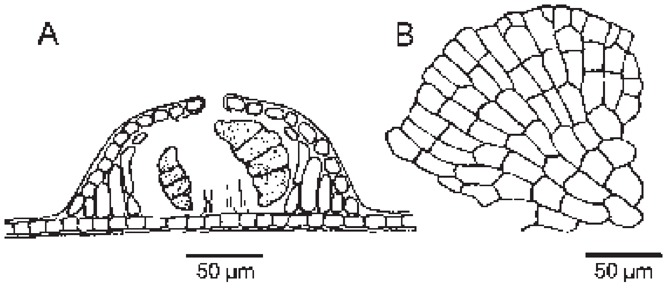

FIGURE 55. *Heteroderma subtilissimum*: A. Transection through mature tetrasporangial conceptacle. B. Surface view of portion of crust (A, B, after Dawson, 1960a: pl. 49: figs. 5,6).

Distribution. Gulf of California: Punta Pelícano, Puerto Peñasco; Bahía San Gabriél, Isla Espíritu Santo to Cabo Pulmo. Eastern Pacific: Isla Guadalupe (off Baja California); El Salvador.

type Locality. Epiphytic on *Corallina pilifera*; reef off Atjatuning, west coast of New Guinea (Dawson, 1960b; Verheij and Woelkerling, 1992).

Remarks. The taxonomic status of Gulf of California specimens referred to *H. subtilissima* is in need of further elucidation (see also Remarks for *Heteroderma*).

Fosliella M. Howe

Fosliella M. Howe, 1920:587.

Algae are thin, calcified crusts, usually less than 200 µm thick, and epiphytic and firmly adherent on various macroalgae and seagrasses. Internally (as seen in vertical section), they are dorsiventrally organized and dimerous, composed of two types of filaments. Primigenous (first order) filaments form a single layer growing parallel (horizontal) on the host; and postigenous (second order) filaments grow more or less upward (vertical). Erect filaments may sometimes consist of only a single epithallial cell. Cells in adjacent filaments are sometimes joined by cell fusions, secondary pit connections are unknown. Trichocytes are sometimes present as terminal cells of the first-order filaments or intercalary in second-order filaments.

Tetrasporangia and sometimes bisporangia are developed within uniporate conceptacles, without apical sporangial plugs. Each spore germinates into a characteristic 4-celled sporeling, which then continues to develop the crustose thallus. Gametangia are poorly known.

REMARKS. The taxonomic status of the genus *Fosliella* is problematic, since the generitype of *Fosliella* M. Howe (1920), *F. farniosa* (J.V. Lamouroux) M. Howe, has been considered to be a *Hydrolithon*, i.e., *H. farinosum* (J.V. Lamouroux) D. Penrose et Y.M. Chamberlain (1993). If these two are recognized as being congeneric, then the generic placement of the other species of "*Fosliella*" is in question, and those not already studied need to be reinvestigated, including the type of *F. paschalis* (Me. Lemoine) Setchell et N. L. Gardner, i. e., *Melobesia paschalis* Me. Lemoine (in Børgesen, 1924). Johansen (in Guiry and Guiry, 2009) commented that *Fosliella* is most closely related to *Pneophyllum* and *Spongites*.

There is one reported species of "*Fosliella*" in the northern Gulf of California (included in "Key to Genera of C. subfam. Mastophoroideae").

Fosliella? paschalis (Me. Lemoine) Setchell et N. L. Gardner

Melobesia paschalis Me. Lemoine in Børgesen, 1924:289, figs. 32f,g; Santelices and Abbott, 1987:8; Andersson and Athanasiadis, 1992:31; Woelkerling, 1998:378; Woelkerling et al. 1998:624, fig. 336.

Fosliella paschalis (Me. Lemoine) Setchell et N. L. Gardner, 1930:176; Dawson, 1959c:4; 1960b:31; 1961b:415; Hollenberg, 1970:65; Johansen, 1976a:399, fig. 345; Stewart and Stewart, 1984:143; Mendoza-González and Mateo-Cid, 1986:423; Afonso-Carrillo, 1989:331, figs. 1–10 (holotype), 11–27; Sánchez-Rodríguez et al., 1989:42; R. Aguilar-Rosas et al., 1990:124; Ramírez and Santelices, 1991:205; Dreckmann, 1991:35; Mendoza-González and Mateo-Cid, 1992:18; Andersson and Athanasiadis, 1992:32; León-Álvarez and González-González, 1993:461; Serviere-Zaragoza et al., 1993a:483; Stout and Dreckmann, 1993:14; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:397; Woelkerling, 1998:378; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; Riosmena-Rodríguez and Woelkerling, 2000:343; Fernández-García et al., 2011:61.

Crustose coralline, epiphytic on other macroalgae; crusts forming pink, prostrate patches, broadening up to a few mm in width, with rounded or lobed margins (not becoming superimposed), or may encircle algal host; monostromatic and very thin, irregularly arranged in more or less radiating rows, usually less than 25 µm thick in vegetative portions; with more cell layers in the vicinity of conceptacles. Cells in surface view, rounded, more or less quadrangular or irregular, 11–15 µm long, 7–8 µm wide, sometimes with cell fusions between cells of contiguous filaments. Trichocytes present, often frequent.

Sporangial conceptacles often crowded over surface; hemispherical to dome shaped, 100–160 µm in diameter, with a single pore; bisporangia and tetrasporangia up to about 60 µm long. Gametangial conceptacles not observed (after Dawson, 1960b).

HABITAT. Epiphytic on *Laurencia* and *Pterocladiella* and probably other macroalgae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Bahía Kino; Bahía Concepción; Isla San Ildefonso to Punta Palmilla; Nayarit to Jalisco. Eastern Pacific: Laguna Beach, southern California to Bahía Magdalena, Baja California Sur; Islas Todos Santos and Isla Guadalupe, off Baja California; Isla Clarión (Islas Revillagigedo); Colima to Oaxaca; Isla Clipperton; La Perouse to Hanga Piko, Rapa Nui (Easter Island; Isla de Pasqual), Chile.

TYPE LOCALITY. Hanga Piko, Rapa Nui (Easter Island; Isla de Pasqual), Valparaíso Region, Chile.

REMARKS. *Fosliella? paschalis* is included in the "Key to Species of *Hydrolithon* and *Fosliella*" (see herein under *Hydrolithon*). The generic status of the taxon *F.? paschalis*, as well as specimens from the Gulf of California referred to the species, should be reinvestigated (see also Remarks under *Fosliella*). Until its generic status is resolved, its placement remains uncertain.

Pneophyllum Kützing

Pneophyllum Kützing, 1843:385; Penrose and Woelkerling, 1991:495; Penrose, 1996b:266.

Calcified crusts are without protuberances, mostly epiphytic on other algae and seagrasses but some may grow on rocks, and strongly adhere to host or substratum by cell adhesion. Crusts are pseudoparenchymatous, some less than 200 µm thick and of 2–3(–5) cell layers, and others much thicker, of numerous cell layers in vegetative parts. Crusts develop from a germination disc with an 8-celled center. Crusts are dorsiventrally organized and dimerous in construction, with 2 orders of filaments; the first-order (primigenous) filaments produce a unistratose basal layer (hypothallium) of nonpalisade cells that gives rise to second-order (postigenous) filaments that grow perpendicular (usually more or less erect) to the substratum or host and form the perithallium. The erect filaments are either unicellular, consisting only of an epithallial cell, or multicellular with subepithallial meristematic cells of the filaments issuing epithallial cells toward the thallus surface and vegetative cells inward. Some cells in adjacent erect filaments are joined by cell fusions; secondary pit connections are absent. Outermost walls of epithallial cells are rounded or flattened, not flared. Trichocytes, when present, are intercalary within first-order filaments or terminal on second-order filaments; single or in groups at the crust surface.

Sporangial conceptacles are uniporate and are more or less even with or sunken below the crustal surface. Bisporangia or zonately divided tetrasporangia are developed over the chamber floor or peripheral to a central columella, and lack apical plugs. The conceptacle roof is formed by filaments that are peripheral to or interspersed between the sporangial initials. The pore canal is surrounded by numerous cells that are oriented parallel to the conceptacle roof or with upward extending filaments. Gametangial thalli are dioecious or monoecious (carpogonia and spermatangia rarely in the same conceptacle). Carposporophytes with carposporangia that develop on short gonimoblast filaments that arise from the peripheral margins of a large central fusion cell. Spermatangial conceptacles with unbranched spermatangial filaments produced from the chamber floor.

Remarks. *Pneophyllum* is differentiated from the genera *Fosliella* and *Spongites* by its 8-celled sporeling and by trichocytes that are intercalary in first-order filaments. However, molecular studies are needed to further evaluate the species and the distinction of these genera. At least one member of the genus consists of unconsolidated filaments, i.e., *Pneophyllum confervicolum* f. *minutulum* (Foslie) Y. M. Chamberlain (1983; basionym: *Melobesia minutulum* Foslie, 1904; =*Heteroderma minutula* (Foslie) Foslie, 1909; *Fosliella minutula* (Foslie) Ganesan, 1963).

Two species are reported in the southern Gulf of California and Pacific Mexico. *Pneophyllum confervicolum* (Kützing) Y. M. Chamberlain (1983; basionym: *Phyllactidium confervicola* Kützing, 1843) is recorded from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985, as *Heteroderma minutula*; Riosmena-Rodríguez and Paul-Chávez, 1997; Mateo-Cid and Mendoza-González, 2009), Bahía San Quintín (R. Aguilar-Rosas et al., 2005) and Isla Guadalupe (Baja California), Bahía Tortugas, inside southeast Bahía San Bartolomé (Baja California Sur) (Dawson, 1960b), Michoacán (Stout and Dreckmann, 1993), and Oaxaca (Dawson, 1960b; Huerta-Múzquiz and Tirado-Lizárraga, 1970). The Pacific Mexico species *Pneophyllum conicum* (E. Y. Dawson) Keats, Y. M. Chamberlain et Baba (1997a; basionym: *Hydrolithon conicum* E. Y. Dawson, 1960b; type locality: Isla Socorro, Islas Revillagigedo) has also been reported from Bahía de La Paz (Cruz-Ayala et al., 2001), Punta Arena and Cabo Pulmo, and Nayarit to Jalisco (Mateo-Cid et al., 2000; Mateo-Cid and Mendoza-González, 2009).

Two species of *Pneophyllum* are reported in the northern Gulf of California.

KEY TO THE SPECIES OF *PNEOPHYLLUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts thin, mostly 15–20 µm thick; sporangial conceptacle pore without extending upward filaments; sporangial conceptacle without columella; sporangial and carposporangial conceptacles not as wide, 60–100 µm in inside diameter, 40–50 µm tall . . . . ***P. fragile***

1b. Crusts thicker, usually 30–50(–100) µm (or more) thick; conceptacle pore with extending upward filaments; sporangial conceptacle with columella; sporangial and carposporangial conceptacles larger, 160–210 µm inside diameter, 75–90 µm tall . . . . ***P. nicholsii***

Pneophyllum fragile Kützing

Pneophyllum fragile Kützing, 1843:385; 1869: pl. 93: figs. a–c; Chamberlain, 1983:356, figs. 24–27; Penrose and Woelkerling, 1991:495, figs. 2–27; Chamberlain, 1994:141, figs. 64, 65; Penrose, 1996b:269, fig. 123; Yoshida, 1998:609; Mendoza-González and Mateo-Cid, 1999:42, fig. 6; Mateo-Cid et al., 2000:65; Mateo-Cid and Mendoza-González, 2003:11; Fragoso and Rodríguez, 2002:126, figs. 29–31; Mateo-Cid et al., 2006:56; Mateo-Cid and Mendoza-González, 2009:610, figs. 13–16, 21.

Melobesia lejolisii Rosanoff, 1866:62, pl. 1: figs. 1–13, pl. 7: figs. 9–11; Suneson, 1937:7, figs. 1–5; Suneson, 1943:23, pl. 4: fig. 18, pl. 5: fig. 21.

Heteroderma lejolisii (Rosanoff) Foslie, 1909:56 [generitype of *Heteroderma*]; Dawson, 1960b:55, pl. 50: figs. 4–6;, 1961b:417; González-González et al., 1996:317.

Fosliella lejolisii (Rosanoff) M. Howe, 1920:588; Masaki, 1968:23, pls. 12, 49, 50; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Tseng, 1983:78, pl. 42: fig. 1; Dreckmann, 1991:34; González-González et al., 1996:311.

Pneophyllum lejolisii (Rosanoff) Y. M. Chamberlain, 1983:359, figs. 28–32; González-González et al., 1996:121.

Crusts very thin, small, purple-pinkish, of epiphytic, 1–2 cell layers in vegetative portions, 15–20 µm thick; 3–5 cell layers in reproductive regions, 20–30(–45) µm thick; initially subdiscoid (suborbicular), 2–4 mm in diameter; later expanding, occasionally covering most of host, often overlapping; firmly attached to host algae or sea grass by cell adhesion. Hypothallium a single, basal layer of first order filaments parallel to host; of squarish to slightly rectangular (nonpalisade) cells, (7–)10–13 µm long, (6–)10–12 µm in diameter. Perithallium of single cell layer or multicellular layers of second order simple or branched filaments more or less perpendicular to hypothallial filaments; of cells (3–)5–11 µm tall, 5–14 µm in diameter. Cell fusions common, secondary pit connections absent. Epithallium a single layer of small cells, 3–6 µm tall and 4–7 µm wide, terminal on perithallial filaments at thallus surface. Trichocytes absent, or if present, usually singular at surface, seen in surface view 15–19 µm long, 10–12 µm in diameter.

Reproductive conceptacles with roof slightly protruding or more or less even with crust surface. Sporangial conceptacles uniporate, convex, protruding; inside chamber with or without columella, 40–80 µm tall, 130–160 µm in diameter; bisporangia or tetrasporangia on floor, 30–48 µm long, 22–29 µm in diameter. Carposporangial conceptacles more or less even with crust surface; with chambers (30–)50–150 µm tall and 110–200 µm in diameter, with tall cells at conceptacle periphery; carposporangia 25–42 µm long, 30–45 µm in diameter. Spermatangial conceptacle chambers (30–)45–90 µm tall, (55–)80–110 µm in diameter; spermatangial filaments only develop from floor of chamber; pore of spermatangial conceptacle with a protruding, elongated mucilaginous tube (after Penrose, 1996b).

Habitat. Epiphytic on algae, such as *Padina,* and seagrasses; intertidal.

Distribution. Gulf of California: Puerto Peñasco; Punta Arena to Cabo Pulmo. Eastern Pacific: Bahía San Quintín, Baja California; Colima; Oaxaca. Western Pacific: China; Korea; Japan.

Type Locality. On *Sphaerococcus coronopifolius*; from an unknown locale in the Mediterranean Sea (Chamberlain, 1983).

REMARKS. *Pneophyllum fragile* is the type species of the genus (Chamberlain, 1983:356, figs. 26, 27).

Pneophyllum nicholsii (Setchell et L. R. Mason) P. C. Silva et P. W. Gabrielson

Heteroderma nicholsii Setchell et L. R. Mason, 1943b:96; Mason, 1953:336; Dawson, 1959a:20; 1960b:57; Dawson et al., 1960b:16; Dawson, 1961b:417; Dawson et al., 1964:44, pl. 33: fig. A; Dawson, 1965:27; Hollenberg and Abbott, 1966:61; Johansen, 1976a:399, fig. 346; Sánchez-Rodríguez et al., 1989:42; Dreckmann et al., 1990:30, pl. 4: fig. 7; Ramírez and Santelices, 1991:207; Dreckmann, 1991:34; Stewart, 1991:78; Mateo-Cid and Mendoza-González, 1991:19; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:224; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:343.

Pneophyllum nicholsii (Setchell et L. R. Mason) P. C. Silva et P. W. Gabrielson in Gabrielson et al., 2004:94; Mateo-Cid and Mendoza-González, 2009:612, figs. 17–21.

Pneophyllum nicholsii (Setchell et L. R. Mason) Woelkerling ex Mateo-Cid and Mendoza-González, 1992:20, *comb. invalid.*

Pneophyllum nicholsii (Setchell et L. R. Mason) Chamberlain ex Dreckmann, 1991:34 *comb. invalid.*; Mendoza-González and Mateo-Cid, 1992:18; Stout and Dreckmann, 1993:14; Mateo-Cid et al., 1993:47; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid and Mendoza-González, 1994b:40; Mendoza-González et al., 1994:106; González-González et al., 1996:405.

Fosliella nicholsii (Setchell et L. R. Mason) G. M. Smith, 1944:225, pl. 50: fig. 8; Dawson, 1945d:43.

Lithophyllum pustulatum f. *australis* sensu Nichols, 1909:356, pl. 10: figs. 4, 5, pl. 13: figs. 21–24 [non *Lithophyllum pustulatum f. australis* Foslie, 1905a:117].

Crusts epiphytic on various algae; pinkish, mostly 30–50(–100) µm thick (occasionally to 350 µm), initially in surface view more or less discoid, later becoming irregular in outline; composed of 4–7 cell layers; often becoming confluent with only margins monostromatic; construction dimerous, attached by a base layer (hypothallium) of small cells, 2.0–3.5 µm tall, 3.5–5.0 µm in diameter, parallel to host surface. Cells of erect postigenous filaments (2nd order, perithallium) 10–12 µm tall, 7.0–8.0 µm wide. Epithallium a single layer of cells 1.5–2.0 µm tall, 3.5–4.5 µm wide. Cell fusions present; secondary pit connection absent. Trichocytes solitary and intercalary (Mateo-Cid and Mendoza-González, 2009).

Sporangial conceptacles protruding above vegetative surface, up to 200–350 µm outside diameter; hemispherical with a flattened top, and a single pore with extending filaments. Tetrasporangial conceptacle chamber, 40–60(–100) µm tall and 170–215 µm inside diameter; with central columella and pore with extending filaments; tetrasporangia zonately divided, 35–45 µm tall, 18–20 µm in diameter. Gametangial thalli monoecious, with separate carposporangial and spermatangial conceptacles on same thallus, each with a single pore with extending filaments. Carposporangial conceptacle chamber elongate, 30–40 µm tall, 185–230 µm in inside diameter; carposporangia about 30 µm tall, 22–25 µm in diameter. Spermatangial conceptacle chamber, ovoid, 40–45 µm tall and 60–65 µm inside diameter; spermatangial filaments arising from floor of chamber.

HABITAT. On various brown algae, such as *Padina, Dictyota,* and *Dictyopteris*, and probably also on red algae and seagrasses; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Coloradito to Bahía San Carlos; Isla Tiburón (Islas de la Cintura); Isla San Pedro Nolasco; Bahía Concepción to La Paz; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Del Norte County, northern California, to Todos Santos, Baja California Sur; Isla San Gerónimo and Isla Cedros (both off Baja California); Colima to Michoacán; Peru.

TYPE LOCALITY. On *Dictyota binghamiae* (=*Pachydictyon coriaceum*), La Jolla, San Diego County, California, USA.

Spongites Kützing

Spongites Kützing, 1841:30; Woelkerling, 1985a:123; Penrose and Woelkerling, 1992:87; Penrose, 1996c:273.

Melobesia sect. *Spongites* (Kützing) Decaisne, 1842b:126.

Crustose corallines vary from flattened crusts to warty or fruticose thalli to entirely composed of protuberances; may be epizoic, attached to substrate or others may be unattached, free-living rhodoliths. Crustose parts of thalli are dorsiventrally organized and may be monomerous, dimerous, or both; protuberances if present have radially arranged filaments and are monomerous. Monomerous portions composed of a core of noncoaxial filaments ventrally arranged, and a peripheral area where the distal portions of these filaments (or their derivatives) curve outward toward the surface. Dimerous portions composed of a single basal layer of primigenous filaments usually consisting of nonpalisade cells, and many layers of postigenous filaments which arise from the dorsal side of cells of the basal primigenous filaments. Postigenous filaments (2nd-order filaments, perithallium) generally greater than 10 cells thick and more than 200 µm thick. Some cells of adjacent filaments are joined by cell fusions, secondary pit connections are absent. Terminal or subepithallial meristematic cells produce epithallial cells outward and vegetative cells inward. The epithallium may be up to several cell layers thick, the outermost epithallial cells have rounded or flattened (not flared) walls. Trichocytes may be absent, or when present, may be single at the surface, or in vertical or horizontal rows, or in horizontal fields. Trichocytes have not been observed in primigenous filaments (hypothallium).

Vegetative reproduction by fragmentation has been reported in some. Reproductive conceptacles have a uniporate roof. Sporangial conceptacles develop zonate tetrasporangia, or sometimes bisporangia, along the chamber floor or peripheral to a central columella. Each sporangium is without an apical plug. The conceptacle roof is formed by filaments peripheral to sporangial initials or by filaments peripheral and interspersed among sporangial initials. The roof pore has elongated cells protruding into the pore canal, and can be with or without extended filaments. Gametangial crusts are monoecious or dioecious. Carposporangia and spermatangia are developed in separate conceptacles. Carposporangial conceptacles contain a carposporophyte composed of gonimoblast filaments developing peripherally from a large central fusion cell bearing terminal carposporangia. Spermatangial conceptacles contain unbranched spermatangial filaments that develop only on the chamber floor.

There are two species of *Spongites* reported in the northern Gulf of California.

KEY TO THE SPECIES OF *SPONGITES* IN THE NORTHERN GULF OF CALIFORNIA

1a. Surface smooth; reproductive conceptacle chambers less than 200 μm in diameter; thallus construction dimerous; trichocytes absent . . . . ***S. decipiens***

1b. Surface more or less smooth to grainy; reproductive conceptacle chambers up to 250 μm in diameter; thallus construction monomerous; trichocytes present at thallus surface . . . . ***S. yendoi***

Spongites decipiens **(Foslie) Y. M. Chamberlain**

FIGURE 56

Lithothamnion decipiens Foslie, 1897:20; 1898:7; Woelkerling, 1993:70.

Spongites decipiens (Foslie) Y. M. Chamberlain, 1993:113, figs. 26, 27, 30, 35, 36, 47–53; Dreckmann, 1990:35; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; L. Aguilar-Rosas et al., 2000:129, 131; Mateo-Cid et al., 2000:65; Paul-Chávez and Riosmena-Rodríguez, 2000:147; Riosmena-Rodríguez and Woelkerling, 2000:337; Serviere-Zaragoza et al., 2007:11; Vidal et al., 2008:176, tbl. 1; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:64.

Lithophyllum decipiens (Foslie) Foslie, 1900f:71; 1929:33, pl. 53: fig. 14; Dawson, 1944a:270, pl. 57: fig. 20; Mason, 1953 [in part, only southern California specimens]:338, pl. 40 (isotype); Dawson, 1957a:5; 1960b:37 [in part], pl. 26: figs. 1, 2, pl. 27: figs. 1–3; Dawson et al., 1960a:16; Dawson, 1961a:416; 1966a:19; Adey and Lebednik, 1967:16; Masaki, 1968:33, pl. 19, pl. 21: figs. 1–5, pl. 57: figs. 6–8; pl. 58; Smith, 1969 [in part, only southern California specimens]:672; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Dreckmann, 1991:33; Woelkerling, 1993:70; González-González et al., 1996:237, 401; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; Pacheco-Ruíz et al., 2008:208.

Hydrolithon decipiens (Foslie) W. H. Adey, 1970:11; Johansen, 1976a [in part, only southern California specimens]:399, fig. 347; Littler and Littler, 1981:153; 1984:22; Stewart, 1991:78; Dreckmann, 1991:34; Mateo-Cid and Mendoza-González, 1991:20; Mendoza-González and Mateo-Cid, 1992:18; Mateo-Cid and Mendoza-González, 1992:20; León-Álvarez and González-González, 1993:461; Mateo-Cid et al., 1993:46; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:106; González-González et al., 1996:226, 397; Riosmena-Rodríguez et al., 1998:26; Cruz-Ayala et al., 2001:191; CONANP, 2002:139.

Pseudolithophyllum decipiens (Foslie) Steneck et R. T. Paine, 1986:237; Pacheco-Ruíz and Zertuche-González, 2002:467.

Crusts thin, (120–)150–240(–300) μm thick, with a relatively smooth surface without protuberances; attached directly to substratum. Construction dimerous with a single basal layer (hypothallium) of slightly elongated cells 6–10(–15) μm long by 6–10 μm in diameter. Erect second-order filaments (perithallium) form the major portion of thallus thickness; of relatively squarish cells, 5–11 μm tall by 6–10 μm wide. Cell fusions common, secondary pit connections absent. Epithallium usually a single layer; upper surface of rounded and relatively thick-walled epithallial cells, 1–2 μm tall by 4 μm wide. Trichocytes absent.

Reproductive conceptacles small, mostly less than 200 μm outside diameter, with a single pore opening; roof usually white, more or less conspicuous against the crust. Sporangial conceptacles 50–100 μm tall, 100–175 μm inside diameter; tetrasporangia develop around chamber periphery. Carposporangial conceptacles 80–100 μm inside diameter. Spermatangial conceptacles 40–50 μm tall by 100–175 μm inside diameter.

HABITAT. On rocks, small stones, mollusk shells, shell fragments, and other hard surfaces and in tide pools; intertidal to shallow subtidal, probably down to 14 m depths (Dawson, 1960b).

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo San Lucas; Isla Ángel de la Guarda; Mazatlán; Sinaloa to Jalisco; Islas Marías (Islas Tres Marías). Eastern Pacific: southern California to Bahía Magdalena, Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Jalisco to Oaxaca; Costa Rica; Panama; Colombia. Western Pacific: Japan.

TYPE LOCALITY. On small stone; San Pedro, Los Angeles County, southern California, USA.

REMARKS. *Spongites decipiens* had been reported in the markedly differing seawater temperatures of the boreal to cold temperate Pacific coast of British Columbia to Washington (e.g., Johansen, 1976a, as *Hydrolithon decipiens*), in the northern Gulf of California (Dawson, 1944a, 1966b), and the warm waters of the southern California (type locality). Steneck and Paine (1986, as *Pseudolithophyllum decipiens* (Foslie) Steneck et R. T. Paine) showed that specimens from the boreal northeastern Pacific were incorrectly identified, referred them to *P. whidbeyense* (Foslie) Steneck et R. T. Paine (1986; basionym: *Lithophyllum whidbeyense* Foslie, 1906a), and restricted the distribution of *Spongites decipiens* to those from southern California and Japan. This suggests there may be others mistakenly referred to *S. decipiens*. For the time being, those in the northern Gulf are tentatively referred to *S. decipiens*.

Although Gulf of California specimens can sometimes seem similar in the field, generally they can be separated on surface texture differences. *Spongites decipiens* has smooth surfaces and *S. yendoi* has less smooth to grainy surfaces. Internally *S. decipiens* is dimerous, has conceptales less than 200 μm in diameter, and lacks trichocytes, whereas *S. yendoi* is monomerous, has

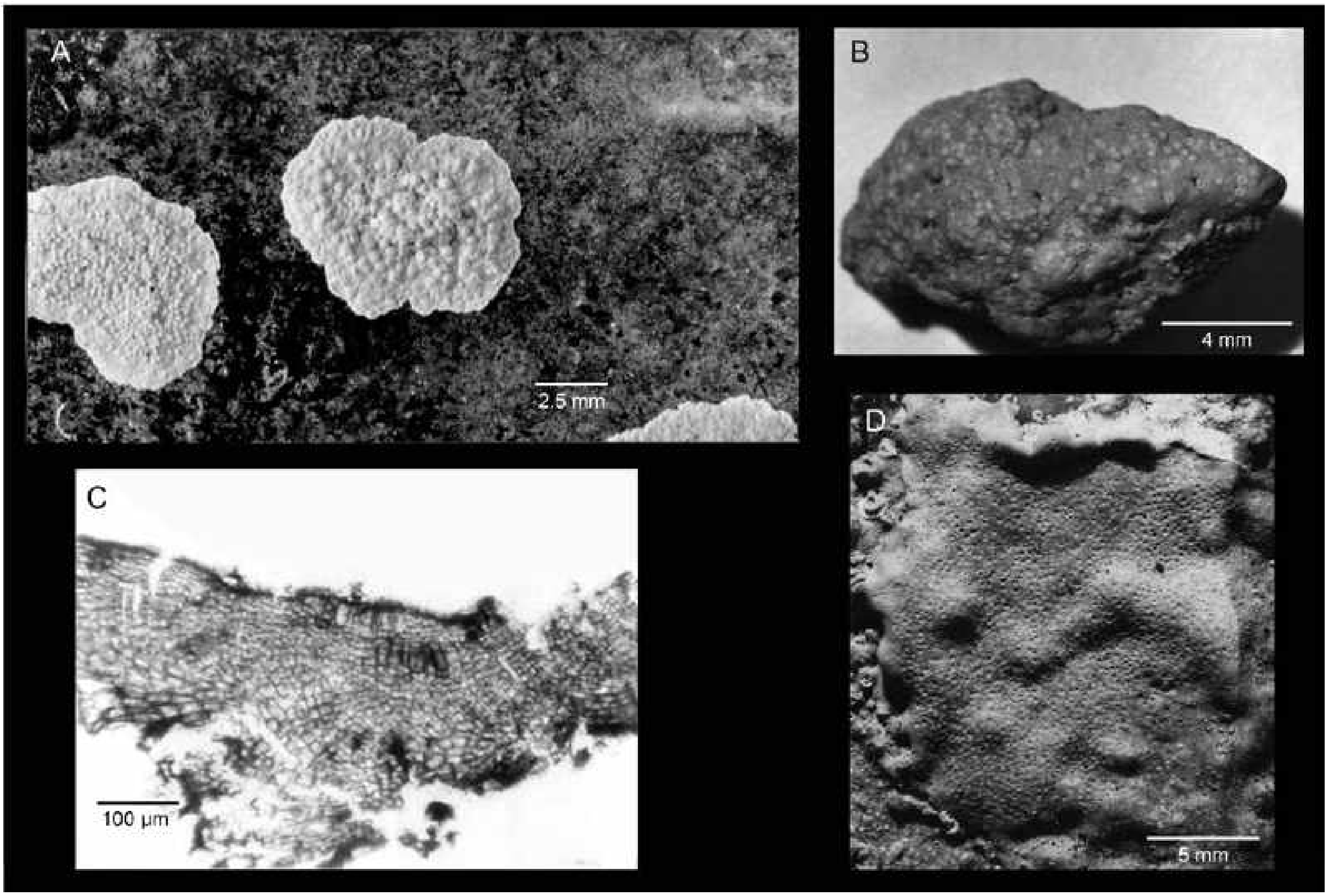

FIGURE 56. *Spongites decipiens*: A. Habit (*EYD-10967*, AHFH, now UC). B. Crust covering rough surface of rock (*JN-3839*, US Alg. Coll.). C. Transection of decalcified crust (*JN-3932,* US Alg. Coll.). D. Surface detail of crust (*JN-3504*, US Alg. Coll.).

trichocytes, and usually has larger conceptacle chambers. The Gulf specimens need further study and molecular testing with types of each of these species to evaluate their taxonomic status and phylogenetic relationship.

Spongites yendoi **(Foslie) Y. M. Chamberlain**

Goniolithon yendoi Foslie, 1900a:25; 1904: pl. 11, fig. 1; Woelkerling, 1993:238.

Spongites yendoi (Foslie) Y. M. Chamberlain, 1993:102, figs. 2–25, 34; Keats et al., 1993:143, figs. 4–23; Penrose, 1996c:280; Yoshida, 1998:615; L. Aguilar-Rosas et al., 2000:131; Fragoso and Rodríguez, 2002:127, fig. 35; Mateo-Cid et al., 2006:56; Vidal et al., 2008:176, tbl. 1.

Lithophyllum yendoi (Foslie) Foslie, 1900a:20; 1929:pl. 53: fig. 16.

Lithothamnion yendoi (Foslie) Me. Lemoine, 1965:10.

Pseudolithophyllum yendoi (Foslie) W. H. Adey, 1970:14.

Lithophyllum decipiens sensu Dawson, 1944a:270 [in part]; 1960b:37 [in part; non *Lithophyllum decipiens* Foslie, 1897:20, which is now *Spongites decipiens* (Foslie) Y. M. Chamberlain, 1993:107, 113].

Crusts initially more or less discoid, later spreading to more than 2 cm; individuals of 3–4 cell layers, 200–500 µm thick; may overgrow each other, becoming up to 0.5 mm thick; surface smooth, or become irregular and grainy; firmly adherent to substratum. Construction monomerous, with a single system of continuously branched filaments that forms a ventral core parallel to the substrate, and then these filaments or their derivatives curve outward toward the thallus surface, forming the peripheral region. Cells of filaments oblong, 5–22 µm long, 2–6 µm in diameter. Epithallial cell terminating filaments at thallus surface. Cell fusions present between adjacent filaments, secondary pit connections absent. Trichocytes at dorsal surface, single or in horizontal fields.

Sporangia conceptacles more or less even with crust surface, mostly up to 250 µm outside diameter; chambers 80–85 µm tall, 175–180 µm inside diameter; roof of 3–5 cells with a pore canal lined with elongated cells that protrude into pore canal but do not extend above pore opening; tetrasporangia zonately divided (after Penrose, 1996c). Gametangial thalli unknown in northern Gulf.

Habitat. On rocks or shells or epizoic on mollusks, such as *Fissurella*; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas. Eastern Pacific: Islas Los Coronados (off northern Baja California) to Isla Margarita, Bahía Magdalena (Baja California Sur); Guerrero. Western Pacific: Japan.

Lectotype Locality. Shimoda, Shizuoka Prefecture, southern Japan.

Remarks. The presence of *Spongites yendoi* , a tropical to subtropical species, is based on its report in the northern Gulf from Puerto Peñasco (Mateo-Cid et al., 2006). Chamberlain (1993) referred some of the earlier Mexican specimens of Dawson (1960b:38, as "*Lithophyllum decipiens*") to *Spongites yendoi*. Upon reexamining some of the same Mexican specimens of Dawson (1960b), Fragoso and Rodríguez (2002) found that some were species of *Hydrolithon*, but none of those they examined were *Spongites*. Thus the presence and distribution of *S. yendoi* the northern Gulf requires further study.

Uncertain Record:
***Spongites fruticulosa* Kützing**

Spongites fruticulosa Kützing, 1841:33; Woelkerling, 1985a:123, figs. 23–32; Penrose, 1991:438, figs. 1–3; 1996c:277, fig. 126.

Lithothamnion fruticulosum (Kützing) Foslie, 1895a:46; Dawson, 1960b: 14 [in part, southern Gulf of California specimens only], pl. 4: figs. 21–25.

Remarks. *Spongites fruticulosa,* a rhodolith described from the Mediterranean Sea (Woelkerling, 1993; Basso and Rodondi, 2006), is the lectotype species of the genus (Woelkerling, 1985a). It has been reported in the southern Gulf from Isla Carmén and Punta Los Frailes (Dawson, 1960b, 1961b, as "*Lithothamnion fruticulosum*"). However, the presence of *S. fruticulosa* in the Gulf needs to be verified since the "*L. fruticulosum*" specimens of Dawson (1960b) were later identified to be *Mesophyllum crassiusculum* (Foslie) Lebednik (in Athanasiadis et al., 2004) by Johansen (1976a, as *L. crassiusculum* (Foslie) L. R. Mason, in Setchell and Mason, 1943b). If that is correct and no other records are found, it would exclude *S. fruticulosa* from the Gulf of California.

CORALLINACEAE SUBFAM. NEOGONIOLITHOIDEAE

Corallinaceae subfam. Neogoniolithoideae A. Kato et M. Baba, in Kato, Baba and Suda, 2011:669.

Calcified crusts and rhodoliths have lateral cell fusions joining cells of contiguous filaments. Secondary pit connections are absent, and the basal layer is without palisade cells. Trichocytes may be present or absent, but if present, not in tightly packed horizontal fields. Sporangial conceptacles are produced by filaments peripheral to the fertile area. Spermatangial filaments develop from both the floor and roof of spermatangial conceptacle chambers.

A recently described monotypic subfamily, C. subfam. Neogoniolithoideae is represented by its single genus in the northern Gulf of California.

Neogoniolithon Setchell et L. R. Mason

Neogoniolithon Setchell et L. R. Mason, 1943a:92; Johansen, 1976b: tbl. 2, figs. 9, 10, 32; Penrose, 1992:339, figs. 1–29.

Calcified crusts vary from flattened crusts to fruticose thalli with protuberances, attached directly to substratum (lack haustoria) or may grow as free living, unattached rhodoliths. Crustose portions are dorsiventrally organized, constructed of a single system of continuously branching filaments (monomerous), with a ventral core of coaxial or noncoaxial filaments (see Kato et al., 2013: figs. 16, 17), which curve outward toward the thallus surface, forming a wide region. Protuberances, when present, have filaments that are radially arranged, with a central core of filaments that curve outward. Each vegetative filament has a terminal or subterminal meristematic cell that divides to produce epithallial cells outward to the thallus surface and additional vegetative cells inward. Some cells of adjacent filaments are linked by lateral cell fusions, and without secondary pit connections. Epithallial cells are rounded or flattened (not flared). Trichocytes are intercalary or terminal, may occur singly, in vertical rows, or in horizontal fields, but not in large or tightly packed horizontal fields.

Vegetative reproduction presumably occurs by fragmentation. Reproductive cells develop within conspicuously protruding, uniporate conceptacles. Sporangial conceptacles are borne on separate crusts from the gametophytic crusts. The sporangial chamber roof is developed by filaments either surrounding or interspersed among sporangial initials, and several cells thick (up to 25 cells thick), with a single, prominent pore lined with cells laterally extending into the pore canal. Zonate tetrasporangia or bisporangial are produced along the chamber floor and walls, either without a columella or, if present, develop peripheral to central columella. Each sporangium is without an apical plug. Gametophytes are monoecious or dioecious, with carposporangia and spermatangia usually in separate conceptacles (rarely within the same conceptacle). Carposporophytes have terminal carposporangia borne on short gonimoblast filaments that arise from the dorsal surface of a thin, flattened fusion cell on the chamber floor (cf. Masaki, 1968; Penrose, 1992). Unbranched spermatangial filaments develop from the floor, walls and roof of the male conceptacle chamber (Penrose, 1992).

Remarks. There is one species recognized in the southern Gulf of California: *Neogoniolithon setchellii* (Foslie) W. H. Adey (1970; basionym: *Lithothamnion setchellii* Foslie, 1897; =*Hydrolithon setchellii* (Foslie) Setchell et L. R. Mason, 1943a), reported from Punta Arena to Cabo Pulmo (Mateo-Cid et al., 2000; Cruz-Ayala et al., 2001), Mazatlán (Mendoza-González et al., 1994), Bahía de Banderas (Serviere-Zaragoza et al., 1993a), Nayarit (Mateo-Cid and Mendoza-Gonzalez, 1992; León-Álvarez and González-González, 1993), and Jalisco (Mendoza-González and Mateo-Cid, 1992), and in Pacific Mexico from Isla Guadalupe (Dawson, 1960b; Stewart and Stewart, 1984).

One species of *Neogoniolithon* is recorded in the northern Gulf of California.

Neogoniolithon trichotomum (Heydrich) Setchell et L. R. Mason

FIGURE 57

Lithothamnion trichotomum Heydrich, 1901b:538; Woelkerling, 1998:364; Woelkerling et al., 1998:592, figs. 304–306.

Neogoniolithon trichotomum (Heydrich) Setchell et L. R. Mason, 1943a:92; Tseng, 1983:82, pl. 44: fig.2; Mendoza-González and Mateo-Cid, 1992:18; Mateo-Cid et al., 1993:46; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; Mendoza-González and Mateo-Cid, 1994:51; Mendoza-González et al., 1994:106; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:131; Cruz-Ayala et al., 2001:191; Riosmena-Rodríguez and Woelkerling, 2000:346; Hinojosa-Arango and Riosmena-Rodríguez, 2004:110, 118; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:11; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:62; Kato et al., 2013:18, figs. 3–15, tbl. 2.

Lithophyllum trichotomum (Heydrich) Me. Lemoine, 1929a:45; Dawson, 1944a:267, pl. 55, fig. 2: pl. 58: figs. 1(lectotype), 4–6, pl. 60; Taylor, 1945:180; Dawson, 1959a:20; 1960b:51, pl. 44, figs. 2, 3, pl. 45: figs. 1, 2, pl. 46; 1961b:417; 1966a:19; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Huerta-Múzquiz and Mendoza-González, 1985:48; Dreckmann, 1991:33; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:239, 401; Mateo-Cid et al., 2000:65.

Crustose corallines 100–1000 μm or more thick, ranging from 10–110 cell layers; fruticose, with numerous, slender, subcylindrical to compressed protuberances. Initially a small encrusting form, later may spread up to 10 cm or more, with lobed margins; surface with simple to subdichotomously or trichotomously branched protuberances of more or less uniform diameter. Some may become free living rhodoliths, up to 5 cm or more in diameter. Protuberances 1.0–1.5 mm in diameter and up to 15 mm in length, with rounded or truncated apices;

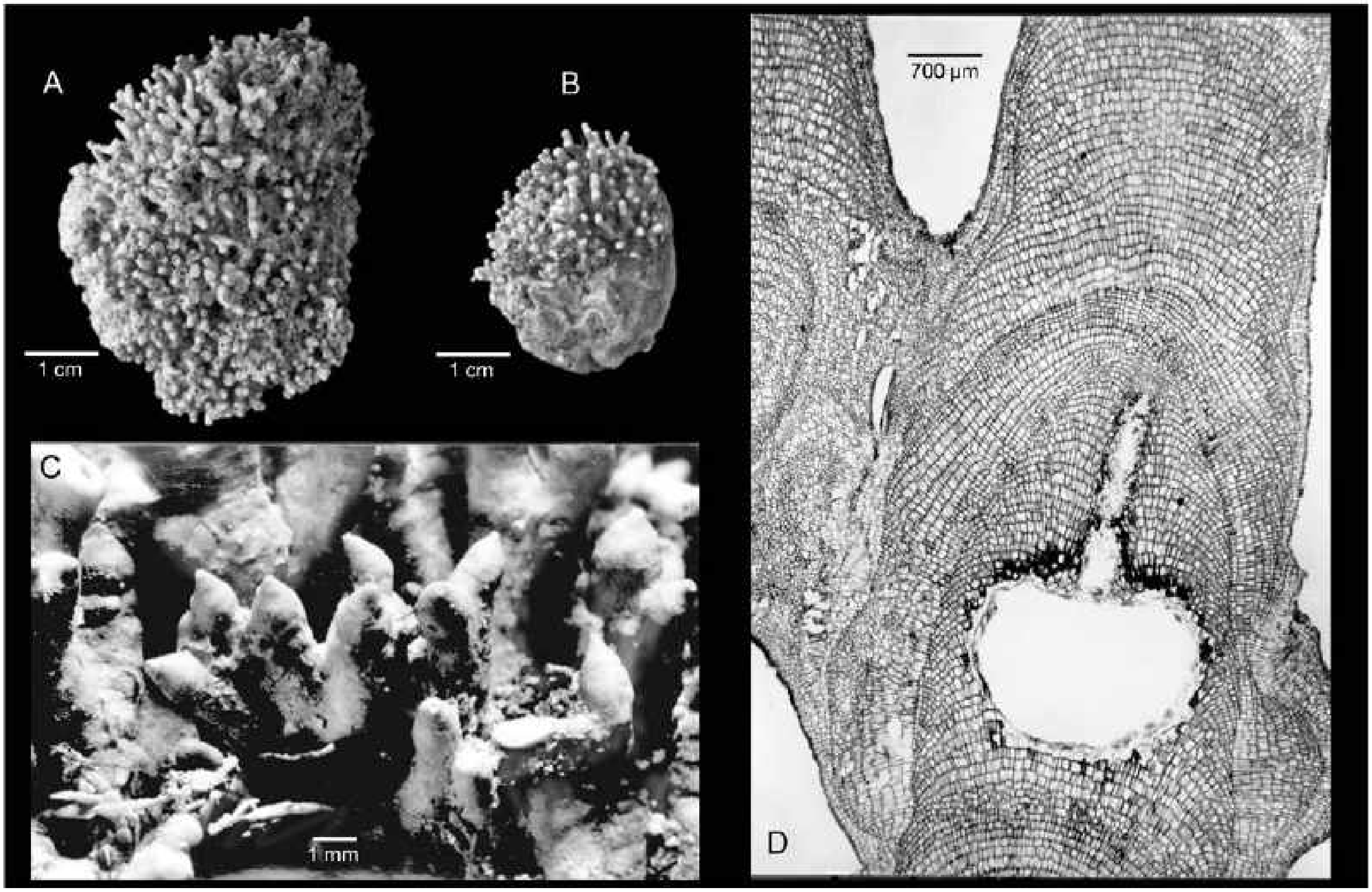

FIGURE 57. *Neogoniolithon trichotomum*: A. Habit (isotype, *L. Diguet-1894*, UC). B. Habit (*EYD-619-40,* AHFH, now UC). C. Close-up showing surface detail of tips of branches (*EYD-1972*, AHFH, now UC). D. Longitudinal section through an erect divided fertile branch, with empty conceptacle (*EYD-226-40*, AHFH, now UC).

becoming abundant or densely congested or sometimes anastomosing. Monomerous; crustose portions with a ventral core of filaments oriented parallel to the substratum (hypothallium) up to 13 cell layers thick, of cells 12–40 µm long, about 10–17 µm in diameter; upward curved filaments (perithallium) of cells progressively decreasing in size toward thallus surface, 6–25 µm tall by 5–17 µm in diameter. Filaments of protuberances of quadrangular cells, 17–40 µm tall by 8–14 µm wide in central portions; outward cells smaller, 14–18 µm long, 9–14 µm wide, in fewer, less-defined layers. Epithallial cells about 4.5–7 µm tall and 9–12 µm wide, terminal on each filament at thallus surface, forming a single layer above elongated subepithallial cells, 7–20 µm tall by 8–15 µm wide. Cellular fusions present between some cells of adjacent filaments. Secondary pit connections absent. Trichocytes present, scattered and in vertical rows (after Dawson, 1960b; and in part Kato et al., 2013).

Reproductive conceptacles conical to dome-shaped, often terminal on branch apices. Sporangial conceptacles large, about 350 µm in length, usually single and terminal on the tips of the protuberances; chambers up to 290 µm tall by 450–1000 µm inside diameter, without a central columella; roof with a prominent central pore. Zonate tetrasporangia, 30–60(–100) µm tall and 60–160 µm in diameter; on floor and walls of conceptacle chamber. Gametophytes not known in northern Gulf of California. Carposporangial conceptacles with chambers, 120–310 µm tall by 310–640 µm inside diameter; gonimoblast filaments arising from a flattened fusion cell over the chamber floor, with terminal carposporangia about 25–50 µm in diameter. Spermatangial conceptacles with chambers 125–160 µm tall and about 370 µm inside diameter; unbranched spermatangial filaments along floor, walls, and roof of chamber; spermatangial parent cells cut off from basal cell of filaments; each spermatangial parent cell produces 2–3 spermatangia, 2–3 µm tall by 3–5 µm in diameter (gametophytes descriptions after Kato et al., 2013).

HABITAT. On rocks, shells, or corals; in sand-covered tidal crevices and in tide pools; or as free-living rhodoliths; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo; Mazatlán, Sinaloa to Jalisco; Isla María Magdalena (Islas Marías). Eastern Pacific: Isla Clarión and Isla Socorro (Islas Revillagigedo); Baja California; Jalisco to Oaxaca; Costa Rica; Panama. Western Pacific: China (Zhang and Zhou, 1980); Vietnam; Japan.

TYPE LOCALITY. Near La Paz, Baja California Sur, Gulf of California, Mexico (Heydrich, 1901b; Woelkerling, 1998).

REMARKS. Described from the southern Gulf of California, *Neogoniolithon trichotomum* is relatively common throughout the Gulf. In the field it is distinguished from other Gulf crustose corallines by its characteristic slender, mostly subcylindrical protuberances and the large terminal conceptacles of up to 450–1000 µm inside diameter. Although *N. trichotomum* can sometimes resemble some *Lithophyllum pallescens*, microscope examination will distinguish *L. pallescens* by its secondary pit connections linking adjacent cells of the perithallial filaments (cell fusions absent) and much smaller sporangial conceptacles less than 400 µm inside diameter.

CORALLINACEAE SUBFAM. POROLITHOIDEAE

Corallinaceae subfam. Porolithoideae A. Kato et M. Baba, in Kato, Baba and Suda, 2011:669.

Calcified crusts have lateral cell fusions between some cells of adjacent filaments. Trichocytes are present in large, tightly packed horizontal fields. Secondary pit connections are absent, and the basal layer is composed of nonpalisade cells. Sporangial conceptacles are produced by filaments peripheral to the fertile area and interspersed among tetrasporangial initials. Spermatangial filaments develop on the chamber floor of the spermatangial conceptacle.

The C. subfam. Porolithoideae is represented by *Porolithon* in the Gulf of California.

***Porolithon* Foslie**

Porolithon Foslie, 1909:57; Kato et al., 2011:669; Bittner et al., 2011:710.

Crusts usually found growing on rocks, shells, or other hard surfaces. Anatomically, thalli are primarily monomerous in construction. The hypothallium is up to several cell layers thick, composed of a noncoaxial core of filaments parallel to the substrate. The perithallium is multilayered, consisting of the continuation of the core filaments and their branches as they curve upward toward the dorsal thallus surface. Lateral cell fusions are present between some cells of adjacent filaments, and secondary pit connections are absent. Trichocytes are present in large, horizontal, postulate (=pustulous of Adey, 1970) fields without any filaments between the individual trichocytes. The epithallium is of 1–3 cell layers.

Sporangial conceptacles formed by filaments peripheral to the fertile area and interspersed among the sporangial initials, conceptacles open by a single pore. Spermatangial filaments develop from the floor of the male conceptacle chamber.

REMARKS. Penrose and Woelkerling (1992) considered the generitype, *Porolithon onkodes* (Heydrich) Foslie (1909), to be congeneric with *Hydrolithon*, as *H. onkodes* (Heydrich) D. Penrose et Woelkerling (1992). If this is followed, then the other taxa placed in *Porolithon*, including the Gulf of California *P. sonorense*, would need to have their generic placement clarified.

On the basis of their morphological and molecular analyses *Porolithon* has been resurrected by Kato et al. (2011). Bittner et al. (2011) restricted *Porolithon* to include members that were primarily monomerous in construction and with trichocytes in large, horizontal, postulate fields that lack any vegetative filaments between the individual trichocytes. Kato et al. (2011) studied Japanese specimens of *P. onkodes*, and Bittner et al. (2011) studied specimens from New Caledonia. In order to corroborate their conclusions, morphological and molecular studies need to be undertaken on the type and topotype material of *P. onkodes* (type locality: Tami Island, Gulf of Huon, Papua New Guinea). Bittner et al. (2011) also suggested, along with several other taxa, that *Hydrolithon samoënse* should be referred to *Porolithon*. Woelkerling et al. (2012) did not accept them as distinct genera, noting that the "*Hydrolithon–Porolithon* complex," needs more morphological, anatomical and molecular analyses to resolve their taxonomic status.

Two species of *Porolithon* are present in the northern Gulf of California.

KEY TO THE SPECIES OF *POROLITHON* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crust surface of undulate or wavy to convoluted raised ridges (up to 1 cm high), plate-like crusts with distinct rounded, lighter-colored margins .... ***P. sonorense***

1b. Crust surface relatively smooth; later expanding and overlapping, surface becoming somewhat warty or lumpy .... ***P. onkodes***

Porolithon onkodes (Heydrich) Foslie

Lithothamnion onkodes Heydrich, 1897a:6, pl. 1: fig. 11a, b; 1897c:410 [as "*L. oncodes*"]; Woelkerling, 1993:164; 1998:357; Woelkerling et al., 1998:575–576, figs. 287–288.

Porolithon onkodes (Heydrich) Foslie, 1909:57; Taylor, 1950:125, pl. 9, pl. 61: figs. 1–2, pl. 62: figs. 1–2, pl. 63: figs. 1–2; Lemoine, 1966:10, figs. 5–6, pl. 1: figs. B–D; Dawson, 1959d:4; 1960a:43; 1961b:415; Adey and Lebednik, 1967:46; Littler, 1971:92; Adey et al., 1982:7, figs. 2–4; Tseng, 1983:82, pl. 3: fig. 2, pl. 44: fig. 4; Santelices and Abbott, 1987:8; Ramírez and Santelices, 1991:223; León-Álvarez and González-González, 1993:462; González-González et al., 1996:257; Kato et al., 2011:669.

Hydrolithon onkodes (Heydrich) D. Penrose et Woelkerling, 1992:83, figs. 4, 5; Penrose, 1996a:261, fig. 119A–D; Keats et al., 1997b:281, figs. 7–10; Yoshida, 1998:561, fig. 3-22(A–D); Fragoso and Rodríguez, 2002:120, figs. 22–24; Mateo-Cid et al., 2006:56; Mendoza-González et al., 2009:225, figs. 4–5; Bernecker, 2009:CD-Rom p. 59; Fernández-García et al., 2011:62.

Goniolithon onkodes (Heydrich) Foslie, 1898:8; 1899:5.

Lithophyllum onkodes (Heydrich) Foslie, 1900c:8; 1909:38; 1929:36, pl. 67: figs. 3–4, 6–7.

Lithophyllum onkodes (Heydrich) Heydrich, 1901b:533.

Spongites onkodes (Heydrich) D. Penrose et Woelkerling, 1988:159, 173, tbl. 2, figs. 10–14; Dreckmann, 1991:35.

Crusts pink to yellowish pink, initially subspherical, later expanding and overgrowing layers; surface somewhat flat to warty or lumpy, rough appearance due to abundant trichocyte fields (groups); variable in thickness, (105–)200–950 µm (in Gulf mostly less than 1.0 mm thick) as reported elsewhere from a few millimeters thick (Mendoza-González et al., 2009) and up to several centimeters thick (Adey et al., 1982). Epithallium of 1–2(–3) cell layers; composed of rounded cells, 2–6 µm tall and 5–9 µm in diameter. Intercalary meristematic cells below epithallium, of cells 4–11 µm long, 4–8 µm in diameter. Perithallium multilayered, of cells 4–13 µm long and 4–10 µm in diameter; cell fusions abundant. Trichocytes 10–30 µm long and 4–15 µm in diameter; forming compact linear fields (groups) of 4–12 cells, up to 100 µm in diameter throughout perithallium. Hypothallium multilayered, 50–150(–350) µm thick; of cells 11–24 µm long and 5–14 µm in diameter.

Reproductive conceptacles usually slightly raised above surface; conceptacle roofs of 3–6 cell layers; uniporate. Tetrasporangial conceptacles scattered; 110–230 µm inside diameter; tetrasporangia zonately divided, 50–75 µm long, 20–40 µm in diameter. Cystocarpic conceptacles 150–210 µm inside diameter; carposporangia 35–70 µm long, 25–70 µm in diameter. Spermatangial conceptacles 130–210 µm inside diameter; spermatia elongated to ellipsoidal, 3–5 µm long, 1–2 µm in diameter.

HABITAT. On rocks and shells and other hard substratum; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco. Eastern Pacific: southern California; Guerrero to Chiapas; Clipperton Island; Costa Rica; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: China; Japan; Papua New Guinea.

TYPE LOCALITY. Tami Island, northwest side of Gulf of Huon, Papua New Guinea.

REMARKS. The generitype of *Porolithon* is *Lithothamnion onkodes. Porolithon onkodes* was reported in the upper Gulf from Puerto Peñasco by Mateo-Cid et al. (2006); as I have not seen their material, the description for the species is based in part on Adey et al. (1982) and Mendoza-González et al. (2009).

Porolithon sonorense E. Y. Dawson

FIGURES 8F, 58

Porolithon sonorense E. Y. Dawson, 1944a:273 [as "*P. sonorensis*"], pl. 57: figs. 17–19, pl. 61: fig. 2; 1960b:25, pl. 15: figs. 1, 2, pl. 16: fig. 1; 1961b:415; 1966a:19; Littler and Littler, 1981:153; Johansen, 1981:2, fig. 2D; Littler and Littler, 1984:27; Anderson, 1991:35; Dreckmann, 1991:35 [as "*Spongites sonorensis*"]; González-González et al., 1996:257; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Rodríguez-Morales and Siqueiros-Beltrones, 1999:23; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:345; Cruz-Ayala et al., 2001:191; CONANP, 2002;139; Pacheco-Ruíz and Zertuche-González, 2002:467.

Crusts forming plate-like lobes, loosely attached, with a tendency to overgrow each other and to form upraised, undulate or wavy ridges where they meet, becoming convoluted, up to 1 cm high. Individual crusts 150–200 µm thick, with distinct rounded, light-colored margins. Hypothallium, where evident, 8–10 cell layers thick; cells 18–26 µm long by 9–14 µm wide. Perithallium of squarish cells, 6–9 µm long by 6–7 µm wide. Epithallium of 2–4 layers of flattened cells, 4–5 µm tall by 6 µm wide. Trichocytes 20–25 µm long by 9–12 µm wide, grouped together

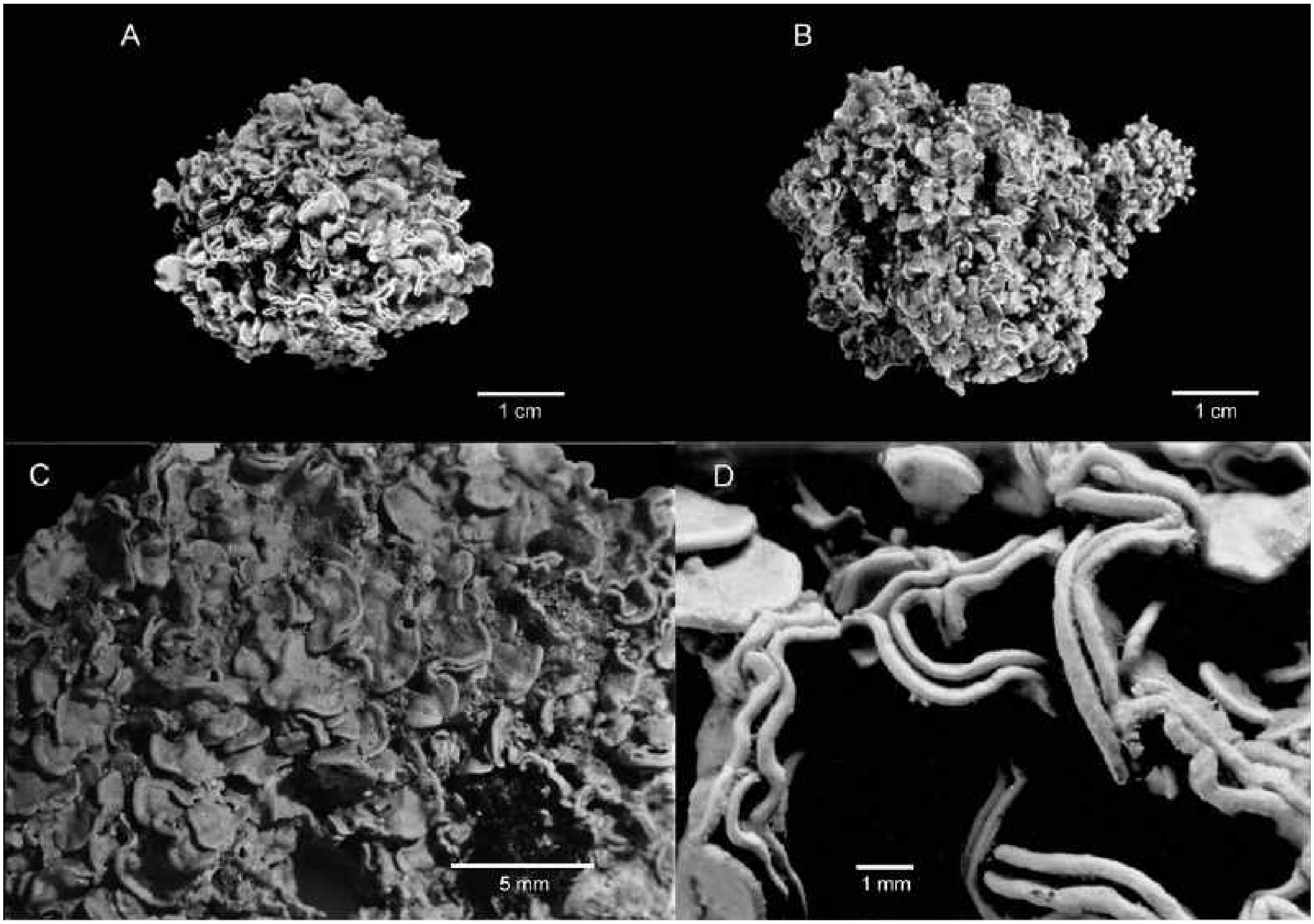

FIGURE 58. *Porolithon sonorense*: A, B. Habits of type collection (*EYD-226a-40*, AHFH-25, now UC). C. Detail of crusts, showing adjacent undulating plates abutting each other (*JN-3775*, US Alg. Coll.). D. Close up of erect, outer edges of abutting undulate plates (*EYD-984,* AHFH, now UC).

in horizontal rows of 6–7 cells; sometimes visible near the surface, or deep within the perithallium.

Tetrasporangial conceptacles immersed or slightly protruding, and scattered over surface, 175–250 µm in diameter, with a single pore opening; tetrasporangia 60 µm in length or more. Gametangial thalli not yet reported.

Habitat. Usually common where found; loosely attached to hard surfaces; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía de La Paz. Eastern Pacific: Bahía Sebastián Vizcaíno, Baja California.

Type Locality. On rocky shore; west side of Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

Remarks. *Porolithon sonorense* is recognized in the field by its upraised, undulate or wavy to convoluted ridges (up to 1 cm high), with distinct rounded, lighter-colored margins (Figure 58C, D). Of the known species of *Porolithon, P. sonorense* is a relatively thin crust in comparison to other members of the genus, which includes the massive species that occur in exposed reef fronts of the central Pacific (Adey et al., 1982).

HAPALIDIACEAE

Hapalidiaceae J. E. Gray, 1865 [1864]:22; Harvey et al., 2003a:995.

The Hapalidiaceae include taxa of the Corallinales whose tetrasporangia produce zonately arranged spores and whose tetrasporangia and/or bisporangia are borne in conceptacles with a multiporate plate. Each sporangium produces an apical plug at the multiporate plate.

Remarks. Doweld (2012) proposed the name Melobesiaceae Früh (1891) for conservation over Hapalidiaceae J. E. Gray (1865) and Lithothamniaceae H. J. Haas (1886, as 'Lithothamnieae'; *fide* Doweld, 2012:680). Herein Hapalidiaceae J. E. Gray is used, following Harvey et al. (2003a), until the proposal has been considered by the International Botanical Nomenclature Committee.

There are two subfamilies of the Hapalidiaceae represented in the northern Gulf of California.

KEY TO THE SUBFAMILIES OF THE HAPALIDIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus without cell fusions and without secondary pit connections between cells of adjacent filaments; sporangial conceptacles with multiporate plate that is acellular at maturity, composed of a calcium carbonate matrix recessed below a single pore opening . . . . **H. subfam. Choreonematoideae**

1b. Thallus with cell fusions adjoining some cells of adjacent vegetative filaments, secondary pit connections absent; sporangial conceptacle roof with a multiporate plate that is cellular at maturity . . . . **H. subfam. Melobesioideae**

Hapalidiaceae subfam. Choreonematoideae

Hapalidiaceae subfam. Choreonematoideae Woelkerling, 1987a:125; Harvey et al., 2003a:994.

The subfamily Choreonematoideae is characterized by nongeniculate thalli; without cell fusions and without secondary pit connections between cells of vegetative filaments; conceptacle roof and walls composed of a single cell layer; presence of an apical plug terminal on each tetrasporangium or bisporangium. Sporangial conceptacle roof with an inner multiporate plate, composed only of a calcium carbonate matrix (acellular) at maturity, recessed below a single pore opening. Spermatangial filaments developed on the floor, walls, and roof of the spermatangial conceptacles.

Remarks. The Choreonematoideae includes a single genus and species, *Choreonema thuretii,* known to occur on the articulated coralline genera *Jania*, *Haliptilon,* and *Cheilosporum*, all members of Corallinaceae subfam. Corallinoideae tribus Janieae (Johansen, 1981). *Choreonema* has also been reported on *Corallina* (Setchell and Gardner, 1930) and *Amphiroa* (Dawson, 1960b).

Choreonema F. Schmitz

Choreonema F. Schmitz, 1889:455; Woelkerling, 1987a:122; Broadwater et al., 2002:1157.

Endosiphonia Ardissone, 1883:450, *nom. illeg.* [non *Endosiphonia* Zanardini, 1878:35].

Minute subspherical conceptacles are the only visible portion of the thallus, whereas the vegetative portions are endophytic within the algal host's tissue. Reproductive conceptacles are lightly calcified and protrude above the intergenicula surface of the host articulated coralline. The vegetative portion is filamentous with largely diffuse and unconsolidated, mostly simple or branching filaments that penetrate into its host; these filaments become pseudoparenchymatous to consolidated in areas of conceptacle production. Lenticular cells on the endophytic filaments produce processes (visible only with transmission electron microscope) that become connected to host cells, indicating its parasitism. Epithallial cells are absent from endophytic filaments but present on conceptacles. Haustoria and trichocytes are lacking. Cells of contiguous filaments are not linked by cell fusions or secondary pit connections.

Reproductive structures develop within the hemispherical to spherical, calcified conceptacles on the host. Conceptacles arise from groups of noncalcified, endophytic filaments cells to form a pseudoparenchymatous patch just below the surface of the coralline host. Sporangial conceptacle roofs are composed of a single layer of cells produced from the filaments peripheral to the sporangial initials. Tetrasporangial initials are developed without columella from the chamber floor of their conceptacles. Each tetrasporangium is zonately divided and produces a mucilaginous apical plug that blocks its pore in the multiporate plate above them; the mucilage of the group of plugs extends outward, obstructing the single outer conceptacle opening prior to sporangia release. Carpogonia and spermatangia are produced within separate uniporate conceptacles on different individuals (dioecious). Each carpogonial conceptacle contains carpogonia that are terminal on 2–3 celled unbranched filaments arising from the chamber floor. Carposporophytes develop after presumed fertilization and, when mature, are composed of a central fusion cell and several-celled filaments that bear terminal carposporangia. Spermatangia are produced on unbranched filaments arising from the floor, walls, and roofs of the spermatangial conceptacle chamber.

Remarks. *Choreonema* is a monotypic genus. The only known species is currently considered to be cosmopolitan. Reported in the southern Gulf, it likely occurs in the northern Gulf of California as well.

Choreonema thuretii (Bornet) F. Schmitz

Melobesia thuretii Bornet in Thuret et Bornet, 1878:96, pl. 50: figs. 1–8; Woelkerling, 1998:381; Woelkerling et al., 1998:629, fig. 341.

Choreonema thuretii (Bornet) F. Schmitz, 1889:455; Suneson, 1937:53, figs. 33–35, pl. 3: figs. 10–12; Hamel and Lemoine, 1953:110, figs. 74–76, pl. 22: fig. 3; Setchell and Gardner, 1930:175; Taylor, 1945:184, pl. 45; Hollenberg, 1948:157; Dawson, 1960b:60, pl. 1: figs. 1–3; 1961b:417; Johansen, 1976a:397, fig. 344; Cabioch, 1980:707; Johansen, 1981:54: fig. 9A,B; Schnetter and Bula-Meyer, 1982:128, pl. 23: fig. B; Stewart and Stewart, 1984:143; Woelkerling, 1987a:113, figs. 1–5; 1988:90; Dreckmann et al., 1990:30; Ramírez and Santelices, 1991:201; Dreckmann, 1991:35; León-Álvarez and González-González, 1993:461; Bula-Meyer, 1995:34; González-González et al., 1996:191, 388; Mendoza-González and Mateo-Cid, 1996a:23, figs. 1–7; Broadwater and La Pointe, 1997:396, figs. 1–27; Yoshida, 1998:548, fig. 3-18A–F; Dreckmann and Gamboa-Contreras, 1998:75; Riosmena-Rodríguez and Woelkerling, 2000:346; Broadwater et al., 2002:1157, figs. 1–8; Dreckmann et al., 2006:154; Fernández-García et al., 2011:61.

Melobesia deformans Solms-Laubach, 1881:53, 57, pl. 1: fig. 5, pl. 3: figs. 12, 26; Woelkerling, 1987b:277, figs. 1–7; 1998:371; Woelkerling et al., 1998:611, fig. 323.

Minute semi-endophytic parasite on articulated corallines; reproductive conceptacles, subspherical lightly calcified, external to host (only visible portion of the thallus). Thallus construction mostly diffuse, with pseudoparenchymatous areas that produce the conceptacles. Endophytic, noncalcified, filaments of elongated cells, unconsolidated, and simple or branched; endophytic filaments penetrate tissue of the algal host with lenticular cells and processes (only seen with TEM) connecting its cells to host cells; supporting its probable parasitism. Filaments lack cell fusions or secondary pit connections; cells multinucleate and without mature plastids.

Reproductive conceptacles (seen with SEM) have a reticulate surface pattern of calcified ridges above a layer of calcified plates (see Broadwater et al., 2002: fig. 2a–f). Sporangial conceptacles (50–)75–100 μm tall and 90–120 μm outside diameter; chamber about 75 μm inside diameter, walls about 13 μm thick; exit pore in outermost region of the conceptacle is a single opening, but inside the opening is a slightly recessed, inner multipore plate with about 15–30 sieve-like openings (see Broadwater et al., 2002: figs. 2f, 3a–c). Tetrasporangia zonately divided, 45–55 μm long, 18–22 μm in diameter, along conceptacle floor, each with terminal mucilaginous plug at the multiporate plate. Gametangial thalli dioecious. Carposporangial conceptacles 105–120 μm tall, 105–126 μm outside diameter; inside chambers about 60 μm tall, 56 μm inside diameter, walls about 30 μm thick; with central fusion cell and gonimoblast filaments consisting of several cells, cells progressively larger upward to terminal carposporangium. Spermatangial conceptacles, 96–135 μm tall, about 100–125 μm outside diameter; inside chamber flask shaped, about 45 μm tall, about 60–70 μm wide, with roof about 20 μm thick; spermatia spherical to ovoid, in chain-like rows (reproductive characters after Chamberlain and Irvine, 1994a; Mendoza-González and Mateo-Cid, 1996a).

HABITAT. Semi-endophytic parasite on species of *Corallina, Jania,* and *Amphiroa*; intertidal.

DISTRIBUTION. Gulf of California: Bahía Agua Verde to Cabeza Ballena. Eastern Pacific: Santa Catalina Island and San Clemente Island (California Channel Islands); Corona del Mar (Newport Beach) to La Jolla (southern California); Isla Guadalupe; Punta Santa Rosaliita (Baja California) to Punta Malarrimo, Bahía Sebastián Vizcaíno (Baja California Sur); Isla Socorro (Islas Revillagigedo); Colima to Oaxaca; Costa Rica; Isla de Gorgona, Colombia; Galapágos Islands; Chile; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: Japan.

TYPE LOCALITY. On the coralline *Haliptilon squamatum* (Linnaeus) H. W. Johansen, L. M. Irvine et A. Webster; Pointe de Querqueville, WNW of Cherbourg, Normandy, Atlantic France.

HAPALIDIACEAE SUBFAM. MELOBESIOIDEAE

Corallinaceae subfam. Melobesioideae Bizzozero, 1885:109.

Hapalidiaceae subfam. Melobesioideae (Bizzozero) A. S. Harvey, Broadwater, Woelkerling et Mitrovski, 2003a:995; Harvey et al., 2003b: 648, 652.

Corallinaceae subfam. Lithothamnioideae Foslie, 1908:19.

The subfamily Melobesioideae is characterized by nongeniculate thalli; some cells of adjacent vegetative filaments adjoined by cell fusions; lack of secondary pit connections; and sporangial conceptacle roofs with multiporate plate composed of cells at maturity. Sporangial conceptacles with tetrasporangia (zonately divided) or bisporangia, underneath the multiporate plate, each sporangium has a terminal apical plug below its outer pore in the conceptacle roof. Carpogonial and spermatangial conceptacles are uniporate. Spermatangia are developed on unbranched or branched filaments issued from the chamber floor, walls, and roof of the spermatangial conceptacles.

The Hapalidiaceae subfam. Melobesioideae is represented by three genera in the Gulf of California.

KEY TO THE GENERA OF HAPALIDIACEAE SUBFAM. MELOBESIOIDEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thin, lightly calcified crusts, usually epiphytic; thallus construction dimerous, consisting of 2 distinct groups of filaments: a lowermost hypothallium of a monostromatic layer of palisade or nonpalisade cells and second order of filaments forming the perithallium or epithallium arising more or less perpendicular from the cells of the lowermost layer ...... ***Melobesia***

1b. Thallus construction monomerous, consisting of a single system of branching filaments that form a ventral or central core and a peripheral region where portions of the core filaments curve outward toward the thallus surface; crusts growing on rocks or as unattached nodules (rhodoliths) or epiphytic 2

2a. Crusts on rocks or epiphytic on articulated corallines; with margins free; may be rhodoliths in other places; thallus contains a ventral and/or central core of coaxial filaments; in vertical section outermost cell walls of terminal epithallial cells rounded or flattened but not flared .... ***Mesophyllum***

2b. Crusts with different surfaces: some smooth; others with extended protuberances; firmly attached to hard substratum or free-living, unattached nodules (rhodoliths); hypothallium of noncoaxial filaments; in vertical section, outermost cell walls of terminal epithallial cells normally flattened and flared .... ***Lithothamnion***

Lithothamnion Heydrich

Lithothamnion Heydrich, 1897c:412, *nom. cons.*

Lithothamnium Philippi, 1837:387, *nom. rej.* [see Woelkerling, 1985b:303, 1988:169].

Thalli are crustose and spreading, with an upper surface that may be smooth to irregular or may be entirely composed of simple to branched protuberances, often short, wart-like, knobby, or stubby. Many are firmly attached to hard substratum, such as rocks, shells, or other hard surfaces. Some species become unattached and form irregularly shaped, free-living nodules (rhodoliths). All are pseudoparenchymatous in structure, with a dorsiventral organization in crustose portions, and radially arranged in the protuberances. Thalli are monomerous; internally composed of branching, laterally adjoined filaments, noncoaxial, in lower (ventral) core or central core, and then filaments outwardly curving toward the thallus surface, forming a peripheral area (perithallium), with filaments terminating with epithallial cells. Some cells of filaments are joined by cell fusions; secondary pit connections are absent; and trichocytes are absent in most species, occasional in some. Epithallium a unistratose layer of cells that are distinctively angular in vertical section; outermost walls of terminal epithallial cells are uniquely flattened and flared (see Woelkerling, 1988: fig. 192).

Assumed vegetative reproduction is apparently by fragmentation. Sporangial conceptacles, multiporate and without columella, develop zonately divided tetrasporangia or bisporangia on the chamber floor. Each tetrasporangium or bisporangium produces an apical plug that blocks its roof pore prior to spore release. The conceptacle roof is formed by thick-walled apices of sporangial filaments that are interspersed among the sporangia but do not persist among sporangia. Gametangial thalli may be dioecious or monoecious, with carpogonia and spermatangia developed in separate uniporate conceptacles. Carpogonia terminate 2- to 3-celled filaments that develop from the conceptacle chamber floor. Carposporophytes are composed of short, gonimoblast filaments that bear terminal carposporangia and lack a conspicuous fusion cell. Roofs of spermatangial and carposporangial conceptacles are formed by overgrowth of surrounding tissue. Spermatangia filaments may be unbranched or branched and bear spermatia in clusters and arise from the conceptacle floor, sides, and roof.

Currently, three species of *Lithothamnion* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *LITHOTHAMNION* AND *MESOPHYLLUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts relatively thin, up to 200 µm thick; with smooth to slightly irregular surfaces, lacking any protuberances or branches . . . . ***Lithothamnion microsporum***

1b. Crusts thicker, with protuberances or protuberant branches; encrusting or free-living, unattached rhodoliths 2

2a. Crusts or rhodoliths with small, close together protuberances of more or less similar size; hypothallium composed of patches of coaxial filaments (arching tiers of laterally aligned cells) . . . . ***Mesophyllum crassiusculum***

2b. Crusts or rhodoliths with protuberances not as above; hypothallium filaments mostly noncoaxial (cells not laterally aligned in arching tiers) 3

3a. Rhodoliths; rounded to irregularly shaped nodules either with short, knobby protuberant branches (2–3 mm in diameter), or slender subcylindrical branched protuberances longer than 6 mm, 1–2 mm in diameter . . . . . . ***Lithothamnion australe***

3b. Rhodoliths; rounded, lumpy-shaped nodules, with extending simple or branched warty protuberances, shorter, up to 6 mm tall; . . . . ***Lithothamnion muelleri***

Lithothamnion australe Foslie

FIGURE 59

Lithothamnion australe Foslie in Weber-van Bosse and Foslie, 1904:24, pl. 2: fig. 10; Dawson, 1960b:11, pl. 4: figs. 1–20, pl. 5: fig. 2, pl. 47: figs. 5–10; 1961b:413; Adey and Lebednik, 1967:82; Adey, 1970:19; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Johansen, 1976a:383, fig. 322; Huerta-Múzquiz, 1978:340; Adey et al., 1982:53, figs. 37, 39, 40; Stewart and Stewart, 1984:143; Ortega et al., 1987:73 [with query], pl. 4: fig. 21; Stewart, 1991:78; Dreckmann, 1991:34; Woelkerling, 1993:34; Serviere-Zaragoza et al., 1993a:484; Mendoza-González and Mateo-Cid, 1994:51; González-González et al., 1996:239; Foster et al., 1997:133; Riosmena-Rodríguez and Paul-Chávez, 1997:71; Woelkerling, 1998:330; Riosmena-Rodríguez and Woelkerling, 2000:334; Serviere-Zaragoza et al., 2007:10; Fernández-García et al., 2011:62.

Lithothamnion corallioides f. *australis* Foslie, 1895b:8, figs. 6, 7.

Lithothamnion australe Foslie,1900e:13, *nom. nud.*

Lithophyllum australe (Foslie) Me. Lemoine, 1917:131; Chávez-Barrear, 1972b:269; Huerta-Múzquiz, 1978:340; Huerta-Múzquiz and Mendoza-González, 1985:48; León-Álvarez and González-González, 1993:461.

Lithothamnion australe f. *americana* Foslie in Weber-van Bosse and Foslie, 1904:25; Dawson, 1944a:271, pl. 56: figs. 5–10, pl. 57: figs. 11–16; Taylor, 1945:173; Dreckmann, 1991:34; León-Álvarez and González-González, 1993:462; González-González et al., 1993:240; Riosmena-Rodríguez and Woelkerling, 2000:334.

Lithothamnion australe f. *americana* Foslie, 1904:25, *nom. invalid.* [see Woelkerling, 1993:25].

Crusts unattached rhodoliths, variable in form; some compact rounded to irregularly shaped nodules (up to 4 cm long, 0.5–2.5 cm in diameter) with conspicuous short, irregular knobby protuberant branches 2–3 mm in diameter; others forming irregularly organized clumps (or individual branches) of long, mostly slender, divaricate to irregular branched, subcylindrical branches, 0.5–2 mm diameter. Hypothallium cells 10–20(–24) µm long by 7–11(–14) µm wide. Perithallium relatively thin, of quadrangular cells, 6–11 µm long by 5–11 µm in diameter.

Sporangial conceptacles apparently rare in Gulf of California, slightly protruding, 400–550 µm in outside diameter; multiporate. Gametangial thalli not recorded in Gulf of California (Dawson, 1960b).

HABITAT. Rhodolith nodules; subtidal, 4–12 m depths, dredged down to 30 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura); Bahía Concepción

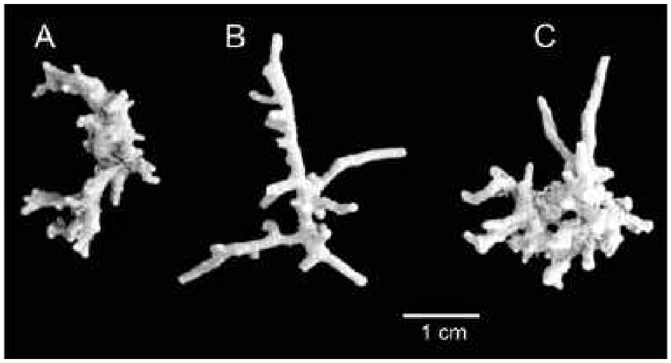

FIGURE 59. *Lithothamnion australe:* Free-living rhodoliths, subcylindrical branches with a wide range of forms. A, B. *EYD-61-40*; C. *EYD-593a* (AHFH, now UC).

to Isla Espíritu Santo and La Paz; Laguna Agiabampo; Sinaloa to Jalisco; Isla María Magdalena (Islas Marias). Eastern Pacific: Santa Catalina and Anacapa Island (California Channel Islands) to northern Baja California; Isla Guadalupe; Isla Cedros; Isla Clarión and Isla Socorro (Islas Revillagigedo); Guerrero; Panama.

Type Locality. Gulf of California (Foslie in Weber-van Bosse and Foslie, 1904:25); "Probably on sublittoral banks," vicinity of La Paz (Dawson, 1960b:11), Baja California Sur, Gulf of California, Mexico.

Remarks. Free-living nodules of *Lithothamnion australe* can often form extensive rhodolith beds at 10–30 m depths. Their movement within the benthic rhodolith beds may exclude the growth of some other algae and invertebrates, as well as remove them, either seasonally or during storms, such as the chubascos (violent squalls with rough seas) that originate in the Gulf of California or off Pacific Mexico and move into the Gulf.

Lithothamnion microsporum (Foslie) Foslie

FIGURE 60

Lithothamnion californicum Foslie f. *microsporum* Foslie, 1902:5; Woelkerling, 1993:149.

Lithothamnion microsporum (Foslie) Foslie, 1929:51; Johansen, 1976a:386, fig. 326; Pacheco-Ruíz and Aguilar-Rosas, 1984:76; Stewart and Stewart, 1984:143; Dreckmann, 1991:34; Mateo-Cid and Mendoza-González, 1991:20; Stewart, 1991:79; González-González et al., 1996:241; L. Aguilar-Rosas et al., 2000:131; Riosmena-Rodríguez and Woelkerling, 2000:342; Fernández-García et al., 2011:62.

Leptophytum microsporum (Foslie) Athanasiadis et W. H. Adey, 2006:101, figs. 123–125 [lectotype], 126–141; Athanasiadis, 2007:240.

Lithothamnion lenormandii sensu Dawson, 1960b:20, pl. 11: figs. 4–6, pl. 14: fig. 2; 1961b:414 [non *Lithothamnion lenormandii* (Areschoug) Foslie, 1895a:178; basionym: *Melobesia lenormandii* Areschoug, 1852:514; =*Phymatolithon lenormandii* (Areschoug) W. H. Adey, 1966b:325 (see Johansen, 1976a:386)].

Crusts pinkish to rose, often spreading 2 cm or more in diameter, with smooth surface (or sometimes slightly irregular or squamulose under magnification); thin, Gulf material mostly 100–200 µm thick; closely adherent to substratum. Hypothallium mostly 50–70(–100) µm thick; of 7–8 layers of small cells; cells about 12 µm long, 5 µm wide; with occasional patches of coaxial filaments (arching tiers of laterally aligned cells). Perithallium 25–100(–200) µm thick; of subspherical, periclinally slightly compressed or ovoid cells, 3–6 µm tall, (4–)5–7 µm wide. Epithallium of flattened cells (in vertical section), although often missing due to sloughing.

Reproductive conceptacles flush with the surface or only very slightly raised (up to 80 µm above surface); 160–280(–330) µm in outside diameter. Sporangial conceptacles multiporate, with (16–)25–40 pores per conceptacle; each pore in surface view surrounded by a rosette of 6–7 epithallial cells; tetrasporangia 70–90 µm long, 20–40 µm in diameter; bisporangia 60–110 µm

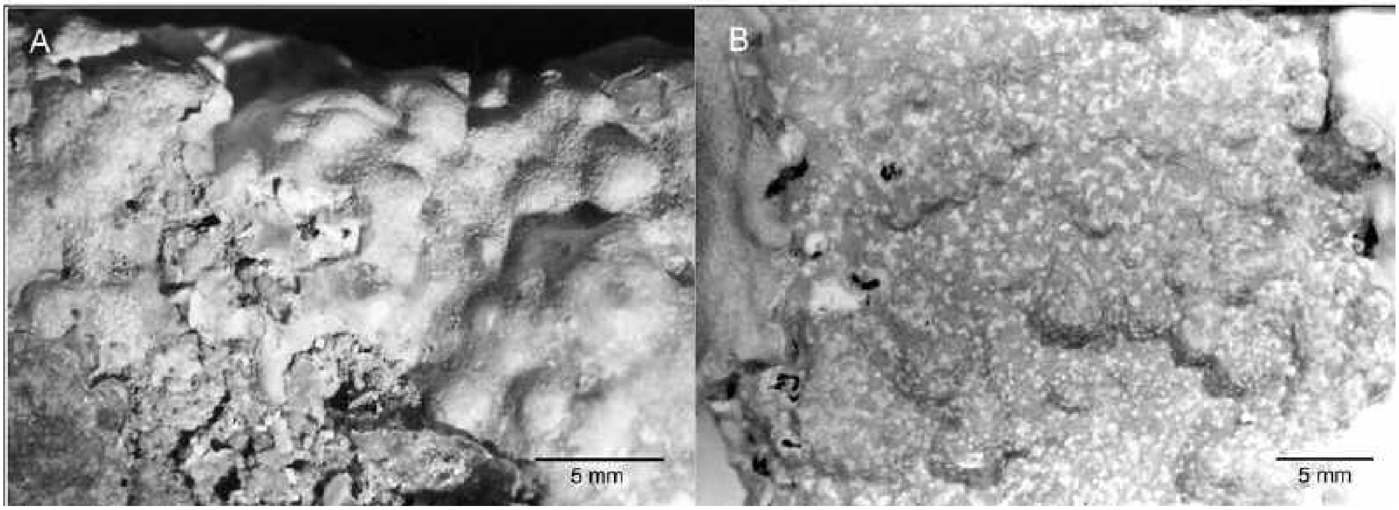

FIGURE 60. *Lithothamnion microsporum*: Surface view of two crusts. A. *JN-3532*; B. *JN-3462* (both US Alg. Coll.).

long, 15–50 µm in diameter. Carposporangial conceptacles uniporate, "about 300 µm in outside diameter" (Dawson, 1960b:20; but not found on his material by Athanasiadis and Adey, 2006). Spermatangia unknown in Gulf (description after Athanasiadis and Adey, 2006, as *Leptophytum microsporum*).

HABITAT. On hard surfaces, usually on pebbles or rocks or sometimes on other crustose corallines; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to San Felipe; Guaymas. Eastern Pacific: Puget Sound, Washington, to Santa Catalina Island (California Channel Islands); Popotla (south of Rosarito), Baja California; Isla Magdalena (west side of Bahía Magdalena), Baja California Sur; Isla Guadalupe; Colima; Oaxaca.

TYPE LOCALITY. On pebbles and sandstone; Pacific Beach, near San Diego, San Diego County, southern California, USA.

REMARKS. Distinctions between the Gulf of California *Lithothamnion microsporum* and some of the other species with smooth surfaces are often unclear, and its species limits and taxonomy need to be clarified in comparisons with type materials. In the field it can sometimes be confused with *Spongites decipiens*; however, differences in the sporangial conceptacles, seen with hand lens or microscope, distinguish these two: the multiporate conceptacles of *L. microsporum* versus uniporate tetrasporangial conceptacles in *S. decipiens*.

Lithothamnion microsporum has been treated as *Leptophytum microsporum* (Foslie) Athanasiadis et W. H. Adey (2006). However, the generitype, *Leptophytum leave* (Strömfelt) W. H. Adey (1966b) was based on *Lithophyllum leave* Strömfelt (1886), which as a later homonym of *Lithophyllum leave* Kützing (1847) is an illegitimate name. Düwel and Wegeberg (1996) treated *Leptophytum* W. H. Adey as a new name based on a designated epitype, and concluded the type materials were conspecific with *Phymatolithon lenormandii* (Areschoug) W. H. Adey (1966b), making *Leptophytum* a heterotypic synonym of *Phymatolithon* Foslie (1898; see also: Woelkerling et al., 2002; Maneveldt et al., 2008; Guiry and Guiry, 2011). An earlier proposal by Athanasiadis and Adey (2003) to conserve *Lithophyllum leave* with a new conserved type was rejected (Compère, 2004; Barrie, 2006; Prud'homme van Reine, 2011). Therefore a new genus may be needed for the generic concept of "*Leptophytum* sensu Adey" (Adey, 1966b; Adey et al., 2001; Athanasiadis and Adey, 2003; Athanasiadis, 2004; Athanasiadis and Adey, 2006). The other species, including *L. microsporum*, need reinvestigation to determine whether they belong in *Lithothamnion, Phymatolithon*, in another genus, or possibly a new one.

Lithothamnion muelleri Lenormand ex Rosanoff

Lithothamnion muelleri Lenormand ex Rosanoff in Rosanoff, 1866:101, pl. 6: figs. 8–11; Woelkerling, 1983b:190, figs. 29–33; Wilks and Woelkerling, 1995:553, figs. 1–6; Woelkerling, 1996a:181, figs. 76A–E, 77A–B; Rivera et al., 2004:235; Foster et al., 2007:367; Riosmena-Rodríguez et al., 2010:58, tbl. 3.1, fig. 3.3C.

Lithothamnion crassiusculum sensu Frantz et al., 2000:1773 [non *Lithothamnion crassiusculum* (Foslie) L. R. Mason, in Setchell and Mason, 1943b:93; basionym: *Lithothamnion rugosum* f. *crassiusculum* Foslie, 1901a:4, which is now *Mesophyllum crassiusculum* (Foslie) Lebednik in Athanasiadis et al., 2004:152; Athanasiadis, 2007:223].

Crusts spreading on substratum or forming rhodoliths; 1.0–4.0 cm wide, 0.1–4 mm thick, with a lumpy surface; protuberances simple to branched, 1–6 mm long, 1–4 mm in diameter; attached by cell adhesion. Structure pseudoparenchymatous; dorsiventrally organized in crustose portions; radially arranged in protuberances. Thallus construction monomerous, with a single system of branched filaments giving rise to a ventral core in crustose portions and central core in protuberant branches and forming the peripheral areas where portions of core filaments or their branches curve outward to thallus surface; some cells of adjacent filaments adjoined by cell fusions; cells of filaments, 2.0–15 µm in diameter and to 2.0–30 µm long. Epithallial cells, 1.0–8.0 µm long and 2.0–8.0 µm in diameter, terminating most filaments at thallus surface, with distal cell walls flattened and flared. Secondary pit connections, haustoria, and trichocytes unknown.

Sporangia developed in multiporate conceptacles, with flush to protruding roofs; zonately divided tetrasporangia, 100–175 µm tall, 30–140 µm in diameter, with an apical plug that blocks the roof pore prior to spore release. Pore canals, in vertical section, with bordering filaments with cells similar in size and shape to other roof filaments. Gametangial thalli not reported in Gulf (description of species after Woelkerling, 1996a).

HABITAT. Usually a rhodolith, often in sediment patches and among rocks and *Sargassum*, mostly in wave-exposed sites; intertidal to shallow subtidal, down to 12 m depths.

DISTRIBUTION. Gulf of California: Cabo Los Mochis (entrance to Bahía Concepción) to La Paz.

TYPE LOCALITY. Western Port Bay, Victoria, Australia.

REMARKS. *Lithothamnion muelleri* has been recently reported in the Gulf of California (Foster et al., 2007; Riosmena-Rodríguez et al., 2010). Usually considered a cool-water species, *L. muelleri* had been known from southern Western Australia to South Australia and Tasmania and Victoria (Woelkerling, 1996a). Woelkerling (1996a) also noted that records of *L. muelleri* from the subantarctic (Papenfuss, 1964b) and southern Chile (Hariot, 1895; Ramírez and Santelices, 1991) need to be confirmed. The finding of *L. muelleri* in the warm waters of the Gulf is interesting and, if confirmed, represents an extraordinary disjunct distribution from Australia and in the Gulf of California.

Melobesia J. V. Lamouroux

Melobesia J. V. Lamouroux, 1812:186 [see Mason, 1953:320, 335; Woelkerling, 1988: 113, 119, 186].

Melobesia Heydrich, 1897c:408, *nom. illeg.* [later homonym of *Melobesia* J. V. Lamouroux, 1812]; Mason, 1953:320, 335.

Melobesia Foslie, 1898:10, *nom. illeg.* [later homonym of *Melobesia* J. V. Lamouroux, 1812]; Foslie, 1909:56; Mason, 1953:320, 335; Woelkerling, 1988:119; Woelkerling and Lamy, 1998:278].

Epilithon Heydrich, 1897c:408.
Hapalidium Kützing, 1843:385.

Crusts thin, lightly calcified, usually epiphytic on other algae (or rarely epizoic), normally encrusting and attached to the surface of various hosts or substrates. Crusts flat or with undulating surfaces; without protuberances or branches. Thalli dorsiventrally organized and dimerous in construction. A single basal layer of first-order (primigenous) filaments is composed of palisade or nonpalisade cells. Second-order (postigenous) filaments of one or more cells may arise perpendicularly from the dorsal surface of the cells of the basal primigenous filaments. Some cells of adjacent filaments are adjoined by cell fusions; secondary pit connections and trichocytes are unknown. Each upright row of cells (filament) usually terminates with an outermost round or flattened epithallial cell or cells.

Sporangial conceptacles are multiporate and produce zonately divided tetrasporangia or bisporangia. Each sporangium produces an apical plug that blocks its pore in the conceptacle roof prior to its release. Gametophytes are monoecious or dioecious. Carpogonia and spermatangia (where known) are developed in separate, uniporate conceptacles. Unbranched carpogonial filaments of 2–3 cells develop from the chamber floor within carposporangial conceptacles. Carposporophytes have 1 or possibly more inconspicuous fusion cells (or lack an evident fusion cell), with gonimoblast filaments of several cells that bear terminal carposporangia. Spermatangia are developed on unbranched filaments arising from the chamber floor, walls, and roof of the spermatangial conceptacle (after Harvey et al., 2003a).

REMARKS. The generic name *Melobesia* has been used three times to describe different taxa, i.e., Lamouroux (1812), Heydrich (1897c), and Foslie (1898). The last two are later homonyms, which are not to be taxonomically confused with *Melobesia* J. V. Lamouroux (Woelkerling in Guiry and Guiry, 2009). This has led to a confused taxonomic history and associated nomenclature (Mason, 1953; Woelkerling, 1988). Taxonomic and morphological data elucidating *Melobesia* can be found in Chamberlain (1985), Wilks and Woelkerling (1991), Woelkerling (1996, 1998), Woelkerling and Lamy (1998), Harvey et al. (2003a, 2003b), Woelkerling and Chamberlain (2007), Le Gall and Saunders (2007), and Woelkerling et al. (2008).

Five species of *Melobesia* are presumed to be in the Gulf of California. In this treatment, two of these species are reported in the southern Gulf, and one is from the oceanographic entrance to the Gulf of California. They are all included since these small, often delicate, epiphytic crusts are easily overlooked and are probably more widespread in the Gulf of California than current records indicate. All Gulf specimens are in need of critical morphological and genetic study to determine their generic placement and specific status.

KEY TO THE SPECIES OF *MELOBESIA* IN THE GULF OF CALIFORNIA

1a. Crusts of only 1–2 layers of cells in vegetative portions 2
1b. Crusts more than 2 layers thick, multilayered, of 7–25 layers of cells in vegetative portions 3
2a. Crust only a single layer of cells in vegetative portions (overgrowth of individuals may form up to 5–6 layers); conceptacles hemispherical, 100–180 µm in diameter . . . . ***M. accola***
2b. Crusts of 1–2 cell layers (50–100 µm thick) in vegetative portions; sporangial conceptacles mostly 110–130 µm in diameter . . . . ***M. membranacea***
3a. Mature crusts of 12–25 layers of cells; conceptacles immersed (not prominent), with many cell layers below chamber floor . . . . ***M. polystromatica***
3b. Mature crusts usually thinner; up to 12 cell layers thick; conceptacles protruding above surface (not immersed), with only 1–2 cell layers below chamber floor 4
4a. Epiphytic on various, noncalcified algae; juvenile crusts orbicular in outline, later forming confluent, irregularly shaped patches, up to 9 mm across; 50–150 µm thick; sporangial conceptacles up to 120 (rarely to 150) µm in outside diameter, with 10–12 pores . . . . ***M. marginata***
4b. Epiphytic on sea grass blades; irregular in outline, up to 2 mm wide; usually less than 50 µm thick; overlapping individuals coalescing, up to 200 µm thick; sporangial conceptacles up to 210 µm in outside diameter, with 9–14 pores . . . . ***M. mediocris***

Melobesia accola (Foslie) Me. Lemoine

Litholepis accola Foslie, 1907:22; Setchell and Gardner, 1930:176; Dawson, 1960b:59; 1961b:417; Adey and Lebednik, 1967:36; Stewart and Stewart, 1984:143; Woelkerling, 1993:15; González-González et al., 1996:237,400; Woelkerling, 1998:296, 397, figs. 140 (holotype), 141; Serviere-Zaragoza et al., 2007:10.

Melobesia accola (Foslie) Me. Lemoine, 1924:289, fig. 32e.

Lithoporella accola (Foslie) W. H. Adey, 1970:14; Ramírez and Santelices, 1991:213.

Lithophyllum accola (Foslie) Woelkerling ex Dreckmann, 1991:34, *comb. inval.*; León-Álvarez and González-González, 1993:470; Fragoso and Rodríguez, 2002:112.

Crusts small, epiphytic on other crustose corallines; thin, monostromatic (a single layer of cells), individual crusts overgrowing each other and becoming up to 5–6 cell layers thick. Cells (in vertical section) rectangular to slightly vertically elongated or irregular, 5–10 µm tall, 5–12 µm wide; cells (in surface view) rectangular to rounded, 7–10 µm by 5–7 µm, arranged in rows.

Conceptacles numerous, hemispherical-conical, 100–180 µm in diameter, with a single pore. Gametangial conceptacles unknown (after Dawson, 1960b).

Habitat. Growing on other crustose coralline algae; intertidal.

Distribution. Gulf of California: Jalisco. Eastern Pacific: Isla Guadalupe; Isla Clarión and Isla San Benedicto (Islas Revillagigedo); Colima to Oaxaca; Hanga Piko, Rapa Nui (Easter Island; Isla de Pascua).

Type Locality. Tahiti (Dawson, 1960b); Hao (Haorangi), east of Tahiti, coral atoll in central part of Tuamotou Archipelago, French Polynesia (Woelkerling, 1998).

Remarks. *Melobesia accola* has not been recently collected, and it remains poorly known in the Gulf (Dawson, 1960b, as *Litholepis accola*). Dawson (1960b) noted conceptacles with a single pore in Pacific Mexico specimens and questioned if they were asexual. However, only multiporate sporangial conceptacles are known in the genus *Melobesia*. The specimens and more collections are needed for further study to confirm their identification and its presence in the Gulf of California.

Melobesia marginata Setchell et Foslie

Melobesia marginata Setchell et Foslie in Foslie, 1902:10; Smith, 1944:219, pl. 49: fig. 2, pl. 50: fig. 1; Taylor, 1945:176; Mason, 1953:321; Dawson, 1960b:6, pl. 1: fig. 6, pl. 2: fig. 1; 1961b:413; Dawson et al., 1964:42, pl. 33: fig. B; Johansen, 1976a:388, fig. 331; Silva, 1979:319; Stewart and Stewart, 1984:143; Pacheco-Ruíz and Aguilar-Rosas, 1984:76; Scagel et al., 1989:209; R. Aguilar-Rosas et al., 1990:124; Dreckmann, 1991:34; Stewart, 1991:79; Ramírez and Santelices, 1991:218; León-Álvarez and González-González, 1993:462; Woelkerling, 1993:145; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; González-González et al., 1996:243, 323, 403; Riosmena-Rodríguez and Woelkerling, 2000:342; Serviere-Zaragoza et al., 2007:11; Fernández-García et al., 2011:62.

Lithothamnion marginatum (Setchell et Foslie) Nichols, 1909:350, pl. 10: fig. 1, pl. 11: figs. 7–9, pl. 13: fig. 25.

Crusts thin, of 2 cell layers in vegetative portions, 50–100 µm thick; initially in surface view orbicular, later forming confluent, irregularly shaped patches, up to 9 mm wide, with lobed margins; of 8–12 cell layers thick centrally; central cells square to rectangular, 3–6 µm wide, 6–20 µm long. Basal layer of cells, 3–9 µm in diameter; epithallial cells somewhat triangular in vertical section.

Sporangial conceptacles crowded, protruding, usually 50–100 µm tall; mostly 110–120 µm (rarely up to 150 µm) outside diameter; roof with 10–12 pores; tetrasporangia zonately divided, 40–60 µm long, 18–30 µm in diameter. Carposporangial conceptacles 95–125 µm tall, 125–150 µm outside diameter. Spermatangial conceptacles conical, 100–125 µm outside diameter (after Mason, 1953; Dawson, 1960b).

Habitat. Epiphytic on *Sargassum*, *Gelidium,* and *Laurencia* and probably other algae; intertidal.

Distribution. Gulf of California: Cabeza Ballena; Jalisco. Eastern Pacific: northern British Columbia to Punta Hughes, northwest side of Isla Magdalena (Bahía Magdalena), Baja California Sur; Islas Todos Santos, Isla Guadalupe, and Isla Cedros (Baja California); Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Oaxaca; El Salvador; Costa Rica; Ecuador; Peru; Galápagos Islands.

Type Locality. On *Gymnogongrus* and *Laurencia*; Bodega Bay, Sonoma County, northern California, USA.

Melobesia mediocris (Foslie) Setchell et L. R. Mason

Lithophyllum zostericola f. *mediocris* Foslie, 1900d:5.

Melobesia mediocris (Foslie) Setchell et L. R. Mason, 1943b:95; Smith, 1944:219, pl. 49: fig. 1; Taylor, 1945:176; Dawson, 1950a:68; 1951:52; Mason, 1953:320, pl. 31: fig. a; Dawson, 1957a:7; 1960b:7, pl.1: fig. 5, pl. 2: figs. 2, 3; Dawson et al., 1960a:68, pl. 19: figs. 4, 5; Dawson, 1961b:413; R. K. S. Lee, 1970:437; Abbott and North, 1972:76; Johansen, 1976a:389, fig. 332; Huerta-Múzquiz, 1978:335; Silva, 1979:319; Stewart and Stewart, 1984:143; Pacheco-Ruíz and Aguilar-Rosas, 1984:71, 76; Ortega et al., 1987:73; Scagel et al., 1989:209; R. Aguilar-Rosas et al., 1990:124; Dreckmann, 1991:34; Stewart, 1991:79; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; González-González et al., 1996:243; Silva et al., 1996b:232.

Lithothamnion mediocre (Foslie) Foslie et Nichols in Nichols, 1908:347, pl. 9.

Crusts thin, epiphytic on sea grasses; initially more or less discoid, spreading and often coalescing to become irregularly shaped (surface view outline), up to 2 mm wide; margins 7–12 µm thick; central vegetative portions 15–25 µm thick; fertile portions mostly 30–65 µm thick (overgrowing or coalescing portions may be up to 200 µm thick). Margins of (1–)2 cell layers; centrally 7–11 cells thick, forming 3 different layers: basal (hypothallium) of 1–2 layers of cells, 6–8(–14) µm in diameter; erect filaments (perithallium) of 4–7 layers of cells about 10 µm tall, 8 µm wide; epithallium of 2 layers of flat cells, 1–4 µm tall, 12 µm wide.

Reproductive conceptacles protruding above surface. Sporangial conceptacles dome shaped, 140–210 µm in diameter, 90–140 µm tall; multiporate, with (4–)9–14 pores; tetrasporangia zonately divided, 50–125 µm tall, 35–80 µm in diameter. Carpogonial conceptacles 125–190 µm in diameter, 70–150 µm tall. Spermatangial conceptacles 75–120 µm in diameter, 65–75 µm tall; spermatia ovoid with minute knob on each end, about 3.7–4.0 µm long, 1.8–2.0 µm in diameter.

Habitat. Epiphytic on sea grasses; intertidal to very shallow subtidal.

Distribution. Gulf of California: Laguna Agiabampo (Sonora and Sinaloa). Eastern Pacific: northern British Columbia to Punta Hughes, northwest end of Isla Magdalena (Bahía Magdalena), Baja California Sur; Islas Todos Santos and Isla Guadalupe, Baja California; Rocas Alijos, Baja California Sur.

Type Locality. On the sea grass *Phyllospadix*; Santa Cruz, Santa Cruz County, northern California, USA.

Remarks. *Melobesia mediocris* is very similar to *M. marginata*; the two are generally separated by their alga or plant hosts. *Melobesia mediocris* is epiphytic on sea grasses, and *M. marginata* is on various fleshy algae. The obligate specificity of their plant or algal hosts needs to be tested, and their relationship needs to be elucidated by molecular studies.

Melobesia membranacea (Esper) J. V. Lamouroux

Corallina membranacea Esper, 1796: pl. *Corallina* XII: figs. 2–4.

Melobesia membranacea (Esper) J. V. Lamouroux, 1812:186; Mason, 1953:319; Dawson, 1960b:8, pl. 25: figs. 1–3; 1961b:413; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Chamberlain, 1983:297–298; 1985:673, fig. 2; Woelkerling, 1988:189; Dreckmann, 1991:34; León-Álvarez and González-González, 1993:462; Chamberlain and Irvine, 1994b:196, figs. 7B, 39A, 75, 93, 94; González-González et al., 1996:323, 403; Riosmena-Rodríguez and Woelkerling, 2000:342; Fragoso and Rodríguez, 2002:130; Serviere-Zaragoza et al., 2007:11; Woelkerling and Chamberlain, 2007:233.

Epilithon membranaceum (Esper) Heydrich, 1897c:408; Hamel and Lemoine, 1953:112, figs. 77–81, pl. 22: figs. 6, 7.

Crusts thin, delicate, orbicular, spreading up to 1 cm (or more) in diameter, usually epiphytic on various larger algae, rarely epizootic or on rocks; flattened, closely adherent to host; only 1–2 cell layers and 25–45 µm thick in vegetative portions; 4–5 cell layers and 55–90 µm thick in reproductive regions. Dimerous with cell fusions present and trichocytes absent. Single basal layer (hypothallium) of cells in vertical section about 7–23 µm tall, 2–6 µm in diameter; erect filaments (perithallium) either absent or up to 7 cells; if present, cells about 2–13 µm tall, 3–10 µm in diameter (cell sizes not given by Dawson, 1960b; after Chamberlain and Irvine, 1994b). Epithallial cells irregularly present; very small, ⅓ to ½ diameter of vegetative cells (Dawson, 1960b).

Sporangial conceptacles prominent, dome shaped or hemispherical, small (80–)110–130(–150) µm outside diameter, single or grouped, sometimes confluent; roof multiporate, 7–20(–30) pores; tetrasporangia 35–90 µm long, mostly zonately divided with a apical pore plug. Carposporangial conceptacles dome shaped, 120–200(–300) µm outside diameter. Spermatangial conceptacles conical, about 100 µm inside diameter, up to 250 µm outside diameter.

Habitat. Epiphytic on *Chaetomorpha* and probably on other algae; intertidal.

Distribution. Gulf of California: Cabeza Ballena; Jalisco. Eastern Pacific: Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Guerrero.

Type Locality. On red algae, west coast of France.

Remarks. *Melobesia membranacea* is the type species of the genus *Melobesia*. The species is easily overlooked and is probably more widely distributed in the Gulf of California than current records indicate.

Melobesia polystromatica E. Y. Dawson

Melobesia polystromatica E. Y. Dawson, 1960b:8, pl. 1: fig. 4, pl. 22: fig. 2; Dawson, 1961b:413; Anderson, 1991:32; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:243, 403; Riosmena-Rodríguez and Woelkerling, 2000:344; Fernández-García et al., 2011:62.

Crusts, epiphytic on *Sargassum*, mostly 5–8 mm in diameter, individuals unevenly thick, varying 100–200 (or more) µm in thickness. Initially a thin, lightly calcified single cell layer of radiating rows of quadangular cells, 6–10 µm long by 3–5 µm wide; soon becoming polystromatic, thicker and heavily calcified, confluent, and somewhat mounded; spreading on flat surfaces or surrounding cylindrical portions of algal host. A single basal layer (hypothallium) (in vertical section) of squarish cells, 6–7 µm in diameter; erect filaments (perithallium) of 15–20 cells in vertical rows, cells 7–12 µm long, epithallium of 4–5 layers of small, quadrate to flattened cells. In surface view, superficial epithallial cells rounded, 4–5 µm in diameter, with thick walls.

Sporangial conceptacles immersed (not prominent), with oval chamber, about 60 µm high by 110 µm inside diameter; conceptacle roof with 20–25 pores; tetrasporangia zonately divided, 25–30 µm long. Carposporangial conceptacles immersed; chambers about 110 µm inside diameter, roof with a single pore. Spermatangial conceptacles with chambers about 80 µm inside diameter (description after Dawson, 1960b).

Habitat. On *Sargassum* and probably other algae; intertidal to shallow subtidal.

Distribution. Gulf of California: Nayarit to Jalisco. Eastern Pacific: Oaxaca; El Salvador.

Type Locality. On *Sargassum liebmannii* J. Agardh: Bahía Tenacatita, Jalisco, Pacific Mexico.

Remarks. A little known species, *Melobesia polystromatica* is distinguished by its polystromatic thallus and immersed reproductive conceptacles. Dawson (1960b) noted *M. polystromatica* had much in common with some of the thin species of *Lithothamnion*. Present in the southern end of the Gulf of California, it is included to call attention to the need for further morphological and molecular study of its taxonomic status.

Mesophyllum Me. Lemoine

Mesophyllum Me. Lemoine, 1928:251; Woelkerling, 1988:193; Harvey et al., 2003a:998; 2003b:647; Le Gall and Saunders, 2007:1118.

Crustose corallines vary in appearance from encrusting with smooth surfaces to those with warty or lumpy protuberances and others that are foliose or fruticose. Species may be epiphytic or epizoic, on rocks or shells, or may form unattached rhodoliths. Thallus construction is monomerous, internally composed of a core of coaxial hypothallial filaments (cells laterally aligned in arching tiers) parallel to the substratum that then shift upward, curving toward the upper surface. The ascending filaments form the more or less stratified perithallium. Most of the filaments terminate with an epithallial cell at the thallus surface. Epithallial cells have rounded or flattened outermost walls that do not flare at the corners. Cell elongation usually occurs within the dividing subepithallial meristematic cells that are usually as long as or longer than their immediate inward derivatives. Cells fusions are present between some cells of adjacent filaments; secondary pit connections are absent (after Guiry and Guiry, 2008–2010). Trichocytes are generally absent but have been reported in a few of the species.

Bisporangia and zonately divided tetrasporangia are developed in sporangial conceptacles with multiporate roofs. Prior to their release, each sporangium has an apical plug that blocks a roof pore. Carpogonia and spermatangia, where known, are produced in separate uniporate conceptacles either on the same or on different thalli. Carpogonia are terminal on 2- to 4-celled unbranched filaments developed from the conceptacle chamber floor. After presumed fertilization the carposporophytes develop in dumbbell-shaped female conceptacle chambers. Mature carposporophytes apparently lack a large central fusion cell but are composed of an irregularly shaped fusion cell or a several-celled fusion cell complex (not always evident). Carposporangia are terminal on gonimoblast filaments of several cells. Spermatangia are developed on unbranched filaments that arise from the conceptacle chamber floor and roof. Spermatangial initials (spermatangial parent cells) in the early stages are covered by a layer of "protective cells" that soon degenerates.

REMARKS. One species is reported in the southern Gulf: *Mesophyllum engelhartii* (Foslie) W. H. Adey (1970; basionym: *Lithothamnion engelhartii* Foslie, 1900f) from Punta Perico (Riosmena-Rodríguez and Vásquez-Elizondo, 2012). Currently there is one species of *Mesophyllum* recorded in the northern Gulf of California.

Mesophyllum crassiusculum (Foslie) Lebednik

FIGURE 61

Lithothamnion rugosum f. *crassiusculum* Foslie, 1901a:4, as '*crassiuscula*.'

Mesophyllum crassiusculum (Foslie) Lebednik in Athanasiadis et al,, 2004:152, figs. 119–149; Athanasiadis, 2007:223, figs. 61–63, tbl. 2.

Lithothamnion pacificum f. *crassiusculum* (Foslie) Foslie, 1906b:10.

Lithothamnion crassiusculum (Foslie) L. R. Mason in Setchell and Mason, 1943b:93; Johansen, 1976a:384, fig. 324; Stewart, 1991:79; Bernecker and Wehrtmann, 2009:225; Fernández-Garcia et al., 2011:63.

Lithothamnion aculeiferum L. R. Mason in Setchell and Mason, 1943b:94; Mason, 1953:326, pl. 33: fig c; Dawson, 1960b:10, pl. 3: figs. 1–3, pl. 5: fig. 1 [note: photo is upside down]; 1961b:413; Hollenberg and Abbott, 1966:59; Masaki, 1968:10, pls. 2, 3, 41; Johansen, 1976a:382, fig. 321; Stewart, 1991:78; González-González et al., 1996:239; Yoshida, 1998:582; Riosmena-Rodríguez and Woelkerling, 2000:334; Pacheco-Ruíz and Zertuche-González, 2002:467.

Lithothamnion fruticulosum sensu Dawson, 1960b:14[in part, southern Gulf of California specimens only; *fide* Johansen, 1976a:384], pl. 4: figs. 21–25 [non *Lithothamnion fruticulosum* (Kützing) Foslie, 1895a:46; which is now *Spongites fruticulosa* Kützing, 1841:33].

Crusts pinkish purple, spreading up to 7 cm wide and 300–800 µm thick; often overgrowing each other, becoming up to 3 mm thick; surface with numerous small close together, short, simple protuberances of more or less similar size, 0.5–1.5 mm tall, (0.5–)1.0–1.5 mm in diameter at base; with angular to rounded or wart-like tops, 1.5–3.0 mm wide; strongly adhering to rocks or covering small pebbles; sometimes becoming nodular as free-living rhodoliths. Monomerous construction; hypothallium irregularly developed and patchy, 50–300 µm thick, predominately of coaxial filaments (laterally aligned cells in arching tiers), of cells 10–25(–30) µm long by 5–13 µm in diameter. Perithallium formed by curving hypothallial filaments as they continue to the thallus surface; perithallium more or less stratified, 50–800 µm thick; filaments of slightly elongate cells in lower portions, 4–23 µm long, (3–)4–9 µm in diameter, upward portions mostly of isodiametric or ovoid cells, 3–9 µm tall, 3–9 µm in diameter. Cell fusions common between cells of contiguous filaments. Epithallium of 1–3 layers of flattened cells, 2–5 µm tall by 3–9 µm wide. Trichocytes absent.

Reproductive conceptacles scattered over crust and protuberances. Sporangial conceptacles crowded, (140–)220 µm tall, 450–750 µm outside diameter; chambers (140–)180–240 µm

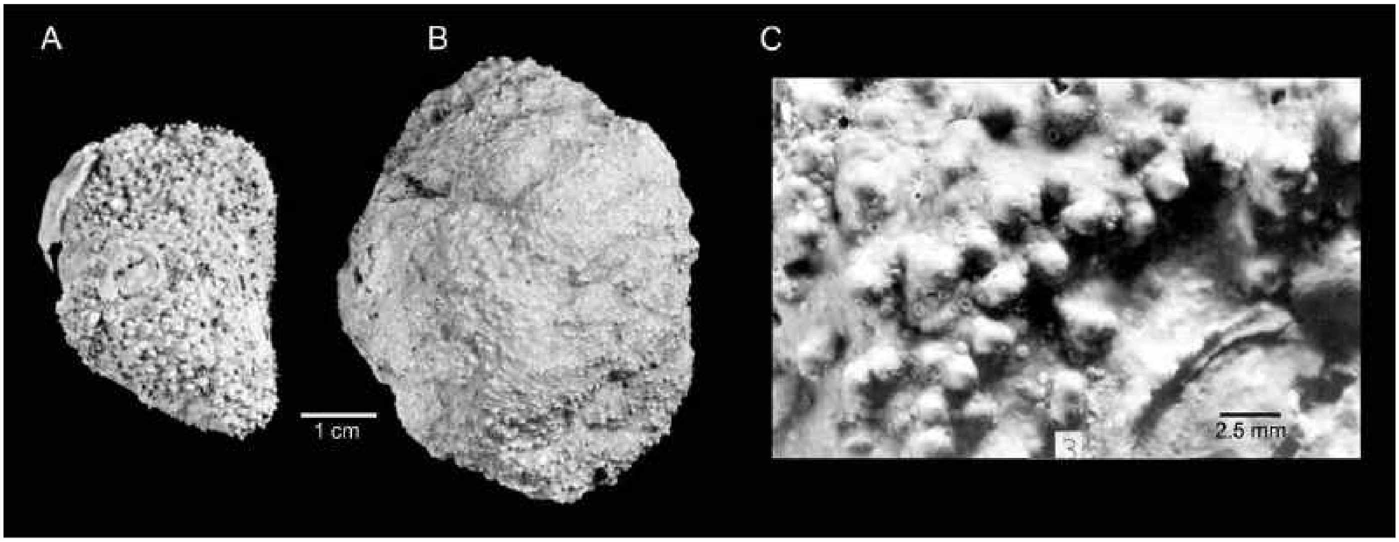

FIGURE 61. *Mesophyllum crassiusculum*: A. Habit (*EYD-4277*, AHFH, now UC). B. Habit (*EYD-2636*, AHFH, now UC). C. Close-up of crust surface showing small short protuberances and sporangial conceptacles (*EYD-2636*, AHFH, now UC).

tall, 300–450 µm inside diameter; multiporate convex roof, (30–) 40–60 µm thick. Pore plates 260–470 µm in diameter, with (15–) 25–50 pores; each pore about 10 µm in diameter, bordered by 6–10 rosette cells in surface view (Athanasiadis, 2007); in vertical section, pore canals straight, bordered by filaments of 6–8(–10) cells, cells thinner and some wider than cells of regular roof filaments. Tetrasporangia 110–175(–200) µm long, 25–70(–100) µm in diameter (after Athanasiadis, 2007). Carposporangial and spermatangial conceptacles not known in the northern Gulf.

Habitat. On rocks of various sizes or sometimes completely covering pebbles forming rhodoliths, or growing on rhodoliths; intertidal to shallow subtidal, down to 6 m depths.

Distribution. Gulf of California: Bahía de Los Ángeles, Bahía de Loreto. Eastern Pacific: Duxbury Reef, Marin County, to La Jolla, California; Cortez Bank (seamount, California Channel Islands); Isla Coronado del Sur (Islas Coronado, off Baja California) to Isla Concha, Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur; Costa Rica. Western Pacific: Japan; Korea.

Lectotype Locality. White Point, White Point Park, San Pedro, Los Angeles County, southern California, USA.

Remarks. *Mesophyllum crassiusculum* has been reported in the northern Gulf from Bahía de Los Ángeles (Pacheco-Ruíz and Zertuche-González, 2002, as *Lithothamnion crassiusculum*) and without comment from Bahía de Loreto (CONANP, 2002, as *L. crassiusculum*); description is based in part on Dawson (1960b) and Athanasiadis (2007). Riosmena-Rodríguez (in Riosmena-Rodríguez and Vásquez-Elizondo, 2012) has suggested that *M. crassiusculum* may belong in the genus *Lithothamnion*. Its presence in the northern Gulf requires further investigation.

AHNFELTIOPHYCIDAE

Ahnfeltiophycidae G. W. Saunders et Hommersand, 2004:1504.

Subclass Ahnfeltiophycidae is characterized by having terminal and sessile carpogonia and a carposporophyte that develops outward. Ultrastructurally, the pit plug cores are either naked, without caps and membranes (Ahnfeltiales), or with cap membranes but without cap layers (Pihiellales; Pueschel and Huisman, 2010).

Remarks. The Ahnfeltiophycidae contains two orders: Ahnfeltiales, which is represented in the Gulf of California, and a monotypic order, Pihiellales Huisman, A. R. Sherwood et I. A. Abbott (2003).

AHNFELTIALES

Ahnfeltiales C. A. Maggs et Pueschel, 1989:349.

Members are distinguished primarily by characteristics of the female gametophyte. The carpogonia are terminal, sessile on filaments of the normal cortical layers within swollen nemathecia. Following fertilization, the carpogonium fuses with morphologically unmodified, contiguous cortical cells and develops outward from the cortex. There are no differentiated auxiliary cells. Gonimoblast filaments grow directly from the carpogonium, spreading over the surface of the sorus, fusing with vegetative and other gonimoblast cells and radiating outward and terminate in carposporangia. Members are agarophytes, with cell walls containing the agarocolloids. Ultrastructure studies have shown pit plugs that lack cap layers and cap membranes.

This order is represented by its single family in the Gulf of California.

AHNFELTIACEAE

Ahnfeltiaceae C. A. Maggs et Pueschel, 1989:348.

Gametophytes are erect thalli arising from a spreading discoid base. Growth is multiaxial, with vegetative cells forming conjunctor cells that result in secondary pit connections and also fusing directly. Sexual reproduction is as for the order, with heteromorphic life histories. Several embryos develop from adjacent zygotes to produce compound external carposporophytes that are not surrounded by a pericarp. Spermatangia are cut off singly and transversely from parent cells on the thallus surface. Male gametophytes may also form monosporangia developed from modified cortical cells. The monospores reproduce the male gametophytes, recycling the male generation.

Monospores may develop from modified cortical cells. Tetrasporophytes are crustose, with the crusts exhibiting direct cell fusions, but lack secondary pit connections. Tetrasporangia develop within sori and are irregularly zonately divided.

The Ahnfeltiaceae is represented by one genus in the northern Gulf of California.

Ahnfeltia Fries

Ahnfeltia Fries, 1836:309; Silva, 1993a:128.

The only genus in the Ahnfeltiaceae, *Ahnfeltia* has the characteristics of the family.

Remarks. The generitype, *Ahnfeltia plicata* (Hudson) Fries (1836; basionym: *Fucus plicatus* Hudson, 1762), has been reported in the southern Gulf of California from El Requesón, Bahía Concepción, to the coral reef of Cabo Pulmo-Los Frailes (Anaya-Reyna and Riosmena-Rodríguez, 1996; Riosmena-Rodríguez et al., 1998).

One species is reported in the northern Gulf of California.

***Ahnfeltia svensonii* W. R. Taylor**

FIGURE 62

Ahnfeltia svensonii W. R. Taylor, 1945:238, pl. 77: fig. 2; Dawson, 1959a:26, fig. 3C; 1961a:247, pl. 42: fig. 1; 1961b:431; Huerta-Múzquiz, 1978:339; Mendoza-González and Mateo-Cid, 1986:424; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:482; Mateo-Cid and Mendoza-González, 1994b:40; González-González et al., 1996:169; CONANP, 2002:136.

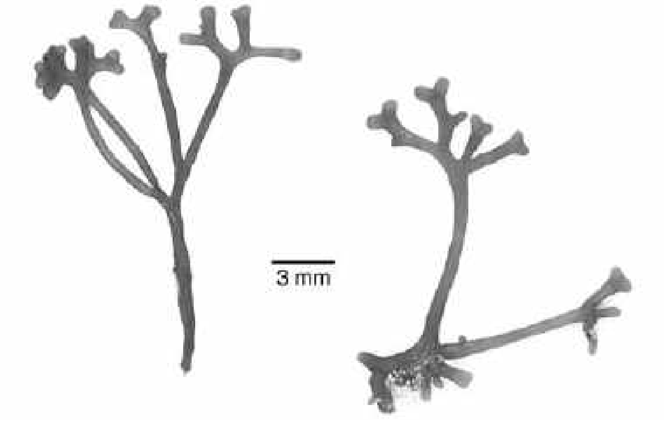

FIGURE 62. *Ahnfeltia svensonii:* Habit (*EYD-18747*, US Alg. Coll.-6444).

Algae in tufts, 2–7 cm tall; dark red to blackish, of cartilaginous, terete to slightly compressed axes, usually 0.7–1.0 mm in diameter (rarely up to 2.0 mm); mostly divaricately dichotomously branched (occasionally polychotomous); upper branches 1–2 mm long in smaller thalli, 5.0–10 mm long in larger thalli. Medulla of thick-walled large cells; surrounded by cortical layer of anticlinal rows of 3–4 small cylindrical cells.

Tetrasporangia not known. Cystocarps immersed within branches, projecting above branch surface; with a large, irregularly shaped pore; carpospore mass without a sterile base or center or pericarp. Spermatangia unknown.

DISTRIBUTION. Gulf of California: Segundo Cerro Prieto to Roca Roja (both Bahía Kino); Loreto; Isla Cholla (off north end of Isla Carmén); Isla Espíritu Santo to Cabo San Lucas; Nayarit to Jalisco. Eastern Pacific: Playa Los Cerritos (south of Todos Santos), Baja California Sur; Galápagos Islands.

TYPE LOCALITY. Black Beach, Isla Floreana (Charles Island; Isla Santa María), Galápagos Islands, Ecuador.

REMARKS. *Ahnfeltia svensonii* has been reported in the southern Gulf (Dawson, 1959a, 1961a) and in the northern Gulf from Bahía Kino (Mendoza-González and Mateo-Cid, 1986). Further collections will be helpful to make morphological and molecular comparisons of Gulf *A. svensonii* with the Galápagos *A. svensonii* from the type locality.

RHODYMENIOPHYCIDAE

Rhodymeniophycidae G. W. Saunders et Hommersand, 2004:1504.

Subclass Rhodymeniophycidae is characterized by pit plugs that are covered by a membrane only, with the exception of the Gelidiales (which have a single inner cap); all others lack cap layers. Life histories, where known, are mostly triphasic. The carposporophyte develops directly from the carposporangium of a carpogonial fusion cell or indirectly from an auxiliary cell that received a transferred diploid nucleus.

REMARKS. The largest subclass of the Florideophyceae, the Rhodymeniophycidae is composed almost entirely of marine species; its members exhibit a very large diversity of morphologies.

The Rhodymeniophycidae is represented by 11 of its orders in the northern Gulf of California.

KEY TO THE ORDERS OF RHODYMENIOPHYCIDAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli primarily uniaxial in construction 2
1b. Thalli primarily multiaxial in construction 7
2a. Thalli medulla of longitudinal filaments, entwined with internal rhizoidal filaments (rhizines or hyphae) in most, but absent in one family; prostrate axes attach by rhizoidal filaments or small brush-like or peg-like holdfasts . . . . **Gelidiales**
2b. Thalli medulla pseudoparenchymatous or filamentous, without rhizines; attached primarily by small or spreading discoid holdfasts or by rhizoidal or stoloniferous outgrowths 3
3a. Auxiliary cells initiate carposporophyte development 4
3b. Auxiliary cells do not initiate carposporophyte development; carposporophyte arises directly from fertilized carpogonium or after its fusion with hypogynous cell 6
4a. Auxiliary cell an intercalary vegetative cell . . . . **Gigartinales (in part)**
4b. Auxiliary cell not an intercalary vegetative cell 5
5a. Auxiliary cell develops from a cell of fertile branch (filament), auxiliary cell normally cut off from the support cell of carpogonial branch after fertilization . . . . **Ceramiales**
5b. Support cell of carpogonial branch functions as an auxiliary cell . . . . **Plocamiales**
6a. Carpogonial branch 2-celled with 2–3 sterile filaments; thalli initially uniaxial in construction (although appearing multiaxial); gametophytes and sporophytes isomorphic . . . . **Gracilariales (in part)**
6b. Carpogonial branch 3- or 4-celled; axial filament usually conspicuous throughout most of thallus; gametophyes and sporophytes isomorphic or heteromorphic . . . . **Bonnemaisoniales**
7a. Thalli mostly crustose (a few partially erect); some with internal calcification, others not calcified; sexual reproductive structures in nemathecia on thallus surface . . . . **Peyssonneliales**

7b. Thalli not usually crustose in habit; not usually calcified; sexual reproductive structures not in nemathecia on thallus surface 8
8a. Gametophytes with medulla of slender filaments and rhizoidal-like filaments; cortex of anticlinal filaments 11
8b. Gametophytes with medulla and cortex not as above, usually pseudoparenchymatous in some portion of thallus 9
9a. Thalli with hollow and solid portions; hollow portions lined by longitudinal filaments, solid portions pseudoparenchymatous . . . . **Rhodymeniales (in part)**
9b. Thalli completely without hollow portions 10
10a. Thalli with a pseudoparenchymatous medulla and cortex 13
10b. Thalli with a filamentous medulla surrounded by a pseudoparenchymatous cortex 12
11a. Algae firm, not usually gelatinous or mucilaginous in texture . . . . **Gigartinales (in part)**
11b. Algae soft, "jelly-like," usually gelatinous or mucilaginous in texture . . . . **Nemastomatales**
12a. Tetrasporangia cruciately to decussately-cruciately divided; either in nemathecia or scattered or in sori over cortex; carposporophyte surrounded by involucres from ampullary filaments (Halymeniaceae) or among cortical filaments without ampullae (Tsengiaceae) . . . . **Cryptonemiales**
12b. Tetrasporangia cruciately to very irregularly divided (superficially appearing zonate), tetrasporangia either in nemathecia (two genera) or in cortex (e.g., Gulf of California *Sebdenia flabellata*); some dorsiventral organized; carposporophyte without involucre filaments, some surrounded by rudimentary cellular pericarp . . . . **Sebdeniales**
13a. Auxiliary cell is terminal cell of a 2-celled filament borne on the supporting cell of carpogonial . . **Rhodymeniales (in part)**
13b. Auxiliary cells absent, do not initiate carposporophyte development . . . . **Gracilariales (in part)**

BONNEMAISONIALES

Bonnemaisoniales Feldmann et Feldmann-Mazoyer, 1952:29.

Algae range from erect, large, and pseudoparenchymatous thalli to small, uniseriate to "polysiphonous-like" filaments, or prostrate crusts. Thalli are uniaxial in structure, with growth from a single apical cell, with subapical cells producing periaxial filaments. Life histories of the species involve isomorphic or heteromorphic gametophytes and sporophytes. Gametophytes may be monoecious or dioecious. Postfertilization development does not involve auxiliary cells; the gonimoblast develops directly from the fertilized carpogonium or after fusion with the hypogynous cell, and it has terminal carposporangia.

Heteromorphic tetrasporophytes are minute to small, uniseriate or trisiphonous filaments; or prostrate single-layered crusts. Cells of the filaments contain discoid chloroplasts that are usually numerous and without pyrenoids. Tetrasporangia are cruciately, tetrahedrally, or irregularly divided.

The order is represented by one of its families in the Gulf of California.

BONNEMAISONIACEAE

Bonnemaisoniaceae F. Schmitz, 1892:20.

Gametophytes are erect, and cylindrical or compressed, and generally much branched, either radially, spirally branched, or distichousand bilaterally branched. The axial row of cells is usually evident and surrounded by branched rows of cells that become compacted outward to form a pseudoparenchymatous cortex of mixed large and small cells in a continuous surface layer. Cells have numerous discoid chloroplasts and are without pyrenoids. Highly refractive, vesicular cells (gland cells) are present in some species.

Life histories, where known, are isomorphic or with heteromorphic life phases. Culture studies of genera occurring in the Gulf have shown the sporophytic phase to be small polysiphonous-like filaments of "*Falkenbergia*" in *Asparagopsis* and uniseriate filaments of "*Trailliella*" in *Bonnemaisonia.* In the female gametophyte, the carpogonial branch is borne terminally on a indeterminate branchlet or borne laterally from inner cortical cells. The carpogonial branch is 3(–4)-celled and, in some genera, has branched sterile filaments from its lower two cells. Fusion of these structures occurs after fertilization as the gonimoblast develops. Gonimoblast filaments arise from this fusion cell and produce terminal carposporangia. Cystocarps are surrounded by a substantial cellular pericarp. Spermatangia are borne in dense superficial sori or on distinct ovoid to clavate stalked branchlets.

REMARKS. The macroscopic gametophytes of two genera of the Bonnemaisoniaceae are present in the northern Gulf of California. Whereas the sporophytic phase, "*Falkenbergia hillebrandii,*" has been collected for northern Gulf *Asparagopsis*, the sporophyte, presumed to be the "*Trailliella*" phase for the Gulf *Bonnemaisonia,* is as yet undetected in the field.

KEY TO THE SPECIES OF BONNEMAISONIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Gametophytes erect, of several bushy (plumose) axes, arising above well-developed system of creeping, stoloniferous axes attached to the substrate by rhizoids; distal portions of ultimate branchlets with a cortex of rectangular, larger cells than those of the bearing branch [Figure 63B] . . . . ***Asparagopsis taxiformis***
1b. Gametophytes erect, mostly epiphytic, entangled with other algae by characteristic hamate (hook-shaped) branchlets [Figure 65C]; ultimate branchlets with cortex of numerous, small, rounded cortical cells similar to the cortex of bearing branch [Figure 65D] . . . . ***Bonnemaisonia hamifera***

Asparagopsis Montagne

Asparagopsis Montagne, 1841:xv.

Falkenbergia F. Schmitz in Schmitz and Falkenberg, 1897:479.

Gametophytes are erect, soft in texture, with several stalked bushy axes, arising from entangled, creeping stoloniferous axes that attach to the substrate by tufts of rhizoids. The main axis and branches are terete to subterete and are richly branched above, but the lower portions are often unbranched. Branching is usually alternate to multifarious, up to several orders, appearing plumose. Each branch is covered with short branchlets on all sides. The medulla is a central axial row of cells, surrounded by an open gelatinous matrix and short, compact, cell rows. These rows of cells branch outward to form a continuous pseudoparenchymatous cortex several cells thick.

Tetrasporangia are produced by the morphologically different small sporophyte, the trisiphonous *Falkenbergia*-phase of the life history. Tetrasporangia are cruciately to irregularly divided. Gametophytes are monoecious or dioecious. Carpogonial branches 3-celled, with lateral nutritive cells from the lower cells. Cystocarps have a subpyriform pericarp with ostiole and are usually borne terminally on short branchlet. Spermatangia form a dense superficial layer on distinct ovoid to clavate head on stalked branchlets.

Remarks. *Asparagopsis* was the first red alga recognized to have a heteromorphic life history (Feldmann and Feldmann, 1939a, 1939b, 1943, 1952; Bonin and Hawkes, 1987; Ní Chualáin et al., 2004). The macroscopic gametophytes of the northern Gulf of California *Asparagopsis* were found to contain interesting secondary metabolites (Fenical, 1974; McConnell and Fenical, 1977a, 1979). Volatile halogenated compounds, mostly brominated and iodinated methanes and acetones, have also been reported in *Asparagopsis* from Hawaii (Burreson et al., 1976) and elsewhere in populations of the smaller, sporophytic phase, *Falkenbergia* (Marshall et al., 1999, 2003).

One species of *Asparagopsis* (with both gametophytic thalli and the sporophytic *Falkenbergia*-phase) has been found in the northern Gulf of California.

Asparagopsis taxiformis (Delile) Trevisan

FIGURE 63

Fucus taxiformis Delile, 1813:295, pl. 57: fig. 2 [note: pls. published 1826].

Asparagopsis taxiformis (Delile) Trevisan, 1845:45, pl. 1; Dixon, 1964:902; Chihara, 1970:64, pl. 32: fig. 4; Abbott and Hollenberg, 1976:340, figs. 282, 283; Huerta-Múzquiz, 1978:337, 340; Schnetter and Bula-Meyer, 1982:111, pl. 11: figs. R–T, pl. 12: fig. A, pl. 15: figs. G,H; Stewart and Stewart, 1984:142; Norris, 1985d:208, fig. 16.1; Huerta-Múzquiz and Mendoza-González, 1985:48; Santelices and Abbott, 1987:8; Sánchez-Rodríguez et al., 1989:42; Stewart, 1991:68; León-Tejera et al., 1993:200; Serviere-Zaragoza et al., 1993a:483; Bula-Meyer, 1995:33; Silva et al., 1996b:232; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:25; Yoshida, 1998:648, fig. 3-41C; Abbott, 1999:174, fig. 43A–D; CONANP, 2002:136; Cruz-Ayala et al., 2001:190; Pacheco-Ruíz and Zertuche-González, 2002:467; Ní Chualáin et al., 2004:1112, fig. 1a; Mateo-Cid et al., 2006:55; Serviere-Zaragoza et al., 2007:9; Y.-P. Lee, 2008:229, figs. A–C; Pacheco-Ruíz et al., 2008:207; Fernández-García et al., 2011:60.

Asparagopsis taxiformis (Delile) Collins et Hervey, 1917:117, *nom. illeg.*; Feldmann and Feldmann, 1943:81; Dawson, 1953a:57; 1957a:7; 1959a:20; 1961b:408; Chihara, 1961:139, figs. 11–19; Chihara, 1962:40–51, tbl. 2; Huerta-Múzquiz and Garza-Barrientos, 1975:8, 11.

Lictoria taxiformis (Delile) J. Agardh, 1841:22.

Asparagopsis delilei Montagne, 1841:xiv, *nom. illeg.*

Asparagopsis sanfordiana Harvey, 1855:544; Harvey, 1858: pl. VI; Okamura, 1908:135, 137, pl. XXVIII: figs. 1–12; Setchell and Gardner, 1930; Okamura, 1936:431; Dawson, 1944a:257; Taylor, 1945:149; Dawson, 1949b:246; González-González et al., 1996:175; Ní Chualáin et al., 2004:1112, fig. 1b.

Asparagopsis sanfordiana f. *amplissima* Setchell et N. L. Gardner, 1924:760, pl. 22: fig. 3, pl. 41; Taylor, 1945:149; González-González et al., 1996:175; Serviere-Zaragoza et al., 2007:9.

Polysiphonia hillebrandii Bornet in Ardissone, 1883:376.

Falkenbergia hillebrandii (Bornet) Falkenberg, 1901:689; Setchell and Gardner, 1930:163; Feldmann and Feldmann, 1943:89, figs. 3–6; Dawson, 1953a3:58; 1959a:20; Chihara, 1960:249; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Abbott and Hollenberg, 1976:340, fig. 283; Pedroche and González-González, 1981:66; Sánchez-Rodríguez et al., 1989:42; Ní Chualáin et al., 2004:1112, fig. 1d; Bernecker, 2009:CD-Rom p. 61.

Gametophytes brownish red to rosy pink to purplish red; composed of numerous erect, soft, plumose fronds up to 45 cm tall; axes arise from a group of terete, prostrate stolons attached to the substratum at various points by rhizoids. Fronds with a prominent, percurrent axis, 1.5–3.0 mm in diameter; densely, more or less alternately to irregularly spirally/multifariously branched, up to several orders; often lacking branches in lower third to half of thallus. Ultimate branchlets slender with pointed apices. Distal portion of ultimate branchlets with several boxy pericentral cells (30–45 µm long and about 30 µm in diameter) around each thin axial filament cell. Uniaxial; axis and principal branches with prominent central axial filament (surrounded by open space) that outwardly produces filaments that form a cylinder of peripheral, pseudoparenchymatous cells. Cortex of small pigmented cells.

Gametophytes dioecious. Cystocarps subspherical, ostiolate, up to 500 µm in diameter; borne terminally on short branchlets. Spermatangial heads terminal on unbranched laterals, heads ovoid to clavate, about 550 µm long and 265 µm wide, covered by dense surface layer of spermatangia.

Habitat. On rocks or sand; low intertidal to shallow subtidal, down to 10 m depths.

Distribution. Gulf of California: Rocas Consag to Punta Los Frailes; Nayarit to Jalisco. Eastern Pacific: Santa Catalina Island and San Clemente Island (California Channel Islands); Islas Los Coronados and Isla Guadalupe to Punta Malarrimo (Baja California); Bahía Magdalena (Baja California Sur); Islas San Benito; Isla Cedros; Isla Socorro, Isla Clarión and Isla San Benedicto (Islas Revillagigedo); Rocas Alijos; El

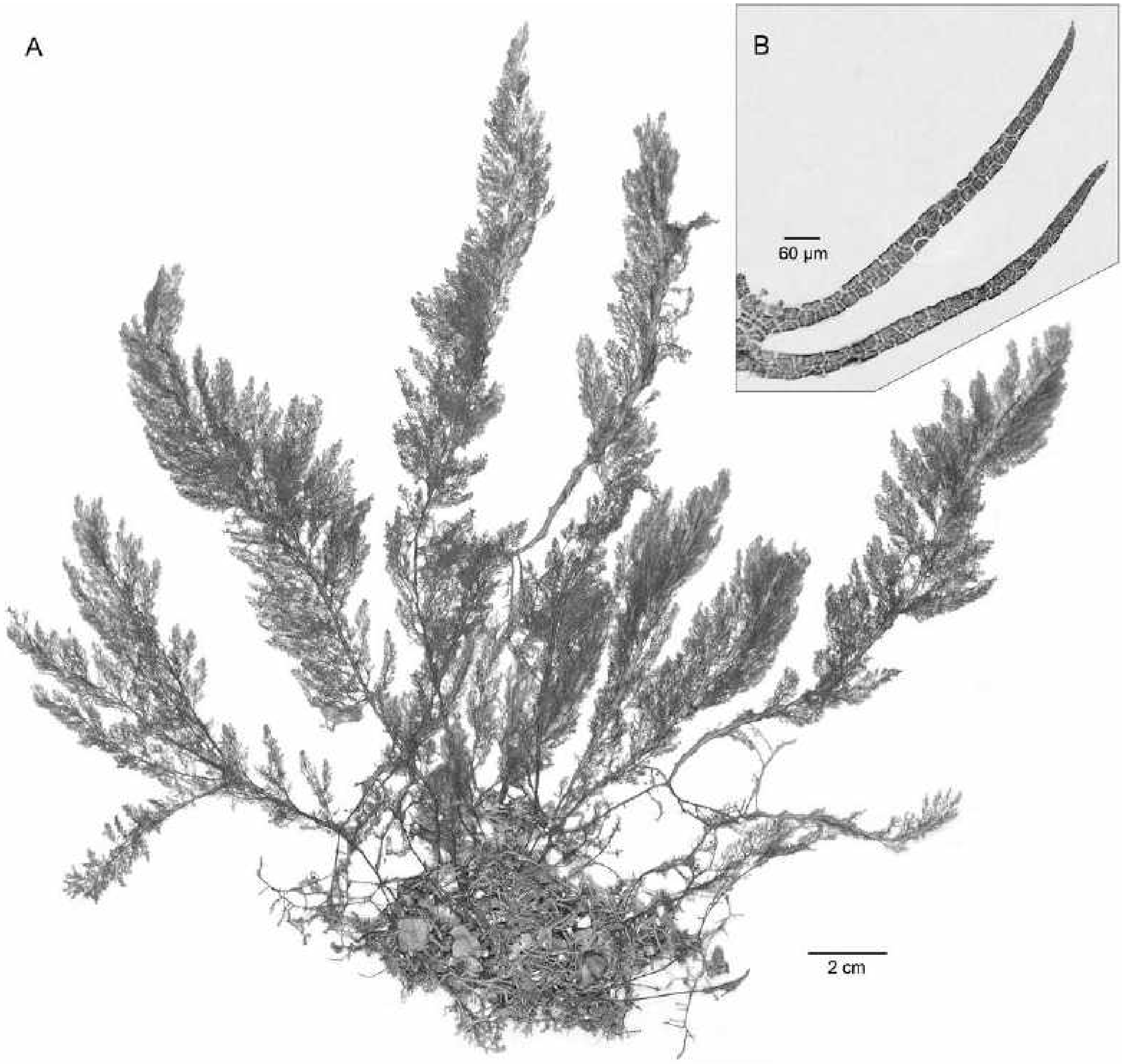

FIGURE 63. *Asparagopsis taxiformis*: A. Habit, plumose gametophyte attached by basal stolons with rhizoids (*JN-3113*, US Alg. Coll.-158607). B. Close-up of ultimate branchlets, showing central axial filament surrounded by 3 pericentral cells, branchlets tapering to acute apex (*JN-4822*, US Alg. Coll. microscope slide 4975).

Salvador; Costa Rica; Panama; Colombia; Ecuador; Galápagos Islands; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: China; Korea; Japan.

TYPE LOCALITY. Near Alexandria, Mediterranean Sea, Egypt.

REMARKS. Since the accounts of Setchell and Gardner (1924, as *Asparagopsis sanfordiana* f. *amplissima*) and Dawson (1944a, as "*A. sanfordiana*"), the Gulf of California material has been referred to a broadly defined *A. taxiformis* (Dawson, 1953a), a reportedly widespread, warm-temperate to tropical species. More recently, Ní Chualáin et al. (2004) found two clades of "*A. taxiformis*" that either represent cryptic sibling species or could possibly be considered as geographically isolated subspecies. Another *Asparagopsis* collected in San Diego, California, was determined to be *A. armata* Harvey (1855), a species described from Western Australia that probably was recently introduced (Ní Chualáin et al., 2004; Miller et al., 2011).

Further study of the northern Gulf specimens referred to *A. taxiformis* is needed to verify their identification. Molecular analyses should be undertaken to compare the northern Gulf material with type locality specimens of the southern Gulf *A. sanfordiana* f. *amplissima* Setchell et N. L. Gardner (1924: type locality: Eureka, Baja California Sur) and the Western Australian species, *A. armata* Harvey and *A. sanfordiana* Harvey, to evaluate their phylogenetic relationships.

Falkenbergia-Phase of *Asparagopsis*

FIGURE 64

Falkenbergia F. Schmitz in Schmitz and Falkenberg, 1897:479.

Sporophyte: small filamentous tufts, 0.3–0.5(–1.0) cm long; of ecorticate, terete filaments; branching irregular; attached by ventral, branched, multicellular holdfasts along various places on the thallus. Growth by a prominent apical cell that initially divides transversely, then lengthwise, to produce 3 pericentral cells surrounding each slender axial filament cell (and of similar length); trisiphonous axes 15–60(–75) µm in diameter; pericentral cells (35–57 µm long and 20–35 µm in diameter). Pericentral cells alternating in position from one segment to the next (spiral). Branches divaricate, developing from middle portion of pericentral cells. Highly refractive small cellular inclusions (gland cells) often conspicuous in live material.

Tetrasporangia cruciately to irregularly divided; single, or in short series, one per segment; derived from a pericentral cell.

HABITAT. Usually entangled among turf algae or occasionally epiphytic on *Sargassum* and other large algae; low intertidal to shallow subtidal.

DISTRIBUTION. *Falkenbergia hillebrandii*-phase. Gulf of California: Puerto Peñasco to Cabeza Ballena; Jalisco. Eastern Pacific: Santa Catalina Island (California Channel Islands; Abbott and Hollenberg, 1976); Islas Todos Santos (R. Aguilar-Rosas et al., 1990) and Isla Guadalupe, Baja California (Setchell and Gardner, 1930) to Bahía Magdalena, Baja California Sur (Sánchez-Rodríguez et al., 1989); Isla Socorro (Islas Revillagigedo); Costa Rica (Bernecker, 2009).

TYPE LOCALITY. *Falkenbergia hillebrandii* (Bornet in Ardissone) Falkenberg (1901; =*Polysiphonia hillebrandii* Bornet in Ardissone, 1883): Elba Island, Tuscan Archipelago, Tyrrhenian Sea, off northwest coast of Italy.

REMARKS. Originally described as a separate genus on the basis of its very different morphology, culture studies of *Falkenbergia* have recognized it to be the sporophyte in the heteromorphic life history of *Asparagopsis* (Feldmann and Feldmann, 1939a, 1939b, 1943; Chihara, 1960, 1961). On the basis of nomenclatural priority, *Falkenbergia* was placed in synonymy with *Asparagopsis*.

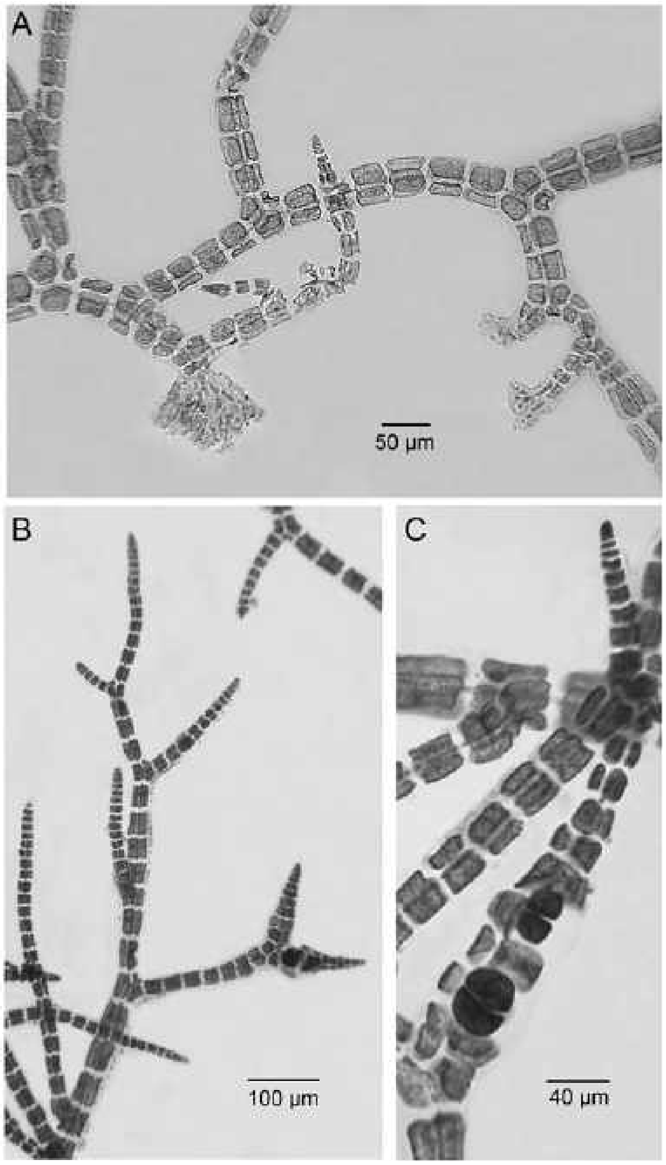

FIGURE 64. *Falkenbergia*-phase of *Asparagopsis* (sporophyte): A. Axes composed of a slender axial filament surrounded by 3 pericentral cells that alternate in position, one segment to the next, prostrate axes attached by multicellular holdfasts (*JN-4438*, US Alg. Coll. microscope slide 4292). B. Axes branch irregularly and tetrasporangia borne one per segment. C. Tetrasporangia derived from pericentral cells, in irregular series (B, C, *JN-4758*, US Alg. Coll. microscope slide 4295).

***Bonnemaisonia* C. Agardh**

Bonnemaisonia C. Agardh, 1822:196.

Gametophytes are erect with terete to slightly compressed axes, branches are bilateral, distichous or spirally arranged. Thalli are attached by a discoid holdfast, or they can be entangled by modified hook-like branchlets to various other algae. Each branch has opposite branchlets of two types. A short, simple to spinose branch occurs on one side, opposed on the other side by a long branch which rebranches, these are regularly alternate in successive pairs. This pattern may be obscured in some species. A single axial filament is evident throughout the thallus, each axial filament cell is associated with two opposite periaxial cells. These further divide outwardly to form the branchlets and develop additional cells that form the cortex. Refractive vesicular cells (gland cells) are present in the outermost cortex.

Tetrasporangia are produced by a heteromorphic sporophyte in most species, either the erect filamentous *Trailliella*-phase or a prostrate single-layered crust (Salvador et al., 2008). In "*Trailliella*," branching is irregular and variable; numerous small secretory (vesicular) cells are borne laterally between adjacent filament cells. The crustose *Hymenoclonium*-phase is formed by frequently branching and anastomosing uniseriate filaments that are appressed to the substrate. Gametophytes are monoecious or dioecious. The carpogonial branch is 3-celled. Urn-shaped cystocarps, with an ostiolate pericarp, are on short branchlets. Spermatangia in dense outer layer on ovoid to elongated heads on short stalked branchlets.

REMARKS. The morphologically different, filamentous *Trailliella* Batters (1896) has long been recognized to be the sporophyte in the life history of *Bonnemaisonia hamifera* Hariot (Feldmann and Feldmann, 1939b, 1943; Harder, 1948; Harder and Koch, 1949; Koch, 1950; Dixon, 1959; Chihara, 1961; Kornmann and Sahling, 1962; Chen et al., 1969) and *B. californica* Buffham (1896) (Chihara, 1965, as "*B. nootkana*"). A crustose tetrasporophyte, *Hymenoclonium serpens* (H. Crouan et P. Crouan) Batters (1895), has been interpreted to be the alternate life history phase of two other species (Salvador et al., 2008), *B. asparagopsis* (Woodward) C. Agardh (1822) (Feldmann and Feldmann, 1939b, 1941, 1943) and *B. clavata* Hamel (1930) (Feldmann and Feldmann, 1939b, 1943; Cortel-Breeman, 1975) (however, this crust has also been suggested to be the juvenile gametophyte; see Kylin, 1945; Feldmann, 1966). Interestingly, in another species, the alternate phase in the life history of the gametophyte of *B. geniculata* N. L. Gardner (1927c) was found to be a morphologically similar tetrasporophyte (Shevlin and Polanshek, 1978). These culture studies suggest that *Bonnemaisonia* is a single genus with diverse life histories or that the genus may be polyphyletic, that is, it includes species that may belong in other genera.

Secondary natural products and their halogenated chemistries have been described in species of *Bonnemaisonia* (McConnell and Fenical, 1977b, 1980; Young et al., 1981). Antimicrobial activity was shown for secondary metabolites from members of the family (McConnell and Fenical, 1979).

There is one species, *Bonnemaisonia hamifera*, reported in the northern Gulf of California, but so far, only the gametophytes have been found.

Bonnemaisonia hamifera Hariot

FIGURE 65

Bonnemaisonia hamifera Hariot, 1891:223; Dawson, 1953a:55, pl. 18: fig. 1; 1961b:407; Chihara, 1961:125, figs. 1–10; 1962:40–51, tbl. 2; 1970:63, pl. 32: fig. 3; Norris and Bucher, 1976:8, fig. 6a; Abbott and Hollenberg, 1976:338, figs. 279, 281; Pacheco-Ruíz and Aguilar-Rosas, 1984:71, 76; Stewart, 1991:68; Perestenko, 1996:82, pl. 45: fig. 3; González-González et al., 1996:176; Yoshida, 1998:649, fig. 3-41D,E; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207; Y.-P. Lee, 2008:230, figs. A–C.

Asparagopsis hamifera (Hariot) Okamura, 1921c:131,144, pl. 183: figs. 10, 11, pl. 184: figs. 10–16; 1936:430, fig. 200; Kylin, 1941:6; Dawson, 1945c:65; González-González et al., 1996:175.

Bonnemaisonia intricata P. C. Silva, 1957b:143.

Acrosymphyton caribaeum sensu Norris, 1973:10, pl. 2; Pacheco-Ruíz et al., 2008:207 [non *Acrosymphyton caribaeum* (J. Agardh) Sjöstedt, 1926:9; basionym: *Calosiphonia caribaeum* J. Agardh, 1899:84].

Gametophytes entangled or epiphytic, up to 20 cm long; of a cylindrical main axis up to 2 mm in diameter, usually without or with few branches in lower portion and plumose in upper portions, with branches opposite but this mostly obscured, appearing spiral to irregular in arrangement. Branches with numerous, terete, short branchlets, up to 2 mm long, 100–150 µm in diameter, and occasional large, specialized, hamate (hook-shaped) branchlets, up to 1.0 cm long by up to 2 mm in diameter. Medulla a central axial filament surrounded by space and 2–3 layers of large globose cells of inner cortex. Outermost cortex a layer of smaller irregularly ovoid cells, about 10–25 µm in diameter, with numerous vesicular cells.

Cystocarps ellipsoid, 520 µm tall and 400 µm wide, with an ostiolate pericarp; borne terminal on a short, simple stalk. Spermatangial heads clavate to ovoid, 390–650 µm long and 240–300 µm wide; spermatangia elongate-ovoid, in dense surface layer covering entire branchlet except short stalk.

HABITAT. Epiphytic and/or entangled on various algae and rarely on gorgonians; low intertidal to subtidal, down to depths of 4.0–20 m.

DISTRIBUTION. Gulf of California: Puerto Calamajue to Bahía de Los Ángeles; Roca Blanca, Puerto Refugio (Isla Ángel de la Guarda). Eastern Pacific: Goleta (southern California) and California Channel Islands to Cabo San Quintín (northern Baja California). Western Pacific: Russia; Korea; Japan.

TYPE LOCALITY. Yokosuka, Kanagawa Prefecture, southeast Honshū, Japan.

REMARKS. Spermatangial fragment, collected from Puerto Calamajue (*JN-4637a*; US Alg. Coll. microscope slide 5165), indicate the northern Gulf *Bonnemaisonia hamifera* may be dioecious. Culture studies of *B. hamifera* by Feldmann and Feldman (1939b, 1943) and Chihara (1961) found the sporophyte to be the morphologically distinct "*Trailliella intricata*." Although the sporophyte of Gulf *B. hamifera* is presumed to be a "*Trailliella,*" it has not yet been encountered in the Gulf of California. The *Trailliella*-phase of *B. hamifera* can be distinguished from similar-looking filamentous tetrasporophytes of other *Bonnemaisonia* species by the small wedge-shaped vesicular cells that alternate from side to side or are irregular along the uniseriate filaments (Guiry and Guiry, 2008–2010; for a description of *T. intricata* Batters (1896) as reported from Alaska to San Quintín, Baja California, see Dawson, 1953a:56, and Abbott and Hollenberg, 1976:338, fig. 281).

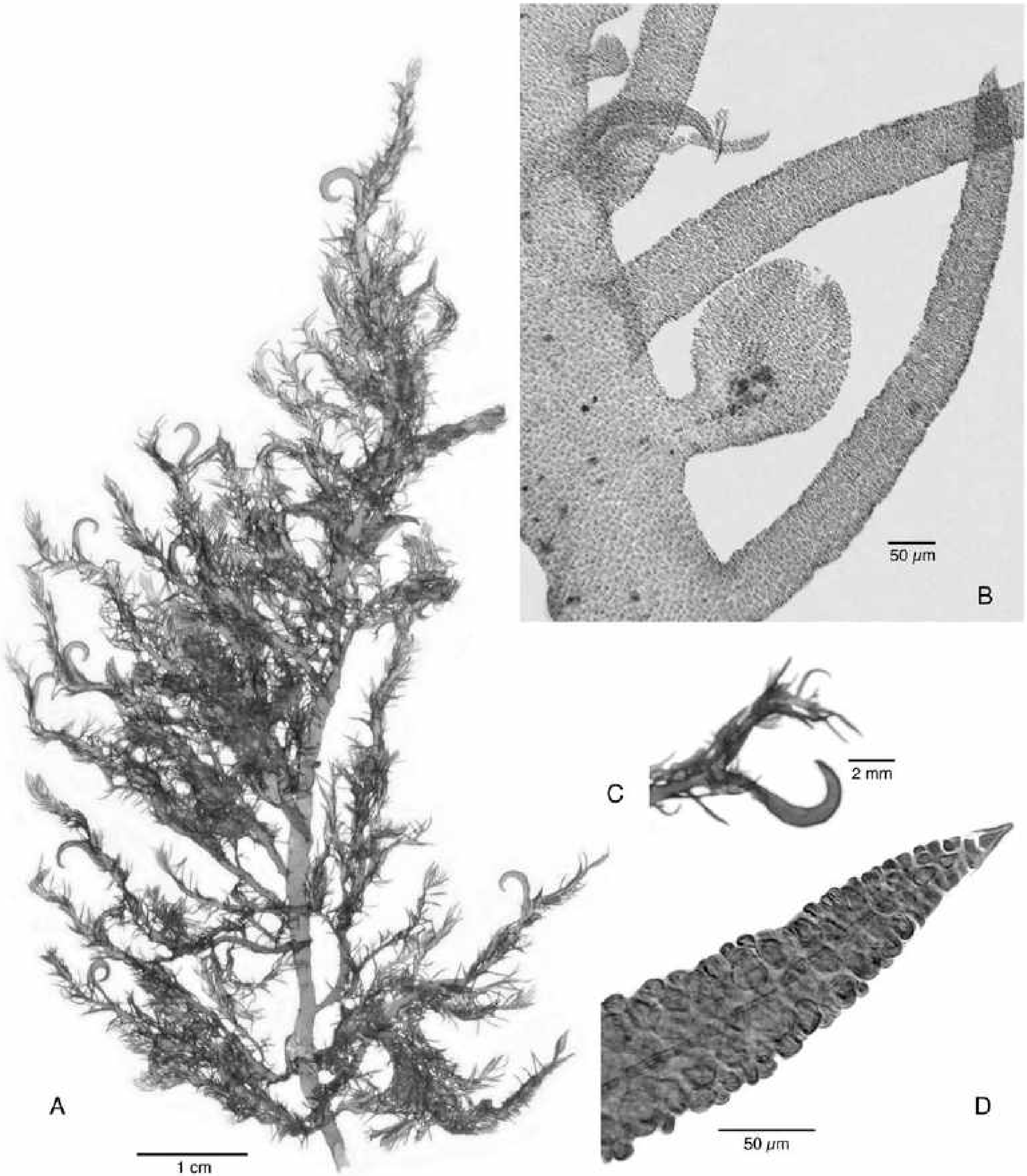

FIGURE 65. *Bonnemaisonia hamifera*: A. Habit (gametophyte) with hook-shaped branchlets for entangling attachment (*JN-5438*, US Alg. Coll.-158653). B. Branch with developing and young cystocarps terminating short branches (*JN-2989*, US Alg. Coll. microscope slide 4277). C. Close-up of a hook branchlet (from A; *JN-5438*). D. Ultimate branchlet showing central axial filament surrounded by cortical cells, tapering to acute apex (*JN-2989*, US Alg. Coll. microscope slide 4277).

CERAMIALES*

Ceramiales Oltmanns, 1904:683.

Members are erect or prostrate or prostrate with erect portions and range from minute uniseriate filaments to polysiphonous axes, foliose blades, to large and pseudoparenchymatous thalli. Members may be simple or lavishly branched, with branches terete to flattened, from radially to distichously or dorsiventrally organized. Growth is initially uniaxial and terminal, but in some members, with age, growth becomes diffuse from marginal or intercalary meristems. Axial cells producing 2–20 (or more) periaxial or pericentral cells, in whorls or with single uniseriate determinate branches. Members may be ecorticate or partially to wholly corticated and may have a filamentous, rhizoidal, or pseudoparenchymatous cortex overlying axial cells. Trichoblasts are present or absent. Cells are uninucleate or multinucleate.

Life histories are triphasic, with isomorphic gametophytes and tetrasporophytes. Gametophytes of most members are dioecious, but some are monoecious. Carpogonial branches are generally four-celled. Formation of the auxiliary cell is directly from the supporting cell after fertilization. Carposporophytes are usually surrounded by involucral filaments or pseudoparenchymatous pericarp and are rarely naked. Spermatangia are in branched clusters, superficial sori, or stichidia. Tetrasporangia (or rarely polysporangia or monosporangia) are borne singly, in clusters, in sori, or in stichidia, on the whorl branches or determinate laterals. Tetrasporangia are tetrahedrally or cruciately/decussately divided.

The Ceramiales is represented by eight families in the northern Gulf of California and includes a large percentage of the genera (about 29%) and species (about 27%) of the red algal subphylum Eurhodophytina that occur in the northern Gulf. Some of these are among the most attractive of the Gulf's species.

KEY TO FAMILIES OF CERAMIALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli narrow to broad foliose blades (flattened), with 2–4 pericentral cells 2
1b. Thalli monosiphonous filaments (axial cells without pericentral cells) or with polysiphonous axes (axial cells with pericentral cells), not generally bladelike 3
2a. Algae generally narrow blades; tetrasporangia in two longitudinal rows . . . . **Sarcomeniaceae**
2b. Algae narrow to broad foliose blades; tetrasporangia not in two longitudinal rows, produced in sori on blades in a single layer or in 2 irregular layers . . . . **Delesseriaceae**
3a. Algae monosiphonous filaments, with or without cortication 5
3b. Algae with polysiphonous axes (axial cell surrounded by pericentral cells); with monosiphonous or polysiphonous determinate branches 4
4a. Axes bearing persistent pigmented determinate pseudolaterals; spermatangia in stichidia-like branchlets of pseudolaterals . . . . **Dasyaceae**
4b. Apices of axes often with colorless determinate branches (trichoblasts); spermatangia produced on branches of trichoblasts or on thallus surface . . . . **Rhodomelaceae**
5a. Radially branched; indeterminate axes nearly fully corticated by alternating bands of short and long cells; determinate branches with narrow cortication bands only at the nodes; carposporophyte surrounded by nonostiolate pericarp . . . . **Spyridiaceae**
5b. Variously branched, cortication not as above or ecorticate; carposporophyte without a surrounding consolidated pericarp . . . 6
6a. Procarp borne from the lower side of a basal cell of a determinate whorl branch or indeterminate branch; gland cells often present; tetrasporangia decussate–cruciate, cruciate, or tetrahedrally divided . . . . **Ceramiaceae**
6b. Procarp formed from a periaxial cell of a fertile axial cell, gland cells generally absent; tetrasporangia tetrahedrally or polyhedrally divided 7
7a. Multicellular fusion cell present in cystocarp of most tribes; each axial cell with 1–6 whorl branches or determinate branchlets . . . . **Wrangeliaceae**
7b. Cystocarp without multicellular fusion cell in most members; each axial cell with 1–4 whorl branches or determinate branchlets . . . . **Callithamniaceae**

CALLITHAMNIACEAE

Callithamniaceae Kützing, 1843:370.

Thalli monosiphonous filaments, usually erect, axial cells bearing determinate branches or 1–4 whorl branches. Gland cells usually absent.

Gametophytes usually dioecious. Spermatangia at ends of whorl branchlets or spermatangial filaments adaxial on cells of the determinate lateral branches (in patches, "tufts," or continuous along cell). Procarp formed from a periaxial cell of a fertile axial cell of an indeterminate axis. This periaxial cell becomes the support cell for the carpogonial branch and lacks a sterile cell or sterile cell group. Carpogonial branches 4-celled, abaxial on the lateral side of the support cell (fertile periaxial cell/basal cell of whorl branchlet or determinate branch). Cystocarps naked or surrounded by loose

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* Contributed by Katina E. Bucher and James N. Norris. K. E. Bucher: Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20013-7012, USA.

involucral filaments arising from cells below the procarp. Meiosporangia are tetrahedrally or polyhedrally (rarely octahedrally) divided, sessile on cells of the whorl branches or determinate laterals.

Four genera of the Callithamniaceae occur in the northern Gulf of California.

KEY TO THE GENERA OF THE CALLITHAMNIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes with 1 lateral branch per axial cell, alternately placed; determinate branches branched or unbranched 2
1b. Axes with 3(–4) determinate branches whorled about an axial cell; determinate branches branched 3
2a. Cells of thallus uninucleate .... *Aglaothamnion*
2b. Cells of thallus multinucleate .... *Callithamnion*
3a. Whorl branches subdichotomous, trichotomous, or quadrichotomously branched, or a mixture of all 3 types; new indeterminate axes forming chains 10–15 cells long before initiating whorl branches; thallus may be mucilaginous or lightly calcified .... *Crouania*
3b. Whorl branches subdichotomously branched; new indeterminate axes forming chains 5–7 cells long before initiating whorl branches; not mucilaginous nor lightly calcified .... *Crouanophycus*

CALLITHAMNIACEAE TRIBUS CALLITHAMNIEAE

Callithamniaceae tribus Callithamnieae F. Schmitz, 1889:450; Hommersand et al., 2005:207.

The tribe Callithamnieae is represented by two genera in the northern Gulf of California.

Aglaothamnion Feldmann-Mazoyer

Aglaothamnion Feldmann-Mazoyer, 1940:451.

Algae are uniseriate branched filaments that are either (1) erect, tufted, and epiphytic, (2) partly endophytic in other algae, or (3), free-living and attached by basal discs or rhizoids issued from the base and the nodes of lowermost portions. Most members are uncorticated, but some are partially corticated by descending rhizoidal filaments. The axial cells produce one lateral branch per cell, resulting in a spiral or radial, alternate-distichous, or pseudodichotomous pattern. Determinate lateral branches are alternately, secundly, or subdichotomously branched. Cells are uninucleate with several discoid to band-shaped plastids.

Tetrasporangia are produced singly or in pairs and are usually sessile, on the adaxial side of the lateral branchlets, tetrahedrally to irregularly divided. Propagules have been reported in both sporophytic and gametophytic thalli of at least one species (Aponte et al., 1994). Procarps are borne in the upper portions of the indeterminate axes. Two opposite periaxial cells develop on an axial cell; only 1 bears a 4-celled carpogonial branch. After fertilization, an auxiliary cell is cut off from each of the opposite periaxial cells, which then develop the paired carposporophytes, composed of gonimolobes that are irregular, lobed, cordate, or reniform in shape. Most mature gonimoblast cells develop into carposporangia. Spermatangia are in clusters, borne on short spermatangial branchlets (usually one to three cells long) along the adaxial side of determinate laterals. The nucleus in the spermantangia is medial, with a mucilaginous vesicle above and below it.

REMARKS. Vegetatively similar in most respects to *Callithamnion*, *Aglaothamnion* is characterized by having species with only uninucleate cells and irregular or lobed gonimolobes in the carposporophyte, whereas species of *Callithamnion* differ in having only multinucleate cells and generally spherically shaped gonimolobes. Harris (1962) reported finding overlapping reproductive characters in some of the uninucleate and multinucleate species and merged the two genera, a conclusion followed by Dixon and Price (1981) and Spencer et al. (1981). However, others (e.g., Itono, 1971b; Abbott, 1972, 1999; L'Hardy-Halos, 1984; Aponte et al., 1994, 1997; Silva et al., 1996a) continue to separate *Aglaothamnion* and *Callithamnion,* using the nuclear condition as a valid character for generic distinction (see also L'Hardy-Halos and Rueness, 1990; Maggs et al., 1991; Maggs and Hommersand, 1993; Maggs and L'Hardy-Halos, 1993).

One species of *Aglaothamnion* is found in the northern Gulf of California.

Aglaothamnion endovagum (Setchell et N. L. Gardner) I. A. Abbott

Callithamnion endovagum Setchell et N. L. Gardner, 1924:771, pl. 28: fig. 62; Kylin, 1941:28, fig. 6B; Dawson, 1944a:312; 1945d:56 (as *Callithamnion* sp.); 1961b:443; 1962a:29, pl. 8: fig.5; 1966b:65.

Aglaothamnion endovagum (Setchell et N. L. Gardner) I. A. Abbott, 1972:262, fig. 7; Abbott and Hollenberg, 1976:617, fig. 559; Stewart, 1991:123; González-González et al., 1996:169.

Acrochaetium grateloupiae E. Y. Dawson, 1950b:153, figs. 22, 23.

Thalli partly endophytic in red algae; endophytic filaments rarely branched, growing intercellularly between the cortical cells of the host, creeping irregularly parallel to the host's thallus surface. Erect portions up to 250 µm tall, rarely with lateral branches; branches, when present, irregularly opposite, alternate, or unilateral. Axial cells up to 20 µm diameter at base, 7–13 µm wide above, with blunt tips.

Tetrasporangia ovoid, 15–18(–23) µm diameter, 23–30 µm long, tetrahedrally divided, sessile, borne on main axis at position of lateral branchlets or rarely terminal. Procarps frequent, alternate along upper axes, and mature gonimoblasts irregularly globular, involucre lacking. Cystocarps appear "twinned" as they originate from auxiliary cells on a pair of opposite periaxial cells. Spermatangia unknown.

Habitat. Endo-epiphytic in blade-like red algae, particularly species of *Grateloupia*; intertidal to shallow subtidal.

Distribution. Gulf of California: Isla San Esteban; Bahía Catalina (at head of inlet to Canal de Guaymas) and Bahía Bocochibampo (west of Heroica Guaymas); Isla San Ildefonso. Eastern Pacific: southern California.

Type Locality. In fronds of *Grateloupia prolongata*; Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

Remarks. Although *Aglaothamnion endovagum* has also been reported from Washington to Oregon, Scagel et al. (1989) noted that its presence in the northeastern Pacific required reinvestigation.

Callithamnion Lyngbye

Callithamnion Lyngbye, 1819:xxxi, 123.

Thalli mostly erect, monosiphonous filaments, ranging from uncorticated, corticated basally by a few descending filaments, to densely rhizoidally corticated. Main axes and major laterals bearing determinate branchlets, 1 per cell, alternately branched. Main branches multifariously, spirally, or distichously arranged. Secondary laterals unbranched or alternately or unilaterally branched. Attached to substratum by short branching rhizoids issued from lower cells of main axes, and slender long rhizoids from the basal cells of primary lateral branches that entwine and descend down the main axes. Cells multinucleate; gland cells absent.

Tetrasporangia tetrahedrally divided, usually sessile; single or in pairs, adaxial on cells of the ultimate determinate branchlets. A few species produce bisporangia (e.g., *C. bisporum* var. *australe*). Gametophytes are usually dioecious. Procarps formed near apex of indeterminate axis, one periaxial cell of a pair functioning as the support cell for a 4-celled carpogonial branch. Twin carposporophytes develop from auxiliary cells borne on each periaxial cell of the pair. Carposporophytes may lack involucres, or if present, issued from cells below the procarp. Spermatangia form short, dense, colorless tufts on the adaxial side of ultimate branchlets, or encircle it.

Five species of *Callithamnion* are reported in the northern Gulf of California.

KEY TO THE SPECIES OF *CALLITHAMNION* IN THE NORTHERN GULF OF CALIFORNIA

1a. Sporangia divide once, forming bisporangia .... ***C. bisporum* var. *australe***
1b. Sporangia divide twice, forming tetrahedrally divided tetrasporangia 2
2a. Branching alternate, predominantly distichous, at least in middle and upper parts, or tending to be distichous rather than multifariously arranged 4
2b. Branching alternate, and predominantly radially or spirally (multifarious) arranged throughout 3
3a. Attenuating considerably upward from base (170–300 μm in diameter basally) to tips (8–10 μm in diameter); densely branched above .... ***C. ramosissimum***
3b. Not as markedly attenuated as above, ultimate branches 0.25 the diameter of main axes; openly branched above .... ***C. marshallense***
4a. Branching to 3 orders; ultimate branchlets relatively sturdy, 40–50 μm in diameter (about 0.5 the diameter of main axes); apices initially incurved, becoming recurved (but not forcipate) .... ***C. rupicola***
4b. Branching to 4–5 orders; ultimate branchlets slender, 15–20 μm in diameter (0.1–0.3 the diameter of main axes); often somewhat corymbose; apices only more or less incurved .... ***C. paschale***

Callithamnion bisporum var. *australe* E. Y. Dawson

FIGURE 66

Callithamnion bisporum var. *australe* E. Y. Dawson, 1962a:26, pl. 9: fig.4; 1966b:65; González-González et al., 1996:181; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211.

Algae of few erect axes, up to 1.0 cm tall, branching alternately from distal end of axial cells, up to 4 orders; attached by multicellular rhizoids. Branches tending to be spirally arranged in lower portions and distichous above; middle portions often without branches for 8–12 cells. Cells to 200 μm in diameter in basal portion of thallus;1.2–1.5 times longer than diameter, gradually attenuating upward; middle portions with cells 4–6 times longer than wide; upper portions 3–5 times longer than diameter; ultimate branchlets somewhat adaxially curved, of 4–8 smaller cells, 10–15 μm in diameter, with blunt apices. Gland cells absent.

Sporangia once divided to form elliptical bispores, 50 μm tall, 30 μm in diameter; sessile, usually single, sometimes 2 on cell. Gametangial thalli unknown.

Habitat. Shallow subtidal, 6–18 m depths.

Distribution. Gulf of California: Bahía de Los Ángeles; Punta Concepción to Puerto Escondido.

Type Locality. Dredged from 6–9 m depths; outer bay, Puerto Escondido, Baja California Sur, Gulf of California, Mexico.

Remarks. Besides its markedly disjunct distribution, the Gulf of California endemic variety *Callithamnion bisporum* var. *australe* differs in having longer ultimate branchlets and smaller bisporangia than those of the northeastern Pacific *C. bisporum* N. L. Gardner (1927e) var. *bisporum* from Puget Sound, Washington (Scagel et al., 1989).

Callithamnion marshallense E. Y. Dawson

Callithamnion marshallense E. Y. Dawson, 1957b:117, fig. 25a–c; 1960a:50; 1961b:443; 1962a:31, pl. 10: figs. 1–3; Huerta-Múzquiz and Mendoza-González, 1985:52; González-González et al., 1996:181; Bernecker, 2009:CD-Rom p. 63; Fernández-García et al., 2011:60.

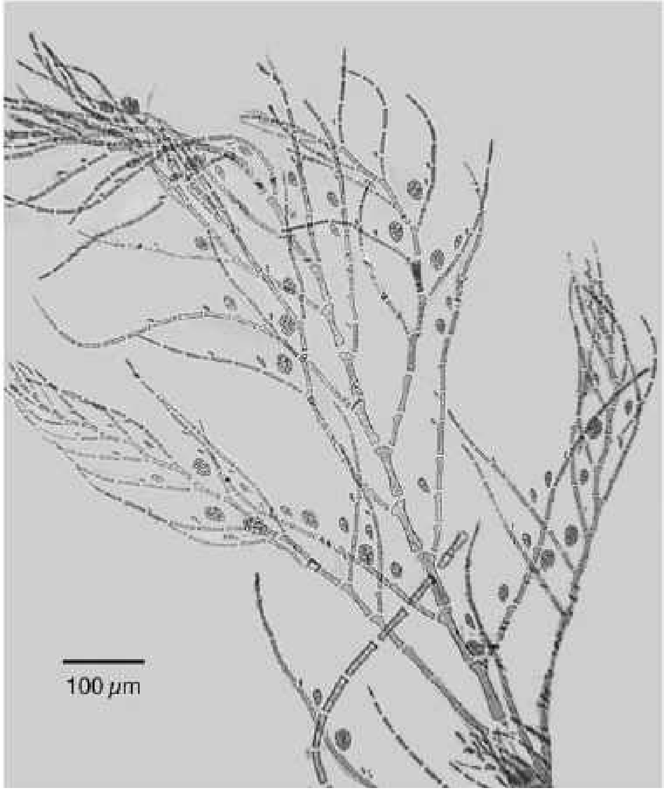


FIGURE 66. *Callithamnion bisporum* var. *australe:* Upper portion of thallus with bisporangia (isotype, *EYD-7190*, US Alg. Coll. microscope slide 333).

Thalli in loose tufts, 4–5 mm tall; main axes of noncorticated cells, up to 80–90 µm in diameter, 80–135 µm long; lower portions partially prostrate, basally attached by modified lateral branchlets with terminal discs (some attachment branchlets of catenate cells, with a few descending rhizoidal filaments; see Dawson, 1962a, pl. 10: fig. 3). Axes alternately branched, but not always from every cell, branchlets usually spirally arranged, often at about ⅕ divergence, sometimes tending in part to be distichous; branching often becoming more open above; ultimate branchlets, mostly simple, lax and curved, 20–30 µm in diameter, long, slightly attenuate, with blunt apices.

Tetrasporangia subspherical, about 40 µm in diameter; sessile, 1 to several on adaxial side of lower half of lateral branchlets. Cystocarps and spermatangia not known.

Habitat. On rocks or shells (also can be epiphytic; Dawson, 1962a) in tide pools; intertidal.

Distribution. Gulf of California: Punta Pelícano (vicinity of Puerto Peñasco); Bahía de La Paz. Eastern Pacific: Punta Santa Rosaliita (“Punta Santa Rosalía”), Baja California to Laguna de San Ignacio, Baja California Sur; Costa Rica; Panama.

Type Locality. On shells and coral rubble, 1.6–3.0 m depths; lagoon, south end of Parry Island, Enewetak Atoll (Eniwetok), Marshall Islands.

Remarks. A single specimen from Punta Pelícano in the upper Gulf of California (*JN-4234,* US Alg. Coll. microscope slide 4684) seems close to *Callithamnion marshallense* and is tentatively referred to this species.

Callithamnion paschale Børgesen

Callithamnion paschale Børgesen, 1924:294, fig. 35a–d; Dawson, 1959a:28, fig. 6b; 1961b:443; 1962a:31, pl. 9: figs. 5, 6; 1966a:26; Abbott and Hollenberg, 1976:613, fig. 555; Huerta-Múzquiz, 1978:338; Mendoza-González and Mateo-Cid, 1985:26; Santelices and Abbott, 1987:9; Ramírez and Santelices, 1991:314; Mateo-Cid et al., 1993:48; González-González et al., 1996:181; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Mendoza-González and Mateo-Cid, 1996b:67, pl. 7: figs. 26–28, pl. 8: figs. 29–32; Riosmena-Rodríguez et al., 1998:26; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:56; Dreckmann et al., 2006:155; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:211.

Callithamnion veleroae E. Y. Dawson, 1944a:312, pl. 50: figs. 3–5; González-González et al., 1996:182.

Algae forming tufts, up to 2.5 cm tall; axes basally to 150 µm in diameter, uncorticated, branched alternately; upper portions often corymbose, dense with branches; upper branchlets of 4–5 orders; ultimate branchlets of up to 15 cells, 6–13(–20) µm in diameter; attached by broad basal cells on other algae (or occasionally with some descending rhizoidal filaments basally). Branches gradually becoming shorter upward; branching of last 2–3 orders usually distichous; lower orders of branches distichous or irregularly multifarious.

Tetrasporangia elliptical, 45–60 µm long, 45–55 µm in diameter, solitary and sessile, adaxial on upper branchlets. Carposporophytes without involucres; usually in pairs, in upper portions of indeterminate axes; each nearly spherical, about 130 µm in diameter. Spermatangia in tufted clusters, adaxial on ultimate branchlets.

Habitat. Usually epiphytic on other algae; mid intertidal to shallow subtidal, down to 2 m depths (also dredged from 22 and 40 m depths; Dawson, 1962a).

Distribution. Gulf of California: Playa Tucson, Bahía La Choya (Bahía Cholla) to Playa Las Conchas (Playa Estación), Puerto Peñasco to Puertecitos; Puerto Refugio, Isla Ángel de la Guarda to Isla Partida Norte (Islas de la Cintura); Bahía Tepoca to Isla Patos (off N end of Isla Tiburón); Bahía Bocochibampo to Punta Los Frailes. Eastern Pacific: San Clemente Island and Santa Catalina Island (California Channel Islands); Isla San Benedicto (Islas Revillagigedo); Chiapas; Rapa Nui (Easter Island; Isla de Pascua).

Type Locality. Hanga Piko, Rapa Nui (Easter Island; Isla de Pascua), Valparaíso Region, Chile.

Callithamnion ramosissimum N. L. Gardner

Callithamnion ramosissimum N. L. Gardner, 1927e:404, pl. 86; Dawson, 1945d:56; 1961b:443; 1962a:32, pl. 10: figs. 6, 7; Schnetter and Bula-Meyer, 1982:159, pl. 29: fig. C; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52;

Stewart, 1991:126; González-González et al., 1996:181; CONANP, 2002:138.

Algae small, mostly 8–12 mm high, principal axes 170–300 µm in diameter at the base; uncorticated or with a few descending filaments. Abundantly branched above, branching alternate and multifarious; ultimate branchlets slender, of 6–10 cells, attenuating to 10 µm in diameter or less, 2–5 diameters long, curved up and inward; with blunt apices.

Tetrasporangia ellipsoidal, 50–65 µm long (including thick envelope), sessile, and borne adaxially in a series (2–4) on branchlets in upper portion of thallus. Cystocarps unknown. Spermatangia forming dense tufts on the adaxial side of ultimate branchlets.

Habitat. Lowermost intertidal or in tide pools, epiphytic on *Sargassum* and other large algae.

Distribution. Gulf of California: Puerto Peñasco; Bahía de Loreto to Bahía de La Paz. Eastern Pacific: Santa Catalina Island (California Channel Islands); La Jolla, southern California; Isla Guadalupe (off Baja California); Isla Gorgona, Colombia. Western Pacific: Vietnam (Nguyen et al., 2013).

Type Locality. Epiphytic on *Hypnea*; La Jolla, San Diego County, California, USA.

Remarks. *Callithamnion ramosissimum* is apparently rare in the northern Gulf of California. Dawson (1945d) noted *C. ramosissimum* was "infrequent and commonly overlooked," and it was not treated in the California flora by Abbott and Hollenberg (1976). It has not been recently collected from the type locality in La Jolla (Stewart, 1991).

Callithamnion rupicola C. L. Anderson

Callithamnion rupicola C. L. Anderson, 1894:360, figs. A,B [as "*C. rupicolum*"]; Smith, 1944:319, pl. 81: fig. 3; Taylor, 1945:260 "*prox.*"; Dawson, 1951:53; 1961b:443; 1962a:33, pl. 11: fig. 1; Abbott, 1971:354, fig. 2c; Abbott and Hollenberg, 1976:613, fig. 557; Stewart and Stewart, 1984:145; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Mendoza-González and Mateo-Cid, 1986:425; R. Aguilar-Rosas and Machado-Galindo, 1990:188; R. Aguilar-Rosas et al., 1990:125; Stewart, 1991:127; R. Aguilar-Rosas and Aguilar-Rosas, 1994:523; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:181; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138.

Callithamnion breviramosum N. L. Gardner, 1927e:403, pl. 84; Dawson, 1961b:442; 1962a:27, pl. 8: figs. 3, 4; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; González-González et al., 1996:181.

Callithamnion rigidum E. Y. Dawson, 1962a:33, pl. 10: figs. 4, 5; Stewart and Stewart, 1984:145; González-González et al., 1996:181.

Callithamnion uncinatum E. Y. Dawson, 1962a:35, pl. 11: fig. 4; González-González et al., 1996:182.

Callithamnion varispiralis E. Y. Dawson, 1949b:16, figs. 29, 30, 54; 1954e:340; 1961b:443; González-González et al., 1996:182.

Algae in small tufts, mostly up to 10(–20) mm tall; of numerous uncorticated axes, 80–100(–150) µm in diameter, with cells 400–800 µm long in lower portions; cells becoming shorter above, to about 1 diameter long; axes abundantly, mainly distichously branched to 1–2 times pinnately, second-order branches mostly alternate but can become pinnately to bipinnately branched; ultimate branchlets, usually simple, coarse, sturdy (somewhat rigid), straight or recurved, with attenuated, rounded, blunt, or uncinate apices; attached by loose, uniseriate, multicellular rhizoids descending near base; rhizoids with or without digitate ends (basal descending rhizoids may entangle or coalesce, giving pseudocorticated-like appearance to basal portion of thallus).

Tetrasporangia subspherical to ellipsoidal, (45–)55–70 µm long, (26–)50–60 µm in diameter; sessile, adaxial on branchlets. Carposporophytes irregularly shaped, subterminal on main axes and branches. Spermatangia forming continuous clusters along adaxial side of lateral branchlets.

Habitat. Epiphytic on *Codium, Gracilaria,* and other algae or on rocks; low intertidal to shallow subtidal, down to 4 m depths.

Distribution. Gulf of California: Puertecitos to Bahia de Loreto; Guaymas. Eastern Pacific: northern California to Todos Santos, Baja California Sur; Islas Todos Santos (off Ensenada), Isla Guadalupe, Islas San Benito, and Isla Cedros, Baja California; Oaxaca; Colombia; Galápagos Islands.

Type Locality. On rocks; Monterey Bay, Monterey County, central California.

Remarks. *Callithamnion rupicola* as currently interpreted is a highly variable species (Abbott, 1971; Abbott and Hollenberg, 1976) that includes several species described from the eastern Pacific: *C. varispiralis* from Santa Catalina Island, California Channel Islands (Dawson, 1949b) to Bahía de Sebastián Vizcaíno, Baja California (Dawson, 1954e), *C. breviramosum* from La Jolla (Gardner, 1927c), *C. rigidum* from Isla Guadalupe, Baja California (Dawson, 1962a), and *C. uncinatum* from Salina Cruz, Oaxaca (Dawson, 1962a).

The Gulf of California *C. rupicola* should be compared molecularly to *C. rupicola* specimens from the type locality of Monterey Bay, California, and the other species that are considered conspecific to assess their phylogenetic relationships and confirm their taxonomic identities.

CALLITHAMNIACEAE TRIBUS CROUANIEAE

Callithamnion tribus Crouanieae F. Schmitz, 1889:451.

Two genera of the tribe Crouanieae are reported in the Gulf of California.

Crouania J. Agardh

Crouania J. Agardh, 1842:83.

Algae are erect, partially erect with prostrate axes or sometimes wholly prostrate, branching up to eight orders. Axes terete, and may be ecorticate or corticated by rhizoids, and some species are mucilaginous and/or lightly calcified. Thalli are composed of monosiphonous filaments, each axial cell bearing a whorl of three branched determinate branchlets and attached to the substratum by multicellular rhizoids issued from the basal cells of whorl branches and lower cells of the axial filament. Thalli are freely branched with lateral indeterminate branches replacing one of the branchlets in a whorl or adventitious indeterminate branches also developing from the basal cell of whorl branches. Indeterminate branch initials originating at irregular intervals, typically developing chains of 10–15 (or more) cells before initiating the whorl branches. Whorl branches are dichotomously, trichotomously, or occasionally quadrichotomously branched or frequently a combination of all three. Some of the whorl branches terminate in a hair cell. Gland cells are usually absent, but occasionally present in some species.

Tetrasporangia are sessile, subspherical to ovoid, tetrahedrally divided, and borne on the basal cell or proximal cells of whorl branches (except in *C. pleonospora,* where tetrasporangia are also borne on more distal cells). Gametophytes are dioecious. Procarps are borne in place of a determinate whorl branch near the apices of indeterminate axes. The carpogonial branch is four-celled on a supporting cell (fertile periaxial cell) that develops an auxiliary cell (after fertilization) that forms the carposporophyte. The carposporophyte consists of globose clusters of carposporangia without involucral filaments but is subtended by elongating whorl branches from axial cells below. Spermatangial parent cells are terminal on the ultimate cells of whorl branches, each bearing clusters of 2–3 spermatangia.

There is one species of *Crouania* reported in the northern Gulf of California.

Crouania attenuata (C. Agardh) J. Agardh

FIGURE 67

Mesogloia attenuata C. Agardh, 1824:51.

Crouania attenuata (C. Agardh) J. Agardh, 1842:83; Setchell and Gardner, 1930:167; Dawson, 1952:431; 1957a:7; 1961b:438; 1962a:23, pl. 7: fig. 4; Stewart and Stewart, 1984:145; Sánchez-Rodríguez et al., 1989:44; González-González et al., 1996:307; Silva et al., 1996b:233; Abbott et al., 2002:306, fig. 13; Serviere-Zaragoza et al., 2007:9.

Thalli soft and lax, erect up to 2(–3) cm tall, up to 250 µm in diameter, may be mucilaginous or lightly calcified. Axes ecorticate, irregularly branched up to 3 orders, with axes covered with short determinate whorl branches. Thalli attached by digitate discs at the ends of uniseriate, multicelluar rhizoids that are

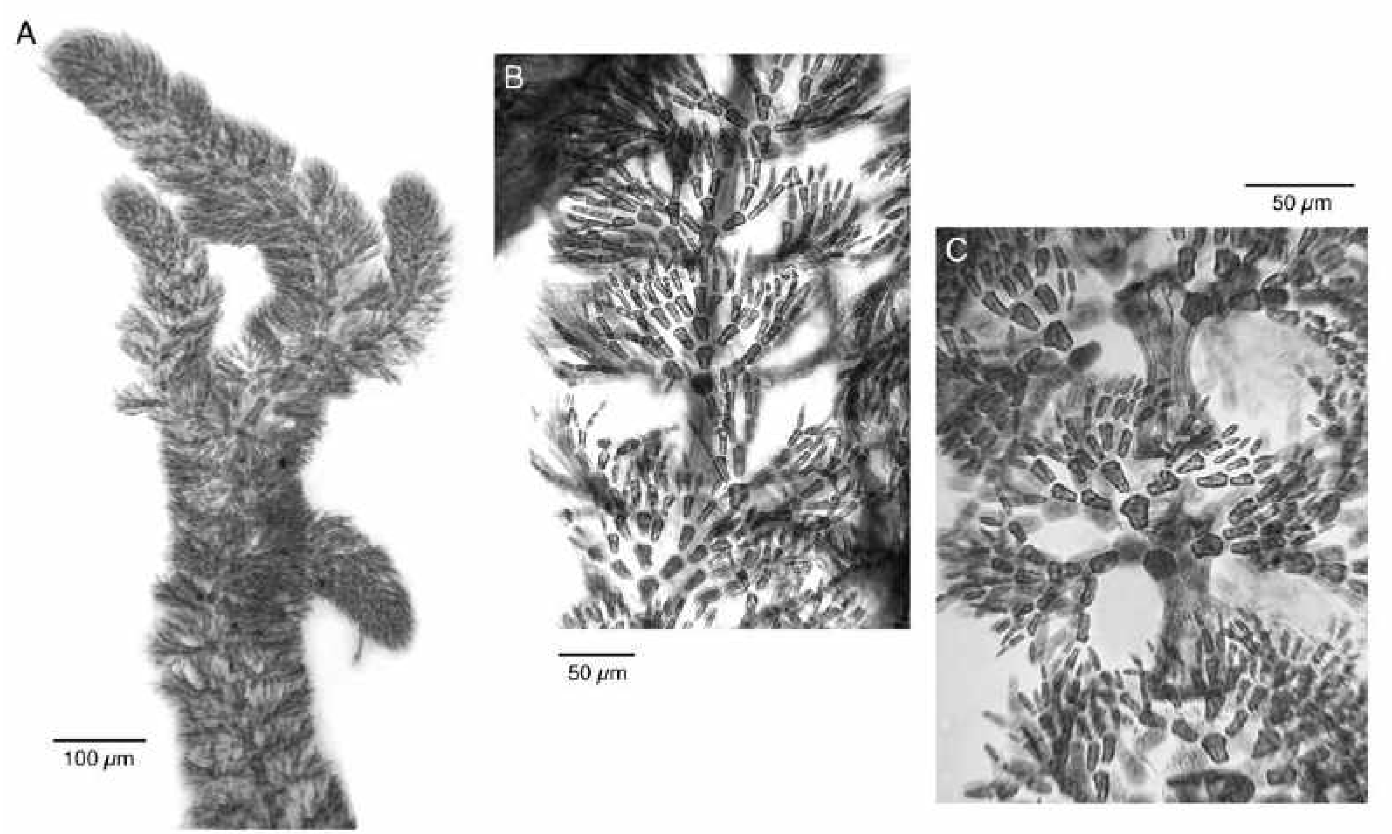


FIGURE 67. *Crouania attenuata*: A. Upper portion of erect axis. B. Mid-portion of branch showing much-branched whorl branches that are upturned toward branch apex. C. Whorl branches dichotomously, trichotomously, and quadrichotomously branched; whorl branches with elongate terminal cells (A–C, *JN-4842*, US Alg. Coll. microscope slide 4705).

issued from the basal cells of lower whorl branches or prostrate axes. Each axial cell bears 3 compound whorl branches toward its distal end. Indeterminate lateral branches borne in place of a whorl branch; adventitious indeterminate laterals may develop from basal cell of whorl branches. Axial cells cylindrical, up to 75(–90) µm in diameter in basal portions, thinner above; axial cell length about 2–3 times its diameter. Axes taper rapidly near apices. Branching of erect thallus monopodial at first, later becoming sympodial to ramisympodial, sometimes irregular. Determinate whorl branches repeatedly branched, up to 5 orders, the first-order to some of the third-order divisions trichotomous (occasionally quadrichotomous), higher-order divisions usually subdichotomous. The cells of the whorl branches are progressively smaller in diameter outward, basal cells obovoid, 7–18 µm in diameter, and outermost cells cylindrical and elongate, about 3 µm in diameter by 9 µm long, ultimate cells terminate in rounded tip, occasionally with a terminal hair cell. Mature whorl branches are 66–105(–150) µm long and curve upward toward apex of axes. Consecutive whorls may be widely separated from each other basally, whorls more crowded above, sometimes concealing axial cells.

Tetrasporangia subspherical to ovoid, tetrahedrally divided, 50–60 µm diameter (including thick wall), sessile on the upper side of basal cell of whorl branches. Procarps formed near apices, cystocarps with several rounded groups of carposporangia. Spermatangia about 2.0–4.5 µm in diameter, borne in clusters of (2–)3–5 on spermatangial parent cells at the tips of fertile whorl branches in the middle and upper portions of the thallus.

Habitat. Epiphytic on larger algae; intertidal to shallow subtidal, 8–28 m depths; also dredged from 47 m depth.

Distribution. Gulf of California: Puerto Peñasco to Puerto Libertad; Cabeza Ballena. Eastern Pacific: Isla Guadalupe (off Baja California); Punta Eugenia (“San Eugenio”) (Bahía Sebastián Vizcaíno) to Bahía Magdalena, Baja California Sur; Rocas Alijos (off Baja California Sur); Isla Clarión (Islas Revillagigedo); Chile; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: China; Japan; Korea; Vietnam.

Type Locality. “Atlantic Ocean” (Agardh, 1824); “probably Atlantic Coast of France” (Dawson, 1962a:24). Lectotype locality: Brittany, France (see Dixon, 1962:256).

Crouanophycus Athanasiadis

Crouanophycus Athanasiadis, 1998:517.

Crouaniella Athanasiadis, 1996a:196, *nom. illeg.* [a later homonym of *Crouaniella* (P. Saccardo) Lambotte, 1888:320].

Algae are composed of monosiphonous, ecorticate filaments, with erect and prostrate axes. Each axial cell bears 3 determinate subequal whorl branches. The whorl branches are composed of elongate cells, with the periaxial cell being smaller, equal, or greater in size than the contiguous cells. Whorl branches are subdichotomously branched (up to fourth order), with divisions beginning at the periaxial cell, and their flat side toward the bearing axis. Indeterminate lateral branches are borne as a fourth branch in a whorl of determinate branches at irregular intervals. New indeterminate laterals form chains of 5–7 cells before initiating the whorl branches. Adventitious development of new indeterminate laterals from basal cells of whorl branches was not observed. Thalli are attached by multicellular rhizoids developed from axial cells in the basal region and from periaxial cells. Gland cells are lacking.

Tetrasporangia are spherical to oblongate, tetrahedrally divided, and sessile, usually borne singly, and adaxially on the basal cell of whorl branches (=periaxial cells). Procarps are unknown. Carposporophytes borne singly in the apical region of an axis (Athanasiadis, 1996a). Spermatangial structures are short branchlets issued by lower cells of the whorl branches, composed of a cell bearing a group of spermatangial parent cells that each produce one to several terminal spermatangia.

Remarks. In the generitype, *Crouanophycus latiaxis* (I. A. Abbott) Athanasiadis (1998), proximal whorl branch cells issue single cells that bear several spermatangial parent cells, 1–4(–6) that each produce 1–3 (typically a pair) terminal spermatangia (see Bucher and Norris, 1995: fig. 9, as *Antithamnionella latiaxis* I. A. Abbott, 1979). Spermatangia are borne in a manner similar to those of *Scageliopsis* E. M. Wollaston (Wollaston, 1981:178, fig. 10; Athanasiadis, 1996a:205).

There is one species of *Crouanophycus* in the Gulf of California.

Crouanophycus mcnabbii (E. Y. Dawson) Athanasiadis

FIGURE 68

Crouanophycus mcnabbii (E. Y. Dawson) Athanasiadis, 1998:517.

Antithamnion mcnabbii E. Y. Dawson, 1959a:28, fig. 7c; 1961b:439; 1962a:18, pl. 5: fig. 4; González-González et al., 1996:174.

Antithamnionella mcnabbii (E. Y. Dawson) D. N. Young, 1981:97, figs. 3, 4.

Crouaniella mcnabbii (E. Y. Dawson) Athanasiadis, 1996a:199, figs. 107A–C, 108A–C.

Algae monosiphonous filaments with prostrate and erect axes, up to 8 mm tall; with 3 subequal whorl branches from the distal end of axial cells, whorl branches closely spaced along axis; algae attached by rhizoids from axial cells in basal portions of erect axes and basal cells of whorl branches (periaxial cells). Axial cells in basal regions to 115 µm long by 60–75 µm in diameter, decreasing in size toward tips. Whorl branches subdichotomously branched, 3(–4) times, divisions starting after periaxial cell. Whorl branches short, 5–7 cells long and 80–130 µm in length. Basal cells of whorl branches equal or larger than contiguous branch cells, 30 µm long and 12 µm in diameter, cells decreasing in size outward, 8 µm long and 4.5 µm in diameter at blunt tips. Indeterminate laterals multifariously arranged, develop as a fourth lateral of a whorl, at irregular intervals, at every fourth to fifth (or more) axial cell. Gland cells absent.

Tetrasporangia subspherical to oblong, tetrahedrally divided, up to 50 µm long, 35 µm in diameter; borne singly, adaxially, and sessile on basal cell of whorl branches. Sexual reproduction unknown.

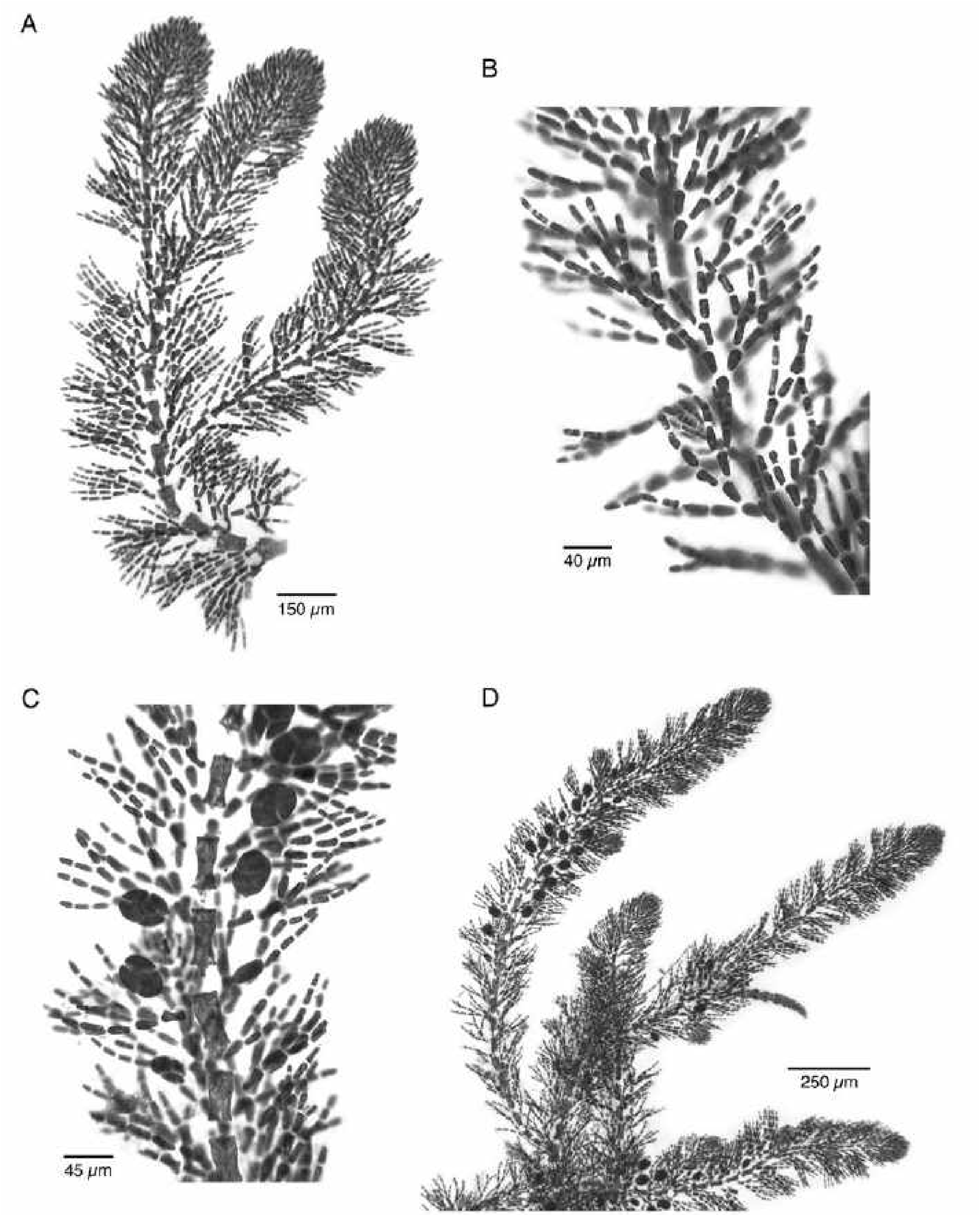


FIGURE 68. *Crouanophycus mcnabbii*: A. Upper portion of branched axis. B. Subdichotomously branched whorl branches. C. Tetrasporangia borne singly and sessile on basal cell of whorl branches. D. Habit of tetrasporangial axes (A–D, *JN-3406*, US Alg. Coll. microscope slide 4717).

Habitat. On rocks, with other turf algae, and epiphytic on *Dictyota*; low intertidal to shallow subtidal, 1.0–9.5 m depths.

Distribution. Gulf of California: Caleta Santa María (north of Puerto Santa Rosalía) to Roca El Solitario, Bahía Agua Verde. Eastern Pacific: Costa Rica; Galápagos Islands.

Type Locality. On rocks; Roca El Solitario, Bahía Agua Verde, Baja California Sur, Gulf of California, Mexico.

Remarks. *Crouanophycus mcnabbii* has also been reported in the western Pacific from southern Japan (Itono, 1969, as "*Antithamnion mcnabbii*"); however, Itono (1977a) later considered the Japanese record to be doubtful. It has also been reported in India (Silva et al., 1996a, as "*Antithamnionella mcnabbii*").

Ceramiaceae

Ceramiaceae Dumortier, 1822:71, 100.

Algae are monosiphonous filaments (uniaxial), with axial cells bearing one to many determinate laterals or whorl branches. Thalli are erect, decumbent, or prostrate, and many are uncorticated, although others may be wholly or partly corticated by rhizoidal-like filaments or small-celled filaments. Cells are mostly uninucleate, and gland cells are often present.

Most produce tetrasporangia that are decussate-cruciately, cruciately, or, less commonly, tetrahedrally divided. Tetrasporangia are borne singly, clustered, or in whorls, sessile or pedicellate, and may be naked, involucred, or more or less covered by the cortex of ordinary branches. Gametophytes are dioecious or occasionally monoecious. Carpogonial branches are four-celled and borne abaxial on the lower lateral side of the supporting cell. After fertilization, an auxiliary cell is formed and cuts off a single gonimoblast initial. The carposporangia may be formed by all or most cells or only by the terminal cells of gonimoblast filaments. Cystocarps are composed of one to several gonimolobes and may be surrounded by sterile involucral filaments, flanked by one or more adventitious laterals, or naked. Multicellular fusion cells are absent. Spermatangia are terminal and either form colorless patches covering the cortex of portions of certain species or are borne terminally on specialized determinate branchlets.

There are nine genera of the Ceramiaceae represented in the marine flora of the northern Gulf of California.

KEY TO THE GENERA OF THE CERAMIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a.	Ultimate order of branches of axes usually uncorticated	2
1b.	Ultimate order of branches of axes incompletely or completely corticated	6
2a.	Axial cells bearing opposite or whorled branches	3
2b.	Axial cells bearing zero or only 1 or 2 opposite branches	***Irtugovia***
3a.	Pair of opposite whorl branches per axial cell; periaxial cells at base of whorl branches smaller than adjacent cells	4
3b.	One to 4(–5) whorl branches per axial cell; periaxial cells about the same size as contiguous cells in whorl branch	5
4a.	Descending and ascending rhizoid-like filaments developing from periaxial cells, forming a loose to dense pseudoparenchymatous cortex around axial row; gland cells on basal cells of whorl-branches (periaxial cell) attached by thin cytoplasmic thread	***Balliella***
4b.	Rhizoids developing from periaxial cells not producing loose to dense pseudoparenchymatous cortex around axial row; gland cells on special short branchlets, bridging 2 cells of branchlet	***Antithamnion***
5a.	Whorl branches all of approximately equal length	***Antithamnionella***
5b.	Whorls each with 2 opposite pairs; juxtapose pairs often of different lengths and different branching patterns	***Pterothamnion***
6a.	Axes nearly or entirely covered by cortication, cortex composed predominately of basipetal filaments; basipetal corticating filaments with rectangular cells arranged in regular longitudinal rows	7
6b.	Axes often with internodal space between nodal bands; if entirely corticated cortex not predominately composed of basipetal filaments; basipetal cortical cells more ovoid to angular and not typically arranged in regular longitudinal rows	8
7a.	Spines usually present, especially at apices; 3 cortical initials cut off per periaxial cell; tetrasporangia emergent from cortex; spermatangia borne at the nodes, produced terminally on branched monosiphonous filaments issued from the upper ends of periaxial cells	***Centroceras***
7b.	Spines absent or rare; 4 cortical initials cut off per periaxial cell; tetrasporangia entirely or partially embedded in cortex, spermatangia cover cortical surface cells	***Corallophila***
8a.	Erect axes with alternate branching pattern; 3 cortical initials cut off per periaxial cell, the third being basipetally directed and divided off transversely, cell initially appearing horizontally elongated; rhizoids are unicellular and develop only from periaxial cells	***Gayliella***
8b.	Axes subdichotomously or irregularly branched; (1–)3–5 cortical initials per periaxial cell; basipetal cells not horizontally elongated; rhizoids multicellular, developing from periaxial and inner and outer cortical cells	***Ceramium***

CERAMIACEAE TRIBUS ANTITHAMNIEAE

Ceramiaceae tribus Antithamnieae Hommersand, 1963:330.

One of the five genera of the tribe Antithamnieae is represented in the northern Gulf of California.

Antithamnion Nägeli

Antithamnion Nägeli, 1847:202.

Thalli are delicate, often epiphytic, and composed of erect axes that arise from prostrate axes or decumbent axes or occasionally are mostly prostrate. Axes are uniseriate, uncorticated, and bear an opposite pair of determinate whorl branches (or rarely 3 in some species) on the axial cells of erect axes. Whorl branches are distichously to decussately arranged along bearing axis and may be simple to variously branched, up to 4 orders. Each whorl branch has an isodiametric basal cell (periaxial cell) that is noticeably shorter than adjacent cells and lacks side branches, but may issue 1–3 rhizoids, an adventitious indeterminate branch, or carpogonial branch. New indeterminate branches occur in three situations depending on the species: (1) replacing 1 whorl branch in a pair, (2) opposite whorl branch suppressed, with new indeterminate branch occurring alone on axial cell, or (3) new indeterminate branch issued from the basal cell of whorl branches. Gland cells are often present, borne laterally or terminally on modified short, 2–6(–9)-celled branchlets; each gland cell covers 2 to several cells. Vegetative cells are uninucleate.

Tetrasporangia are generally cruciately divided but sometimes may be irregularly divided and usually ovoid to oblong when mature. Tetrasporangia may be sessile or pedicellate and borne on the inner (proximal) cells of opposite whorl branches or often replacing branchlets of the final order. Gametophytes are usually dioecious, rarely monoecious. Carpogonial branches are 4-celled, borne singly on the basal cells of successive whorl branches near apices of indeterminate branches. Only one carposporophyte maturing per axis, borne near the apex of the fertile axis, naked or subtended by elongated whorl branches from the axial cell(s) below. Spermatangia clustered on spermatangial parent cells that are whorled about short-celled branchlets (cylindrical heads or clusters) that are usually borne adaxially on successive inner cells of whorl branches or second-order branchlets.

REMARKS. Two species are reported in southern Gulf of California: *Antithamnion antillanum* Børgesen (1917) from north of Cabo Pulmo (Dawson, 1962a; as *A. lherminieri*), and *A. hubbsii* E. Y. Dawson (1962a) from Bahía de Loreto (CONANP, 2002). Two other taxa originally described as species of *Antithamnion* from the southern Gulf are now recognized to belong in other genera: *A. pseudocorticatum* E. Y. Dawson (1962a) is now *Balliella pseudocorticata* (E. Y. Dawson) D. N. Young (1981), and *A. mcnabbii* E. Y. Dawson (1959a) is now *Crouanophycus mcnabbii* (E. Y. Dawson) Athanasiadis (1998). Another taxon, *Antithamnion plumulum* (Ellis et Solander) Thuret ex Le Jolis (1863) var. *plumulum* as reported from Isla Santa Cruz in the southern Gulf of California (Dawson, 1966b), should be reinvestigated. The Isla Guadalupe "*A. plumulum* var. *plumulum*" of Dawson (1962a) and Stewart and Stewart (1984), was noted by Athanasiadis (1996a:57) to probably be a species of *Pterothamnion* Nägeli.

There are three species of *Antithamnion* found in the northern Gulf of California.

KEY TO THE SPECIES OF *ANTITHAMNION* IN THE NORTHERN GULF OF CALIFORNIA

1a. Determinate whorl branches predominately alternately branched; tetrasporangia sessile . . . . ***A. decipiens***

1b. Determinate whorl branches predominately pectinate or secund; tetrasporangia usually pedicellate 2

2a. Indeterminate branches borne singly on an axial cell, without an opposite determinate whorl branch; gland cells often on branchlet of 3 or more cells . . . . ***A. defectum***

2b. Indeterminate branches usually borne opposite a determinate whorl branch; gland cells often on short branchlet of 2(–3) cells . . . . ***A. kylinii***

Antithamnion decipiens (J. Agardh) Athanasiadis

FIGURE 69

Callithamnion decipiens J. Agardh, 1842:70.

Antithamnion decipiens (J. Agardh) Athanasiadis, 1996a:151, fig. 70A–G.

Callithamnion fragilissimum Zanardini, 1860:11, table III, B.

Antithamnion fragilissimum (Zanardini) De Toni, 1903:1408.

Antithamnion ogdeniae I. A. Abbott, 1979:218, figs. 11–14.

Thallus with erect axes, up to 1.3 cm tall, arising from prostrate portions. Axial cells of erect filament develop an opposite pair of determinate whorl branches at their distal end; whorl branches subdistichously to decussately arranged along bearing axis, somewhat congested toward the apices. Cells of main axes 30–120 µm in diameter and 96–120(–240) µm long. Shorter cuboidal cell, 10–35 µm long, at the base of whorl branches. Whorl branches of a pair are of nearly equal development (subequal). Whorl branches are branched in alternate pattern, but occasionally an opposite pair of short branchlets develops at the lowest part of a whorl branch. Most whorl branches 250–700(–950) µm long and gently attenuate. Indeterminate laterals paired with an opposite determinate whorl branch along the axes, new indeterminate laterals commonly also develop from the cuboid basal cell of determinate whorl branches. Gland cells occasional to frequent, 8–16 µm in diameter; borne on short 2, 3(–5)-celled second-order branchlets, each gland cell resting on 2 cells. Gland cell branchlets more common on cells in the lower half of whorl branches. Rhizoids issued by cuboid basal cells of whorl branches, unicellular or multicellular, of variable lengths, occasionally terminating in a digitate attachment disc.

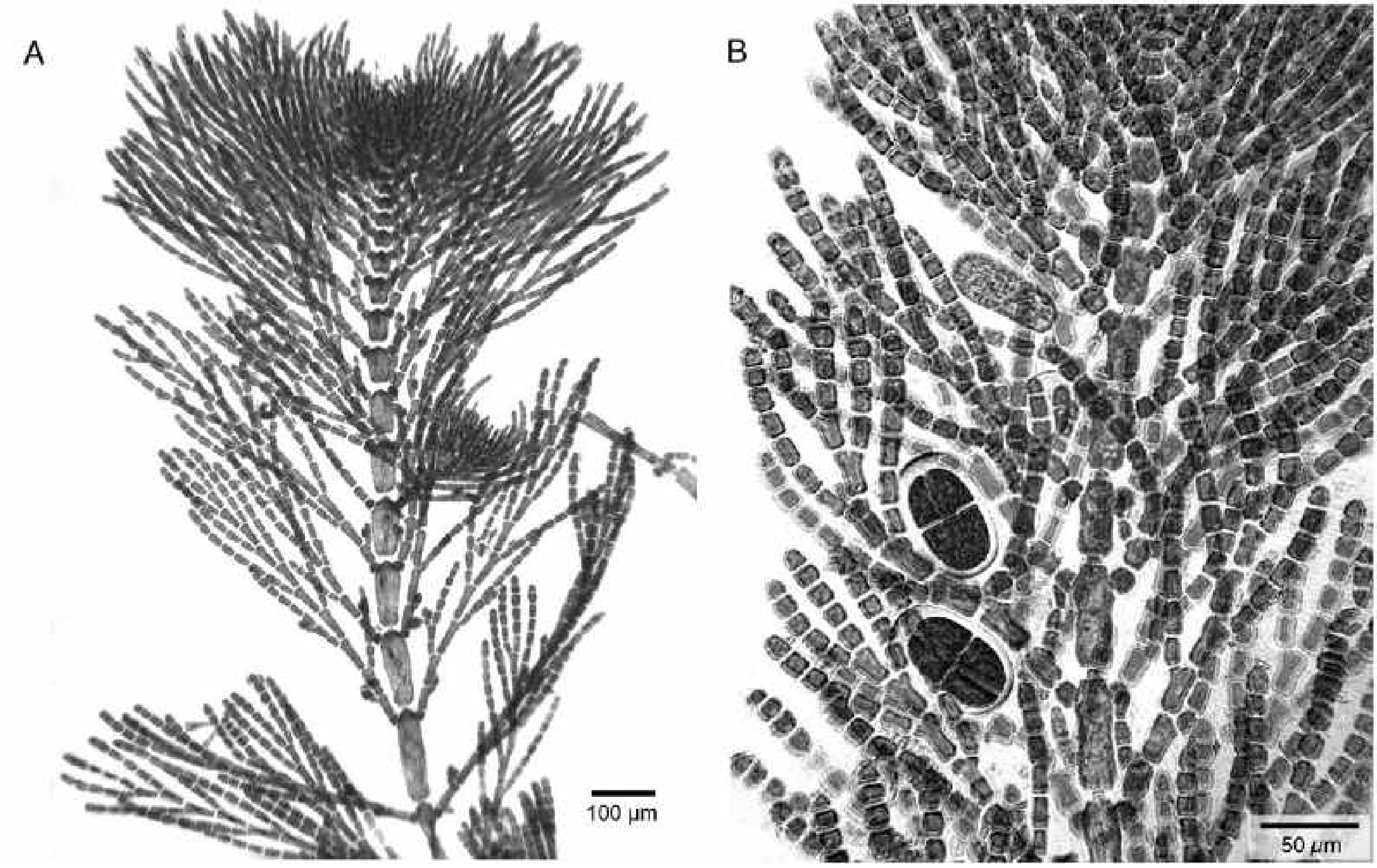


FIGURE 69. *Antithamnion decipiens*: A. Erect axis showing alternately branched whorl branches with gland cells borne on short branchlets and an indeterminate branch (*JN-4921*, US Alg. Coll. microscope slide 4750). B. Tetrasporangia sessile borne on first order branchlets (*JN-4146*, US Alg. Coll. microscope slide 4719).

Tetrasporangia sessile, 60–70(–75) µm long, 30–47 µm in diameter, oblong-ellipsoidal to obovate, borne adaxial on the basal cell (or contiguous cells) of first order branchlets (alternate branchlets) of the whorl branches. Gametangial thalli not seen in Gulf of California material.

Habitat. Epiphytic on *Sargassum* and other algae; lowermost intertidal to shallow subtidal, down to 10 m depths.

Distribution. Gulf of California: Punta Pelícano (vicinity of Puerto Peñasco) to El Desemboque; Caleta de Santa María (north of Puerto Santa Rosalía) to Cabeza Ballena. Central Pacific: Hawaiian Islands.

Type Locality. Nice, Provence-Alpes-Côte d'Azur, France, western Mediterranean Sea.

Remarks. Specimens from Punta Pelícano (*JN-4230, JN-4242*), Puerto Peñasco (*JN-4394*), El Desemboque (*JN-5168, JN-5191*), Punta Robinson (*JN-4866*), Punta Cirio (*JN-4921*), Sonora and Caleta de Santa María (*JN-3404*) and Cabeza Ballena (*JN-4145, JN-4146*), Baja California Sur, establish *Antithamnion decipiens* in the Gulf of California.

Antithamnion defectum Kylin

FIGURE 70

Antithamnion defectum Kylin, 1925:46, fig. 27a,b; Smith, 1944:308, pl. 78: figs. 1, 2; Inagaki, 1950:24, fig. 3; Dawson, 1961b:438; West and Norris, 1966:55, fig. 6; Wollaston, 1972a:75, figs. 1–4; Wollaston, 1976:573, fig. 517; Devinny, 1978:359; Young, 1979:42, figs. 1–13; Young and West, 1979:49, figs. 1–18; Young, 1980:119, figs. 1–5; Lindstrom and Gabrielson, 1989:222, fig. 1; Scagel et al., 1989:141; R. Aguilar-Rosas et al., 1990:125 ; González-González et al., 1996:173; S.-R. Lee et al., 2005:534, fig. 1.

Antithamnion pygmaeum N. L. Gardner, 1927e:413, pls. 91–93; Smith, 1944:309, pl. 78: fig. 4, pl. 80: fig. 1; Dawson et al., 1960b:24; Dawson, 1961b:438; 1962a:21, pl. 6: fig. 2; Dawson and Neushul, 1966:182; West and Norris, 1966:55, fig. 2; Norris and West, 1967:144; González-González et al., 1996:174.

Antithamnion setaceum N. L. Gardner, 1927d:373, pls. 73, 74.

Antithamnion secundatum sensu Dawson, 1962a:22, pl. 7: fig. 3; González-González et al., 1996:174 [non *Antithamnion secundatum* N. L. Gardner, 1927e:413; see Wollaston, 1972a:79].

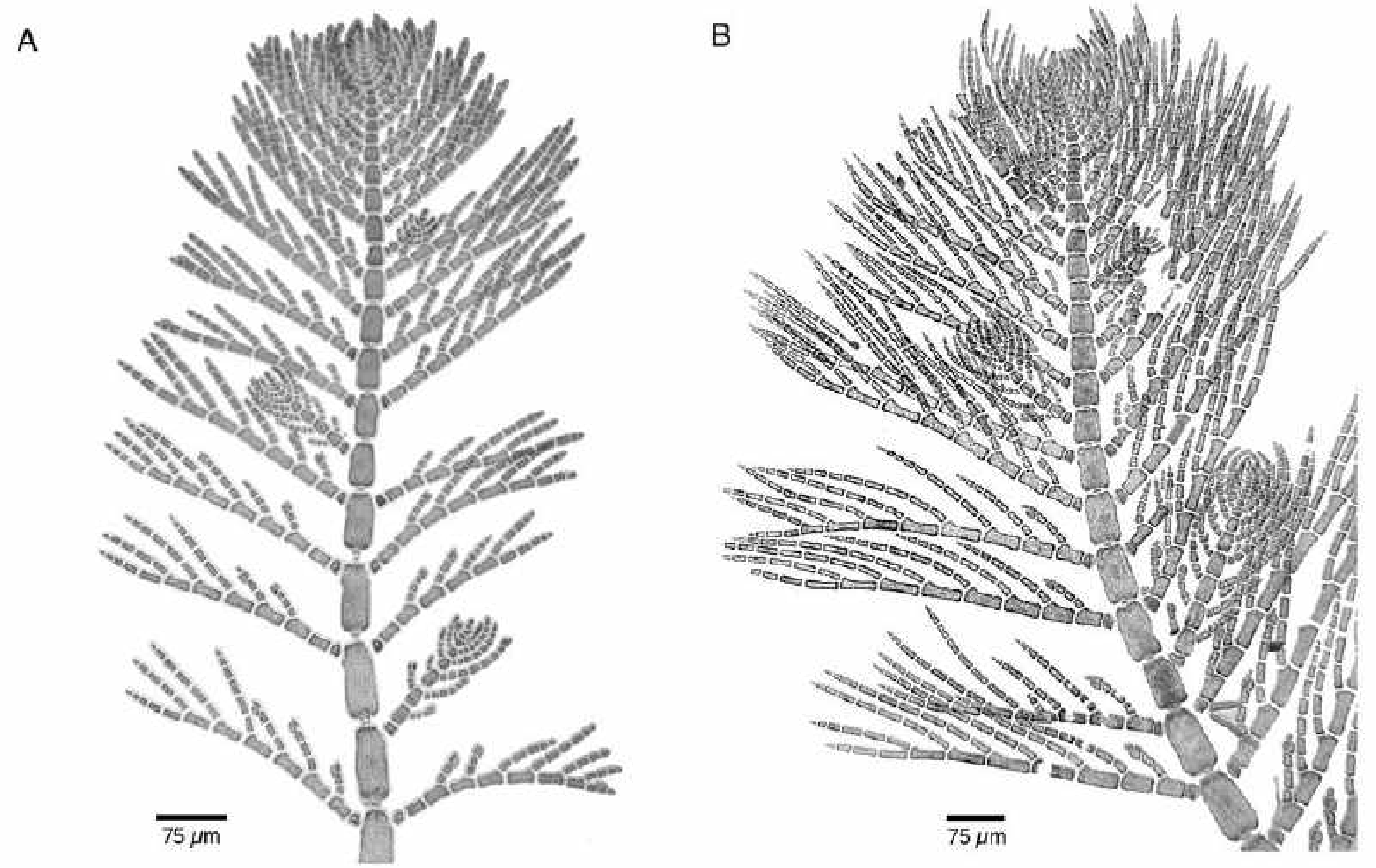


FIGURE 70. *Antithamnion defectum*: Upper portion of axes showing new axes (indeterminate branches) issued without an opposite paired whorl branch, and gland cells borne distally on inner branchlets. A. *JN-4758b*, US Alg. Coll. microscope slide 4295. B. *JN-4757*, US Alg. Coll. microscope slide 4731.

Antithamnion dendroideum sensu Norris, 1975:436; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211 [non *Antithamnion dendroideum* G. M. Smith et Hollenberg, 1943:217].

Algae to 2(–7) mm high, main axes percurrent, indeterminate laterals alternately and distichously arranged along axes, without a paired determinate whorl branch opposite them. Axial cells cuboid above, cylindrical below, up to 105 μm in diameter and up to 245 μm long. Each axial cell at their distal end bears 2 opposite whorl branches. Whorl branches distichously arranged along bearing axes. Cells at the base of whorl branches are shorter (23–35 μm) than adjacent cells and can develop rhizoids that often end in digitate attachment discs. Whorl branches 10–13 cells long, up to 725 μm in length; whorl branches bearing secundly a single order of up to 8 simple adaxial branchlets. Adaxial branchlets somewhat outwardly curved. Ultimate cells of all branches and branchlets acute. Gland cells usually borne on inner branchlets of whorl branches, branchlets usually 3 or more cells long, gland cells common near tip or in upper half of branchlet, overlying 2(–3) cells.

Tetrasporangia ovoid, up to 80 μm long, cruciately divided, borne on unicellular pedicels (apparently reduced ultimate branchlets) or terminally and laterally off inner ultimate branchlets (see Gardner, 1927e: fig. 93). Carpogonial branch as for genus. Spermatangia in terminal whorls on short cylindrical heads, arising adaxially in place of branchlets on the inner cells of whorl branches and second-order branchlets (reproductive information after Abbott and Hollenberg, 1976).

HABITAT. On rocks or epiphytic on other algae; subtidal, 12–26 m depths.

DISTRIBUTION. Gulf of California: Isla Ángel de la Guarda; Islas de Los Gemelos (Los Hermanitos), Bahía de Los Ángeles; Canal de San Lorenzo (between southern end of Isla Espíritu Santo and north of Punta San Lorenzo). Eastern Pacific: Alaska to Islas Todos Santos (off Ensenada), Baja California.

TYPE LOCALITY. Syntype localities (Kylin, 1925): Friday Harbor (San Juan Island), Canoe Island (off SE of Shaw Island and NW end of Lopez Island), and Peavine Pass (channel between Orcas Island and Blakely Island), all San Juan County, Washington, USA. Lectotype locality: Friday Harbor, San Juan Island (Smith, 1944), and, later, Canoe Island (Lindstrom and Gabrielson, 1989; Athanasiadis, 1996a).

REMARKS. *Antithamnion defectum* is known in the northern Gulf (Dawson, 1962a, as *A. secundatum*). The species has been variously interpreted, but herein it is recognized as a distinct species.

It has been considered conspecific with *A. densum* (Shur) M. Howe on the basis of morphological studies (Athanasiadis, 1990, 1996a; Maggs and Hommersand, 1993). More recently, S.-R. Lee et al. (2005), using molecular analyses, concluded material identified as "*A. densum*" should be treated as three separate species. The North Atlantic "*A. densum*" was genetically distinct from the North Pacific "*A. densum*," which was found to be two different species (S.-R. Lee et al., 2005). One, *A. defectum* Kylin, was restricted in distribution to the northeastern Pacific, and the other, *A. sparsum* Tokida (1932; Yoshida, 1981), was restricted to the western Pacific. The third, *A. densum* (Suhr) M. Howe (1914; basionym: *Callithamnion densum* Suhr, 1840; type locality: Peru), was thought to be restricted to Peru and northern Chile (Dawson et al., 1964; Ramírez and Santelices, 1991), but it has also been reported in the northeastern Atlantic (L'Hardy-Halos, 1968b; Guiry and Maggs, 1991; Maggs and Hommersand, 1993), where it may have been introduced (Athanasiadis, 1990).

Antithamnion kylinii N. L. Gardner

FIGURE 71

Antithamnion kylinii N. L. Gardner, 1927e:411, pl. 89: fig. 1; Smith, 1944:307, pl. 77: fig. 1, pl. 78: fig.5; Dawson, 1954e:342; Dawson et al., 1960b:24; Dawson, 1961b:438; Wollaston, 1972a:78, figs. 10–13; 1976:574, fig. 520; Scagel et al., 1989:142; Lindstrom and Gabrielson, 1989:222, fig. 2; Stewart, 1991:124; González-González et al., 1996:174; Athanasiadis, 1996a:160, fig. 76A–C; Pacheco-Ruíz et al., 2008:211.

Antithamnion densum sensu Howe, 1914:153, fig. 14 [in part; his description only, excluding the type; non *Antithamnion densum* (Suhr) M. Howe, 1914:151[type specimen only; see Athanasiadis, 1996a:162].

Antithamnion secundatum N. L. Gardner, 1927e:413.

Antithamnion nematocladellum R. E. Norris, 1987b:26, figs. 11, 12, 15 [see Athanasiadis, 1996a:160].

Algae in tufts, up to 2 cm high; most cells of indeterminate axes producing at their distal end 2 opposite whorl branches. Cells of main axes small and cuboid above; cylindrical and 75–120 μm in diameter and 200–600 μm long basally. Whorl branches are not strictly distichously arranged, diverging to decussate, with a small cuboid cell, 8–23 μm diameter at the base of each whorl branch. Determinate whorl branches 12–15 cells long (to 720 μm long), adaxially ramified, with up to 8 pectinate branchlets; opposite whorl branches often unequal. Whorl branches and branchlets tapering to an acute apical cell. Indeterminate branches replacing a whorl branch in a pair, borne opposite a determinate whorl branch that is often simple or less branched than neighboring whorl branches. Successive indeterminate laterals alternately positioned along bearing axes. Gland cells, 12 μm wide by 13–23 μm long, frequently on short 2- to 4(–6)-celled branchlets. Typically, 1 gland cell per branchlet, gland cell in contact with 2 cells.

Tetrasporangia cruciately divided, ovoid, about 70 μm long; borne on 1-celled pedicels, along several successive inner cells of whorl branches on the adaxial side. Cystocarps not seen in northern Gulf specimens. Spermatangia terminal on spermatangial parent cells whorled about cells of short fertile branches, forming cylindrical heads borne in a series on the adaxial side of inner cells of whorl branches.

HABITAT. On mollusk shells and epizoic on the carapace of the black sea turtle (*tortuga negra*), *Chelonia mydas agassizii*; subtidal, down to at least 15 m depths.

DISTRIBUTION. Gulf of California: Canal de Infiernillo (between Isla Tiburón and Sonora). Eastern Pacific: southern British Columbia to Punta San Hipólito, Baja California; Galápagos Islands; Peru. Western Pacific: Korea.

TYPE LOCALITY. On log floats; Victoria Harbor, Victoria, Vancouver Island, British Columbia, Canada.

REMARKS. Our collections from Canal de Infiernillo (between Isla Tiburón and the Sonoran coast), *JN-4733* and *JN-4735*, subtidal, on shells, west of Campo Viboras, and *JN-4780, JN-4781, JN-4783*, and *JN-4784* from the carapace of a sea turtle, *Chelonia mydas agassizii,* vicinity of Campo Ona, now establish *A. kylinii* in the northern Gulf of California.

CERAMIACEAE TRIBUS DOHRNIELLEAE

Ceramiaceae tribus Dohrnielleae Feldmann-Mazoyer, 1940 ['1941']:241.

The tribe is represented by two genera in the northern Gulf of California.

Antithamnionella Lyle

Antithamnionella Lyle, 1922:347, figs. 1–4.

Algae are monosiphonous filaments that may be erect or of erect axes arising from prostrate axes and uncorticated throughout, with a variable number of branches per whorl, 1–6 subequal or irregularly unequal whorl branches cut off from each axial cell. Whorl branches may be simple but are usually branched. In different species whorl branches can be consistent or inconsistent in number and arrangement. The basal cell of whorl branches (periaxial cells) may be smaller, similar, or larger in size than adjacent whorl branch cells (depending on species). Lateral indeterminate axes generally replace a whorl branch, and new axes can also develop from basal cells of whorl branches. Rhizoids develop from the periaxial cells of prostrate axes and from axial cells of erect axes near basal regions. Cells are uninucleate. Depending on the species, gland cells are absent or few to common and sessile, borne on a single cell, laterally on cells of whorl branches and branchlets, sometimes in a short series on successive cells.

Tetrasporangia are ovoid to near spherical, and tetrahedrally, oblique-cruciately, or cruciate-decussately divided and

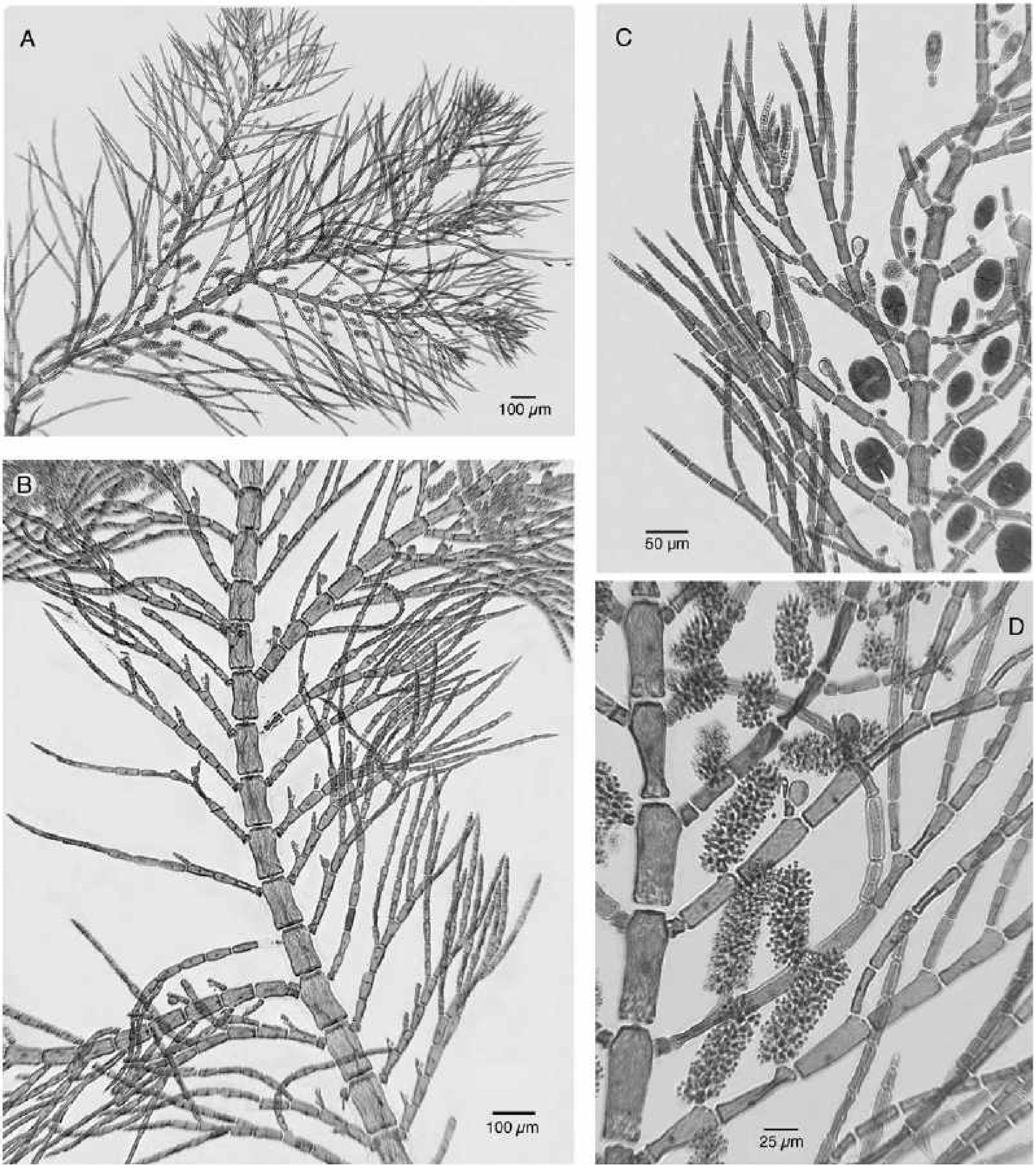


FIGURE 71. *Antithamnion kylinii:* A. Bushy habit with opposite whorl branches arranged distichous to decussate (*JN-4780*, US Alg. Coll. microscope slide 4741, male gametophyte). B. Portion showing new axes issued with an opposite whorl branch; whorl branches with adaxial unbranched branchlets, and gland cells on short branchlets (*JN-4780*, US Alg. Coll. microscope slide 4736). C. Tetrasporangia on single-celled pedicels, borne adaxially on the inner cells of whorl branches (*JN-4735*, US Alg. Coll. microscope slide 4729). D. Spermatangial structures borne adaxially on the inner cells of whorl branches (*JN-4780*, US Alg. Coll. microscope slide 4735).

sessile or pedicellate on the inner cells of whorl branches or branchlets, typically on basal cells (periaxial cells). Gametophytes are mostly dioecious but are monoecious in some species. Carpogonial branches are four-celled and borne on the basal cells of whorl branches and may suppress the growth of the whorl branch and/or bearing axis. Carposporophytes are surrounded by subtending whorl branches from the axial cell below the fertile segment. Spermatangial structures consist of a file of spermatangial parent cells (SPC) forming a filament with several spermatangia whorled about each SPC, these structures borne in a series usually adaxially on whorl branch and branchlet cells (after Athanasiadis, 1996a).

Three species of *Antithamnionella* are reported in the northern Gulf.

KEY TO THE SPECIES OF *ANTITHAMNIONELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Whorl branches commonly unbranched or rarely unilaterally branched; whorl branches, relatively short, up to 120 µm long, frequently in pairs, distichous-opposite or decussately arranged along axis . . . . ***A.* cf. *spirographidis***
1b. Whorl branches frequently subdichotomously branched, appearing distichous-alternately branched; whorl branches typically longer than above, frequently in whorls of 3 2
2a. Three (or occasionally 2) whorl branches per axial cell; whorl branches up to 240 µm long . . . . ***A. breviramosa***
2b. Two (to three) subequal whorl branches per axial cell; whorl branches up to 360 µm long . . . . ***A. sublittoralis***

***Antithamnionella breviramosa* (E. Y. Dawson) E. M. Wollaston**

FIGURE 72

Antithamnion breviramosus E. Y. Dawson, 1949b:14, figs. 28, 57; 1954e:342; 1957c:7; 1959a:28; 1960a:50; 1961b:438; 1962a:14, pl. 5: fig. 3, pl. 15: fig.1; 1966a:26; 1966b:65; Itono, 1969:30, fig. 1A–D.

Antithamnionella breviramosa (E. Y. Dawson) E. M. Wollaston in Womersley and Bailey, 1970:322; Wollaston, 1972a:84, figs. 22–25; Abbott and Hollenberg, 1976:580, fig. 523; Schnetter and Bula-Meyer, 1982:147, pl. 24: figs. E,F; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:20; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:41; Mendoza-González et al., 1994:108; Bula-Meyer, 1995:36; González-González et al., 1996:174; Mendoza-González and Mateo-Cid, 1996b:67, pl. 6: figs. 21–25; Athanasiadis, 1996a:105, fig. 46A–E; Abbott, 1999:253, figs. 71A–C; Pacheco-Ruíz and Zertuche-González, 2002:468; Dreckmann et al., 2006:155; Fernández-García et al., 2011:60.

Antithamnionella elegans sensu Riosmena-Rodríguez et al., 1998:26; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; 2002:235; CONANP, 2002:138; Mateo-Cid et al., 2006:56; Bernecker, 2009:CD-Rom p. 64 [non *Antithamnionella elegans* (Berthold) J. H. Price et D. M. John in J. H. Price et al., 1986:16; basionym: *Antithamnion elegans* Berthold, 1882a:516; see also Cormaci and Furnari, 1989:264].

Algae up to 3 mm high, composed of creeping prostrate axes and erect axes; attached by simple uniseriate rhizoids that sometimes end in multicellular digitate discs. Axial cells in middle portions 30 µm in diameter and 60–150 µm long (2–5 times the diameter in length). Axial cells at their distal end issuing whorl branches, usually in whorls of 3 (basally sometimes only 2 laterals in a whorl). Indeterminate branches arise irregularly and replace one of the whorl branches in the whorl or may arise from basal cells (periaxial cells) of whorl branches. Whorl branches up to 150(–240) µm long, composed of 7–11(–13) cells, gradually attenuated, with branch tips mostly blunt. Whorl branches subdichotomously branched, commonly appearing distichous-alternately branched, 2–4(–5) times divided starting at the second to third cell in branch, sometimes unbranched. Cells of whorl branches 10–15 µm in diameter. Gland cells elliptical, 9–14 µm in length, often frequent; borne single, laterally, developed at apex on terminal whorl-branch cells. Gland cells sometimes in a short series on successive cells.

Tetrasporangia tetrahedrally divided, ovoid to oblongate, up to 40 µm long; borne sessile and adaxial on basal or second cell of whorl branches. Gametophytes unknown in the Gulf of California, as known elsewhere, monoecious or dioecious with carpogonial branches borne on basal cells of short 2-celled branches. Cystocarps single, borne near apex of bearing branch, inhibiting its growth. New axis sympodially developing from a periaxial cell of whorl branches below the carposporophyte. Carposporophytes surrounded by subtending whorl branches from below the fertile segment. Spermatangia in clusters on short (up to 2-celled) filament, adaxial on inner 3–5 cells of whorl branches.

HABITAT. Epiphytic on *Prionitis* or other larger algae; subtidal, down to 16 m depths.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Cabo San Lucas; Mazátlan, Sinaloa to Jalisco. Eastern Pacific: southern California to Todos Santos, Baja California Sur; Colima; Chiapas; El Salvador; Costa Rica; Colombia; Galápagos Islands. Central Pacific: Hawaiian Islands. Western Pacific: Korea; Wake Island (northern Marshall Islands).

TYPE LOCALITY. Drift, epiphytic on *Sargassum palmeri* Grunow; Pebbly Beach, southeast of Avalon, Santa Catalina Island, California Channel Islands, southern California, USA.

REMARKS. Cormaci and Furnari (1988) consider *Antithamnionella breviramosa* to be a synonym of *A. elegans* (Berthold) J. Price et D. M. John (in J. Price et al., 1986; basionym: *Antithamnion elegans* Berthold, 1882a), a conclusion that was followed by some phycologists (e.g., Lawson and John, 1987; Stewart, 1991; Silva et al., 1996a). However, on the basis of differences in the numbers of whorl branches, their branching pattern, place of gland cell initiation, and gametophyte structure, other researchers (e.g., Itono, 1969; G.-H. Kim and Lee, 1990; Athanasiadis, 1996a; Abbott, 1999) recognize *A. breviramosa* and *A. elegans* as distinct species. *Antithamnionella breviramosa* with carpogonial branches on reduced 2-celled laterals, and spermatangial parent cells forming 2-celled filament, while *A. elegans*

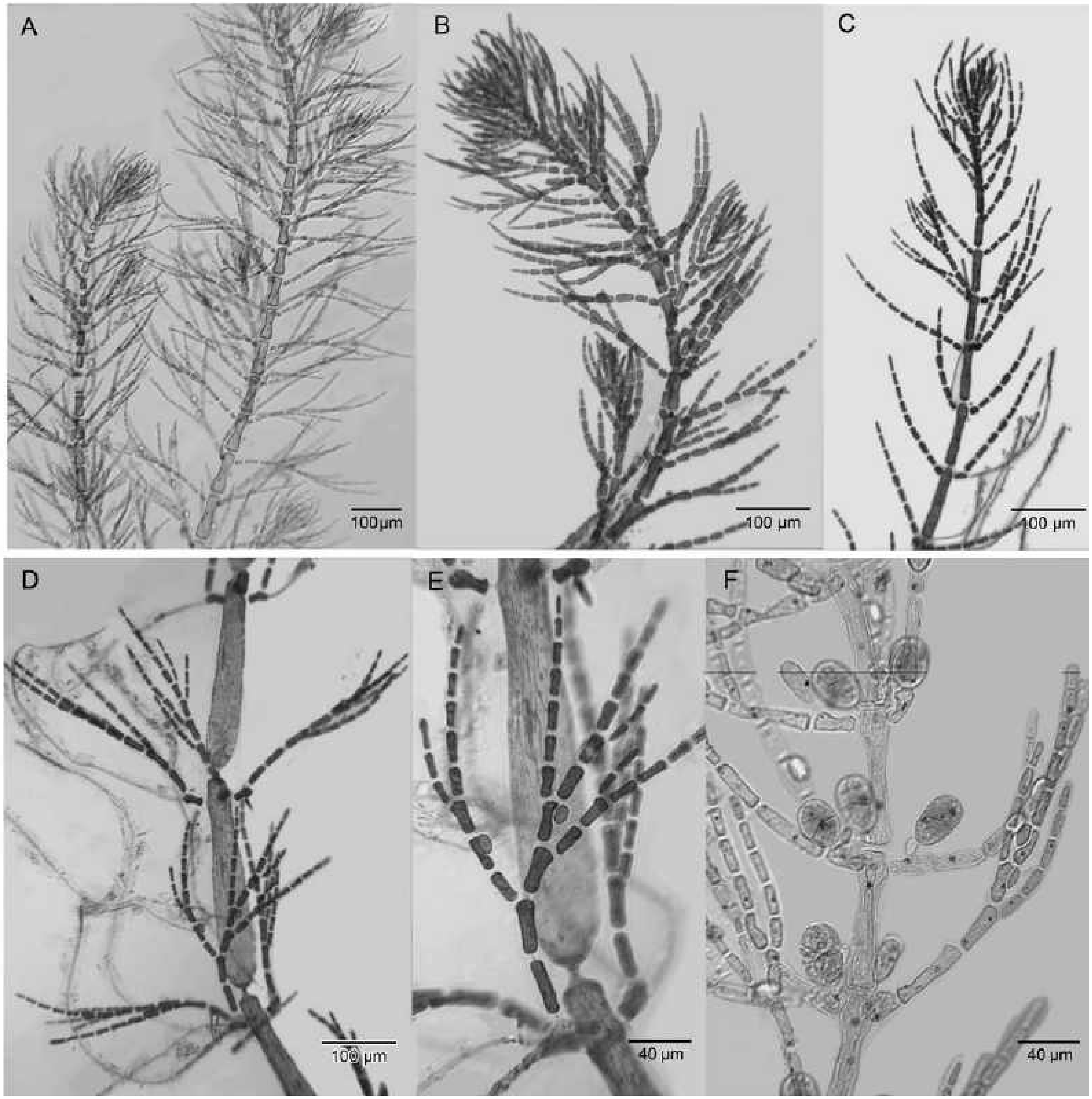


FIGURE 72. *Antithamnionella breviramosa*: A. Habit, long whorl branches repeatedly divided (*JN-4435*, US Alg. Coll. microscope slide 4727). B. Habit, whorl branches branching a moderate amount (*JN-4908*, US Alg. Coll. microscope slide 4751). C. Habit, most of the whorl branches are unbranched, with some rhizoids (*JN-5064b*, US Alg. Coll. microscope slide 4840). D. Lower portion of axis showing 3 whorl branches per axial cell and rhizoids developing from periaxial cells (*JN-5042*, US Alg. Coll. microscope slide 4757). E. Distichous, alternately branched whorl branch with gland cells borne on a single cell (*JN-5042*, US Alg. Coll. microscope slide 4757). F. Tetrasporangia borne on proximal cells of whorl branches (*EYD-26126,* US Alg. Coll. microscope slide 788).

has carpogonial branches on normal size whorl branches and spermatangial parent cells forming filaments up to 4 cells long (Athanasiadis, 1996a). Japanese records of "*Antithamnionella breviramosa*" of Itono (1969, 1977a: fig. 49H) should be reexamined, as Athanasiadis (1996a) has questioned their identification and generic placement. *Antithamnionella breviramosa* is also reported in the western Atlantic (Wynne, 2005, 2011).

Antithamnionella cf. _spirographidis_ (Schiffner) E. M. Wollaston

FIGURE 73

Antithamnion spirographidis Schiffner, 1916:137, figs. 19–27.

Antithamnionella spirographidis (Schiffner) E. M. Wollaston, 1968:345, fig. 29A–T; Lindstrom and Gabrielson, 1989:227, fig. 4; Athanasiadis, 1996a:121, fig. 57A–G.

Thallus of northern Gulf specimen: prostrate and erect axes, up to about 3 mm long; basal portion with attachments apparently missing; axial cells bearing 1 to 3 whorl branches. Whorl branches often in pairs in a spiral-decussate arrangement; occasionally with a single whorl branch or with 3 branches forming a whorl. Indeterminate branches branching similar to their bearing branches; irregular in occurrence, with the number of axial cells between indeterminate branches variable. Indeterminate branches can develop either (1) in place of one of the whorl branches in a pair, (2) as the third branch to form a whorl, or (3) on periaxial cells or infrequently from the second cell of whorl branches. Axial cells in lower regions of thallus up to 55 µm in diameter and to 190 µm in length. Whorl branches mostly simple, sometimes sparsely secundly branched; gradually attenuated distally, ending in a blunt tip; periaxial (basal) cell of whorl branch usually similar in size to adjacent cells of whorl branch but occasionally may be smaller or larger in size. Rhizoids apparently not abundant, issued from periaxial cells of whorl branches. In upper portions of thallus whorl branches short, up to 80–120 µm long, somewhat stiff looking, with short cells, isodiametric 7–13 µm in size; in midportions of thallus whorl branches more or less straight out (near 90 degrees) from axial cell; in lower portions of thallus whorl branches appear more flexible and longer, up to 280 µm long, with cylindrical cells about 12–15 µm in diameter by 25–30 µm long. Gland cells frequent, 7–10 um long, lateral on parent cell, usually a middle to lower cell (commonly third or fourth cell) of a whorl branch; generally only one gland cell per whorl branch. No reproductive structures found.

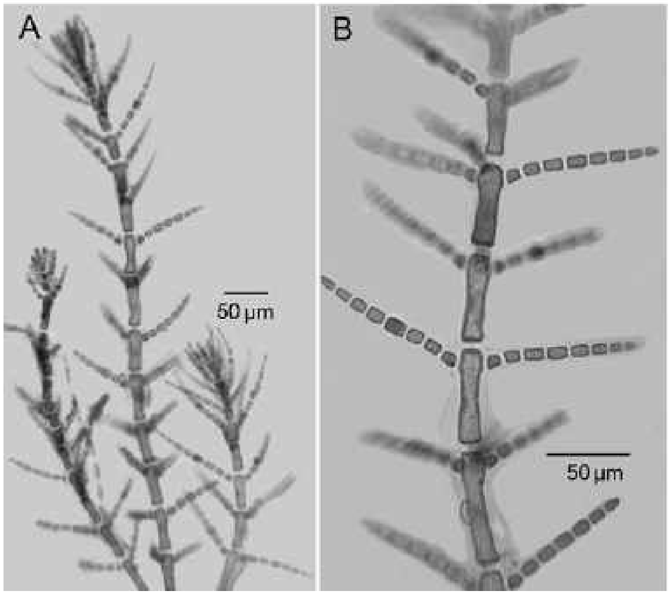


FIGURE 73. *Antithamnionella* cf. *spirographidis*: A. Habit, showing whorl branches decussately arranged. B. Close-up of short whorl branches composed of short, squarish cells (A, B, *JN-4769*, US Alg. Coll. microscope slide 4734).

HABITAT. Epizoic on carapace of a living black sea turtle, *Chelonia mydas agassizii* (collected by Seri fishermen); surface to subtidal.

DISTRIBUTION. Gulf of California: Canal de Infiernillo, between Campo Ona and Campo Viboras off the mainland coast of Sonora and between the east coast of Isla Tiburón.

TYPE LOCALITY. Sacchetta, Gulf of Trieste, Adriatic Sea, Italy.

REMARKS. As currently interpreted in the eastern and western Pacific, *Antithamnionella spirographidis* (Schiffner) E. M. Wollaston (1968) is quite broadly defined with a high degree of morphological variability that has resulted in a number of previously described species being considered conspecific (Wollaston, 1972a, 1976; Lindstrom and Gabrielson, 1989; Athanasiadis, 1996a; H.-S. Kim and Lee, 2012)—*Antithamnionella glandulifera* (Kylin) Wollaston (1972a; basionym: *Antithamnion glanduliferum* Kylin, 1925), *Antithamnion gardneri* G. De Toni (1936a; =*A. tenuissimum* N. L. Gardner, 1927d; non *A. tenuissimum* (Hauck) Schiffner, 1916), and *Antithamnionella miharae* (Tokida) Itono (1977; basionym: *Antithamnion miharae* Tokida, 1942).

This wide range of variability could include our single specimen of *Antithamnionella,* which was found growing on a sea turtle carapace. Although in habit it somewhat resembles *Antithamnion glanduliferum* Kylin (1925: fig. 28e; Dawson, 1962a: pl. 4: fig. 7), our northern Gulf specimen differs in several ways from *Antithamnionella spirographidis* sensu Lindstrom and Gabrielson (1989), and it may be a different or possibly new taxon. Examination of Dawson's (1962a) Pacific Mexico material identified as *Antithamnion glanduliferum* (*EYD-20267*, and *-20396*; US Alg. Coll. microscope slides 207 and 206) show the whorl branches on his specimens to be distichously arranged, mostly 2 whorl branches (rarely with 3 whorl branches) per axial cell, and whorl branch initials at the axial apex that develop in a clearly unilateral alternating series (see Athanasiadis, 1996a: fig. 57a; Lindstrom and Gabrielson, 1989: fig. 4). In our Gulf specimen, perhaps due to its decussate-spiral branching or the more common occurrence of 3-branch whorls, the axial apex is more congested and whorl branch initials do not appear to develop in a unilateral alternating series. Many of the whorl branches in midportions of the thallus extend more or less straight out from the axial cell, in contrast those of *A. spirographidis* that bend upward (e.g., see Kim and Lee, 2012: figs. 38a–f, 39a–f). The Gulf specimen is sterile, thus reproductive structures could not be compared.

Other specimens from the Gulf of California reported as *Antithamnionella spirographidis* by Pacheco-Ruíz et al. (2008) may be this species but need to be re-examined. Dawson (1966b, as "*Antithamnion glanduliferum*") concluded that his southern Gulf material from Isla Salsipuedes was an "intermediate condition" with both blunt and acute tips on whorl branches and related it to the Galápagos *Antithamnion veleroae* W. R. Taylor (1945). More recently Athanasiadis (1996a:128) considered *A. veleroae* to be a synonym of *Antithamnionella ternifolia* (J. D. Hooker et Harvey) Lyle (1922).

For now our northern Gulf of California specimen (*JN-4769*; US Alg. Coll. microscope slide 4734) is tentatively referred to *Antithamnionella* cf. *spirographidis* until more material from the northern Gulf can be collected, studied, and genetically compared with type material of other species.

Antithamnionella sublittoralis (Setchell et N. L. Gardner) Athanasiadis

Antithamnion sublittorale Setchell et N. L. Gardner, 1937:86, pl. 6: fig. 15; Dawson, 1944a:313; 1961b:439; 1962a:22, pl. 7: fig.2; Stewart and Stewart, 1984:145; González-González et al., 1996:174.

Antithamnionella sublittoralis (Setchell et N. L. Gardner) Athanasiadis, 1996a:119, fig. 55A,B.

Algae composed of a sparingly branched creeping axis and erect axes, up to 1 cm tall; each axial cell usually bearing 2(–3) whorl branches, arranged in spiral pattern around axes (decussate). Axial cells of main axes 55–65 µm in diameter and 165–260 µm in length (3–4 times as long as wide). Whorl branches 200–300(–360) µm long; unbranched or mostly distichous-alternately branched, usually incurved; up to 12 cells long. Cells of whorl branches 15–30 µm long and 10–15 µm in diameter. New axes replacing a whorl-branch at irregular intervals. Gland cells develop adaxially from intercalary cells near apices. Gland cells borne singly or in a series of up to 3, on successive whorl branch cells, smaller than bearing cell.

Tetrasporangia sessile, borne on periaxial and second cell of whorl branches. Carpogonial branches borne on 2-celled whorl branches near apices. Carposporophytes borne singly, subtended by 3 whorl branches, which may be longer (up to 520 µm long and up to 15 cells long) than regular whorl branches.

HABITAT. Epiphytes on larger algae; subtidal, 4–30 m depths (dredged down to 40 m depths).

DISTRIBUTION. Gulf of California: Bahía Salinas, Isla Carmén; Canal de San Lorenzo (off southern end of Isla Espíritu Santo) to San José del Cabo. Eastern Pacific: Isla Guadalupe (off Baja California).

TYPE LOCALITY. Epiphytic, dredged at 37 m depth; San José del Cabo, Baja California Sur, Gulf of California, Mexico.

Irtugovia Perestenko

Irtugovia Perestenko, 1996:140 [in Russian], 204 [in Latin].

Algae are erect, monosiphonous branched filaments, attached by rhizoids developed from lowermost cells near the base or having erect axes arising from prostrate axes, uncorticated with a variable number of branches per whorl, 1–6 subequal or irregularly unequal whorl branches borne on each axial cell. In different species, whorl branches can be consistent or inconsistent in number and arrangement. Whorl branches may be simple or branched. The basal cell of whorl branches (periaxial cells) may be smaller, similar, or larger in size than adjacent whorl branch cells. Lateral indeterminate axes replacing a whorl branch and new axes can also develop from basal cells of whorl branches. Growth is apical. Gland cells absent to common, sessile, borne laterally on cells of whorl branches, sometimes in a short series on successive cells, one per cell. Cells uninucleate.

Tetrasporangia are cruciately divided and ovoid to near spherical, sessile or pedicellate on inner cells of whorl branches or branchlets. Gametophytes are monoecious or dioecious. Carpogonial branches 4-celled; borne on basal cells of whorl branches, may suppress the growth of whorl branch or bearing axis. Carposporophytes are surrounded by subtending whorl branches. Spermatangia are grouped on spermatangial structures borne adaxially on whorl branches and branchlets.

REMARKS. *Irtugovia* is similar to *Antithamnionella,* but it is distichously branched and with successively dividing tetrasporangia, borne in short branches, appearing clustered. Womersley and Wollaston (in Womersley, 1998) commented that *Antithamnionella* was separated on vegetative features (number and branching of whorl branchlets, position of gland cells) and tetrahedrally divided tetrasporangia. Athanasiadis (1996a) noted that *Irtugovia* was not monophyletic but lacked distinctive characters and was in need of further study. Later, Athanasiadis (2002) found that the distinction of *Irtugovia* from *Antithamnionella* was cladistically supported, and included both in the tribe Dohrnielleae. However, it remains a little-understood genus in need of further elucidation.

Athanasiadis (2002) also noted the genus name *Irtugovia* is a later homonym of *Haplocladium* Nägeli (1862; generitype: *H. floccosum* (O. F. Müller) Nägeli). There is also a bryophyte genus, *Haplocladium* (Müller Hal.) Müller Hal. (1896; basionym: *Hypnum* sect. *Haplocladium* Müller Hal., 1879), but it also is a later homonym. Thus, the use of the name *Irtugovia* would need to be conserved over *Haplocladium* Nägeli (Athanasiadis, 2002).

One species of *Irtugovia* has been reported in the northern Gulf of California.

Irtugovia pacifica (Harvey) Perestenko

Callithamnion floccosum var. *pacificum* Harvey, 1862:176.

Irtugovia pacifica (Harvey) Perestenko, 1996:142, pl. 18: figs. 13, 14, pl. 22: fig. 5.

Antithamnion floccosum f. *pacificum* (Harvey) Setchell et N. L. Gardner, 1903:341.

Antithamnion pacificum (Harvey) Kylin, 1925:47, figs. 28C,D, 29A–F; Dawson, 1944a:313; Smith, 1944:310; Dawson, 1961b:439; 1962a:19, pl. 4: figs. 8, 9; González-González et al., 1996:174.

Antithamnionella pacifica (Harvey) E. M. Wollaston, 1972a:87, figs. 31–36; Wollaston, 1976:582, fig. 525; Scagel et al., 1989:226; Lindstrom and Gabrielson, 1989:226, tbl. 1, fig. 4.

Algae erect, uniseriate filaments, lower portions often entangled, distichously branched; usually (1–)2 opposite whorl branches per axial cell; periaxial cells smaller than adjacent cells in whorl branch. Whorl branches unbranched (except for fertile branchlets with reproductive structures). Indeterminate lateral branches arising in place of whorl branch. Lower axial cells very long, 20(–30) times longer than in diameter. Gland cells are usually entirely absent but are also noted to be rare.

Tetrasporangia cruciately divided, developing by successive divisions (often tetrahedral in appearance); borne terminally or laterally on short branches on the adaxial side of whorl branches. Carpogonial branches single on basal cell of whorl branches near apex of axis; carposporangia in more or less elongate groups. Spermatangia on short spermatangial branches borne adaxially on inner cells of whorl branches (after Wollaston, 1976).

HABITAT. Epiphytic on larger algae, subtidal (dredged 22–36 m depths; Dawson, 1944a).

DISTRIBUTION. Gulf of California: Bahía Tepoca; Guaymas. Eastern Pacific: Alaska to Baja California. Western Pacific: Russia.

TYPE LOCALITY. Syntypes: Orcas Island, Washington; Esquimalt, British Columbia, Canada (Harvey, 1862). Lectotype locality: Orcas Island, San Juan Islands, San Juan County, Salish Sea, Washington, USA (Lindstrom and Gabrielson, 1989).

REMARKS. Dawson (1962a) noted that his earlier collected northern Gulf of California specimens identified as "*Antithamnion pacificum*" (Dawson, 1944a) were missing and presumed to be misfiled (AHFH to LAM, now UC). Until his specimens are found, more collections are needed to verify the presence of *Irtugovia pacifica* in the Gulf of California.

CERAMIACEAE TRIBUS DELESSERIOPSEAE

Ceramiaceae tribus Delesseriopseae Itono et Tak. Tanaka, 1973:251.

There is one genus of the tribe Delesseriopseae found in the northern Gulf of California.

Balliella Itono et Tak. Tanaka

Balliella Itono et Tak. Tanaka, 1973:249.

Algae are uniseriate branched filaments and either erect or with both erect and prostrate portions. Axial cells bear determinate branches in one plane (distichous) or slightly rotated, which are opposite pairs of branches of unequal lengths. Indeterminate lateral branches are produced regularly or irregularly depending on species, replacing one of the determinate branches of a pair. In mature portions of the axes, ascending and descending branched, rhizoid-like filaments arise from the basal cells of the determinate branches (i.e., periaxial cells) and encircle the axial row of main axes and indeterminate laterals, eventually forming a loose or dense pseudoparenchymatous cortex. Spherical vesicular cells (gland cells) are generally on the basal cells of branches (periaxial cells) or occasionally on contiguous cells borne adaxially, abaxially, or both, and may also occur on the rhizoid-like filaments corticating the axes. Vesicular cells are attached to the parent cell by a thin cytoplasmic thread.

Tetrasporangia are spherical to ovoid and cruciately divided and can be sessile or pedicellate, single or in clusters, and borne adaxially as well as abaxially on the periaxial (and occasionally second) cells or can be on short branchlets arising from the periaxial cells. Carpogonial branches are four-celled, with the procarps formed at successive levels along main axes, and borne singly on periaxial cells; sometimes an axial cell supports fertile periaxial cells to both sides. Carposporophytes are surrounded by accessory involucral filaments or naked. Spermatangial branchlets of 1–4 fertile cells, each with whorl of spermatangial parent cells that cut off both spermatangia and new spermatangial parent cells. Spermatangial structures develop along lateral branch cells, starting on proximal cells and extending distally, borne abaxially and/or adaxially.

REMARKS. Additional distinguishing features have been tentatively recognized for the genus, pending their discovery in the generitype *Balliella crouanioides* (Itono) Itono et Tak. Tanaka (1973; basionym: *Antithamnion crouanioides* Itono, 1971a). These characters include the absence of adventitious development of new axes from periaxial and contiguous cells of determinate branches, and the origin of vesicular cells from axial cells near the apices and transference to periaxial cells (Huisman and Kraft, 1984; Athanasiadis, 1996a). There is one species of *Balliella* known in the Gulf of California.

***Balliella pseudocorticata* (E. Y. Dawson) D. N. Young**

Antithamnion pseudocorticatum E. Y. Dawson, 1962a:20, pl. 7: figs. 1–5; González-González et al., 1996:174.

Balliella pseudocorticata (E. Y. Dawson) D. N. Young, 1981:94, figs. 1, 2; Athanasiadis, 1996a:43; CONANP, 2002:138.

Bakothamnion curassavicum C. Hoek, 1978:48, figs. 1, 2.

Algae minute, up to 5 mm high; with both prostrate and erect axes, upper axes sinusoidal, attached to substratum by long, multicellular rhizoids. Axial cells 100–120 µm in diameter by 270–300 µm in length; bearing at their distal end an opposite pair of distichous, unequal branches. Determinate branches with slightly smaller cell than contiguous cells at their base; oppositely pinnately branched up to 2 orders. In mature portions, branched rhizoid-like filaments issued by periaxial cells loosely corticate the axial row of main axes and indeterminate lateral branches. Secondary indeterminate lateral branches replacing a branch in pair, borne alternately at irregular intervals, up to 5(–10) axial cells apart. Vesicular (gland) cells round, up to 13 µm in diameter, borne abaxially and singly (up to 2 in older portions of thallus) on basal cells of lateral branches (periaxial cells). Corticating rhizoid-like filaments may also bear vesicular cells.

Reproductive structures have not been observed in Gulf of California material. Tetrasporangia, described from specimens from Seychelles, are borne adaxially and sessile from basal cells of lateral branches (Huisman and Kraft, 1984).

Habitat. On rocks, coral rubble, and worm tubes; shallow subtidal (also dredged to about 20 m depths).

Distribution. Gulf of California: Bahía de Loreto to La Paz. Eastern Pacific: Isla Fernandina, Galápagos Islands.

Type Locality. Dredged 4–10 fathoms (7.3–18.3 m); Canal de San Lorenzo (channel between the southern end of Isla Espíritu Santo and northern peninsula from Punta Coyote to Punta San Lorenzo), near entrance to Báhia de La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. *Balliella pseudocorticata* is apparently uncommon in the Gulf of California. It has a wide distribution: reported in the western Atlantic from Bermuda (Schneider and Searles, 1997), Florida (Dawes and Mathieson, 2008), Puerto Rico (Ballantine and Wynne, 1986), the Greater Antilles (Littler and Littler, 2000), Curaçao (Hoek, 1978, as "*Bakothamnion curassavicum*"), and Colombia (Díaz-Pulido and Díaz-Ruíz, 2003); in the Indian Ocean from the Seychelles (Huisman and Kraft, 1984) and Maldive Islands (Silva et al., 1996a); and in the Pacific from the Galápagos Islands (Young, 1981) and New Zealand (Adams, 1994).

Ceramiaceae tribus Ceramieae

Ceramiaceae tribus Ceramieae Fries, 1836:302; Athanasiadis, 1996a:180.

There are four genera of the tribe Ceramieae present in the northern Gulf of California. Athanasiadis (1996a) noted that the entire group is in need of a systematic revision.

Centroceras Kützing

SEE FIGURE 89A

Kützing, 1842 [1841]:731; Kylin, 1956:379.

Algae erect, often from prostrate axes, composed of cylindrical uniseriate axial filaments entirely corticated by a single layer of smaller cells; basipetal cortical cells rectangular, arranged in closely spaced longitudinal rows parallel to the axes. Apices often forcipate; branching is subdichotomous, trichotomous, tetrachotomous, alternate, subsecund, or irregular, with all orders of branching similarly corticated. The cells of the axial filament each cut off a ring of 6–20 periaxial cells at their upper end. The first periaxial cell issues 4 cortical initials, while each of the other periaxial cells cut off 3 cortical initials that develop the cortical filaments—2 short acropetal filaments and 1 basipetal filament. One of the acropetal initials also cuts off a basipetal (descending) filament secondarily, and this filament and the basipetal-initial-produced filament (i.e., 2 descending filaments per periaxial cell) extend to match the elongation of the axial cell. Axes completely corticated, with a segmented appearance as successive axial cells are individually corticated. The majority of cortical growth is in the basipetal direction, and cells of the long basipetal filaments are rectangular. Most species have one to many spines formed at the nodes by the acropetally produced cortical cells, and gland cells are present in many species (although they may be inconspicuous). Rhizoids are uniseriate and multicellular, issued at nodes by periaxial cells, rarely by cortical cells.

Tetrasporangia develop from the periaxial cells and are usually tetrahedrally divided; initial issued abaxial and subsequently become whorled at nodes. Tetrasporangia protrude from the cortex and may be naked or subtended by involucral filaments or spines or both. Gametophytes are dioecious. Carpogonial branches 4-celled, issued by periaxial cells in a row along upper portions of fertile thalli. Mature cystocarps are sessile, spherical, and encircled by several short involucral branches. Spermatangia form dense sori, whorled about the nodes. Spermatangia are minute elliptical to clavate cells borne terminally, singly or in groups of twos and threes on specialized monosiphonous freely branched filaments that arise from the anterior portion of periaxial cells.

Remarks. Although not observed in Gulf of California specimens of *Centroceras*, specialized asexual reproductive structures termed "missiles" have been reported in *C. clavulatum* from the Red Sea (Lipkin, 1977). They are proposed to be the alga's response to intense grazing pressure.

Two species of *Centroceras* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *CENTROCERAS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Gland cells at nodes flattened; tetrasporangia projecting from cortex, involucres absent . . . . ***C. clavulatum***
1b. Gland cells at nodes ovoid; tetrasporangia with 4- to 6-celled involucres . . . . ***C. gasparrinii***

Centroceras clavulatum (C. Agardh) Montagne

Ceramium clavulatum C. Agardh in Kunth, 1822:2.

Centroceras clavulatum (C. Agardh) Montagne, 1846b:140; J. Agardh, 1851:148; Harvey, 1853:211, pl. 33: fig. C; Howe, 1911:509; Setchell and Gardner, 1924:779; Okamura, 1936:743, fig. 355; Kylin, 1941:30; Smith, 1944:328, pl. 84: figs. 5, 6; Dawson, 1944a:321; 1962b:68, pl. 26: fig. 7, pl. 27: fig. 3; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:9; Abbott and Hollenberg, 1976:604, fig. 547; Itono, 1977a:35, 118, 201, figs. 16A,B, 39A,B; Huerta-Múzquiz, 1978:335; Pedroche and González-González, 1981:66; Stewart and Stewart, 1984:145; Boo and Lee, 1985:298, figs. 1–6; Mendoza-González and

Mateo-Cid, 1986:425; Sánchez-Rodríguez et al., 1989:44; Dreckmann et al., 1990:32; Stewart, 1991:127; Mateo-Cid et al., 1993:48; León-Tejera et al., 1993:200; González-González et al., 1996:184; Anaya-Reyna and Riosmena-Rodríguez, 1996:864. tbl. 1; Yoshida, 1998:886, fig. 3-84C–E; Abbott, 1999:261, fig. 73A–F; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; Cruz-Ayala et al., 2001:191; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:9.

Algae tufts, 0.5–3.0 cm tall; with axes 150–320 µm in diameter; subdichotomously branched or occasionally trichotomous; branching at intervals of 9–10 axial cells in the main axes and intervals of 6–9 axial cells in lateral axes. Apices forcipate and slightly inrolled. Short proliferous branches with undivided inrolled apices common in lower portions of thallus. Periaxial cells 12–16 at a node; first periaxial cell produces 4 cortical initials; all other periaxial cells each cut off 3 cortical initials, 2 acropetally and 1 basipetally. First cortical initial may cut off 1 or 2 cells acropetally; one a cortical cell and the other may be a spine; or 1 flattened gland cell; or 2 cortical cells. Second cortical initial cuts off 1 cell acropetally and a filament basipetally. The third cortical initial produces a descending (basipetal) file of cells. The 2 basipetally directed filaments keep pace with the elongation of the axial cell, completely corticating the thallus. Cortical cells subrectangular, 10–18 µm high, 5.0–10.5 µm wide; arranged in unbranched longitudinal rows. Acropetal cortical filaments 2 cells long (including cortical initial); basipetal filaments 18–25 cells long. Straight, 3-celled spines few to many, up to 50 µm long; whorled about the nodes, adding to the segmented appearance of the thallus. Segments reach 360–600 µm in length at the basal dichotomies; decreasing in length toward apices. Rhizoids 1 to several cells long, issued from periaxial cells at the nodes, often ending in a multicellular attachment pad.

Tetrasporangia tetrahedrally divided, 35–45(–50) µm in diameter; emergent and whorled about the nodes (see Joly, 1965: fig. 502; Itono, 1977a: fig. 39A, B); usually borne in distal segments of erect axes or in short proliferous branches. Gametophytes dioecious. Cystocarpic thalli were not found in Gulf collections. Spermatangial clusters of 2–3 clavate spermatangia, terminal on specialized, freely branched, uniseriate filaments arising from the upper end of periaxial cells; densely whorled at the nodes.

Habitat. On rocks, tidal platforms, or other algae; low intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Eureka; Mazatlan, Sinaloa to Narayit. Eastern Pacific: Santa Cruz, California, to Peru; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Guererro to Oaxaca. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea.

Type Locality. Callao (west of Lima), Provincia Constitucional, Peru.

Remarks. Cystocarps, although not found in Gulf material, have been described for *C. clavulatum* elsewhere: cystocarps of western Atlantic specimens were bilobed and partly surrounded by several involucral filaments and borne laterally (Taylor, 1960). Molecular and morphological studies on the broadly defined "*Centroceras clavulatum* complex" found it to include a number of distinct species (Won et al., 2009). On the basis of phylogenetic analyses and consistent morphological differences, three previously described species were resurrected, including *C. gasparrinii*, along with two others that were described as new species (Won et al., 2009). In light of this study, all Gulf of California and Pacific Mexico specimens referred to "*Centroceras*" should be re-examined to determine if they are correctly identified or represent other species.

Centroceras gasparrinii (Meneghini) Kützing

FIGURE 74

Ceramium gasparrinii Meneghini, 1844a:186.

Centroceras gasparrinii (Meneghini) Kützing, 1849:689; Won et al., 2009:231, figs. 3a–o, 4a–h,11a–d, 14b,h.

Centroceras inerme Kützing, 1849:688; Kützing, 1863:7, pl. 17, figs. e–g; Titlyanova et al., 2006:202.

Centroceras clavulatum var. *inerme* (Kützing) Piccone, 1886:54; Dawson, 1966a:27; 1966b:65; González-González et al., 1996:184.

Ceramium clavulatum var. *inerme* (Kützing) Weber-van Bosse, 1923:322.

Thalli of erect and prostrate axes, up to 6 cm high and to 265 µm in diameter, subdichotomously or occasionally trichotomously branched (rarely a tiny fourth branch occurs), with the third branch in the middle of a fork and smaller. Erect axes with forcipate tips, inrolled to some degree; branching at intervals of 10–12 axial cells in both the main and lateral axes, and adventitious branches may develop from periaxial cells at the nodes in lower portions of thallus. Nodes with 12–19 periaxial cells; all periaxial cells initiate smaller-celled filaments that form the cortex. Mature cortex of rectangular cells (about 10 µm in diameter by 14–25 µm in length) in regular longitudinal rows, completely covering the axial cells. Except for the first periaxial cell produced at a node, most periaxial cells issue 2 acropetal initials at their anterior end and 1 basipetal initial at their posterior end. Acropetal ascending filaments 1–2 cells long (except when with spines and longer tetrasporangial involucres), and the basipetally directed filaments (one from the acropetal initial and one from the basipetal initial), 13–23 cells long. Straight, 3-celled spines (including the cortical initial) in a whorl at each node throughout the thallus. Gland cells ovoid, at distal end of node, about 10 µm in diameter. Multicellular uniseriate rhizoids, 25–40 µm in diameter, issued at the nodes by periaxial cells, often end in digitate pads and attach the alga to its host or the substratum.

Tetrasporangia tetrahedrally divided, 30–45 µm in diameter and about 50 µm long (excluding the sheath), emergent, subtended by unbranched involucral filaments, 4–6 cells long, arising from first cortical initials or transformed from spines. Tetrasporangia whorled about nodes usually borne in distal segments of erect axes or in short proliferous branches.

Habitat. On rocks and in algal turf; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía San Carlos; El Tecolote, Bahía de La Paz to Cabeza Ballena. Eastern Pacific: California; Baja California; Panama. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea.

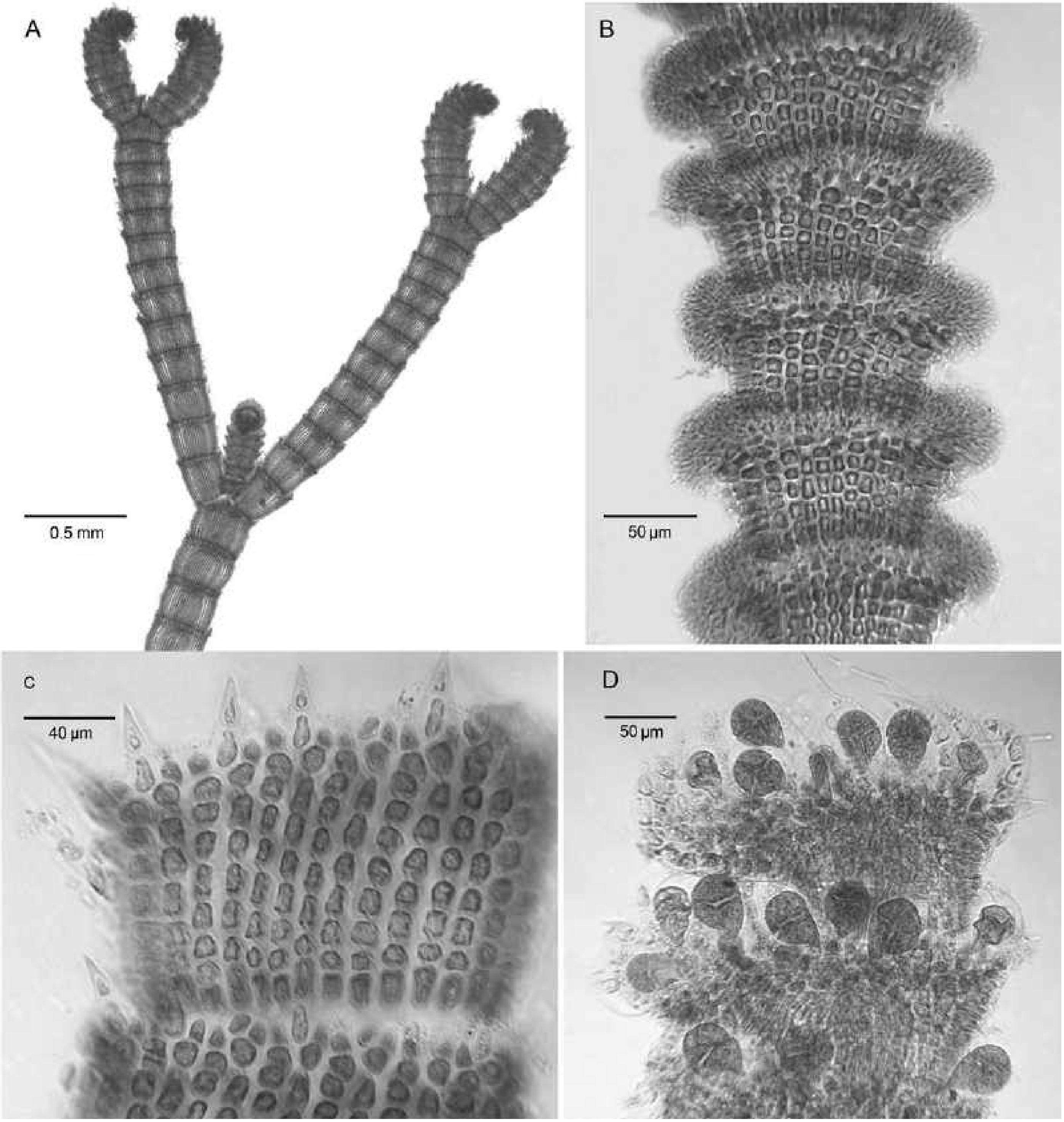


FIGURE 74. *Centroceras gasparrinii*: A. Apical region showing dichotomously to trichotomously branched axis, forcipate and inrolled apices, with numerous spines (*JN-4285*, US Alg. Coll. microscope slide 4792). B. Spermatangial branchlets whorled at nodes (*JN-4131a*, US Alg. Coll. microscope slide 4784). C. Detail of cortex showing cells arranged in longitudinal rows and spines whorled at nodes (*JN-4131b*, US Alg. Coll. microscope slide 8700). D. Tetrasporangia whorled at nodes, subtended by 5- to 6-celled involucres (*JN-4131e*, US Alg. Coll. microscope slide 4759).

Type Locality. Palermo, northwest coast of the island of Sicily, Mediterranean Sea, southern Italy.

Remarks. On the basis of molecular and morphological differences, Won et al. (2009) distinguished *Centroceras gasparrinii* from others of the "*Centroceras clavulatum* complex." The characteristic emergent tetrasporangia, involucres, and spines now recognized for *C. gasparrinii* were illustrated by Norris and Bucher (1982: fig. 102, as "*C. clavulatum*").

Ceramium Roth

Ceramium Roth, 1797:146.

Algae are monosiphonous, generally terete filaments, with both prostrate and erect or decumbent axes that are subdichotomously, alternately, or irregularly branched. Axes are composed of a central axial row of larger cells that each produce at their distal end a ring of 4 or more smaller periaxial cells that each usually give rise to (1–)3–5 cortical initials that develop smaller-celled filaments of limited growth, acropetal filaments (ascending toward apices), and/or basipetal filaments (descending toward base) that form the relatively consistent cortical pattern. In some species pseudoperiaxial cells divide off laterally from periaxial cells, increasing the number of cells in the periaxial ring; these pseudoperiaxial cells may also issue cortical filaments. Axes are completely or incompletely corticated (leaving a noncorticated internodal space) by ovoid to angular cells. In some species the cortex is completed early, whereas in others development continues to elaborate the cortical pattern, making nodal bands more variable from young to older portions. Diagnostic characters for species separation are the number of periaxial cells in the ring at a node, the presence or absence of pseudoperiaxial cells, the number and positions of cortical filament initials, the development and mature pattern of cortical filaments that form the cortex, tetrasporangial features, and the thallus branching pattern. Multicelluar rhizoids develop from both periaxial and inner and outer cortical cells and can be blunt tipped or terminate in a multicellular digitate or discoid pad. Gland cells are present on cortical filaments of some species.

Tetrasporangia are sessile and borne in a variety of positions: solitary, opposite, or whorled at the nodes; and naked or surrounded by an involucre formed by upward growth of the cortical filaments or embedded completely in the cortex. Tetrasporangia are usually derived from the periaxial cells, but in some, especially robust fully corticated species, later tetrasporangia may arise from any inner cortical cell, and so tetrasporangia may appear scattered (Itono, 1977a; Womersley, 1978). Gametophytes are dioecious. Carpogonial branch is 4-celled, developed from a periaxial cell, abaxial on the lower lateral side of the supporting cell (a periaxial cell). Cystocarps may be terminal or intercalary on a branch or in the axils of branch dichotomies. Cystocarps have spherical gonimolobes that may be naked or more commonly are surrounded by 1 to several involucral branches that arise from the node below. Spermatangial parent cells develop from cortical cells and produce spermatangia terminally, forming an external layer of minute, colorless cells that cover the surface cortical cells in upper portions of thalli.

Remarks. The genus *Ceramium* is well represented with 26 species reported in the Gulf of California. Species of *Ceramium* are frequently epiphytic on larger algae or sea grasses and some are also found on solid substrata.

Four species are recorded only in the southern Gulf: *Ceramium codii* (H. Richards) Feldmann-Mazoyer (1938; basionym: *Ceramithamnion codii* H. Richards, 1901) from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985, as *C. mucronatum* Segi, 1944), *C. personatum* Setchell et N. L. Gardner (1930) from Laguna Agiabampo (Ortega et al., 1987), *C. monacanthum* J. Agardh (1894) from Punta Arena (Mateo-Cid et al., 2000) and Mazátlan (Mendoza-González et al., 1994), and *C. giacconei* Cormaci et G. Furnari (1991) from a rhodolith bed at Punta Perico, northern end of Bahía de los Muertos (Cho et al., 2003b).

Currently, there are 22 species and two varieties of *Ceramium* known in the northern Gulf, two of which are Gulf endemics, *C. obesum* and *C. periconicum*.

KEY TO THE SPECIES OF *CERAMIUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Central axial cells incompletely corticated, corticated at the nodes only (although internodal space may be greatly reduced near apices) 9

1b. Central axial cells completely corticated by smaller cells in some region of the axes; complete cortication may be interrupted at internode above a fork (branching point) and/or in basal regions of axes 2

2a. Central axial cells completely corticated in some portions of axes but with internodal gaps present at least in basal parts 3

2b. Central axial cells completely corticated throughout 5

3a. Interrupted cortication just above branching point (dichotomy); 4 cortical initials cut off per periaxial cell . . . . **C. interruptum**

3b. Cortication not interrupted at first axial cell above a branching point, complete in upper portions of axes; 5 cortical initials cut off per periaxial cell 4

4a. Axes completely corticated only in upper portions, some lower portions with cortical nodes slightly separated . . . . **C. sinicola** var. **sinicola**

4b. Axes completely corticated nearly throughout, only extreme lowermost portion with slim internodes between cortical nodes . . . . ***C. sinicola* var. *johnstonii***
5a. Thalli mainly creeping, sturdy (500–1100 µm in diameter), with thick cortex (200 µm or more) . . . . ***C. obesum***
5b. Thalli mainly erect, more slender (usually less than 500 µm in diameter), with a thinner cortex than above 6
6a. Thalli relatively tall, usually over 2 cm, up to 18 cm; spines sometimes present 7
6b. Thalli shorter, usually less than 2 cm high; spines absent 8
7a. Unicellular (to 2-celled) spines common on apices of main axes and on short lateral branchlets; lateral branchlets of similar lengths, whorled around a segment . . . . ***C. horridulum***
7b. Spines lacking or with infrequent multicellular spines; adventitious lateral branchlets longer and of more variable lengths than branchlets in *C. horridulum*, and radially arranged over several segments . . . . ***C. pacificum***
8a. Thalli sparsely, irregularly branched; with short branch apices tending to be incurved or "hooked" . . . . ***C. howellii***
8b. Thalli subdichotomously branched; epiphytic on *Codium*, attached to host by pigmented rhizoids with bulbous tips . . . . ***C. codicola***
9a. Thalli with spines 10
9b. Thalli without spines 11
10a. Thalli with straight or recurved spines arranged abaxially along upper portions, spines mostly lacking in lower portions (deciduous) . . . . ***C. paniculatum* (in part)**
10b. Spines recurved, whorled at each cortical band throughout much of thallus; spines persistent . . . . ***C. hamatispinum***
11a. Mature cortical band narrow, of 2–3(–4) tiers of cells; no basipetal cortical initials cut off from periaxial cells, acropetal cortical filament development only, or initial may look lateral to side of periaxial cell but not proximal (beneath) periaxial cell 12
11b. Mature cortical band of 3 or more tiers of cells; basipetal development slight to extensive 15
12a. In cortical band, most periaxial cells cut off 3 cortical initials, 2 acropetal initials and 1 lateral appearing initial 13
12b. In cortical band, most periaxial cells cut off 2 acropetal cortical initials; one of which is laterally directed, and this cell often cuts off an acropetal cell 14
13a. Lateral initial produced by a longitudinal (vertical) division of a periaxial cell; the lateral initial does not divide further; tetrasporangia naked, protruding . . . . ***C. periconicum***
13b. Lateral initial may divide further; tetrasporangia with involucres . . . . ***C. mazatlanense* (in part)**
14a. Axes and branches less than 35 µm in diameter throughout . . . . ***C. affine* var. *affine***
14b. Axes and branches larger, greater than 40 µm in diameter . . . . ***C. affine* var. *peninsularis***
15a. Tetrasporangia naked (without involucre), emergent 16
15b. Tetrasporangia involucred or immersed in cortex 18
16a. Gland cells usually present, sometimes giving a green iridescence; apices markedly inrolled (circinate) . . . . ***C. aduncum***
16b. Gland cells absent; apices not markedly inrolled 17
17a. Lower internodes 1.0–2.5 times taller than broad; cortical cell size within node decreasing in distal direction in upper portions of axes; branches less dense and longer in upper portions of thallus . . . . ***C. caudatum***
17b. Lower internodes broader than tall; cortical cell size within a node not changing progressively with direction; branches dense and relatively shorter in upper portions of thallus . . . . ***C. zacae***
18a. Primary axes mostly prostrate, with some erect filaments 19
18b. Primary axes mostly erect, with some prostrate portions 20
19a. Erect axes unbranched or irregularly branched (opposite or alternate branching in prostrate portions); tetrasporangia completely immersed in the cortex of short clavate branches, several tetrasporangia per nodal band . . . . ***C. procumbens***
19b. Erect axes sparsely branched (basal portions unbranched to sparsely branched); tetrasporangia protruding through the cortex, partially surrounded by corticating filaments at their base, usually solitary (or 2) at a node . . . . ***C. serpens***
20a. Axes slender, 100 µm in diameter or less 21
20b. Axes more robust, greater than 100 µm in diameter 22
21a. Internodes of tetrasporangial axes not reduced; tetrasporangia 25–35 µm in diameter . . . . ***C. camouii***
21b. Internodes of tetrasporangial axes abruptly reduced in swollen terminal portions; tetrasporangia 30–40 µm in diameter . . . . ***C. equisetoides***
22a. Posterior end of periaxial cells cuts off basipetal corticating cells in descending direction 23
22b. Periaxial cells cut off pseudoperiaxial cells obliquely in a lateral direction (pseudoperiaxial cells are positioned inbetween periaxial cells in nodal ring) 24
23a. Axes branching subdichotomous; apices forcipate . . . . ***C. paniculatum* (in part)**
23b. Axes branching irregular and sparse; apices nonforcipate . . . . ***C. vagans***

24a. Cortical bands with 7–8 periaxial cells, each cuts off laterally a pseudoperiaxial cell; both periaxial and pseudoperiaxial cells cut off acropetal as well as basipetal initials, and nodal band development occurs in both directions . . . .*C. clarionense*

24b. Cortical bands with 5(–6) periaxial cells; each periaxial cell cuts off a wedge-shaped pseudoperiaxial cell laterally, nodal band development mainly acropetal; only pseudoperiaxial cells may cut off a basipetal initial (appears more or less lateral) . . . . ***C. mazatlanense* (in part)**

Ceramium aduncum Y. Nakamura

FIGURE 75; SEE ALSO FIGURE 78A

Ceramium aduncum Y. Nakamura, 1950:158, figs. 2b, 3; 1954:18, figs. 13-2, 17-4; 1965:138, pl. 2: figs. 1, 2; Noda, 1972:13, fig. 15; Itono, 1972:81, fig. 11A; 1977a:34, 113, 199, 267, figs. 13L(1–7), 38D,E, 60E; Meneses, 1995:166, figs. 1–4; González-González et al., 1996:184; Lewis and Chiu, 1996: figs. 1–2; Yoshida, 1998:889, fig. 3-84F–H; Abbott, 1999:266, fig. 74A–D; CONANP, 2002:138; Abbott et al., 2002:303, figs. 6–7; Mateo-Cid et al., 2006:56; Pacheco-Ruíz et al., 2008:211; H.-S. Kim, 2012:31, figs. 17–19.

Ceramium clarionense sensu Dawson, 1950c:134 [in part], pl. 4: fig. 29; 1954b:448, fig. 55K; 1961b:440; 1962a:53 [in part; Gulf of California specimens], pl. 18: figs. 5, 6; 1966a:26; Phạm-Hoàng, 1969:236, fig. 2.167; Schnetter and Bula-Meyer, 1982:151, pl. 25: figs. C,D, pl. 27: fig. A [non *Ceramium clarionense* Setchell et N. L. Gardner, 1930:170].

Ceramium sp. nov.? sensu Setchell and Gardner, 1930:173, pl. 7: fig. 25; Nakamura, 1950:159 [see Meneses, 1995:166].

Algae up to 1.0 cm tall; axes mostly erect with creeping portions, branching subdichotomously at intervals of 7–8(–12) nodes; individual axes up to 350 μm in diameter basally, tapering upward; cortication restricted to nodes; apices forcipate and noticeably inrolled; lower portions creeping on the substratum, attached by few to many unbranched, uniseriate rhizoids, usually 2–3 cells long, up to 15 μm wide, developed from both cortical and periaxial cells. Axial cells mostly isodiametric or slightly longer than wide. Internodal space about 100 μm long basally, decreasing upward, at times reduced to just a thin line

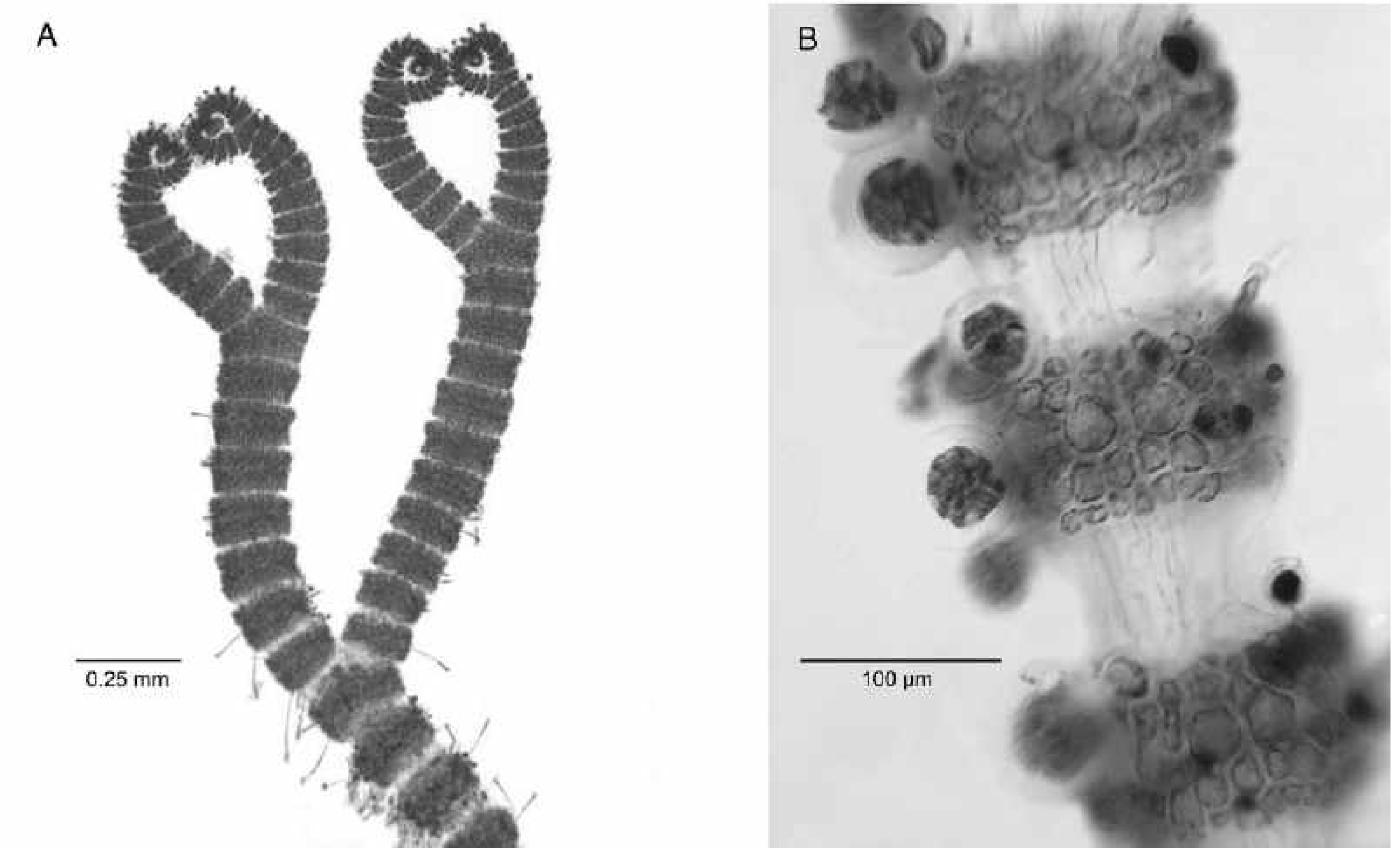


FIGURE 75. *Ceramium aduncum*: A. Upper portion with circinate apices and conspicuous gland cells (*JN-5060*, US Alg. Coll. microscope slide 8701). B. Several emergent tetrasporangia (with a thick hyaline envelope), borne off one side of node (*JN-3098*, US Alg. Coll. microscope slide 8690).

near apices. Cortical bands truncate; up to almost twice as broad as high. Periaxial cells 6–8(–11) in number, depending on axes diameter, each periaxial cell cuts off 2 acropetal cortical initials and 2 basipetal initials. Each initial issues corticating filaments several cells in length. Nodal cortication up to 3 cell layers thick; cortical cell size progressively smaller with successive divisions. Surface cortical layer of small angular cells, 7–15 µm in diameter; surface cells absent in gaps near the center of nodal band, revealing the larger round periaxial cells beneath. Gland cells (10–)24–45 µm in diameter, conspicuous (staining deeply with aniline blue); often numerous in both acropetal and basipetal corticating filaments (may be responsible for iridescence seen in live material); may be sparse or lacking in some specimens.

Tetrasporangia naked, protruding, tetrahedrally divided; surrounded by thick hyaline envelope; 30–40 µm in diameter (not including envelope), initially borne adaxially, several per node; arising from cortical filament cells, rarely from periaxial cells; later scattered throughout the nodal band. Mature cystocarps, 150–180 µm in diameter, surrounded by several involucral branches. Spermatangia minute sessile cells, developing first on the adaxial side of a node, then continuing to develop over the cortical band.

HABITAT. In tide pools, epiphytic on various algae, including corallines, *Sargassum*, *Padina*, and *Codium*, and epizoic on bryozoans and sponges; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena; Nayarit; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: California Channel Islands to Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur; Isla Guadalupe; Rocas Alijos; Oaxaca; Isla Gorgona, Colombia. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Taiwan; Vietnam; Korea.

TYPE LOCALITY. Gôza, Shima Peninsula, Mie Prefecture ("Sima Province," Nakamura, 1965), Honshū Island, Japan.

REMARKS. There has been some confusion on the identity of *Ceramium aduncum* and *C. clarionense* in the Gulf. Reexamination of Dawson's (1962a) Gulf of California specimens identified as "*Ceramium clarionense*" (US Alg. Coll.) revealed them to be *C. aduncum*. Dawson's (1950c:134) expanded description of "*C. clarionense*" was apparently based on *C. aduncum*. Examination of isotype microscope slide labeled "type" of *C. clarionense* (AHFH-124, microscope slide 183; now UC) revealed it to have two species: a sterile *C. clarionense* and a tetrasporic *C. aduncum*. The features distinguishing *C. aduncum* are its isodiametric or slightly longer than broad axial cells, lack of pseudoperiaxial cells in the periaxial ring, refractive gland cells usually being present, circinate apices (inrolled tips), and naked tetrasporangia, whereas *C. clarionense* has spherical axial cells, pseudoperiaxial cells in the periaxial cell ring, lacks refractive gland cells, has strongly incurved apices, and has tetrasporangia that are surrounded by involucres (see also Meneses, 1995).

Ceramium affine Setchell et N. L. Gardner var. *affine*

Ceramium affine Setchell et N. L. Gardner, 1930:172; Dawson, 1944a:317, pl. 51: fig. 4; Taylor, 1945:272 [with a query]; Dawson, 1950c:132; 1961b:439; 1962a:50, pl. 17: fig. 6; 1966a:26; Itono, 1972:78, fig. 5; Abbott and Hollenberg, 1976:592, fig. 531; Itono, 1977a:31, 99, 195, 230, 261, figs. 13B, 15B, 50D, 58D; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; Sánchez-Rodríguez et al., 1989:44; Mateo-Cid and Mendoza-González, 1992:21; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:184; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Yoshida, 1998:889; L. Aguilar-Rosas et al., 2000:131; CONANP, 2012:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Riosmena-Rodríguez et al., 2005a:33; Pacheco-Ruíz et al., 2008:211.

Ceramium affine var. *originale* E. Y. Dawson, 1950c:133, *nom. superfl.*; González-González et al., 1996:185.

Algae epiphytic or entangled with other algae, 4–6 mm high, main axis 20–35(–42) µm in diameter at base; branching irregularly subdichotomous, at intervals of 10–12 axial cells; corticated only at the nodes; branch apices straight to slightly incurved; proliferous branches uncommon; attached by rhizoids developed from periaxial and cortical cells. Periaxial cells number 4(–5), each periaxial cell cuts off 2 acropetal cortical initials. The second initial may be slightly larger than the first and is laterally displaced. Both initials may produce 1(–2) rounded cells acropetally, forming a very narrow cortical node usually only (1–)2–3 cells tall. No basipetal cortical initials or filaments develop. Internodes long and narrow, usually 3–4(–6) times longer than wide, 30–40 µm in diameter in lower portion, 24–28 µm in upper portion; becoming shorter in length toward apex.

Tetrasporangia tetrahedrally divided, oblong, projecting and naked, 27–45 µm in diameter; borne abaxial, usually single, or occasionally with 2 per node. Tetrasporangia are issued from periaxial cells. Cystocarps unknown in Gulf of California collections. Spermatangia forming a layer of tiny colorless cells beginning on one side of a cortical band and later completely covering the band.

HABITAT. Epiphytic on various algae; shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Puerto Refugio, Isla Ángel de la Guarda; Nayarit to Jalisco. Eastern Pacific: southern California to Bahía Magdalena, Baja California Sur; Isla Guadalupe; Ecuador. Western Pacific: Japan; Korea (Y.-P. Lee, 2008; H.-S. Kim, 2012).

TYPE LOCALITY. Epiphytic on *Codium simulans*; Isla Guadalupe, off Baja California, Pacific Mexico.

REMARKS. Although cystocarps are unknown in the Gulf *Ceramium affine* var. *affine*, in specimens from California, they were reported to be 100–120 µm in diameter, with large carposporangia (Abbott and Hollenberg, 1976), and in the Japanese *C. affine,* cystocarps were described as being surrounded by 3–4 involucral branchlets (Itono, 1977a). Specimens tentatively identified as *Ceramium affine* were also reported from the Galápagos Islands (Taylor, 1945, as "*Ceramium affine*, *prox.*"). Barros-Barreto et al. (2006: 912, tbl.3, figs. 2, 4a–h), using morphological and molecular data, have reported *C. affine* in the Western Atlantic from Brazil.

Ceramium affine var. *peninsularis* E. Y. Dawson

FIGURE 76

Ceramium affine var. *peninsularis* E. Y. Dawson, 1950c:132, pl. 2: figs. 16, 17; 1961b:439; 1962a:51, pl. 17: figs. 9, 10; Huerta-Múzquiz and

Tirado-Lizárraga, 1970:129; Huerta-Múzquiz, 1978:340; González-González et al., 1996:185.

Algae 10–12 mm high, subdichotomously branched at intervals of (8–)12–18 axial cells, with occasional adventitious branches; main axes cylindrical, 60–110 μm in diameter near base, tapering abruptly the last several segments to the apex; apices straight to slightly incurved. Axes attached by unbranched rhizoids with blunt tips or multicellular digitate pads. Axes corticated only at the nodes, with narrow cortical bands of only 2–3 tiers of cells. Internodes elongate; mostly (4–)6–8 times as long as broad; below (up to 450 μm long), diminishing in size toward the upper portions of the thallus. Periaxial cells number 4; each cuts off 2 acropetal cortical initials; the second cortical cell initial is larger than the first and is displaced laterally to one side of the periaxial cell (resembling a pseudoperiaxial cell). These laterally directed acropetal cells are slightly smaller than the periaxial cells and often wedge shaped, interposed between the periaxial cells and regularly produce 1 acropetal cell. The cortical band lacks basipetal initials and all basipetal filament development.

Tetrasporangia oblong, up to 60 μm long, 30–50 μm in diameter; protruding, naked, each within a hyaline envelope; 1 to several borne irregularly secund at a node. Cystocarps, to 150 μm in diameter, are surrounded by several involucral branches. Spermatangia clusters covering the surface of cortical cells, starting adaxially, and with time completely coating the nodal band.

HABITAT. Epiphytic or entangled on various algae; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de San Lucas. Eastern Pacific: Corona del Mar, southern California to Laguna Ojo de Liebre, Baja California; Golfo de Tehuantepec, Oaxaca to Chiapas.

TYPE LOCALITY. Dredged from 4–6 m depth; Isla Concha, Laguna Ojo de Liebre (Scammon's Lagoon), Baja California, Pacific Mexico.

REMARKS. *Ceramium affine* var. *peninsularis* is the larger of the two varieties, almost twice the size of *C. affine* var. *affine* in all vegetative dimensions. Although both varieties are reported in the Gulf, only *C. affine* var. *peninsularis* was found in our Gulf collections.

Ceramium camouii E. Y. Dawson

Ceramium camouii E. Y. Dawson, 1944a:319, pl. 51: figs. 2, 3; 1950c:129; 1957a:8; 1961b:440; 1962a:52, pl. 17: fig. 8, pl. 18: figs. 1, 2; Abbott and Hollenberg, 1976:594, fig. 533; Huerta-Múzquiz and Mendoza-González, 1985:52; Mateo-Cid and Mendoza-González, 1992:21; Serviere-Zaragoza et al., 1993a:483; Mendoza-González et al., 1994:108;

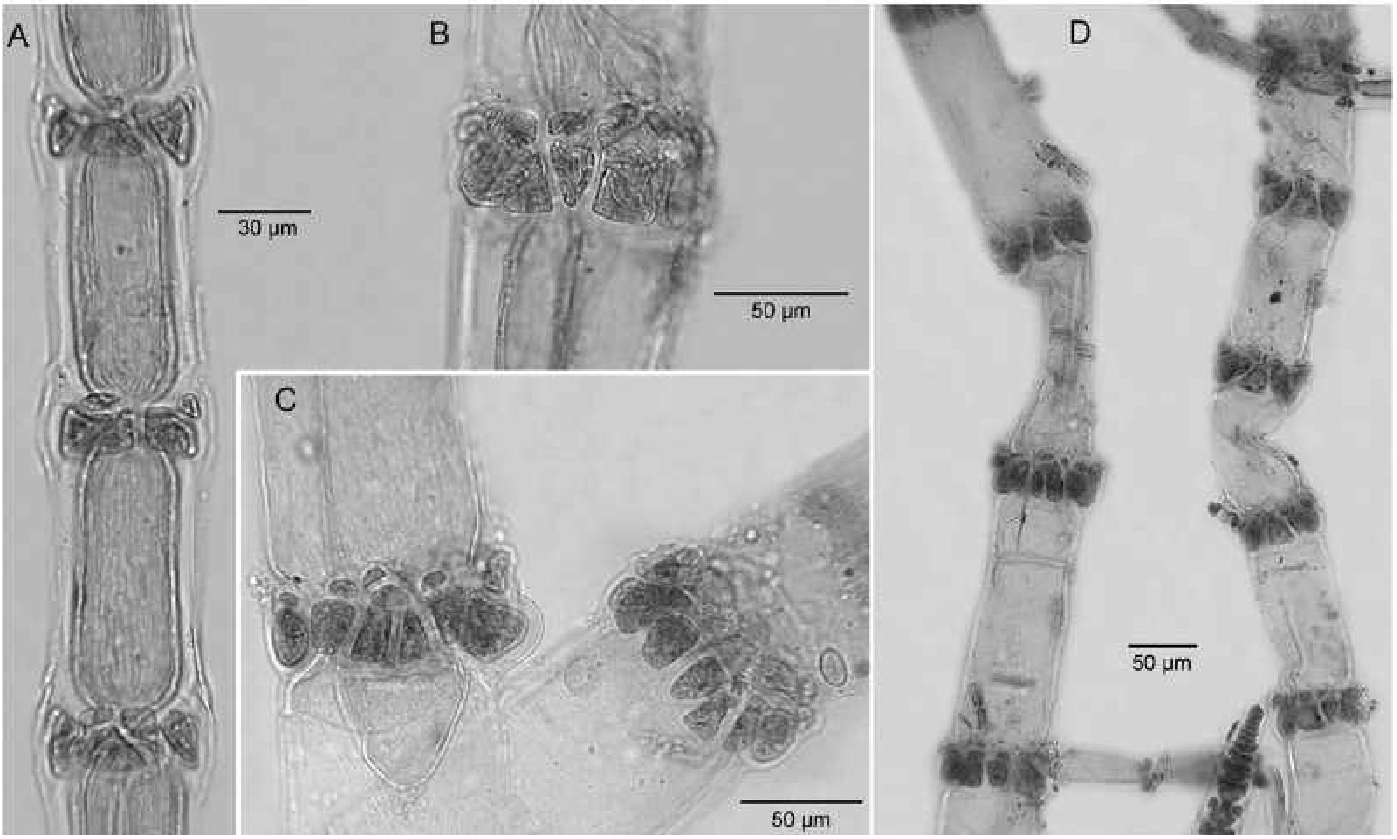


FIGURE 76. *Ceramium affine* var. *peninsularis*: A. Young nodes showing first acropetal cortical initial, and second laterally directed acropetal initial. B, C. Mature nodal cortication. D. Two filaments showing long internodes and short nodes, 2(–3) cells high (A–D, *JN-4002*, US Alg. Coll. microscope slide 8702).

González-González et al., 1996:185; Silva et al., 1996b:233; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138.

Algae up to 3–4 mm high, thin and delicate, 30–60(–80) μm in diameter, corticated only at the nodes, with very short nodal bands of small cells (about 3 cell rows high). Axes sparingly subdichotomously branched, with straight, nonforcipate apices; cortical bands shorter than internodes, internodes long basally; attached by rhizoids issued 1 per node, with blunt tips or digitate attachment pads. Periaxial cells number about 4(–5), each cuts off 2 roundish acropetal cortical initials and 2 basipetal initials. The acropetal initials may produce 1 or 2 more cells acropetally, the terminal cells of the acropetal filaments occasionally bearing a slender hair. Sometimes the original 4 cortical initials may divide in half into more angular smaller cells.

Tetrasporangia 25–35 μm in diameter, surrounded by an open involucre; whorled about the nodes, giving tetrasporangial axes a tumid appearance (Dawson, 1962a). Cystocarpic and spermatangial thalli unknown in Gulf of California material.

Habitat. Epiphytic on or entangled with other algae, such as *Centroceras* and *Polysiphonia*, and in algal turfs; intertidal.

Distribution. Gulf of California: San Felipe; Isla Turner to Ensenada Bocochibampo (west of Guaymas); Bahía de Loreto to Punta Arena (north of Cabo Pulmo); Mazátlan, Sinaloa to Jalisco. Eastern Pacific: southern California to Bahía Todos Santos (near Punta Banda), Baja California; Rocas Alijos. Western Pacific: China.

Type Locality. Among other minute algae scraped from intertidal rocks; Isla Turner (Turners), off SE end of Isla Tiburón (Islas de la Cintura), Gulf of California, Mexico.

Ceramium caudatum Setchell et N. L. Gardner

FIGURES 77, 78C

Ceramium caudatum Setchell et N. L. Gardner, 1924:776, pl. 27: figs. 55–57; Dawson, 1944a:317; 1950c:134; 1959a:30; 1961b:440; 1962a:52 [in part, excluding *C. avalonae*], pl. 18: figs. 3, 4, pl. 19: fig. 7, pl. 20: fig. 1; 1966a:26; Dawson and Neushul, 1966:182; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Abbott and Hollenberg, 1976:594 [in part, excluding *C. avalonae*], fig. 534; R. Aguilar-Rosas, 1982:84; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1986:425; Mateo-Cid et al., 1993:48; Mateo-Cid and Mendoza-González, 1994b:41; Mendoza-González et al., 1994:108; González-González et al., 1996:304; CONANP, 2002:138; L. Aguilar-Rosas et al., 2002:235; Pacheco-Ruíz and Zertuche-González, 2002:468; Hernández-Herrera et al., 2005:147; Pacheco-Ruíz et al., 2008:211.

Algae with erect and prostrate portions, 4–15 mm tall, nodal bands (70–)100–120(–200) μm in diameter, internodes 80–300 μm long in lower portions, shortening upward to 20–30 μm long; apices forcipate and slightly incurved. Nodal band with 5 periaxial cells; each producing 2 acropetal cortical initials; each initial producing several branched acropetal filaments of progressively smaller cells. Basipetal development of cortical band variable and lateral. Young cortical bands may be without any basipetal development, while in mature portions of axes, a cell may be cut off obliquely from the posterior portion of a periaxial cell, laterally to one or both sides of the periaxial cell. The ends of the oblique cells remain level with the ends of the periaxial cells (not below the periaxial cell), resulting in truncate cortical bands. In robust specimens the 2 oblique laterally placed cells may divide further.

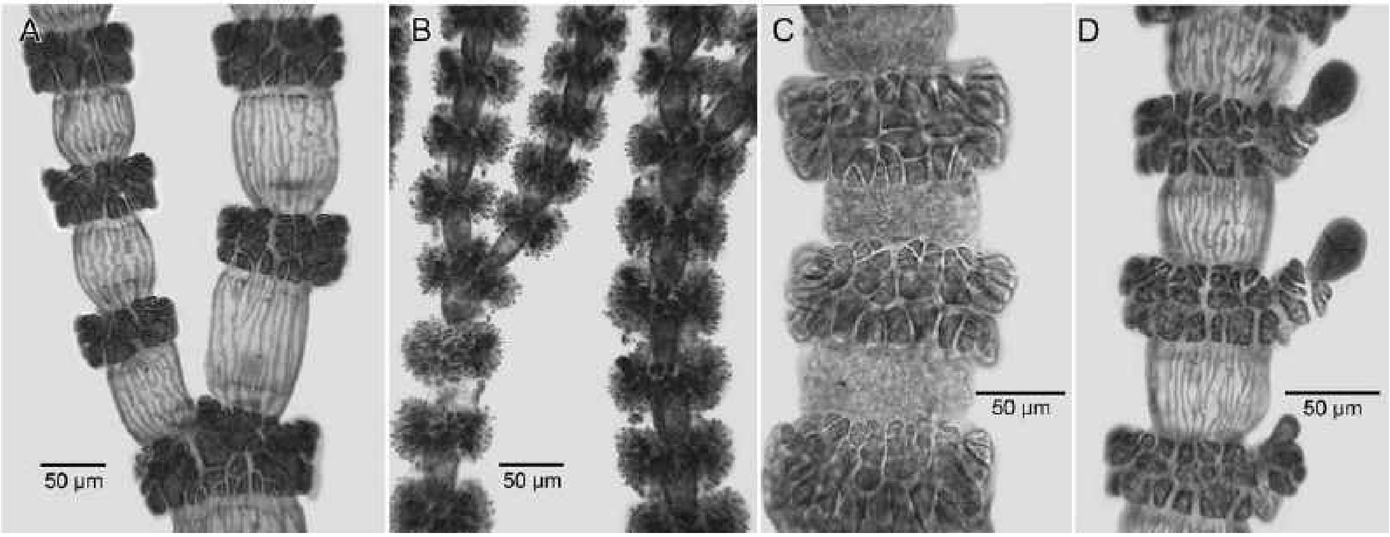


FIGURE 77. *Ceramium caudatum*: A. Nodal cortication (*JN-4904b*, US Alg. Coll. microscope slide 5256). B. Spermatangia covering nodes (*JN-4400*, US Alg. Coll. microscope slide 8709). C. Detail of mature nodal cortication (*JN-4138b*, US Alg. Coll. microscope slide 5223). D. Emergent tetrasporangia (*JN-3289*, US Alg. Coll. microscope slide 5211).

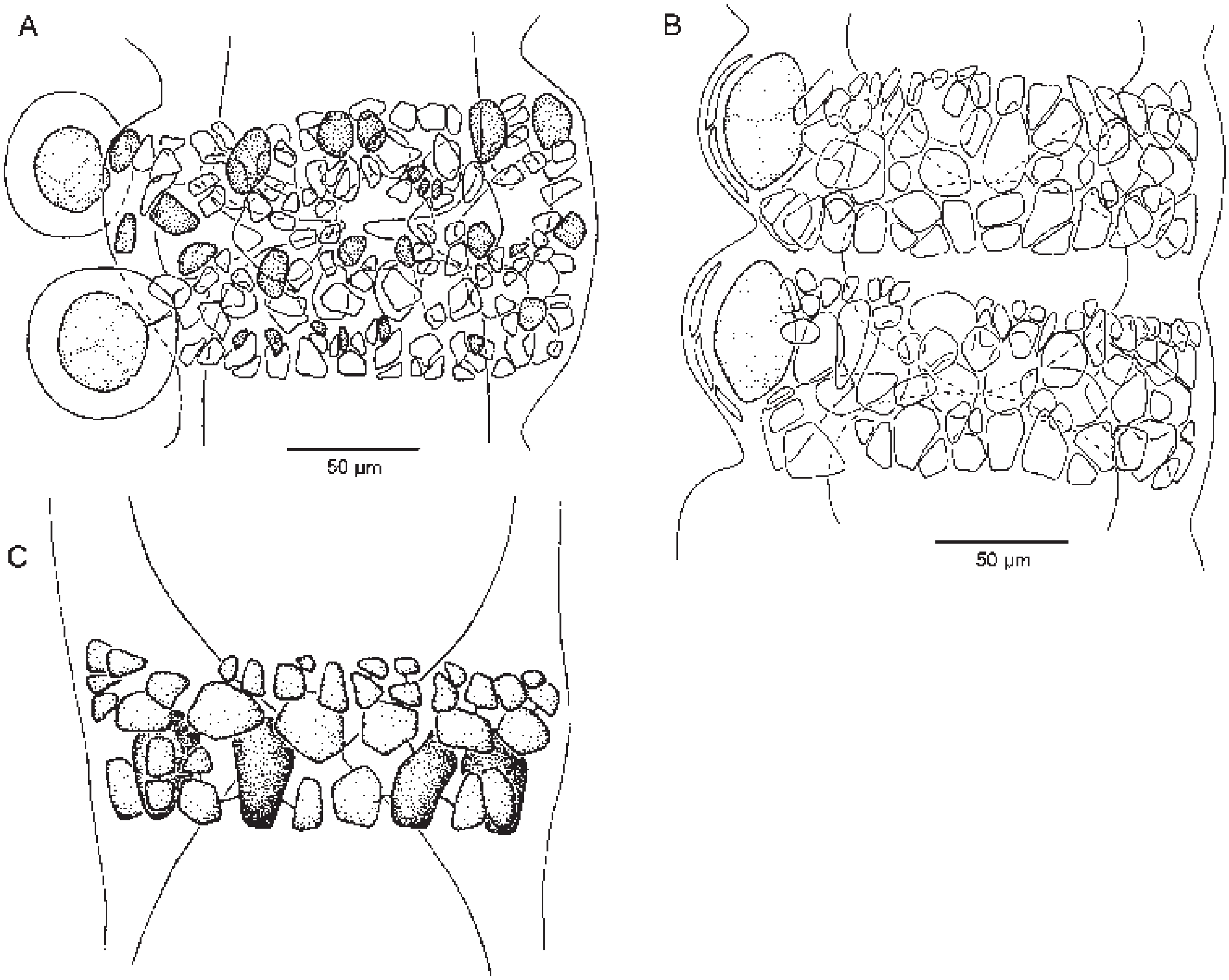


FIGURE 78. Species of *Ceramium*. A. *Ceramium aduncum:* Mature node with gland cells (darkly stippled) and naked exerted tetrasporangia (*JN-3191*, US Alg. Coll. microscope slide 4763). B. *Ceramium clarionense:* Mature node and tetrasporangia with involucres (holotype, *Mason-75*, UC). C. *Ceramium caudatum:* Nodal cortication (diagrammatic; periaxial cells darkly stippled).

Tetrasporangia 45–55(–60) µm wide, to 75 µm long, tetrahedrally divided; projecting and naked; borne abaxial and adaxial, solitary or often whorled at a node. In young stages some tetrasporangia are caudate in shape (with a tail-like appendage). Cystocarps 180–195(–270) µm in diameter; borne laterally off axes, with 2–5 involucral branches that can be long and straight; carposporangia to 55 µm long. Spermatangia forming a dense patch of minute cells, beginning on one side and then completely covering a nodal band.

Habitat. Epiphytic on *Codium* and other algae and epizoic on stalked hydroids and the black sea turtle (*tortuga negra*), *Chelonia mydas agassizii* (sometimes referred to as *C. mydas* Linnaeus or *C. agassizii* Bocourt; see Carr, 1984; Parham and Zug, 1996); occasionally intertidal to subtidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Puerto Peñasco; Isla San Jorge; Roca Rojo, Bahía Kino to Bahía Empalme (south of Guaymas); Bahía Concepción to La Paz; Mazátlan, Sinaloa to Jalisco. Eastern Pacific: California Channel Islands to Isla Guadalupe; southern California to Todos Santos, Baja California Sur; Golfo de Tehuantepec, Oaxaca; Costa Rica.

Type Locality. Floating among other algae; Eureka, near La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. The pattern of the cortical bands of *Ceramium caudatum* varies greatly from upper to lower portions of axes as the corticating filaments develop. Dawson (1962a: pl. 18: fig. 3) illustrates younger nodes, whereas the older nodes in larger specimens have additional basipetal/lateral development with "the angular cells tending to extend down over the larger rounded cells" (Dawson, 1962a:52).

The Santa Catalina Island (California Channel Islands) *Ceramium avalonae* E. Y. Dawson (1949b; 1950c; 1960a; 1962a: pl. 20: fig. 1: type of *C. avalonae*) was later considered conspecific with *C. caudatum* by Dawson (1962a) and Abbott and Hollenberg (1976). However, Womersley (1978) observed the nodal cortical structures of the two were quite different and recognized them as separate species (see also Stewart and Stewart, 1984; González-González et al., 1996).

Ceramium clarionense **Setchell et N. L. Gardner**

FIGURE 78B

Ceramium clarionense Setchell et N. L. Gardner, 1930:170, as "*C. clarionensis,*" pl. 7: figs. 26–27; Dawson et al., 1960b:10 [in part]; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Serviere-Zaragoza et al., 1993a:483; R. Aguilar-Rosas and Aguilar-Rosas, 1994:523; Meneses, 1995:168, figs. 5–10; González-González et al., 1996:185 [in part; Pacific Mexico only]; Silva et al., 1996b:233; Abbott, 1999:269, fig. 75A–C; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:211; Pérez-Estrada et al., 2012:190.

Algae mostly erect, with creeping portions, to 9 mm high, axes 95–200 µm in diameter; axes corticated only at the nodes; internodes reduced to just a line near apices; branching subdichotomous, with intervals of 7–9 nodes between dichotomies in the distal region; numerous adventitious branches often present; apices forcipate and curved inward; attached by rhizoids originating from cortical cells. Axial cells spherical, cytoplasmic strand evident as a midline in axial cells throughout the thallus. Nodal bands with 7–8 periaxial cells; each periaxial cell issues 1 small-celled acropetal corticating filament and 2 (rarely 3) larger-celled basipetal filaments and also typically cuts off a pseudoperiaxial cell (totaling 7–8 at a node). Each pseudoperiaxial cell produces 2 acropetal and 1–2 basipetal corticating filaments. Cortical cells irregularly shaped, angular, or rounded. Cortical nodes sometimes more than twice as wide as tall.

Tetrasporangia cruciately divided, to 50(–65) µm in diameter; tetrasporangia borne within the upper half of cortical node, initially abaxial, at maturity may become whorled; cortical cells issue 3- to 4-celled involucres that subtend each tetrasporangia, bloating the node. Carposporangial thalli irregularly branched; cystocarps surrounded by up to 6 involucral branchlets. Spermatangia cover cortical surface cells in distal portions of the thallus.

HABITAT. Epiphytic on larger algae; intertidal to subtidal.

DISTRIBUTION. Gulf of California: Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985); Nayarit to Jalisco. Eastern Pacific: Rocas Alijos; Isla Clarión (Islas Revillagigedo). Central Pacific: Hawaiian Islands.

TYPE LOCALITY. Growing on *Codium*, Isla Clarión, Islas Revillagigedo, Pacific Mexico.

REMARKS. Study of northern Gulf of California "*Ceramium clarionense*" sensu Dawson (1962b) showed specimens deposited in US Alg. Coll. were actually *C. aduncum* (see also Meneses, 1995, and Remarks under *Ceramium aduncum*). Thus, other records of Gulf of California "*C. clarionense*" that may be based on the interpretation of Dawson (1962a) and deposited in other herbaria (e.g., Huerta-Múzquiz and Mendoza-González, 1985) should be reexamined before the presence of *C. clarionense* in the northern Gulf of California can be confirmed. Using morphological and molecular analyses Barrios-Barreto et al. (2006) have reported *Ceramium clarionense* in the Western Atlantic from Brazil.

Ceramium codicola **J. Agardh**

Ceramium codicola J. Agardh, 1894:23; Setchell, 1905:60; Kylin, 1941:29; Smith, 1944:326, pl. 84: fig. 1; Dawson, 1945d:59; 1950c:117, pl. 1: fig. 6; Dawson et al., 1960b:6; Dawson, 1961b:440; 1962a:54, pl. 19: figs. 5, 6, pl. 20: fig. 5; Abbott and North, 1972:75; Abbott and Hollenberg, 1976:600, fig. 543; L. Aguilar-Rosas, 1981:94; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1985:26; Scagel et al., 1989:163; R. Aguilar-Rosas et al., 1990:125; Stewart, 1991:129; González-González et al., 1996:185; Cho et al., 2002a:557, figs. 57–79.

Ceramium codiophilum Setchell et N. L. Gardner, 1937:89 [as "*C. codiophila*"], pl. 8: figs. 23, 24; Dawson, 1944a:318 [in part]; 1951:53; González-González et al., 1996:186.

Algae epiphytic on *Codium*; mostly erect, up to 1.8 cm tall, branching pseudodichotomously; axes completely corticated, with short, forcipate, incurved apices; attached by rhizoids produced by both periaxial and cortical cells in the basal portions of erect axes; rhizoids pigmented, unbranched, multicellular and with distinctive bulbous tips. Periaxial cells number 5–6, and surround the distal end of nodes; each periaxial cell cuts off 5 cortical initials that produce the corticating filaments that form the cortex. First 2 cortical initials are cut off from the anterior end of a periaxial cell and grow acropetal cortical filaments; second 2 initials are cut off from the posterior end and grow basipetal cortical filaments; a fifth cortical initial is issued on the outside surface of a periaxial cell. The thallus is completely corticated throughout.

Tetrasporangia spherical, 35–40(–50) µm in diameter; embedded, scattered, or whorled in more or less swollen axes. Cystocarps surrounded by involucral branchlets; borne upper 2–3 dichotomies of branches. Spermatangia unknown.

HABITAT. Epiphytic on *Codium*; low intertidal to subtidal.

DISTRIBUTION. Gulf of California: La Paz to San José del Cabo. Eastern Pacific: Alaska to California; Islas Todos Santos, Isla Guadalupe, Isla Cedros, and Islas San Benito, Baja California; Bahía San Bartolomé, Baja California Sur.

TYPE LOCALITY. Epiphytic on *Codium*; Santa Cruz, Santa Cruz County, northern California, USA. Lectotype selected by Cho et al. (2002a:557).

REMARKS. In the field, *Ceramium codicola* can often be recognized by the reddish brown patches it forms on host species of *Codium*. Sometimes resembling *C. sinicola,* the two are most easily differentiated by the nature of their attachment rhizoids. *Ceramium codicola* is attached to its specific host *Codium* by pigmented rhizoids with inflated to bulbous ends.

Ceramium equisetoides E. Y. Dawson

FIGURE 79A–C

Ceramium equisetoides E. Y. Dawson, 1944a:320, pl. 51: fig. 1; 1950c:128; 1957c:21; 1961b:440; 1962b:55, pl. 19: fig. 4; 1966a:27; Abbott and Hollenberg, 1976:595, fig. 536; Mendoza-González and Mateo-Cid, 1985:26; Huerta-Múzquiz and Mendoza-González, 1985:52; Ortega et al., 1987:74, pl. 6: fig. 27, pl. 7: figs. 28–30; Mateo-Cid and Mendoza-González, 1992:21; Mateo-Cid et al., 1993:48; Mateo-Cid and Mendoza-González, 1994b:41; Mendoza-González et al., 1994:108; González-González et al., 1996:186; Mateo-Cid et al., 2000:66; CONANP, 2002:138; Mateo-Cid et al., 2006:56; Bernecker, 2009:CD-Rom p. 64; Fernández-García et al., 2011:60; Pérez-Estrada et al., 2012:191.

Ceramium sp. of Setchell and Gardner, 1924:778: pl. 29: figs. 70, 71.

Algae up to 15 mm high, axis 50–100 µm diameter; with erect and prostrate axes; erect axes branching subdichotomously, apices forcipate or undivided; with numerous adventitious nonforcipate branches; corticated only at the nodes, except near apices of tetrasporangial axes; rhizoids arise from cortical and periaxial cells of prostrate axes, ending in digitate attachment discs or blunt tips. Internodes are long, to 300 µm basally, shortening up right near the apices where several nodes are often clumped closely together. Periaxial cells number 4–5, each divides off 4 cortical initials; 2 acropetal initials that branch and generate ascending filaments of 1–2 small cells long; and 2 basipetal initials that each cut off a cell basipetally. Basipetal and acropetal filaments about equal in length. Cortical bands truncate on both upper and lower edges, cells often rectangular on lower border of bands.

Tetrasporangia 30–40 µm in diameter, immersed in the cortex in terminal portions of main and lateral branches. Tetrasporangial axis nonforcipate and often slightly enlarged with internodes abruptly reduced, usually a single whorl of tetrasporangia at each node, at tip tapering quickly to apex; 1–3 tetrasporangia may be produced by a periaxial cell. Cystocarps lateral, surrounded by several involucral branchlets. Spermatangia minute cells, completely covering surface cortical cells in terminal portions of axes.

HABITAT. Epiphytic on or entangled with other algae; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Arena ("Punta Arenas"; north of Cabo Pulmo); Laguna Agiabampo; Mazátlan, Sinaloa to Nayarit. Eastern Pacific: Newport Harbor, southern California, to Todos Santos, Baja California Sur; Costa Rica.

TYPE LOCALITY. Puerto San Carlos, near Guaymas, Sonora, Gulf of California, Mexico.

Ceramium hamatispinum E. Y. Dawson

FIGURE 79D–G

Ceramium hamatispinum E. Y. Dawson, 1950c:122, pl. 3: figs. 20–22; 1961b:440; 1962a:57, pl. 22: figs. 2–4; Hollenberg, 1968d:75, fig. 2; Mendoza-González et al., 1994:108; González-González et al., 1996:187; Abbott, 1999:275, figs. 77A(holotype)–B; Fernández-García et al., 2011:65.

Axes erect or decumbent, to about 10 mm tall and up to 130 µm in diameter; subdichotomously branched in upper portions, apices circinate (incurved) (Figure 79D, E). Axes corticated only at the nodes, cortical bands up to 50 µm long. Periaxial cells number 6–7 at a node, each issue 1 acropetal and 2 basipetal short filaments. Pseudoperiaxial cells sometimes present, each bearing 2 acropetal and 1 basipetal filaments. Spines abundant and persistent, occurring throughout most of thallus; forming conspicuous whorls of (2–)4–6 spines around the distal part of cortical bands. Spines up to 50 µm long, of 3(–4) pigmented cells in a uniseriate row, and mostly recurved with an acute, hook-like tip (Figure 79F, G).

Reproduction not seen in Gulf specimens.

HABITAT. Growing on rocks, sometimes on crustose corallines, or entangled with other algae; intertidal.

DISTRIBUTION. Gulf of California: Bahía San Carlos; Mazátlan, Sinaloa to Nayarit. Eastern Pacific: Costa Rica. Central Pacific: Hawaiian Islands.

TYPE LOCALITY. Intertidal; Miramar, south of San Blas, Nayarit, Gulf of California, Mexico.

REMARKS. A new record for the northern Gulf of California, *Ceramium hamatispinum* was identified among species of *Gayliella* (*EYD-11019a*) and *Polysiphonia*, all collected from the shallow inner lagoon at Bahía San Carlos and mixed on the same microscope slide (*EYD-11019b*; US Alg. Coll. microscope slide 492). *Ceramium hamatispinum* as reported in the western Pacific from China may be a different species. Illustrations of Zheng et al. (2001; fig. 23:1–6) show its nodes with short, single-celled spines and straight branch apices; lacking the multicelled spines with recurved hook-like apices and incurved branch apices of *C. hamatispinum*.

Ceramium horridulum P. C. Silva

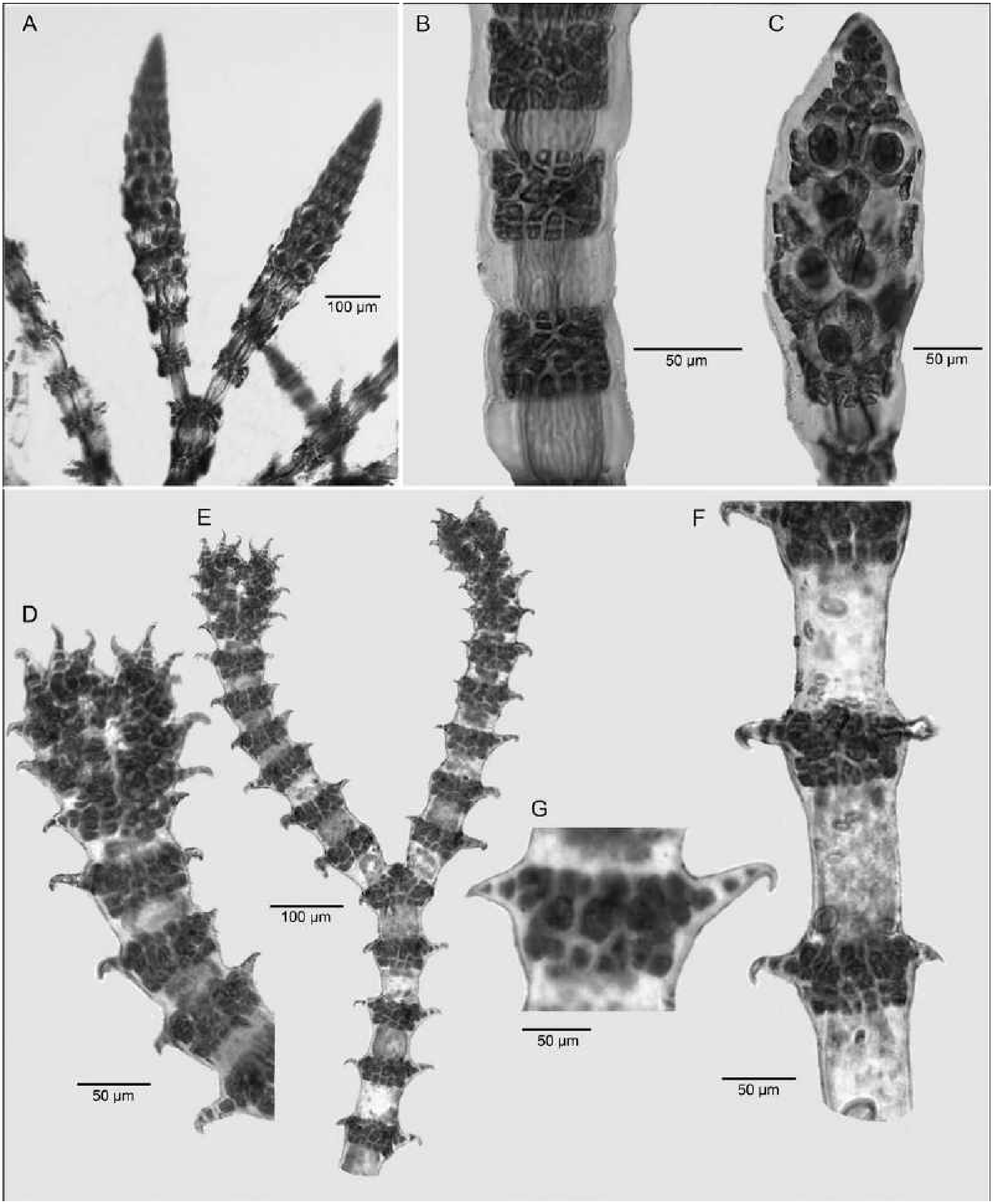
FIGURE 80

Ceramium horridulum P. C. Silva, 1972:204.

Ceramium horridum Setchell et N. L. Gardner, 1924:777, *nom. illeg.* [a later homonym of *Ceramium horridum* Meneghini, 1844a:184], pl. 26: figs. 49, 50, pl. 79; Dawson, 1944a:318; 1950c:116; 1961b:440; 1962a:58, pl. 23: fig. 4; 1963c:12; R. Aguilar-Rosas and Machado-Galindo, 1990:188; R. Aguilar-Rosas et al., 1990:125; González-González et al., 1996:187; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211.

Ceramium pacificum sensu Norris, 1973:15, pl. 6 [non *Ceramium pacificum* (Collins) Kylin, 1925:61].

Algae relatively large, mostly erect, to 6–8(–18) cm tall, main axes in basal portions up to 625 µm in diameter (sometimes axes narrowing at nodes), gradually tapering to forcipate apices; branched subdichotomously, with 0–5 short branchlets whorled around a segment in middle and lower portions of axes, base of branchlets up to 210 µm in diameter; spines frequent with 1- to 2-celled spines terminating both main axes and short lateral branchlets. Periaxial cells number about 9. Axes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G
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FIGURE 79. (Opposite) A–C. *Ceramium equisetoides*: A. Tetrasporangial axes. B. Mature cortication pattern. C. Tetrasporangia immersed in cortex near terminal portions of axes, with internodes abruptly reduced (A–C, *JN-3178e*, US Alg. Coll. microscope slide 4666). D–G. *Ceramium hamatispinum*: D. Upper branch with incurved apices. E. Habit, showing characteristic spines whorled on nodes. F. Portion of axis with longer internodes. G. Detail of cortical node with multicellular spines with recurved tips (D–G, *EYD-11019b*, US Alg. Coll. microscope slide 492).

completely corticated by small angular cells, segments slightly separated only near apical region; cortication thin. Axes with predominantly basipetal cortication, basipetal filaments long, branched, cells in irregular longitudinal rows, acropetal cortical filaments shorter, covering a smaller portion of axial filament cell.

Tetrasporangia about 30–40 µm in diameter; immersed in the cortex, irregularly arranged, making an imprecise band around nodes of both main axes and short whorled branchlets. Whorled branchlets bearing cystocarps slightly wider (240–330 µm in diameter at base) and longer than vegetative branchlets. Cystocarps up to 360 µm in diameter, usually only one per branchlet, gonimolobes surrounded by several (3–4) short, wide (140–180 µm diameter at base) involucral branches, with spines. Spermatangial thalli remain unknown in this species.

Habitat. On rocks and possibly entangled with other algae; subtidal, dredged from 4–32 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Guaymas; Los Mangles, Isla Carmén to Canal de San Lorenzo, off southern end of Isla Espíritu Santo. Eastern Pacific: Islas Todos Santos (off Ensenada), Baja California; Galápagos Islands (Dawson, 1963c).

Type Locality. Cast ashore among other algae; Guaymas, Sonora, Gulf of California, Mexico.

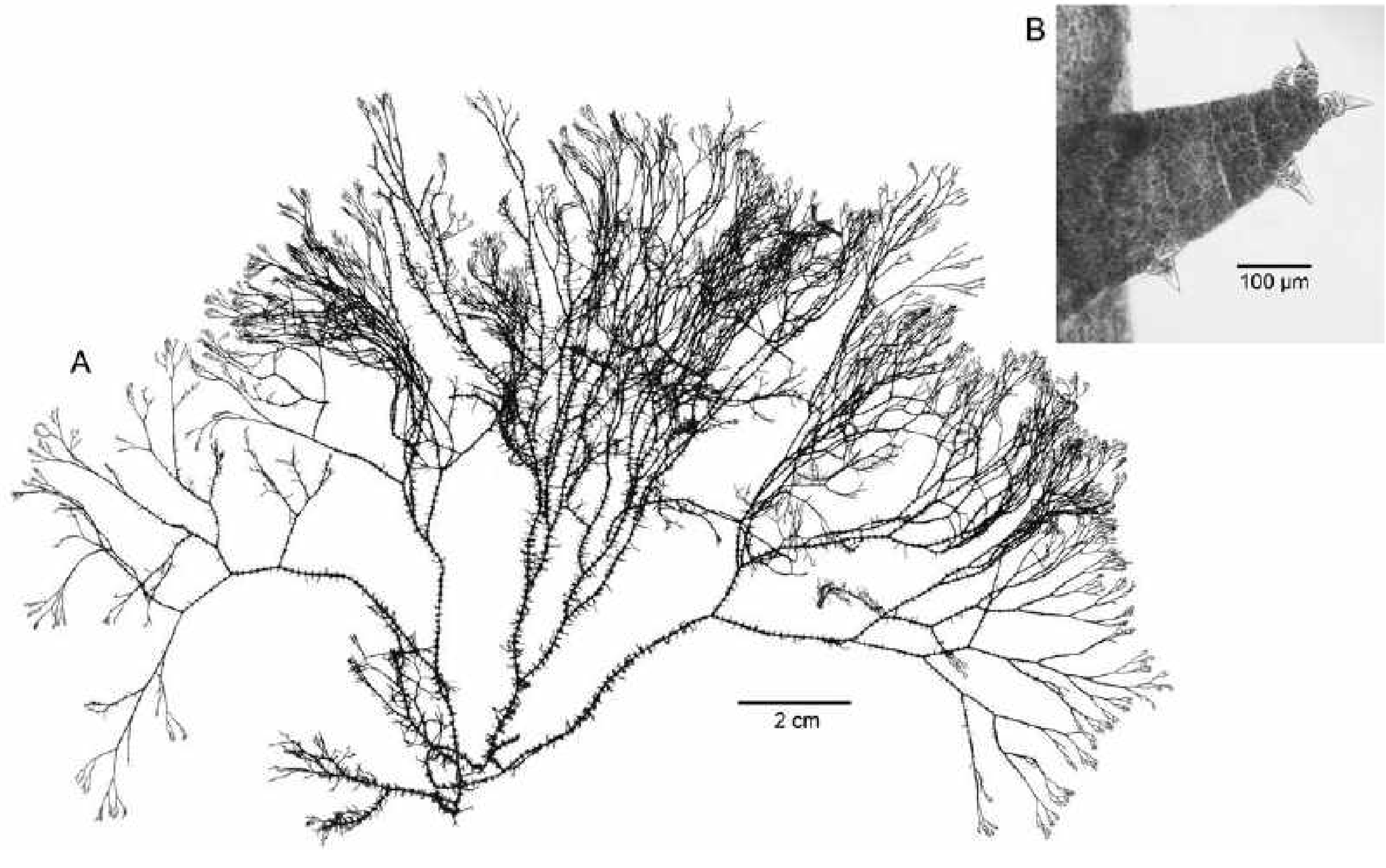


FIGURE 80. *Ceramium horridulum*: A. Habit (*JN-5310*, US Alg. Coll.-217345). B. Detail of one of the short branchlets radially arranged around axes, with several 2-celled spines (*JN-5310*, US Alg. Coll. microscope slide 8703).

Remarks. Among the Gulf species of *Ceramium, C. horridulum* is readily recognized by its large size and numerous short branchlets radially arranged about the axes and adorned with spines. Cystocarpic specimens were found and are described above for the first time for this species (23 m depth from Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda; *JN-5805*, US Alg. Coll. microscope slide 10,132).

In habit *Ceramium horridulum* bears a strong resemblance to *C. pacificum* but differs in several features. *Ceramium horridulum* has about 9 periaxial cells encircling a cortical band, and 1- to 2-celled spines terminal and along the main branches and the short lateral branchlets, whereas *C. pacificum* usually has cortical bands with (5–)6–7 periaxial cells, and spines are not mentioned in most descriptions (i.e., Dawson, 1962a; Cho et al., 2002a; Carlile et al., 2010). However Abbott and Hollenberg (1976) noted 1 or 2 short spines occasionally at apices of *C. pacificum* from California. The arrangement of the adventitious branchlets in middle to lower portions of the axes also differs: the axes of *C. horridulum* usually bear several, short branchlets (mostly 3–5), similar in length, in whorls around a segment; whereas in *C. pacificum* the adventitious branchlets are longer, usually of assorted lengths, and not whorled but more openly radially-arranged along numerous segments. Molecular evidence would help to determine the phylogenetic positions of these two morphologically similar species and their relationship to species in the "*C. sinicola*-complex" sensu Cho et al. (2003a).

Ceramium howellii Setchell et N. L. Gardner

FIGURE 81

Ceramium howellii Setchell et N. L. Gardner, 1937:88, pl. 6: fig. 14; Dawson, 1957a:4; 1961b:440; 1962a:58, pl. 21: fig. 1, pl. 22: fig. 1; Stewart and Stewart, 1984:145; González-González et al., 1996:187.

Algae of both erect and prostrate portions, up to 15 mm tall; axes up to 650 µm in diameter, sparsely and irregularly branched. Erect axes with mostly short branches; branch apices nonforcipate, adaxially curved or "hooked." Axial cells shorter than broad, with a cytoplasmic strand usually visible forming a midline; completely corticated by a thin, mostly single layer of small, irregularly arranged, angular cells (4–)7–12 µm in diameter. Periaxial cells number 10; larger, rounder, and slightly recessed below the thin layer of outer cortical cells.

Tetrasporangia 30–45 µm in diameter; irregularly scattered and embedded in the cortex of both main and lateral branches; sometimes aggregated into indistinct bands, tetrasporangial axes

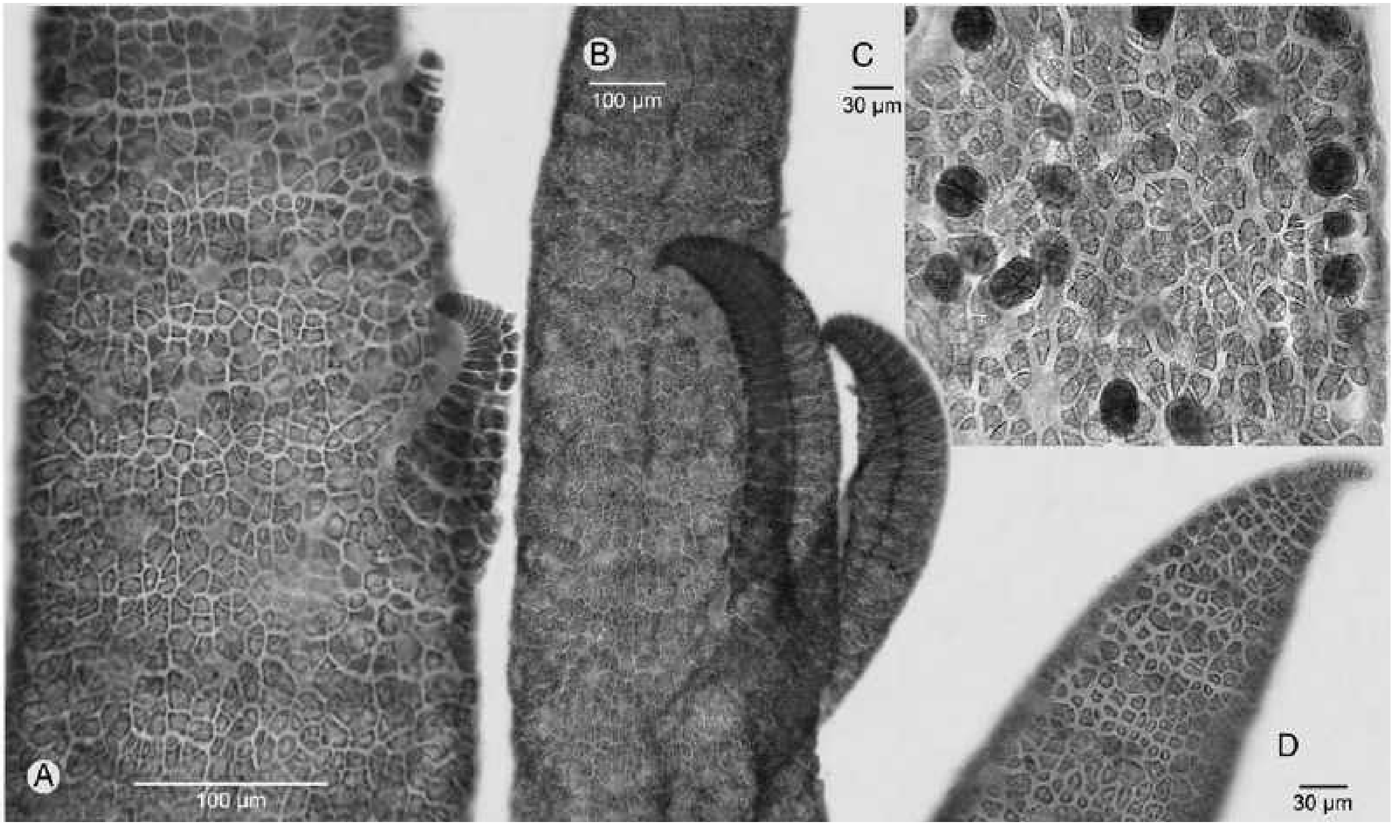


FIGURE 81. *Ceramium howellii*: A. Axial filament nearly completely corticated and developing branch with incurved tip. B. Branches with incurved tips. C. Tetrasporangia immersed in cortex (A–C, *JN-5464*, US Alg. Coll. microscope slide 5271). D. Developing cortication near a tip (*EYD-8425*, US Alg. Coll. microscope slide 479).

up to 850 µm in diameter. Cystocarps borne laterally; enveloped by several involucral branchlets. Spermatangia small, colorless cells covering cortex in upper portions of thallus.

HABITAT. On rocks; intertidal to shallow subtidal, down to 8 m depths (dredged to 30 m; Dawson, 1962a).

DISTRIBUTION. Gulf of California: Punta la Gringa, Bahía de Los Ángeles; Bahía Salinas, Isla Carmén. Eastern Pacific: Isla Guadalupe (off Baja California); Galápagos Islands.

TYPE LOCALITY. On rocks, southeast side of Isla Fernandina (Narborough Island), Galápagos Islands, Ecuador.

REMARKS. *Ceramium howellii* is now reported in the northern Gulf of California from Punta la Gringa, Bahía de Los Ángeles (*JN-5464b,* US Alg. Coll. microscope slide 5271). Apparently rare or possibly overlooked, *C. howellii* in the northern Gulf is known only from this one collection. Its Gulf distribution is extended northward from Isla Carmén in the southern Gulf (Dawson, 1962a).

Ceramium interruptum **Setchell et N. L. Gardner**

FIGURE 82

Ceramium interruptum Setchell et N. L. Gardner, 1924:775, pl. 26: fig. 47; Cho et al., 2003a:778, figs. 1a–j, 2a–i.

Ceramium sinicola var. *interruptum* (Setchell et N. L. Gardner) E. Y. Dawson, 1944a:316; Hollenberg, 1948:158; Dawson, 1950c:119; 1959a:30; 1961b:441; 1962b:65, pl. 27: fig. 8; 1966a:27; González-González et al., 1996:189.

Algae usually epiphytic; of both creeping and erect portions, up to 1.5 cm tall, attached to host by branched rhizoids with blunt or digitate ends; erect axes branched pseudodichotomously, with 7–11 segments between branching points; apices forcipate

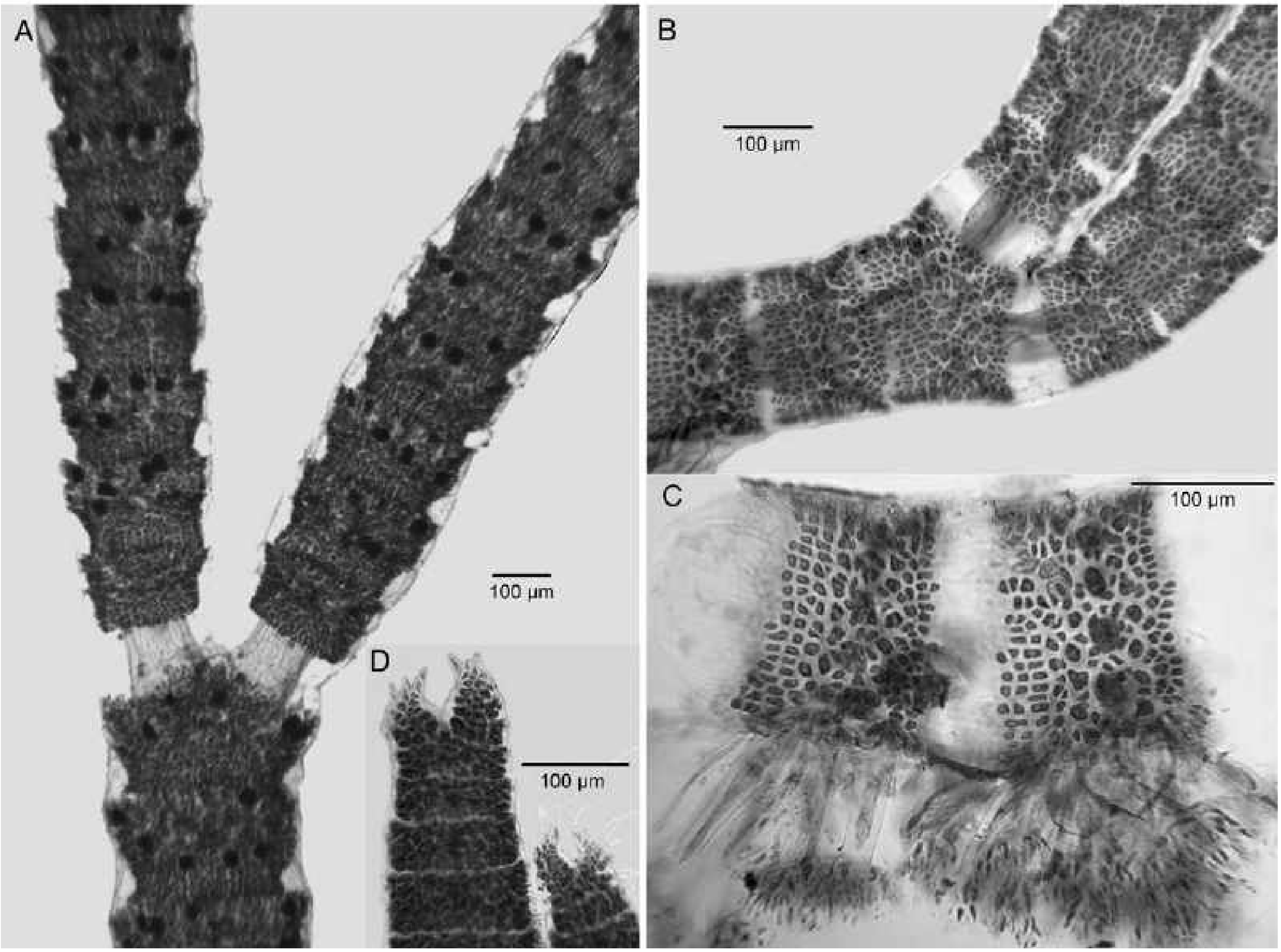


FIGURE 82. *Ceramium interruptum*: A. Tetrasporangial axis cortication interrupted above the dichotomy, and tetrasporangia immersed in the cortex (*JN-4201*, US Alg. Coll. microscope slide 4788). B. Cortical pattern with cortication interrupted above dichotomy. C. Prostrate axis showing numerous rhizoids issued by periaxial and cortical cells of two nodes. D. Spines at apices (B–D, *JN-4404*, US Alg. Coll. microscope slide 4794).

and incurved with occasional abaxial multicellular spines; axes mostly completely corticated, except at the first internode above a dichotomy where the axial filament cell is uncorticated, and incomplete cortication (internodes present) in lower and prostrate portions of thalli. Axial filament cells in the upper portions spherical to ovoid, becoming more cylindrical below. Periaxial cells number 7–9; each periaxial cell obliquely cuts off 4 cortical filament initials; 2 initials from the anterior end of a periaxial cell form acropetal filaments, and 2 initials from the posterior end form basipetal filaments. Mature acropetal and basipetal corticating filaments up to 10–13 cells long. Rhizoids issued from both periaxial and cortical cells of prostrate axes, uniseriate and multicellular, mostly ending in muticellular digitate pads. Gland cells, 10–15 µm in diameter, may develop on cortical filaments.

Tetrasporangia tetrahedrally divided, 46–56 µm long by 35–50 µm in diameter, immersed in the cortex, in distal portions of thallus. Tetrasporangia appear whorled in a ring at the nodes, produced by the periaxial cells; tetrasporangia production continuing through several axial dichotomies, and in more proximal portions, tetrasporangia additionally issued by inner cortical cells and appear scattered or in several whorls per segment. Cystocarps subspherical, 163–287 µm long by 202–302 µm in diameter; borne in upper portions of a thallus, surrounded by 5–7 incompletely corticated involucral branchlets. Spermatangia colorless, elliptical to spherical cells 3–5 µm × 2–4 µm; initially develop on adaxial side and later cover the cortical node.

Habitat. Epiphytic on various algae, including species of *Codium*, *Gelidium*, *Laurencia*, and articulated coralline algae; mid-intertidal tide pools to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco; Isla Coronado (Isla Smith), Bahía de Los Ángeles; Bahía Agua Verde to El Tecolote, Bahía de La Paz. Eastern Pacific: Orange County, southern California.

Type Locality. Eureka, near La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. Recent studies of the *Ceramium sinicola* complex that included *C. sinicola* var. *interruptum* (Cho et al., 2003a) revealed it to be a distinct species, and *C. interruptum* was reinstated on the basis of morphological and molecular data. *Ceramium interruptum* differs from the similar-looking species, *C. sinicola* and *C. codicola,* by its interrupted cortication above branching points, the issuing of only four cortical filament initials per periaxial cell, and its frequent creeping habit.

Ceramium mazatlanense E. Y. Dawson

FIGURE 83

Ceramium mazatlanense E. Y. Dawson, 1950c:130, pl. 2: figs. 14, 15; 1954a:6; 1957c:21; 1959d:4 [with a query]; 1961b:440; 1962a:59, pl. 23: figs. 1, 2; Schnetter and Bula-Meyer, 1982:153, pl. 25: figs. E–K, pl. 27: fig. B; Mendoza-González et al., 1994:108; González-González et al., 1996:187; Abbott, 1999:278, figs. 78C,D; López et al., 2004:11; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:61.

Ceramium macilentum sensu Serviere-Zaragoza et al., 2007:9 [non *Ceramium macilentum* J. Agardh, 1894:15].

Algae with both prostrate and erect portions, mostly 3–10 mm tall, corticated only at the nodes, with relatively short cortical bands, about 25–30(–50) µm high; erect axes 70–120(–150) µm in diameter (cortical bands 2–3 times as wide as tall); branching subdichotomously; apices forcipate and incurved; prostrate axes attached to substrate by uniseriate rhizoids of several cells. Periaxial cells number 5(–6), most periaxial cells laterally cut off a pseudoperiaxial cell, resulting in a ring of up to 10(–12) wedge-shaped (rounded- triangular in surface view) cells at a node (i.e., 5(–6) periaxial cells with 5(–6) pseudoperiaxial cells between them), periaxials usually with narrow ends of cell facing distally (upward), and pseudoperiaxials with their narrow ends facing downward. Each periaxial cell cuts off an acropetal cortical initial that produces a small-celled ascending filament, 2–4 cells long; each pseudoperiaxial cell usually produces 1 acropetal filament (2–4 cells long) and occasionally 1 basipetal initial (appears lateral). In some specimens corticating filaments may be mostly lacking, leaving only periaxial and pseudoperiaxial cells to form the node. Nodal bands (1–)2–4(–5) cells high, with smaller cells at the distal end of the node and larger cells below and beneath them. Internodes elongate in lower parts of thallus.

Tetrasporangia cruciately divided, spherical, (30–)35–50(–65) µm in diameter (occasionally exceeding the cortical band length); issued from periaxial cells; tetrasporangia partially surrounded by a cortical envelope (i.e., covered by corticating cells and a projecting lax involucre of branched cortical filaments). Tetrasporangia borne abaxial, singly or up to several in a group, in a prominent series on successive nodes in upper portions of thalli; in some specimens tetrasporangia may be whorled at node, causing axis to appear tumid. One cystocarp surrounded by 2–3 involucral branchlets, 1 cystocarp per node, often in a short series on the abaxial side. Spermatangia small, colorless cells covering cortical surface cells of fertile bands.

Habitat. Epiphytic on larger algae; mid to low intertidal.

Distribution. Gulf of California: Bahía Kino to Ensenada de San Francisco (vicinity of Guaymas); Mazatlán, Sinaloa. Eastern Pacific: Isla San Benedicto (Islas Revillagigedo); Guerrero; El Salvador; Costa Rica; Colombia; Clipperton Island (?). Central Pacific: Hawaiian Islands. Western Pacific: China.

Type Locality. Epiphytic on *Codium*; **small reef 2 miles (3.22 km) north of** Mazatlán, Sinaloa, Gulf of California, Mexico.

Remarks. Dawson (1954a) commented that the numerous hairs on the cortical bands of *Ceramium mazatlanense* reminded him of *Trichoceras pubescens* Kützing (1862: pl. 85: figs. d–r; =*Ceramium fastigiatum* var. *pubescens* (Kützing) Piccone) and suggested it should be reexamined. However, since then, Dawson (1962a) and others have accepted *C. mazatlanense* as being a distinct species (e.g., Meneses, 1995; Silva et al., 1996a; Abbott, 1999; Zheng et al., 2001; John et al., 2003, 2004).

Although South and Skelton (2000) later placed *Ceramium mazatlanense* in synonymy with *C. macilentum* J. Agardh (1894), most have keep them separate (e.g., Zheng et al., 2001; John et al., 2004). Abbott et al. (2002) noted that specimens previously

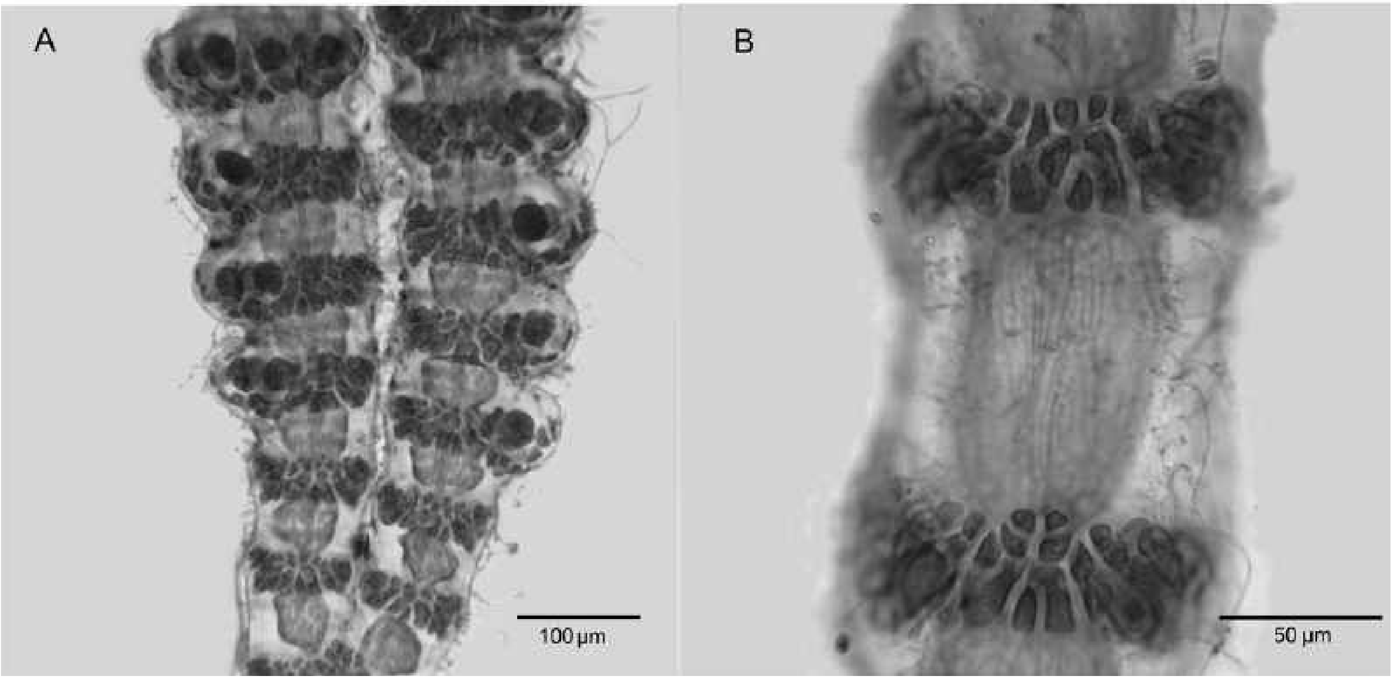


FIGURE 83. *Ceramium mazatlanense*: A. Tetrasporangia with involucres giving tumid appearance. B. Two mature nodes, much wider than tall (A, B, *EYD-11031*, US Alg. Coll. microscope slide 512).

referred to "*C. mazatlanense*" from Vietnam (Dawson, 1954b; Phạm-Hoàng, 1969) were misidentified and actually were *C. macilentum*. Although the cortical patterns of the nodal bands are similar, *C. mazatlanense* may have a slightly greater basipetal (lateral) cortical development in mature nodes. For now the Gulf of California *C. mazatlanense* is recognized as distinct from the Australian *C. macilentum* until each can be tested and compared with molecular analyses.

Ceramium obesum E. Y. Dawson

FIGURE 84A

Ceramium obesum E. Y. Dawson, 1950c:119, pl. 1: figs. 7–9; 1961b:440; 1962a:60, pl. 22: figs. 5, 6; González-González et al., 1996:187; Pacheco-Ruíz et al., 2008:211.

Algae mostly prostrate, with creeping axes, up to 2.2 cm in length; axes cylindrical, sturdy, and broad; 900–1100 µm in diameter (reduced in diameter at apices); infrequently and subdichotomously branched, but with many erect short secondary branches; apices forcipate, short, thick, strongly incurved tips; completely corticated, with thick cortex, composed of several cell layers, an inner layer of thick-walled cells, 25–100 µm in diameter, and a dense surface layer of small, anticlinally elongated cells, 15–25 µm long by 5–9 µm wide; attached to substratum by numerous small rhizoids produced from ventral surfaces.

Reproductive structures unknown.

HABITAT. Growing in algal turfs among other algae and debris; intertidal.

DISTRIBUTION. Gulf of California: Bahía Agua Dulce, Isla Tiburón.

TYPE LOCALITY. Intertidal rocky shore; Bahía Agua Dulce, Isla Tiburón, Gulf of California, Mexico.

REMARKS. An endemic species, *Ceramium obesum* is not well known and has not been recently collected.

Ceramium pacificum (Collins) Kylin

Ceramium rubrum var. *pacificum* Collins, 1913:125.

Ceramium pacificum (Collins) Kylin, 1925:61; Kylin, 1941:29; Smith, 1944:326, pl. 83: fig. 3; Dawson, 1950c:120, pl. 4: fig. 30; t al., 1960a:50, pl. 37: figs. 1, 2; 1961b:441; 1962b:61, pl. 23: fig. 3, pl. 24: fig. 1; Abbott and Hollenberg, 1976:600, fig. 545; R. Aguilar-Rosas, 1982:84; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Scagel et al., 1989:164; Sánchez-Rodríguez et al., 1989:44; Ramírez and Santelices, 1991:321; González-González et al., 1996:187; Pacheco-Ruíz and Zertuche-González, 2002:468; Cho et al., 2002a:565, figs. 117–140; Pacheco-Ruíz et al., 2008:211; Carlile et al., 2010:342, figs. 1–19; Jeong et al., 2013:440, fig. 1A–F.

Ceramium rubrum var. *pacificum* Collins in Hauck and Richter, 1889, *nom. nud.*: Exsiccate *Phykotheka Universalis* No. 302 [lectotype specimen of *Ceramium rubrum* var. *pacificum* Collins; see Carlile et al., 2010: fig. 1].

Ceramium rubrum var. *pacificum* Collins in Collins et al., 1901b, *nom. nud.*: Exsiccate *Phycotheca Boreali-Americana* No. 893.

Ceramium rubrum var. *pacificum* Collins in Setchell et N. L. Gardner, 1903, *nom. nud.*:345

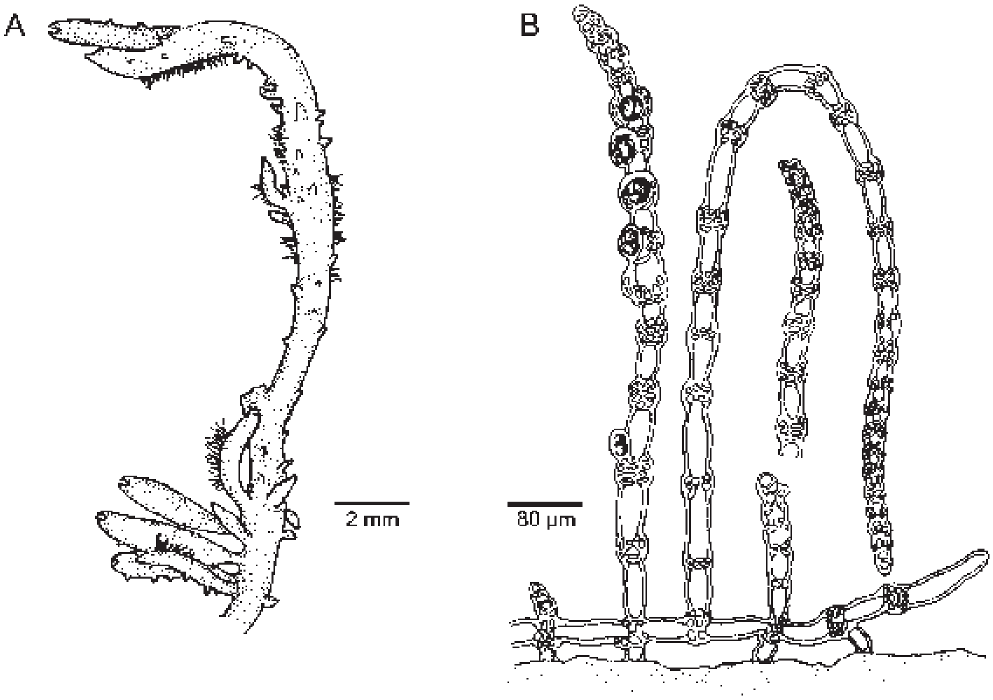


FIGURE 84. Species of *Ceramium*. A. *Ceramium obesum*: Specimen from the type collection displaying stout forcipate apices, thick and complete cortication, and numerous rhizoids (after Dawson, 1962a: pl. 22: fig. 5). B. *Ceramium serpens:* Erect axes with tetrasporangia above prostrate axes attached to substratum (after Dawson, 1962a: pl. 25: fig. 6).

Ceramium washingtoniense Kylin, 1925:62; Carlile et al., 2010:336, 342, fig. 2 [type specimens].

Algae erect with prostrate portions, relatively large, up to 18 cm high; axes about 350 µm in diameter; pseudodichotomously branched; 9–14 axial cells between branches; apices forcipate, inrolled. Axial cells spherical to cylindrical, completely corticated, except for slight gaps between segments near apices; cortication thin. Periaxial cells (5–)6–7 encircle a node; each cutting off 4 cortical initials that are spherical to ovoid and larger than the cells of the corticating filaments they generate. Basipetal growth predominates, with basipetal filaments usually longer than acropetal filaments. Outermost cortical cells angular and small, 10–14 µm in diameter. Small gland cells, 8–14 µm; cut off from cells at the ends of the acropetal corticating filaments. Adventitious lateral branchlets, numerous, relatively short and curved; develop from periaxial cells; radially arranged about the axis in middle to lower portions of thalli. Rhizoids, issued from large cortical cells, mostly rod-shaped with blunt tips.

Tetrasporangia cruciately divided, 42–60 µm in diameter (excluding sheath); develop from periaxial cells or occasionally from large cortical cells; immersed in the cortex, completely covered by cortical cells and forming 1 to 4 whorls about a node. Cystocarps nearly spherical, 280–350 µm in diameter; of 2–3 gonimolobes and surrounded by 4–6 involucral branchlets (after Cho et al., 2002a). Spermatangia produced on spermatangial parent cells derived from surface cortical cells.

Habitat. On rocks or epiphytic; low intertidal to shallow subtidal, down to 4.5 m depths.

Distribution. Gulf of California: Bahía de La Paz. Eastern Pacific: Alaska to California; Punta María, Baja California; Chile. Western Pacific: Korea.

Lectotype Locality. Monterey, Monterey County, central California (Smith, 1944:326); lectotype specimen selected by Cho et al. (2002a:565; Carlile et al., 2010:342, fig. 1).

Remarks. *Ceramium pacificum* is reported in the southern Gulf of California from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985). Although superficially similar in appearance to *C. horridulum, C. pacificum* differs in its lack of 1- to 2-celled spines on main axes and on short radially arranged branchlets, number of periaxial cells, and arrangement of short, adventitious branchlets (see also Remarks under *C. horridulum*). Abbott and Hollenberg (1976) noted the occasional presence of short spines in apices of *C. pacificum*; however others do not mention spines in their descriptions (i.e., Kylin, 1925; Smith, 1944; Dawson, 1962a; Cho et al., 2002a; Jeong et al., 2013).

Reexamination of the "*C. pacificum*" reported from Puerto Refugio, Isla Ángel de la Guarda (Norris, 1973) revealed it to be *C. horridulum*. Other Gulf of California specimens referred to "*C. pacificum*" need to be critically compared with *C. horridulum* and type locality Pacific *C. pacificum* to confirm its presence in the Gulf.

Ceramium paniculatum Okamura

FIGURE 85

Ceramium paniculatum Okamura, 1896:36, pl. 3: figs. 22, 23; 1921:114, 122, pl. 179: figs. 8–16; 1936:737; Dawson, 1944a:319; 1950c:122; 1959a:10, 30; 1960c:97; 1961b:441; 1962b:61, pl. 23: figs. 5–7; Nakamura, 1965:146, figs. 9, 10, pl. 2: fig. 5; Hollenberg, 1968d:75, fig.

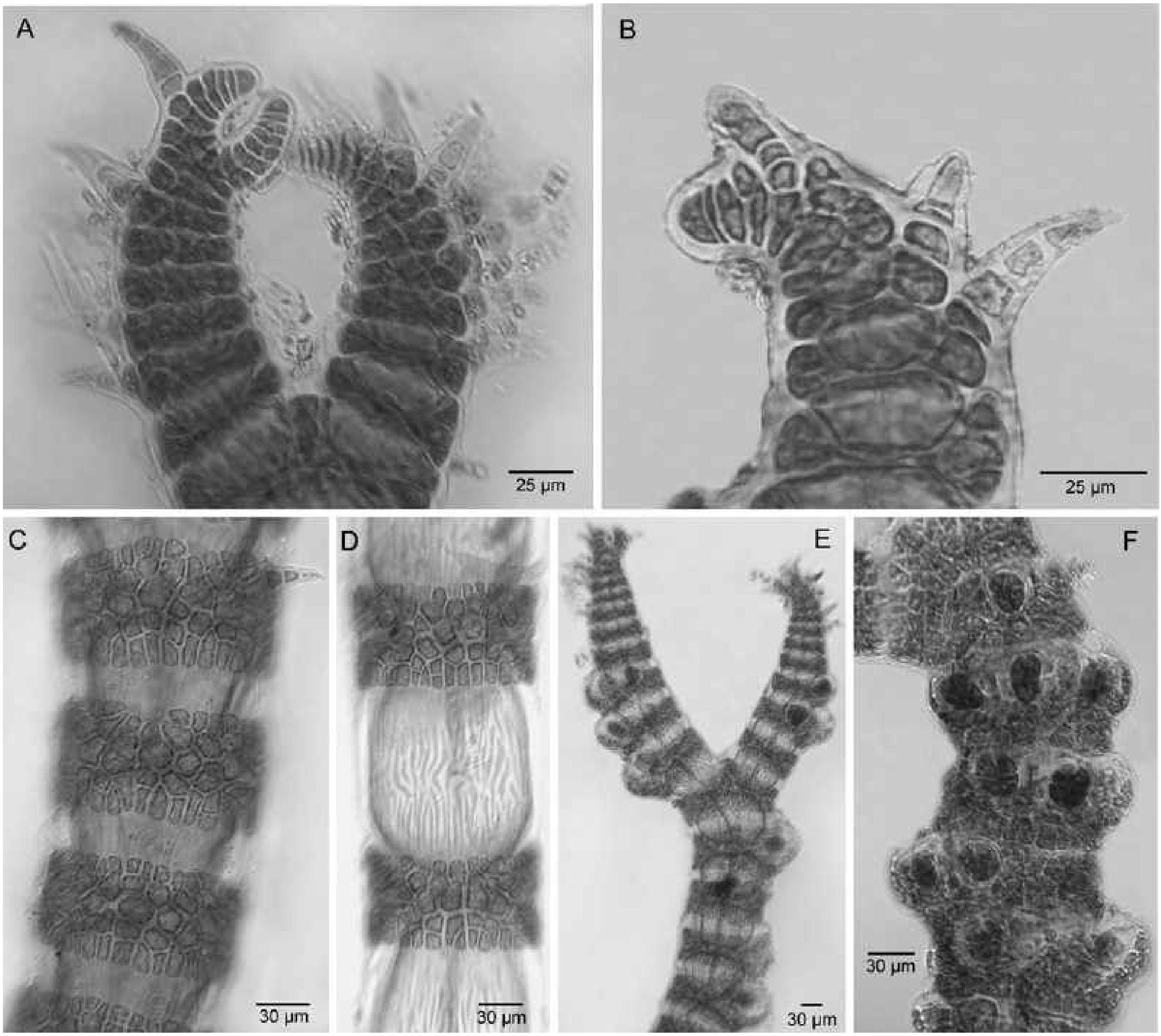


FIGURE 85. A–D. *Ceramium paniculatum*: A. Multicelluar spines near apices. B. Detail of multicellular recurved spines (*JN-4539*, US Alg. Coll. microscope slide 4258). C, D. Several examples of mature cortication pattern, one node with a persistent multicellular spine. E, F. Tetrasporangia develop first on one side then become whorled around nodes, each enfolded by an involucre of several cells, resulting in a tumid appearance (A, C–F, *JN-4396*, US Alg. Coll. microscope slide 8704).

1; Itono, 1972:75; 1977a:32, 101, 263, figs. 13D1-7, 59F–G, 60D; Stewart and Stewart, 1984:145; Tseng, 1983:128, pl. 67: fig. 3; Huerta-Múzquiz and Mendoza-González, 1985:52; González-González et al., 1996:188; Yoshida, 1998:897, figs. 3-86F,G; Abbott, 1999:279, fig. 78E; CONANP, 2002:138; López et al., 2004:11; Pacheco-Ruíz et al., 2008:211; Fernández-García et al., 2011:61.

Algae of erect axes, up to 13 mm tall, above short prostrate portions; axes 120–150 µm wide; axial cells 240 µm long, 135 µm wide in basal regions, tapering very slightly upward to tips; branching subdichotomous; branches occurring at intervals of 6–11 axial filament cells, with few proliferous branches, mostly on the basal parts of erect axes and prostrate axes, arising from periaxial cells; corticated only at the nodes, internodes long below (up to 180 µm), decreasing to quite small above. Apices forcipate, often with a series of acute, (2–)3–4(–5)-celled straight or recurved spines, one per node, 20–50 µm long, arranged abaxially in upper parts of thallus. Multicellular spines deciduous, infrequent on nodes below. Periaxial cells at nodes of decumbent axes issue unbranched to sparingly branched attachment rhizoids. Periaxial cells number 6(–7); each cuts off 4 corticating initials, 2 from the anterior end of the periaxial cell and 2 from the posterior end. The top 2 initials form acropetal corticating filaments, 1–3 cells long, and 2 posterior initials cut off basipetal corticating filaments, 1–3 cells long. Acropetal and basipetal filament growth nearly equal. Nodal bands usually 5(–8) cells high (50–75 µm high), broader than tall, truncate on both upper and lower margins. Cortication appears mostly 1 cell layer thick, except along middle of node; corticating cells large in comparison with those of other Gulf *Ceramium* species; periaxial cells in middle of node largest and roundest (about 20 µm in diameter); ultimate acropetal cortical cells (along upper margin) smallest of node (about 8 µm wide); ultimate basipetal filament cells sometimes vertically elongate. Gland cells absent.

Tetrasporangia, 30–45 µm long, involucred by several bracteate cortical filaments, lower portions covered by corticating cells; 1 to several tetrasporangia at a node, initially abaxial and then becoming whorled, causing nodal band to appear tumid. Cystocarps unknown in Gulf of California material. Spermatangia minute cells covering cortical cells in the upper portions of thalli.

HABITAT. On rocks or epiphytic on other algae, often in tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; Bahía de Loreto to Cabeza Ballena; Mazatlán, Sinaloa. Eastern Pacific: Isla Guadalupe (off Baja California); Guerrero to Oaxaca; El Salvador. Central Pacific: Hawaiian Islands. Western Pacific: Japan; China; Korea.

TYPE LOCALITY. Growing on *Corallina*; Kamahara, formerly Iwaki Province (along sea from Hitachi, Rikuzen, to Iwashiro; Rein, 1884), Tōsandō region (Okamura, 1896), Honshū Island, Japan.

REMARKS. Although cystocarps are unknown in *Ceramium paniculatum* specimens from the northern Gulf, those from Japan (Okamura, 1921) are borne abaxially in a series on upper branches, consist of 2–5 gonimolobes (Itono, 1977a: fig. 59G) and are subtended by up to four short, involucral branchlets.

The habit of Gulf of California *C. paniculatum* differs from Korean material (H.-S. Kim, 2012: fig. 66A–D) in being shorter in thallus height, having shorter internode lengths in lower portions of thallus, and longer intervals between branches (often up to 11 axial cells). The cortical pattern of Japanese (Itono, 1977a: fig. 13D4) and Korean *C. paniculatum* has shorter basipetal cortical filaments than those of Gulf specimens. However in mature lower portions, the cortical pattern of the Korean alga (H.-S. Kim, 2012: fig. 69C) has longer basipetal filaments and is somewhat similar to those of Gulf material. The nodes of Gulf of California *C. paniculatum* also differ in being truncate on both upper and lower margins, and some of the ultimate basipetal cells are slightly longer than wide (Figure 85C, D).

Ceramium periconicum T. O. Cho et Riosmena-Rodriguez

FIGURE 86

Ceramium periconicum T. O. Cho et Riosmena-Rodriguez, 2008:307, figs.1–49.

Algae in short tufts, with prostrate and erect axes, up to 3 mm tall; axes slender, 45–75(–90) µm in diameter; corticated only at the nodes; nodal cortication to about 30(–40) µm high (3(–4) cells high). Apices forked and straight, unequal in length, branching pseudodichotomous and subsequently regularly alternate in mature specimens. Prostrate axes with long internodes; attached by uniseriate, multicellular rhizoids (originating from periaxial cells), often terminating in digitate pad. Periaxial cells 4–5 at a node; each cuts off 3 cortical initials; first 2 cortical initials divide off from the anterior end of the periaxial cell and develop the acropetal filaments, 2(–3) cells long; third cortical initial cut off by a vertical division through a periaxial cell and is directed laterally (only on one side); lateral initial situated between periaxial cells and does not divide further. Cortical bands lack basipetal filaments. Gland cells present or lacking; small, angular, 8–12 µm wide, borne at tips of acropetal corticating filaments.

Tetrasporangia tetrahedrally divided, up to 40 µm long by 35 µm wide (not including hyaline sheath), naked, protruding; borne primarily abaxially in a series in upper portions of thalli, rarely whorled; each periaxial cell may produce up to 2 tetrasporangia. Mature cystocarps in upper portions of thallus, spherical, up to about 200 µm in diameter; with 2–3 gonimolobes subtended by 3–4 involucral branchlets (female reproductive structures described from Baja California Sur specimens; see Cho and Riosmena-Rodriguez, 2008). Spermatangial parent cells arise from cortical cells and produce 1–2 spermatangia terminally, initially developing on one side of nodal band and eventually covering whole band; spermatangia small colorless cells, 1–4 µm in diameter.

HABITAT. In turfs; epiphytic on other algae, including *Gelidium, Amphiroa,* and *Agardhiella,* that grow on hard substrata and in tide pools; mid intertidal to shallow subtidal, down to 10 m depths (also dredged from 20 m).

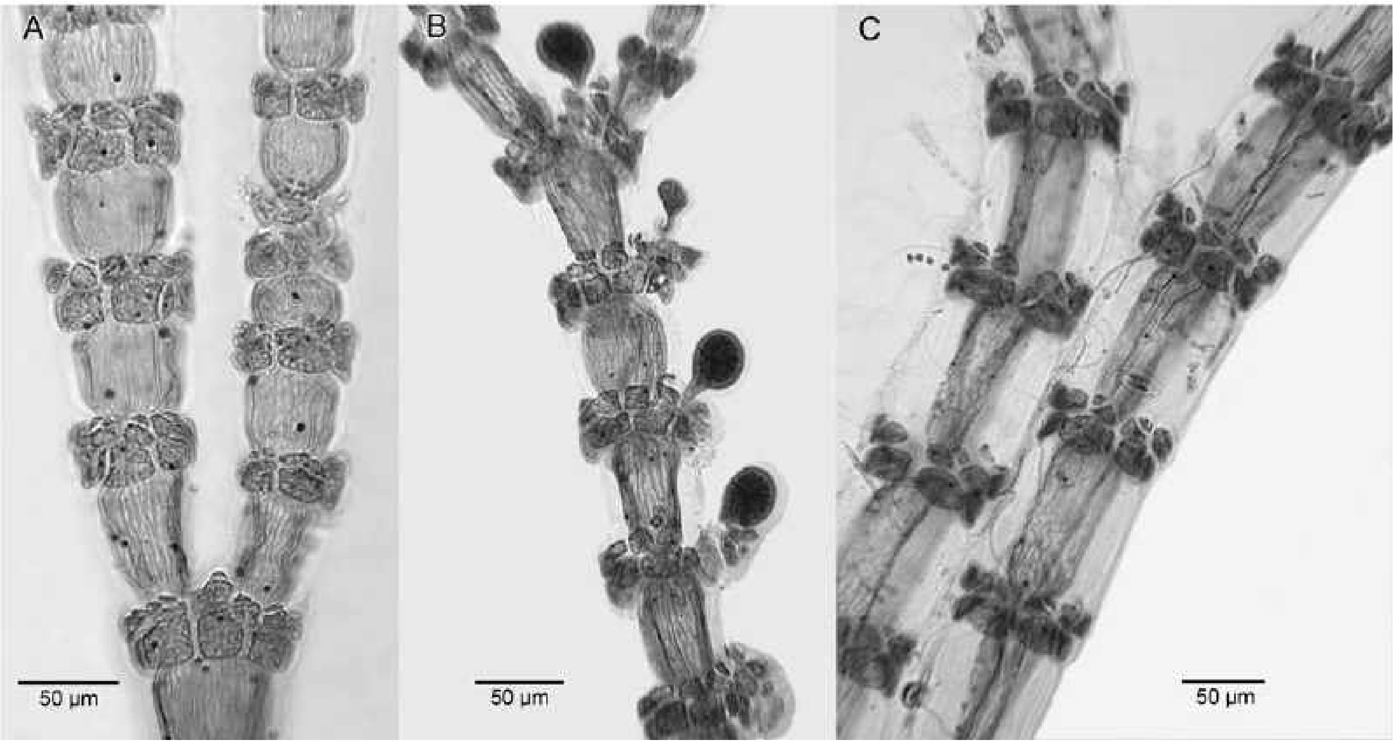


FIGURE 86. *Ceramium periconicum*: A. Cortication pattern at nodes (*EYD-6851a*, US Alg. Coll. microscope slide 557). B. Protruding naked tetrasporangia. C. Cortication pattern, no basipetal cortical filament development, one cell cut off transversely (laterally) (B, C, *JN-4436*, US Alg. Coll. microscope slide 8705).

DISTRIBUTION. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco to Isla la Ventana, Bahía de Los Ángeles; Bahía de La Paz to Bahía de San Lucas.

TYPE LOCALITY. 2–3 m depth; Punta Perico (north of Bahía de los Muertos), Baja California Sur, Gulf of California, Mexico.

REMARKS. A Gulf of California endemic species, *Ceramium periconicum* is now reported in the upper Gulf with its collection from Puerto Peñasco, Sonora (Cumpleaños Tidepool, Playa Las Conchas (Playa Estación): *JN-3906c*, US Alg. Coll. microscope slide 5218). Other northern Gulf collections, from Isla la Ventana, Bahía de Los Ángeles (*JN-4436* and *JN-4459*, US Alg. Coll. microscope slide 5236), are also northward distribution extensions from Punta Perico, Baja California Sur. Some northern Gulf specimens have axes slightly wider in diameter (up to 90 µm), and no gland cells were observed at tips of acropetal cortical filaments. One specimen identified as *C. periconicum*, from Bahía de San Lucas (*EYD-6851a,* US Alg. Coll. microscope slide 557), shows the division of the third cortical initial from some periaxial cells slightly off vertical, tending toward oblique, but the third cortical initial is always laterally directed and does not divide further.

Ceramium procumbens Setchell et N. L. Gardner

FIGURE 87

Ceramium procumbens Setchell et N. L. Gardner, 1924:772, pl. 27: figs. 51–54; Dawson, 1944a:318; Hollenberg, 1948:158; Dawson, 1950c:128; 1959a:30; Dawson et al., 1960b:11, 12, 13; Dawson, 1960a:51; 1961b:441; 1962a:63, pl. 24: figs. 3, 4, pl. 25: figs. 1–3; 1966a:27; Dawson and Neushul, 1966:182; Itono, 1972:85; Abbott and Hollenberg, 1976:597, fig. 539; Itono, 1977a:33, 100, 198, 231, 266, figs. 13G1-6, 15E–J, 37F–G, 50H,I, 58H–J, 59H; Huerta-Múzquiz and Mendoza-González, 1985:52; González-González et al., 1996:188; Yoshida, 1998:897; Mateo-Cid et al., 2000:66; Cho et al., 2001:45–52, figs. 1–28; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:61; Nguyen et al., 2013:211.

Ceramiella procumbens (Setchell et N. L. Gardner) Díaz-Piferrer, 1969a:203.

Algae minute epiphytes; axes mostly prostrate, producing oppositely to irregularly arranged erect axes, 1–2(–3) mm high, 40–100 µm in diameter; cortication incomplete. branching of repent axes and erect branches irregular, with short, erect adventitious branches; Axes attached to host by short uniseriate rhizoids with blunt tips or multicellular digitate pads, rhizoids issued by both periaxial and cortical cells. Apices of prostrate axes slightly

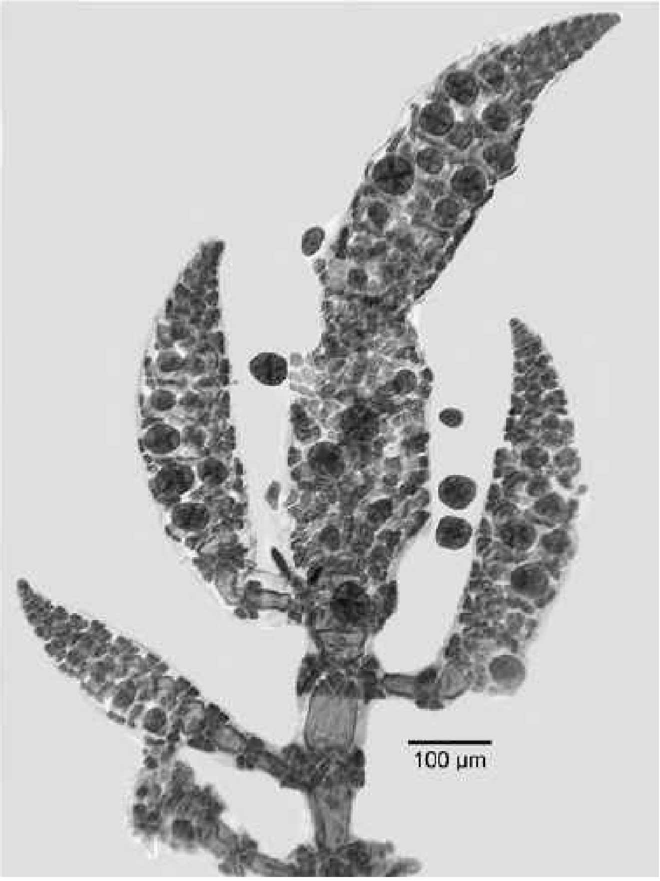


FIGURE 87. *Ceramium procumbens:* Branching pattern and tetrasporangia immersed in clavate branches (*JN-4897*, US Alg. Coll. microscope slide 8706).

forcipate; apices of erect adventitious branches straight, undivided. Erect adventitious branches unilaterally issued by periaxial cells on the dorsal side of prostrate axes. Axial cells cylindrical, up to 150 µm long and to 60 µm in diameter in basal regions; decreasing in size toward the apex, and more spherical in shape. Corticated only at the nodes, cortical bands wider than tall. Internodes 60–105 µm long basally, becoming shorter toward the apex. Periaxial cells number 4 per axial cell; each periaxial cell cuts off 4 cortical initials, 2 are obliquely cut off from the anterior end and form acropetal corticating filaments, and 2 are cut off obliquely from the posterior end of the periaxial cell, producing basipetal corticating filaments. In mature bands acropetal filaments slightly longer (2–3 cells long) than basipetal filaments.

Tetrasporangia irregularly cruciately divided, 30–45(–50) µm in diameter; arranged in a whorl around a cortical band, on a number of bands in succession; a single tetrasporangium produced per periaxial cell; immersed in the cortex of terminal portions of clavate branches. Tetrasporangial branches of varying lengths, swelling to 85–180 µm in diameter to accommodate tetrasporangia; internodes shortened, cortical bands packed tightly together. Gametophytes dioecious. Cystocarps spherical, 50–105 µm in diameter, surrounded by 2–4 involucral branchlets; and appear to be terminal on erect adventitious branches; several upper nodes of these branches broaden in diameter before the cystocarp. Carposporangia 22–30 µm in diameter. Spermatangia minute, colorless cells above spermatangial parent cells produced from cortical cells, covering and swelling terminal end (except apex) of erect adventitious branches (after Cho et al., 2001).

HABITAT. Epiphytic on various algal hosts, including *Laurencia*, *Gelidium*, *Grateloupia,* and especially *Amphiroa*; mid intertidal to shallow subtidal, down to 8 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena. Eastern Pacific: Santa Cruz Island, Anacapa Island and Santa Catalina Island (California Channel Islands) to Punta Santa Rosaliita (“Punta Santa Rosalía”), Baja California; Isla Magdalena (Bahía Magdalena), Baja California Sur; El Salvador; Costa Rica. Western Pacific: Japan; Vietnam.

TYPE LOCALITY. Epiphytic on *Grateloupia prolongata*; Isla Partida (off north end of Isla Espíritu Santo), Baja California Sur, Gulf of California, Mexico.

Ceramium serpens Setchell et N. L. Gardner

FIGURE 84B

Ceramium serpens Setchell et N. L. Gardner, 1924:775, pl. 27: fig. 58; Dawson, 1944a:318; 1949c:244; 1950c:129; 1957a:4, 5; 1961b:441; 1962a:64, pl. 25: fig. 6; Abbott and Hollenberg, 1976:598, fig. 540; Itono, 1972:79, fig. 8; 1977a:33, 109, 198, figs. 13F1-2, 15A, 37H; Schnetter and Bula-Meyer, 1982:155, pl. 26: figs. A–C, pl. 28: fig. C; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1985:26; González-González et al., 1996:188; Yoshida, 1998:898; Abbott, 1999:281, fig. 79C; Pacheco-Ruíz et al., 2008:211.

Algae minute epiphytes; 3–4(–10) mm in height; main axis 45–90 µm in diameter; creeping filaments give rise to sparsely branched erect axes; attached to host by rhizoids. Apices of erect axes nonforcipate or rarely branched, slightly curved. Corticated only at the nodes; internodes rather long (3–5 times nodal band height), except near the apex. Periaxial cells number 4 at a node; each cutting off 4 cortical initials, 2 from the anterior end and 2 from the posterior end of the periaxial cell that initiate cortical filaments. The anterior pair branch once, forming acropetal filaments 2 cells long, and the posterior pair may not divide or may divide obliquely or transversely, forming basipetal filaments 2 cells long. Gland cells absent.

Tetrasporangia cruciately divided, 25–35(–40) µm in diameter; usually solitary (rarely 2) at a node, distributed in a short series along upper portions of erect axes, protruding through the cortex, partially covered by acropetal corticating filaments. Cystocarps and spermatangia unknown.

HABITAT. Epiphytic on larger algae; intertidal.

DISTRIBUTION. Gulf of California: La Paz to Punta Palmilla. Eastern Pacific: Santa Catalina Island (California Channel Islands) to Baja California; Clipperton Island (Dawson, 1957a, with query); Costa Rica (Dawson, 1962a, with query); Colombia; Galápagos Islands (Dawson, 1957a, with query). Central Pacific: Hawaiian Islands; Marshall Islands; Palmyra Atoll. Western Pacific: Japan; China.

TYPE LOCALITY. Epiphytic on *Laurencia*; La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. Although described from the southern Gulf, *Ceramium serpens* is not well known. The collection of gametangial thalli from the type locality, La Paz, and molecular testing of topotype material will be useful in elucidating its taxonomic status. Outside the Gulf of California, *C. serpens* has been rather widely reported: in the western Pacific, central Pacific, South Pacific, Western Australia (Huisman and Borowitzka, 2003), and the Seychelles (Indian Ocean) (Silva et al., 1996a).

South and Skelton (2003) corroborated the interpretation of Millar (1990) and considered Fiji collections of *C. serpens* conspecific with *Ceramium codii* (H. Richards) Feldmann-Mazoyer (1938; basionym: *Ceramithamnion codii* H. Richards, 1901; type locality: Bermuda). It too has been widely reported: in the Atlantic from Florida to Brazil, the Caribbean Sea, Europe, and Africa, and in the Pacific off Japan, Korea, the Hawaiian Islands, Micronesia, and Chile (Guiry and Guiry, 2010) and Rapa Nui (Easter Island; Isla de Pascua; Santelices and Abbott, 1987). Morphological differences between "*C. codii*" from Korea and Bermuda type materials were observed by H.-S. Kim (2012). However, until molecular analyses are completed on those identified as "*C. codii*," Cho and Fredericq (2006) restricted *C. codii* to Bermuda and the Florida Keys, noting it is probably not as widespread in distribution as has been reported, and there may be up to 11 species in the "*C. codii*-complex."

Ceramium sinicola Setchell et N. L. Gardner var. *sinicola*

FIGURE 88

Ceramium sinicola Setchell et N. L. Gardner, 1924:773, pl. 25: figs. 40, 41, pl. 75; Dawson, 1944a:315; 1950c:118, pl. 1: figs. 4, 5; 1957a:5, 8; 1959a:30; Dawson et al., 1960b:12; Dawson, 1961b:441; 1962b:64, pl. 25: figs. 4, 5, pl. 27: figs. 6–8; Abbott and Hollenberg, 1976:602, fig. 546; L. Aguilar-Rosas, 1981:94; Schnetter and Bula-Meyer, 1982:156, pl. 26: figs. D–F, pl. 27: fig. D; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1985:28; 1986:425; Ortega et al., 1987:75, pl. 8: figs. 34–36; Salcedo-Martínez et al., 1988:83; R. Aguilar-Rosas et al., 1990:125; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:188; Silva et al., 1996b:233; Mendoza-González and Mateo-Cid, 1999:44, figs. 20–23; Mateo-Cid et al., 2000:66; Cruz-Ayala et al., 2001:191; Pacheco-Ruíz and Zertuche-González, 2002:468; CONANP, 2002:138; Cho et al., 2003a:778, figs. 3, 4; López et al., 2004:11; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:211.

Ceramium bicorne Setchell et N. L. Gardner, 1924:773, pl. 28: fig. 64, pl. 74; Pacheco-Ruíz et al., 2008:211.

Algae epiphytic, robust, (1–)3–5(–10) mm high; mostly erect axes, 120–250(–690) µm in diameter, often more slender basally, widening above, branching subdichotomous, at intervals of 6–8 axial segments, with frequent short proliferous branchlets above short prostrate axes; attached by multicellular rod shaped rhizoids, produced by periaxial and cortical cells, rhizoids with mostly blunt tips or occasionally multicellular digitate pads. Apices forcipate and slightly incurved, at times with 1 to several multicellular spines. Cortication coverage variable: almost completely corticated in some or internodes evident basally but barely discernable up higher on erect axes (i.e., cortication incomplete in basal portions and prostrate axes with internodes evident). Periaxial cells 7–8 at a node; each periaxial cell cuts off 5 cortical initials; first 2 initials cut off obliquely from the anterior end of the periaxial cell develop acropetal cortical filaments, each 5–7 cells long; second 2 initials are cut off obliquely from the posterior end of the periaxial cell and develop basipetal filaments, each 5–7 cells long; a fifth cortical initial issued on the outside face of a periaxial cell. Cortex composed of small angular cells, 5–7 µm in diameter; covering nearly all of the axial cell in the upper parts of mature erect axes, with a diminutive empty space separating segments.

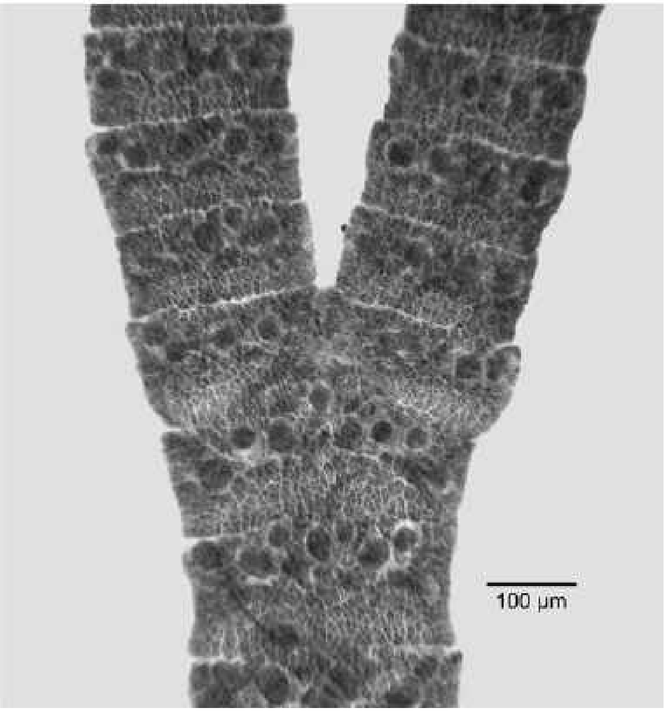


FIGURE 88. *Ceramium sinicola*: Nearly complete cortication covers axial filament with immersed tetrasporangia whorled at nodes (*JN-4584*, US Alg. Coll. microscope slide 4798).

Tetrasporangia tetrahedrally divided, spherical to ellipsoidal, (30–)45–55 µm in diameter; immersed in the cortex, and sporangial production may extend through several axial dichotomies; tetrasporangial axes may be enlarged, up to 690 µm in diameter, occasionally with several short straight spines at the apices. Tetrasporangia in a whorl at a node in distal portions of the thallus when produced only by the periaxial cells (1 per parental cell); in middle regions tetrasporangia also produced by inner cortical cells with additional whorls of tetrasporangia within a segment. Cystocarps spherical, 150–350 µm in diameter; borne abaxial in upper portions of axes, surrounded by 4–6 short involucral branchlets with incomplete cortication. Spermatangia minute, colorless cells, 3–4 µm in diameter; form a dense layer over cortical cells in the upper portions of the thallus; initially adaxial, later encircling cortex (Cho et al., 2003a).

HABITAT. Epiphytic on *Codium*, *Laurencia*, *Tacanoosca*, *Amphiroa*, and other, usually larger, algae; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía Tepoca to Cabeza Ballena; Isla San Pedro Nolasco; Bahía Topolobampo; Laguna Agiabampo, Sonora-Sinaloa to Nayarit. Eastern Pacific: Santa Barbara, California to Todos Santos and Rocas Alijos, Baja California Sur; Islas Todos Santos and Isla Guadalupe, Baja California; Isla San Benedicto (Islas Revillagigedo); Jalisco to Guerrero; Colombia.

TYPE LOCALITY. Bahía de Todos Santos, Ensenada, Baja California, Pacific Mexico.

REMARKS. *Ceramium sinicola* var. *sinicola* is a frequently encountered epiphyte in the Gulf of California. Originally, Setchell and Gardner (1924a) described three similar-looking Gulf species (*C. sinicola*, *C. interruptum*, and *C. johnstonii*) on the basis of differences in degrees of their cortication. Dawson (1944a) reduced these species to taxonomic varieties of *C. sinicola,* as *C. sinicola* var. *sinicola*, *C. sinicola* var. *interruptum,* and *C. sinicola* var. *johnstonii*. Abbott and Hollenberg (1976) did not recognized these varieties, noting that "large numbers of specimens will demonstrate a complete range of the cortication characters by which these varieties are distinguished," thus reducing them to represent a single, variable, more broadly defined species. More recently, Cho et al. (2003a) resurrected one of the taxonomic varieties to specific status, *C. interruptum,* on the basis of phylogenetic analyses of its distinct DNA sequences as well as morphological features. Reports identifying "*C. sinicola*" from the Gulf of California and Pacific Mexico should be reexamined to verify that they are *C. sinicola* var. *sinicola* or possibly *C. sinicola* var. *johnstonii* or *C. interruptum* (see also Remarks under *C. interruptum*).

Ceramium sinicola var. *johnstonii* (Setchell et N. L. Gardner) E. Y. Dawson

Ceramium johnstonii Setchell et N. L. Gardner, 1924:774, pls. 76, 77.

Ceramium sinicola var. *johnstonii* (Setchell et N. L. Gardner) E. Y. Dawson, 1944a:316; 1950c:119; 1961b:441; 1962a:65; González-González et al., 1996:189.

Algae 1–2(–3) cm tall, about 80 µm in diameter; subdichotomously branched; completely corticated, except in basal portions; cortical cells 7.0–10 µm in diameter, not arranged in rows; a slight separation between corticating segments can form a very narrow internodal space in upper portions of axes; apical cell very acute.

Tetrasporangia completely immersed in corticating layer; irregularly scattered in axes and more or less arranged in whorls in short lateral branches (only slightly swelling the branches). Cystocarps and spermatangia unknown in type material (Setchell and Gardner, 1924).

HABITAT. Epiphytic on various algae; intertidal.

DISTRIBUTION. Gulf of California: Bahía Tepoca to La Paz; Isla San Esteban and Isla San Pedro Mártir (Islas de la Cintura).

TYPE LOCALITY. Isla San Pedro Mártir, Gulf of California, Mexico.

REMARKS. Although similar to *Ceramium sinicola* var. *sinicola*, the variety *C. sinicola* var. *johnstonii* differs morphologically in being completely corticated throughout the thallus except in the lowermost basal parts (Dawson, 1962a). The taxonomic status of Gulf of California *C. sinicola* var. *johnstonii* requires further investigation and comparative testing with Pacific Mexico *C. sinicola* var. *sinicola*, particularly with type locality (Ensenada, Baja California) material. The southern California *C. sinicola* was elucidated by Cho et al. (2003a), who also suggested that *C. johnstonii* may be conspecific.

Ceramium vagans P. C. Silva

Ceramium vagans P. C. Silva in Silva et al., 1987:56; Abbott, 1999:284, fig. 80A–D; Abbott et al., 2002:305, fig. 8; López et al., 2004:11; Serviere-Zaragoza et al., 2007:9; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:61.

Ceramium vagabundum E. Y. Dawson, 1957b:121, *nom. illeg*., fig. 27e; 1957c:22; 1961b:441; 1962b:66, pl. 27: fig. 5; Schnetter and Bula-Meyer, 1982:157, pl. 26: figs. G,H, pl. 28: figs. A,B; González-González et al., 1996:189 [a later homonym of *Ceramium vagabundum* (Linnaeus) Roth, 1800:465; basionym: *Conferva vagabunda* Linnaeus, 1753:1167, which is now *Cladophora vagabunda* (Linnaeus) C. Hoek, 1963:144].

Ceramium sp. sensu Dawson, 1954c:6, pl. 4: fig. 2 [see Dawson, 1957c:22].

Algae of erect axes arising irregularly from prostrate axes; mostly less than 2(–5) mm high and 60–135(–165) µm in diameter; erect axes unbranched or sparingly subdichotomously to irregularly branched, with gradual taper to straight nonforcipate apices; attached to substrate by rhizoids issued by periaxial and cortical cells on ventral side of creeping axes. Corticated only at nodes, internodal space narrowing toward apices. Periaxial cells number 6–8; each cuts off 4 cortical initials, 2 acropetal and 2 basipetal. Nodal bands in young stages 3 cell rows high. Each cortical initial produces 2 cells (that elongate then divide); each developing 2 cortical filaments several cells long. Along lower (proximal) margin of the nodes at the elongation stage (before division) the bottom row of elongate cells looks regularly parallel, then cells divide, and the row looks less regular, although nodal cortication remains truncate along bottom edge (upper margin also truncate). Acropetal and basipetal filament growth about equal, with round periaxial cells in middle of band with progressively smaller cells toward edges, ultimate cells angular, <10 µm. Mature nodal bands consist of 7–8 cell rows; bands about 1.5–2.0 times as wide as tall. Gland cells absent.

Tetrasporangial axes swollen, 180–195(–250) µm in diameter; nodal bands closely arranged, forming tumid crowded area near terminal portion of axes. Tetrasporangia typically cruciately divided, 40 µm long, about 25 µm in diameter; whorled within nodes, covered by cortical involucres, bulging out fertile nodes. Sexual plants not observed.

Habitat. On rock, often mixed with other algae in algal turfs; intertidal.

Distribution. Gulf of California: Isla Turner, off SE end of Isla Tiburón (Islas de la Cintura). Eastern Pacific: Isla San Benedicto (Islas Revillagigedo); Guerrero; El Salvador; Costa Rica; Colombia. Central Pacific: Hawaiian Islands. Western Pacific: Philippines; Vietnam.

Type Locality. Growing within tufts of *Asteronema breviarticulatum* (J. Agardh) Ouriques et Bouzon (2000); near the margin of the seaward reef opposite the Enewetak Marine Biology Laboratory, Parry Island, Enewetak Atoll (Eniwetok), Ralik Archipelago, northwest Marshall Islands.

Remarks. *Ceramium vagans* is not well known in the northern Gulf. It has been more widely reported in the tropical Pacific: Philippines (Silva et al., 1987); Enewetak (Dawson, 1957b); Palmyra Atoll; Fiji (South and Skelton, 2000); French Polynesia (Payri et al., 2000); Micronesia (Lobban and Tsuda, 2003). It is also reported in the western Atlantic from Brazil (Villaca et al., 2010).

Ceramium zacae Setchell et N. L. Gardner

Ceramium zacae Setchell et N. L. Gardner, 1937:89, pl. 8: fig. 22a–c; Dawson, 1945c:62; 1950c:134, figs. 27, 28; 1957a:8; 1959a:30; Dawson et al., 1960b:12, 24; Dawson, 1961b:441; 1962b:67, pl. 26: figs. 4–6; Norris and Hollenberg, 1970:118; Abbott and Hollenberg, 1976:598, fig. 542; Mendoza-González and Mateo-Cid, 1986:425; Scagel et al., 1989:165; Mateo-Cid et al., 1993:48; González-González et al., 1996:190; Silva et al., 1996b:233; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; Hernández-Herrera et al., 2005:147; Pérez-Estrada et al., 2012:191.

Algae epiphytic, with prostrate and erect portions, up to 6 mm high; main axes 100–300 µm in diameter, tapering upward with upper branches reduced in diameter; branching subdichotomous, more densely branched toward apices, with occasional proliferous branches. Apices straight and forcipate. Corticated only at the nodes; internodes short throughout the thallus; lower internodes about as long as broad. Periaxial cells number 5; each cuts off 2 cells acropetally that overlap the periaxials. Each acropetal cell cuts off (1–)2 cells acropetally; these in turn, commonly cut off an additional cell acropetally. Periaxial cells in lower nodes cut off 1(–2) cell obliquely basipetal. Nodes truncate on the lower side.

Reproduction not seen in our material. Tetrasporangia naked, emergent, 35–40 µm in diameter; whorled 3–4 at a node, or on either adaxial or abaxial sides of axes. Cystocarps surrounded by involucral branchlets; borne lateral in the upper portion of axes. Spermatangia in adaxial patches on the nodes in upper parts of axes (after Dawson, 1962b).

Habitat. Epiphytic on *Gelidium* and other algae and on red mangrove (*Rhizophora mangle*) prop roots; low intertidal.

Distribution. Gulf of California: Puerto Peñasco; Punta Cirio to Segundo Cerro Prieto, Bahía Kino; Puertecitos to Bahía Agua Verde; Bahía de La Paz to Punta Arena; Jalisco. Eastern Pacific: northern Washington; southern California to Punta Abreojos (inside of Bajos Wright) and Rocas Alijos, Baja California Sur.

Type Locality. Epiphytic on *Codium fragile*; Bahía Tortuga (southeast side of Bahía San Bartolomé), Baja California Sur, Pacific Mexico.

Corallophila Weber-van Bosse

FIGURE 89B

Corallophila Weber-van Bosse, 1923:339.

Algae are prostrate axes that give rise to erect axes that may be unbranched or with subdichotomous or adventitious branching. Axes attach to hosts or substrate by rhizoids that develop from periaxial and inner cortical cells. Axes composed of a central row of large axial cells that are almost completely covered by smaller cells of the corticating filaments, except for narrow gaps separating the adjacent cortical segments of successive axial cells. Each axial cell cuts off 4–12 periaxial cells (depending on species) at its distal end, and each periaxial cell cuts off four cortical initials that develop the cortical filaments [except *C. itonoi* (Ardré) R. E. Norris, 1993, which has pseudoperiaxial cells (see Itono, 1977a, fig. 16P]. Two acropetal initials are cut off from the anterior end of a periaxial cell, and two basipetal initials are cut off from the posterior end. Cortical growth is predominately in the basipetal (descending) direction; basipetal cortical filaments are simple or may branch, consist of three or more rectangular cells aligned in parallel longitudinal rows, and descend to cover the axial cell (internode). The two acropetal cortical filaments are short, ascending, and composed of two to three rounded cells not aligned in longitudinal rows. Cortication is mostly one cell layer thick; axes and branches are similarly corticated. Spines are present in some species.

Tetrasporangia are tetrahedrally divided, partially or completely embedded in the cortical layer (except in *C. itonoi*), and borne toward the end of erect branches or on short, stichidia-like branchlets (Norris, 1993). Cystocarps, currently known for only two of the species (Cho et al., 2000), are borne lateral on erect branches and usually consist of two gonimolobes, without involucres or sterile branches. Spermatangia are in superficial patches on ordinary cortical cells in the upper thallus.

Remarks. Although the distinctiveness of the genus *Corallophila* is controversial (e.g., Wollaston in Guiry and Guiry, 2008–2010), some have recognized the genus (e.g., Price and Scott, 1992; Norris, 1993; Yoshida, 1998; Abbott, 1999). Cho et al. (2000:323, tbl. 1) confirmed the generic concept of *Corallophila* of Norris (1993).

In the Gulf of California, the cortical pattern of *Corallophila* is most similar to *Centroceras,* which also has rectangular cortical cells arranged in somewhat regular longitudinal rows. *Corallophila* is distinguished by two basipetal cortical initials that develop from the posterior end of each periaxial cell, with

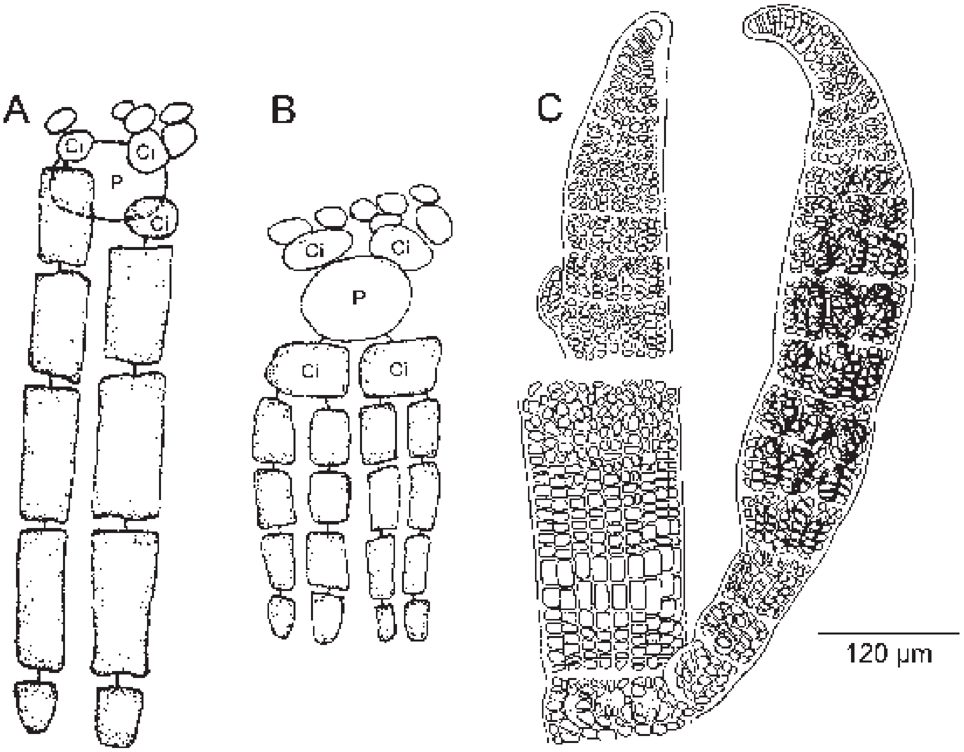


FIGURE 89. Diagrammatic illustrations comparing cortical units of the genera *Centroceras* and *Corallophila* and cortication pattern detail of *Corallophila bella*. A. *Centroceras*: A typical periaxial cell issues 3 cortical filament initials, the first 2 from its distal end and a third from its proximal end. The first distal initial develops only acropetally (short filaments, spines, or gland cells), and the second distal initial grows both acropetally and basipetally, producing a long descending filament. The solitary proximal cortical initial grows only basipetally, cutting off a long descending filament. B. *Corallophila*: In most species a periaxial cell issues 4 cortical filament initials—2 distally that develop short acropetal filaments and 2 proximally that issue basipetal filaments that are longer and branch. (Abbreviations: P, periaxial cell; ci, cortical initial. Basipetal (descending) filaments are stippled. A, B, drawn with modifications after R. E. Norris, 1993, figs. 1b, 2b.) C. *Corallophila bella*: Note slightly curved, undivided apices; upper portion of erect axis with tetrasporangia immersed within the cortex in rings around the nodes; and cortical cells in regular vertical rows (type specimen drawings after Setchell and Gardner, 1924, pl. 26: fig. 48).

each basipetal filament branching once, whereas in *Centroceras* the basipetal filaments do not branch and only one basipetal cortical initial is issued per periaxial cell, with the other descending cortical filament developing basipetally from an acropetal cortical initial (see diagram comparing cortical units in Figure 89A, B).

One species of *Corallophila* occurs in the northern Gulf of California.

Corallophila bella (Setchell et N. L. Gardner) R. E. Norris

FIGURE 89C

Centroceras bellum Setchell et N. L. Gardner, 1924:779, pl. 26: fig. 48, pls. 40c, 78; Dawson, 1944a:321; 1961b:441; 1962b:69, pl. 27: fig. 4; Hommersand, 1963:244, fig. 30b–l; González-González et al., 1996:184.

Corallophila bella (Setchell et N. L. Gardner) R. E. Norris, 1993:395; Abbott et al., 2002:306, with query.

Ceramiella bella (Setchell et N. L. Gardner) Børgesen in Díaz-Piferrer, 1969a:202, *nom. nudum.*

Ceramiella bella (Setchell et N. L. Gardner) Díaz-Piferrer, 1969b:179.

Algae consist of axes arising from prostrate axes and becoming erect, 1.0–1.5 cm tall; completely corticated (except for narrow gaps between cortical segments); branching irregular, subsecund to subdichotomous; adventitious branches common; attached to the substrate by numerous rhizoids issued by the periaxial or inner cortical cells of prostrate axes. Main axes about 110–130 µm in diameter, gradually tapering to a single apical cell; apex slightly curved. Periaxial cells 8–10 at the distal end of an axial cell; each periaxial cell issues 2 acropetal initials that develop into short corticating filaments and 2 basipetal cortical initials. Corticating cells of basipetal filaments are quadrate and arranged in straight rows parallel to the axis. Filament cells midway through a mature cortical segment may be longer than other corticating cells (Setchell and Gardner, 1924; Norris, 1993). Spines absent.

Tetrasporangia cruciately divided; immersed beneath the cortex; in a ring around nodes, in slightly swollen branches. Cortical cells are often smaller in tetrasporangial axes. Carpogonial and spermatangial thalli unknown in Gulf of California material.

HABITAT. Known from drift, cast ashore.

DISTRIBUTION. Gulf of California: Guaymas. Western Pacific: Vietnam.

TYPE LOCALITY. Cast ashore; Guaymas, Sonora, Gulf of California, Mexico.

REMARKS. In the Gulf, *Corallophila bella* is most easily separated from the similar-looking *Centroceras* species by its lack of circinate apices and the absence of spines. Seemingly rare in the northern Gulf of California, *Corallophila bella* remains only known from the type specimen, *Centroceras bellum* Setchell et N. L. Gardner (1924) from Guaymas, Sonora (Dawson, 1962b; Hommersand, 1963). It is apparently more common elsewhere, having been reported in the western Pacific from Vietnam (Abbott et al., 2002), the eastern Atlantic from Sierra Leone (Lawson and John, 1987), and the Persian Gulf and Oman Sea from Iran (Sohrabipour and Rabii, 1999).

***Gayliella* T. O. Cho, L. McIvor et S. M. Boo**

Gayliella T. O. Cho, L. McIvor et S. M. Boo in Cho et al., 2008:723.

Algae epiphytic, composed of prostrate axes that give rise to erect axes, and attach to host by elongate unicellular rhizoids issued only from periaxial cells (1 per periaxial cell), with rhizoids often ending in a digitate pad. Axes are corticated only at the nodes and branch alternately and terminate with forcipate apices. Nodes consist of 4–9 periaxial cells, with each periaxial cell producing (2–)3–4 corticating filament initials. The single basipetally directed cortical initial is developed by a transverse (horizontal) division near the posterior end of a periaxial cell; this basipetal cell is horizontally elongate (about same width as the periaxial or pseudoperiaxial cell) and remains undivided or may undergo further divisions depending on species. Gland cells often present.

Tetrasporangia are developed only by the periaxial cells, a single tetrasporangium per periaxial cell, that is somewhat covered by cortical filament cells. Cystocarps are borne near apices and surrounded by involucral branches. Spermatangial parent cells are issued by cortical cells and produce spermatangia that cover the cortical surface.

Four species of *Gayliella* are currently known in the northern Gulf of California.

KEY TO THE SPECIES OF *GAYLIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Gland cells clavate, projecting markedly from node; often greater than 40 μm long . . . . *G. fimbriata*
1b. Gland cells absent or, if present, spherical to ovoid, not projecting notably from node; smaller, less than 25 μm long . . . 2
2a. Pseudoperiaxial cells present between periaxial cells; nodal cells arranged in regular vertical columns; acropetal and basipetal cortical initials produced by transverse division of periaxial or pseudoperiaxial cells, width of initial nearly equal to that of producing cell; tetrasporangia cruciately divided . . . . *G. recticortica*
2b. Pseudoperiaxial cells not present between periaxial cells; nodal cells not arranged in regular vertical columns; only basipetal cortical initial produced by transverse division of periaxial cells (initial may remain horizontally elongate or may divide further depending on species); tetrasporangia tetrahedrally divided 3
3a. Periaxial cells number 4; horizontally elongate basipetal cortical cells remain apparent in mature cortical pattern . . . . **G. species A**
3b. Periaxial cells number 6–7; horizontally elongate basipetal cortical cells indiscernible in mature cortex as they continue to divide, resulting in numerous smaller cells . . . . *G. taylorii*

***Gayliella fimbriata* (Setchell et N. L. Gardner) T. O. Cho et S. M. Boo**

FIGURE 90

Ceramium fimbriatum Setchell et N. L. Gardner, 1924:777, pl. 26: figs. 43, 44; Setchell and Gardner, 1937:88, pl. 7: fig. 18; Dawson, 1944a:317; 1950c:123; 1959a:30; 1961b:440; 1962a:56, pl. 19: fig. 3, pl. 20: figs. 6, 7; 1966a:27; Chávez-Barrear, 1972b:269; Itono, 1977a:33, 106, 197, figs. 13I, 14E–G, 37D; Huerta-Múzquiz, 1978:338; Pedroche and González-González, 1981:66; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1986:425; Sánchez-Rodríguez et al., 1989:44; Mendoza-González and Mateo-Cid, 1992:20; Abbott, 1999:272, fig. 76A–C; González-González et al., 1996:186; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211.

Gayliella fimbriata (Setchell et N. L. Gardner) T. O. Cho et S. M. Boo in Cho et al., 2008:723, fig. 2a–q; H.-S. Kim, 2012:95: figs. 73–74; Jeong et al, 2013:443, fig. 3.

Algae minute; composed of prostrate axes giving rise to erect axes, up to 8 mm tall, 80–150 μm wide basally; attached to the substratum by unicellular rhizoids issued from periaxial cells. Branching regularly alternate, at intervals of 3–5 axial cells in main axes and intervals of 4–6 axial cells in lateral axes; with forked, slightly incurved apices. Axes corticated only at the nodes, internodes short in upper portions, lengthening markedly in basal and prostrate portions. Axial cells are spherical near apices and elongate to cylindrical below. Periaxial cells number 6–7, each periaxial cell divides off 3 cortical filament initials. The first 2 cortical initials cut off obliquely from the anterior end of the periaxial cell and develop 2 acropetal corticating filaments,

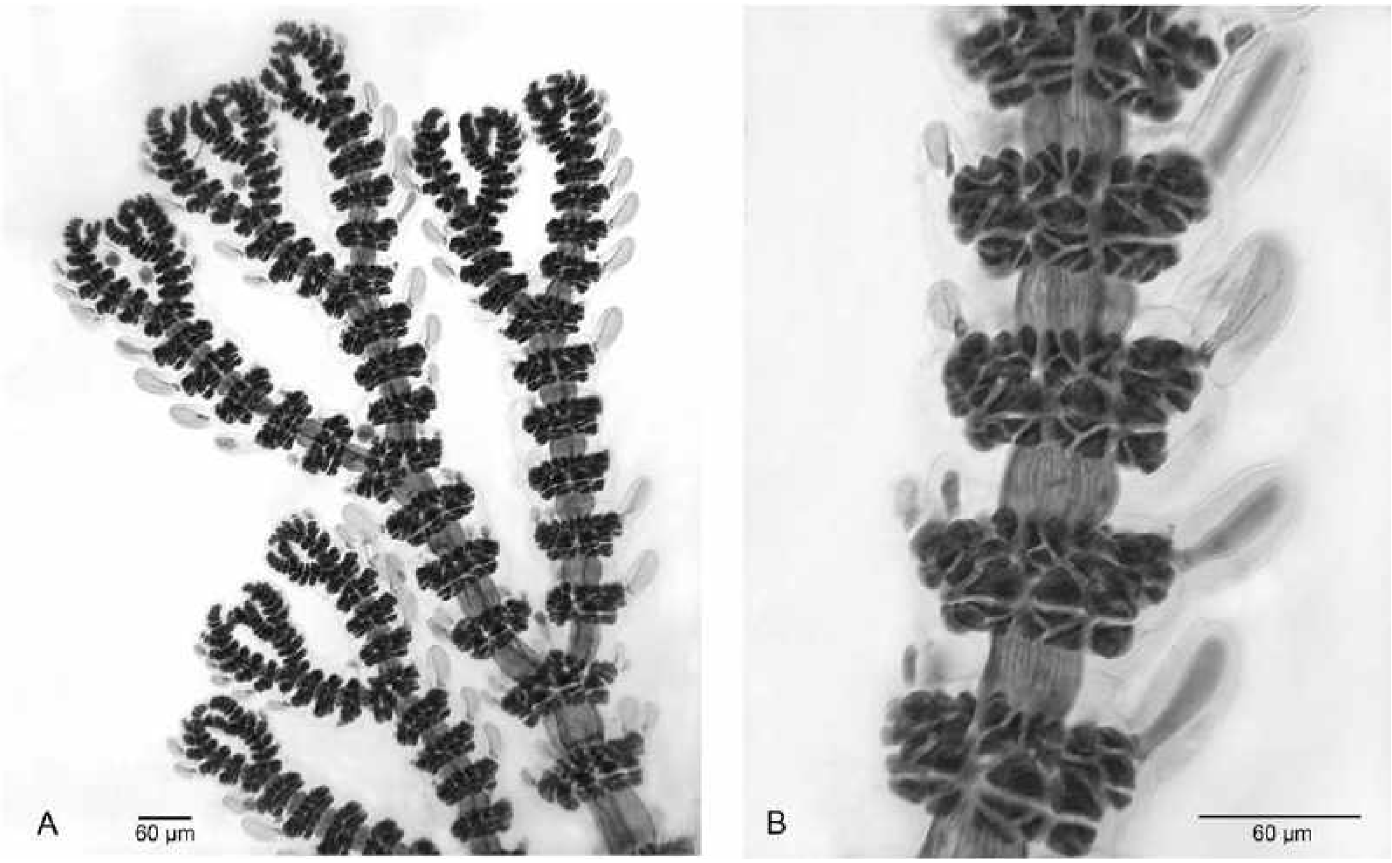


FIGURE 90. *Gayliella fimbriata*: A. Habit of erect axes, with series of protruding gland cells on abaxial side. B. Mature cortical pattern with clavate gland cells, some whorled about node (A, B, *JN-5062*, US Alg. Coll. microscope slide 5263).

and the third initial, cut off transversely (horizontally) from the posterior end of the periaxial cell, is horizontally elongate and later continues to divide. The acropetal corticating filaments are 3–4 cells long, and the basipetal filament is 2–3 cells long. Where a lateral branch occurs, 1 periaxial cell produces an additional cortical initial that develops an extra acropetal cortical filament. Protruding stout, bulbous, clavate gland cells, issued from the cortical cells (initially by terminal cells of acropetal filaments), are at first abaxially arranged and later whorled about the nodes (later may develop on basipetal cortical filament cells also). Gland cells up to 40(–60) µm long and upwardly directed.

Tetrasporangia spherical, 55–65 µm in diameter; whorled at nodes and partially covered by cortical filaments (Dawson, 1962a). Gametophytes not known in the Gulf.

Habitat. Epiphytic on *Padina* and other algae, sometimes entangled with other algae; intertidal to shallow subtidal (also dredged from 40 m depths; Dawson, 1962a:57).

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Punta Banda, Baja California to Punta Eugenia ("San Eugenio"), Baja California Sur; Guerrero. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea.

Type Locality. Floating; Eureka, near La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. The large, protruding, clavate gland cells of *G. fimbriata* distinguish it from other *Gayliella* species. Won and Cho (2010) reported differences in their molecular phylogenetic analysis between Gulf of California type locality *G. fimbriata* and those of Korea; however their data are not yet published (H.-S. Kim, 2012).

Gayliella species A

FIGURE 91

Ceramium gracillimum var. *byssoideum* sensu Dawson, 1957c:21; 1959a:30; 1961b:440; 1962a:57, pl. 20: figs. 2, 3, pl. 21: figs. 2, 3; Abbott and Hollenberg, 1976:597, fig. 538; Huerta-Múzquiz, 1978:338; Schnetter and Bula-Meyer, 1982:152, pl. 25: figs. L–O, pl. 27: fig. C; Mendoza-González and Mateo-Cid, 1986:425; Pacheco-Ruíz and Zertuche-González, 2002:468 [non *Ceramium gracillimum* var. *byssoideum* (Harvey) Feldmann-Mazoyer, 1938:323; 1940:293, fig. 109].

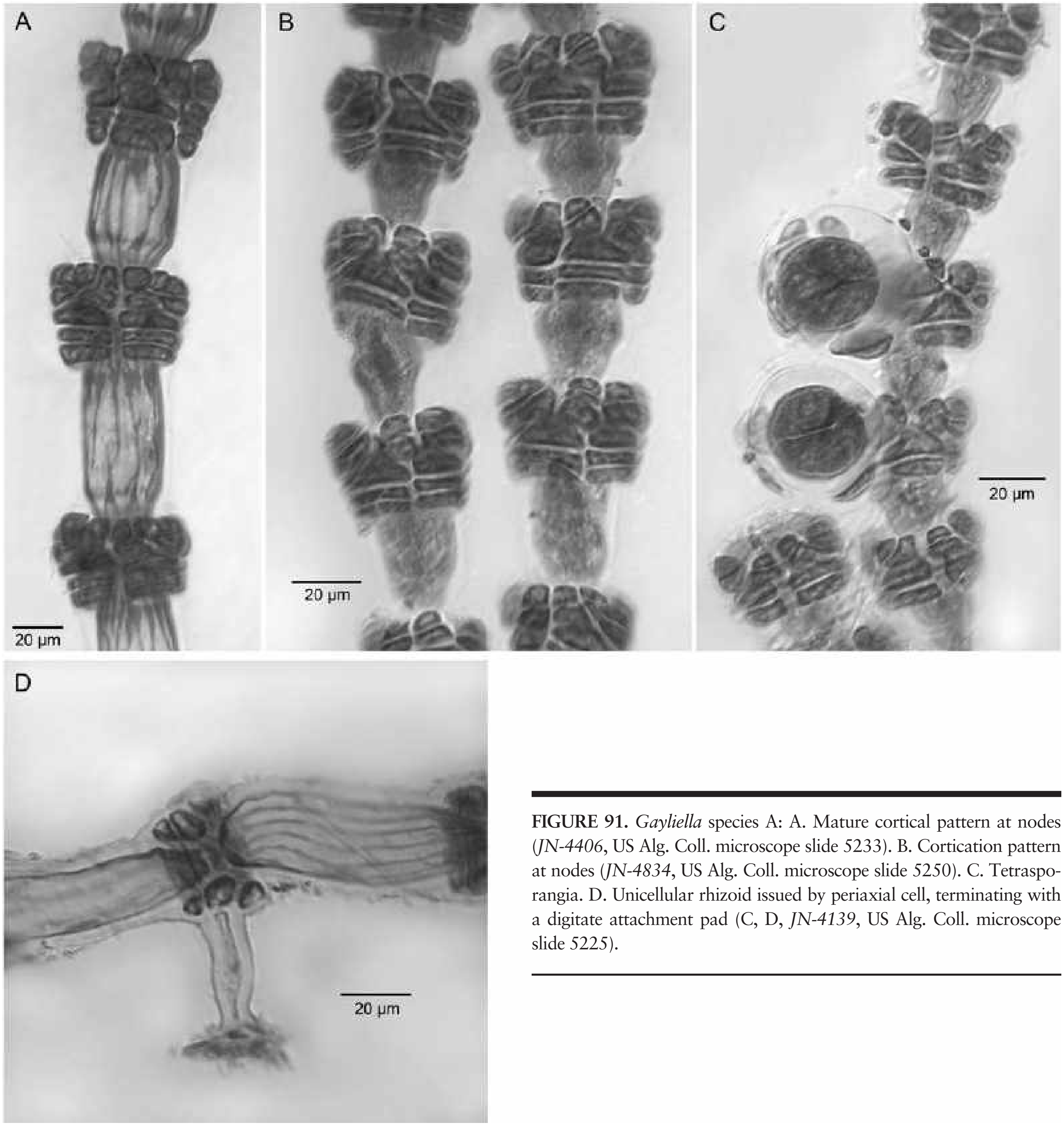


FIGURE 91. *Gayliella* species A: A. Mature cortical pattern at nodes (*JN-4406*, US Alg. Coll. microscope slide 5233). B. Cortication pattern at nodes (*JN-4834*, US Alg. Coll. microscope slide 5250). C. Tetrasporangia. D. Unicellular rhizoid issued by periaxial cell, terminating with a digitate attachment pad (C, D, *JN-4139*, US Alg. Coll. microscope slide 5225).

Thalli forming epiphytic minute tufts, up to 10 mm high, with prostrate and erect axes, up to 80–100 µm in diameter basally; attached by rhizoids from prostrate or lower portions of erect axes. Rhizoids unicellular, developed only from periaxial cells, with blunt tips or with digitate attachment discs. Apices forcipate and slightly incurved. Branching alternately at intervals of 4–6 axial cells in main axes and intervals of 6–10 axial cells in lateral axes. Nodes in midportions up to 65 µm wide and to 45 µm tall (long). Internodes long in prostrate and basal portions of the axes. Four periaxial cells encircle a node, periaxial cells somewhat triangular in shape. Each periaxial cell cuts off 3 cortical initials: 2 from the anterior end of the periaxial cell are cut off obliquely and develop acropetal cortical filaments; 1 cut off transversely from the posterior end is horizontally elongate and may divide transversely again to form a second horizontally elongate cell and infrequently may undergo 1 further transverse division. Each of the acropetal corticating filaments is 2–3 cells long, each basipetal filament is 2–3 cells long. Gland cells occasionally present, ovoid, up to 15 µm in diameter, most often at ends of acropetal cortical filaments.

Tetrasporangia 30–45 µm in diameter, borne singly at a node (Figure 91C) or whorled (Dawson, 1950c, as *Ceramium masonii*), each partially covered by cortical filament cells ("involucres"). Female thalli not found in Gulf material. Spermatangial superficial, covering cortical surface cells (Dawson, 1962a).

Habitat. Epiphytic on other algae; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena.

Remarks. Our northern Gulf specimens (US Alg. Coll.) referred to *Gayliella* species A are in agreement with those that Dawson (1962a) identified as "*Ceramium gracillimum* var. *byssoideum*," which are now recognized to belong in the genus *Gayliella*. They somewhat resemble small *Gayliella mazoyerae* T. O. Cho, Fredericq et Hommersand (in Cho et al., 2008) and *G. transversalis* (F. S. Collins et Hervey) T. O. Cho et Fredericq (in Cho et al., 2008), but *Gayliella* species A differs in that its mature basipetal filaments are 2(–3) horizontally elongate cells long, whereas those of both *G. mazoyerae* and *G. transversalis* have only 1 basipetal horizontally elongate cell. In other species of *Gayliella* slight differences in nodal cortication have been shown to be consistent with differences in molecular sequence data (Cho et al., 2008). It seems best to await DNA sequence data on the Gulf specimens to establish species limits before we describe *Gayliella* species A as a new species solely on the differences in the cortical pattern we observed. It is also similar to *Ceramium dawsonii* A. B. Joly (1957:150, pl. 19: figs. 1a–d) from Brazil, but Cho et al. (2008) found that genetically three different species had been referred to "*Ceramium dawsonii*." Although all three belong in the genus *Gayliella*, the generic status of *C. dawsonii* was left unresolved until its type can be examined and compared to their Brazilian specimens.

Gulf of California specimens identified as "*Ceramium flaccidum* (Harvey ex Kützing) Ardissone (1871)" from Puerto Peñasco (Mateo-Cid et al., 2006), Santa Teresa, and Puertecitos (L. Aguilar-Rosas et al., 2000), Bahía de Los Ángeles (Pacheco-Ruíz et al., 2008), Bahía de La Paz (Pérez-Estrada et al., 2012), and Mazátlan (Mendoza-González et al., 1994) should be reexamined to verify its presence in the Gulf or they may belong here. *Ceramium masonii* E. Y. Dawson (1950c), considered to be a synonym of "*C. gracillimum* var. *byssoideum*" sensu Dawson (1954b, 1962a), also needs to be reexamined so its taxonomic status and relationship to *Gayiella* species A can be resolved.

Gayliella recticortica (E. Y. Dawson) T. O. Cho et S. M. Boo

FIGURE 92

Ceramium recticorticum E. Y. Dawson, 1950c:124, pl. 3: figs. 23, 24; 1961b:441; 1962a:63, pl. 24: figs. 5, 6; González-González et al., 1996:188; Cho et al., 2002b:277–289, figs.1–43; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211.

Gayliella recticortica (E. Y. Dawson) T. O. Cho et S. M. Boo in Cho et al., 2008:736.

Thalli minute tufts, to 3(–5) mm tall; main axes 45–75 µm in diameter, of a uniseriate row of axial cells corticated only at the nodes, with long internodes basally; attached to host by elongate unicellular rhizoids produced by periaxial cells of prostrate and basal portions of erect axes; a periaxial cell produces only 1 rhizoid. Apices forcipate and slightly incurved; branching alternate, at intervals of 4–5 segments along main axes and intervals of 5–7 segments in lateral branches. Four periaxial cells encircle a node, along with 4–5 pseudoperiaxial cells, each cut off laterally on the adaxial side of a periaxial cell, except for the first formed periaxial cell that issues a pseudoperiaxial cell laterally on two sides. Periaxial and pseudoperiaxial cells divide transversely from both anterior and posterior ends to produce rectangular, horizontally elongate acropetal and basipetal corticating cells, which may divide transversely again during further development. First formed periaxial cell produces 3 vertical columns of cells (1 from itself and 1 from each of its 2 pseudoperiaxial cells); the other periaxial cells produce 2 vertical rows (1 from themselves and 1 file of cells from their pseudoperiaxial cell). Cortical pattern of 4–5 columns (vertical rows) visible in lateral view appears orderly as somewhat rectangular periaxial, pseudoperiaxial, and cortical cells of the basipetal filaments and acropetal cortical initials are

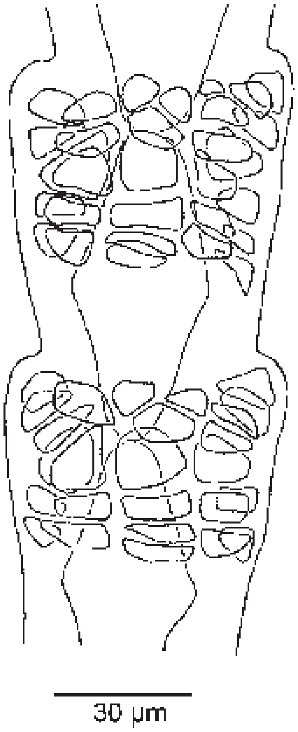


FIGURE 92. *Gayliella recticortica:* Cortication pattern at nodes (*EYD-501-46*, paratype, AHFH, now UC).

of similar width. Ultimate cells of the acropetal filaments smaller and less rectangular. Gland cells spherical to ovoid, small, 9–12 µm in diameter, originate from terminal cells of both acropetal and basipetal corticating filaments (Cho et al., 2002b).

Reproductive structures produced in the upper portions of the thallus. Tetrasporangia cruciately divided, 20–45 µm in diameter, within a hyaline envelope; whorled at the nodes, 1 to 4 tetrasporangia (1 per periaxial cell), covered by cortical cells. Cystocarps spherical; composed of up to 3 gonimolobes and surrounded by 2–4 involucral branchlets. Spermatangia minute, colorless spheres, develop on spermatangial parent cells borne on cortical cells; start on adaxial side and later covering entire cortical surface of a node (Cho et al., 2002b).

Habitat. Epiphytic on *Gastroclonium* and on various other algal hosts; low intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía Bocochibampo, Sonora; Puerto Balandra (east side of Bahía de La Paz) and Punta Perico, Baja California Sur; Mazatlán, Sinaloa. Eastern Pacific: Galápagos Islands.

Type Locality. Epiphytic on *Gastroclonium pacificum*; Bahía Bocochibampo, near Guaymas, Sonora, Gulf of California, Mexico.

Remarks. *Gayliella recticortica* has been reported from the Great Barrier Reef (Price and Scott, 1992:107, as *Ceramium recticorticum*). However, the Australian "*G. recticortica*" may not be the same as the Gulf of California *Gayliella recticortica.* Although both have acropetal and basipetal cortical initials that are horizontally elongate and cortical cells arranged in regular longitudinal rows, nodes of Australian "*G. recticortica*" (see Price and Scott, 1992: fig. 34A, B) are more simple and regular, with all of the nodal cells somewhat equal in width. Also, in the Mexican material including the Gulf of California type of *G. recticortica* (Cho et al., 2002b, as *Ceramium recticorticum*), the acropetal corticating filaments divide, with two little cells and gland cells often present (distal margin more irregular than photo of Australian alga). In the Australian "*G. recticortica,*" pseudoperiaxial cells are apparently absent, so there are fewer longitudinal rows in its cortical band (Price and Scott, 1992:108, fig. 34A–B) than are found in the Gulf of California specimens and the type of *G. recticortica* (Cho et al., 2002b: figs. 2–4, 11–19).

Gayliella taylorii (E. Y. Dawson) T. O. Cho et S. M. Boo

FIGURE 93

Ceramium taylorii E. Y. Dawson, 1950c:127, pl. 2: fig. 13, pl. 4: figs. 31–33; 1954a:6; 1957c:21; 1959a:30; 1961b:441; 1962a:65, pl. 26: figs. 1–3; 1966a:27; Itono, 1972:76, fig. 1B; Abbott and Hollenberg, 1976:598, fig. 541; Itono, 1977a:108, 198, figs. 13J, 14H; Huerta-Múzquiz, 1978:335; Pedroche and González-González, 1981:66; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1992:20; González-González et al., 1996:189; Fernández-García et al., 2011:61.

Gayliella taylorii (E. Y. Dawson) T. O. Cho et S. M. Boo in Cho et al., 2008:727, fig. 4a–l.

Thalli of prostrate and erect axes, to 7–12 mm high and to 120 µm in diameter, alternately branched with forcipate and incurved apices. Main axes with 3–4 axial cells between branching points, and in lateral branches 4–6 axial cells between branches. Unicellular rhizoids issued from periaxial cells in prostrate axes and in the basal portion of erect axes. Axes corticated only at the nodes; axial cells cut off 6–7 periaxial cells at their distal end. Each periaxial cell produces 3 cortical initials that develop corticating filaments: first 2 cortical initials, cut off obliquely from the anterior end of a periaxial cell, form the acropetal filaments; remaining initial, cut off transversely from the posterior end of the periaxial cell, forms a horizontally elongated basipetal cell that undergoes further divisions, developing the basipetal filament. Each acropetal corticating filament 3–4 cells long; basipetal filament 2–3 cells long. Horizontally elongate nature of basipetal cells in mature cortical nodes diminishes as continued divisions break the cell up into smaller angular cells. Small ovoid gland cells, to 12 µm in diameter, develop from acropetal cortical filament cells.

Tetrasporangia whorled at a node, about 30 µm in diameter, covered by acropetal cortical filament cells. Cystocarps surrounded by 5–6 involucral branches; develop near apices. Spermatangia as for genus.

Habitat. Epiphytic on *Prionitis*, *Chaetomorpha*, and probably other algae, also on rocks; intertidal.

Distribution. Gulf of California: Puerto Peñasco; Isla Patos (off north end of Isla Tiburón); Isla Partida; Isla Rasa (Isla Raza); Guaymas, Sonora; La Paz to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: southern California to Bahía Magdalena, Baja California Sur; Isla San Benedicto (Islas Revillagigedo); Guerrero; Oaxaca; El Salvador; Costa Rica. Western Pacific: China.

Type Locality. Cabeza Ballena, Baja California Sur, Gulf of California, Mexico.

CERAMIACEAE TRIBUS PTEROTHAMNIEAE

Ceramiaceae tribus Pterothamnieae Athanasiadis, 1996a:44.

One genus of the tribe Pterothamnieae is represented in the northern Gulf of California.

Pterothamnion Nägeli in Nägeli et Cramer

Pterothamnion Nägeli in Nägeli et Cramer, 1855:66.

Platythamnion J. Agardh, 1892:22.

Algae are erect, richly branched uniseriate filaments, usually with sinusoidal apices, that are attached to substratum or host by multicellular rhizoids issued from the basal region of axes. Thalli are composed of axes of unlimited growth with whorl branches of determinate growth, whorl branches generally of 2 dissimilar pairs. Axial filament cells bear 2 to 4(–5) whorl branches; 2 major subequal or unequal lateral whorl branches opposite each other and may additionally bear 1–2 (rarely 3) transverse minor whorl branches opposite each other. Longer (major) whorl branches may be simple or branched up to 4 orders and are commonly in distichous patterns, tristichous to tetrastichous, and abaxial and/or adaxial or with adaxial pairs of branchlets.

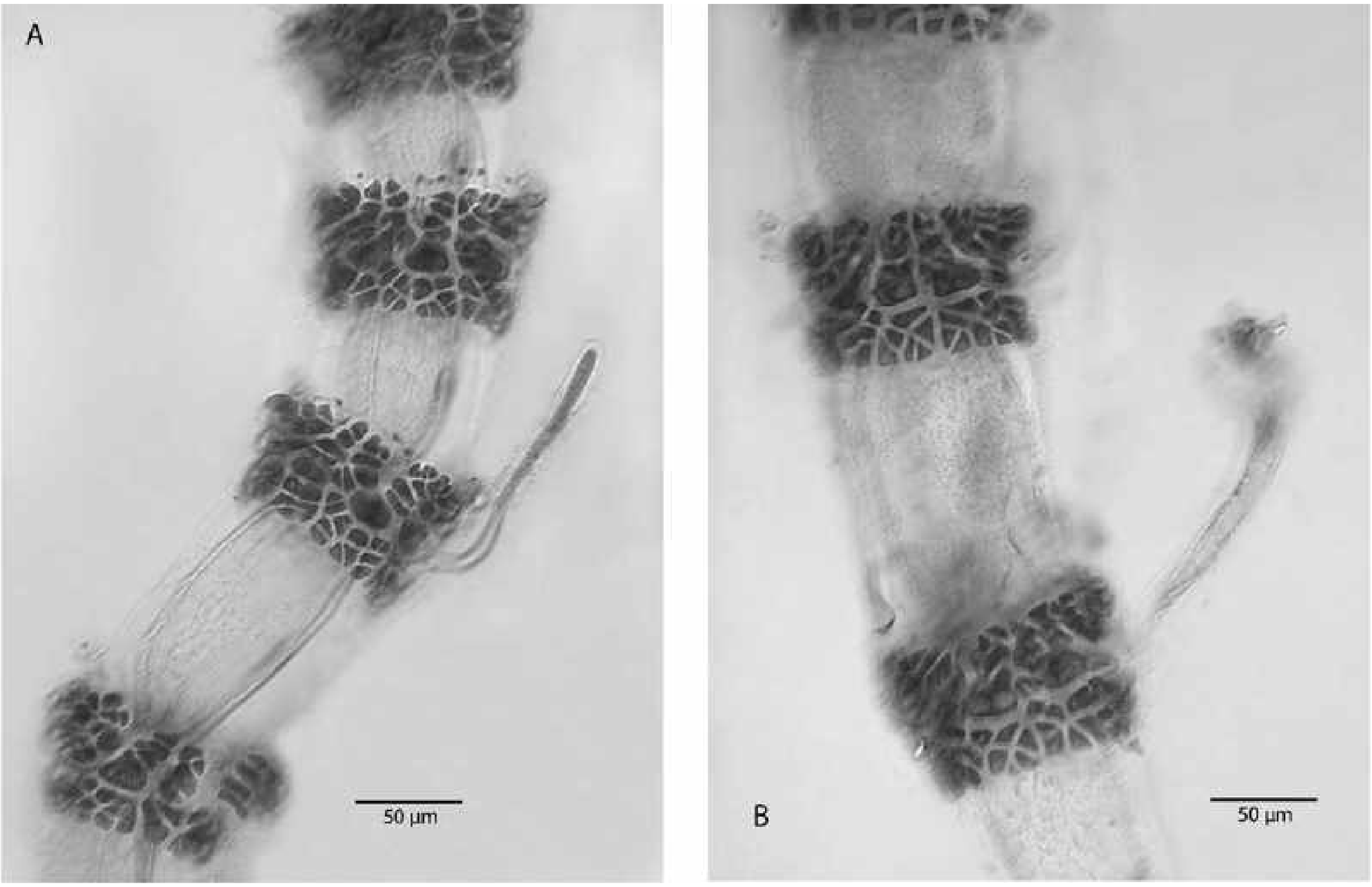


FIGURE 93. Paratypes of *Gayliella taylorii*: A and B. Mature cortication pattern at nodes (A, *EYD-1962*; A, US Alg. Coll. microscope slide 441; B, *EYD-1961*, US Alg. Coll. microscope slide 440).

The minor transverse whorl branch pairs may be dimorphic, distinctly shorter, with a different branching pattern, or just less developed and nearly as long as the major pair of whorl branches. Terminal spines are common in certain species. Indeterminate lateral branches arise in place of long (major) whorl branches in a regular, alternate sequence in the plane of the frond, at intervals of 2–8(–15) cells or irregularly from axial filament cells (Wollaston, 1968:303; Athanasiadis and Kraft, 1994). Adventitious new axes can also develop from the basal cells (and less commonly from other cells) of whorl branches. Axes are usually ecorticated but may be loosely to densely corticated by descending rhizoids in lowermost portions of axes. Gland cells may be common to rare (seldom absent), variable in size and shape, usually sessile, and borne adaxially on an intercalary cell of whorl branches and branchlets.

Mature tetrasporangia are subspherical and cruciately to decussately divided, sessile or pedicellate, and borne singly or in groups, on cells of whorl branches or proximal branchlet cells. Gametophytes usually dioecious, procarps develop near apices of indeterminate axes, carpogonial branches are borne singly, or several in a series, on basal cell of consecutive (and/or opposite) whorl branches that act as support cells. Carposporangia are in several rounded groups (gonimolobes), subtended by whorl branches from the axial cells below. In most species there is usually only 1 carposporophyte per indeterminate axis. Spermatangia are in whorls, terminal on short spermatangial structures that replace various orders of branchlets or branch cells (after Athanasiadis and Kraft, 1994; Athanasiadis, 1996a; Womersley, 1998).

Three species of *Pterothamnion* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *PTEROTHAMNION* IN THE NORTHERN GULF OF CALIFORNIA

1a. Major whorl branches (longer pair) with 3–4 branchlets from each cell (tristichous or tetrastichous), or at least the more proximal cells . . . . **P. *orbignianum***

1b. Major whorl branches with 1 or 2(–3) branchlets from most cells, or at least the more proximal cells 2
2a. Major whorl branches pectinate, branchlets borne nearly exclusively on upper side (adaxial) of whorl branch cells, rarely an abaxial branchlet on periaxial cell . . . . *P. pectinatum*
2b. Major whorl branches distichous and pinnate, branchlets borne on upper and lower sides of proximal whorl branch cells . . . . *P. tepocensis*

Pterothamnion orbignianum **(Montagne) Nägeli**

FIGURE 94

Callithamnion orbignianum Montagne, 1837:351; 1839:7, pl. 7: fig. 4; Kützing, 1861:27, pl. 84: fig. 2.

Pterothamnion orbignianum (Montagne) Nägeli, 1862:376; Athanasiadis, 1996a:51, figs. 9D, 11.

Antithamnion orbignianum (Montagne) De Toni, 1903:1403; Dawson et al., 1964:76, pl. 71: fig. C, pl. 73: figs. A–C; Ramírez and Santelices, 1991:308.

Platythamnion orbignianum (Montagne) J. Agardh, 1892:23; Howe, 1914:154; Taylor, 1947:82.

Platythamnion heteromorphum f. *reversum* Setchell et N. L. Gardner, 1903:345, pl. 25.

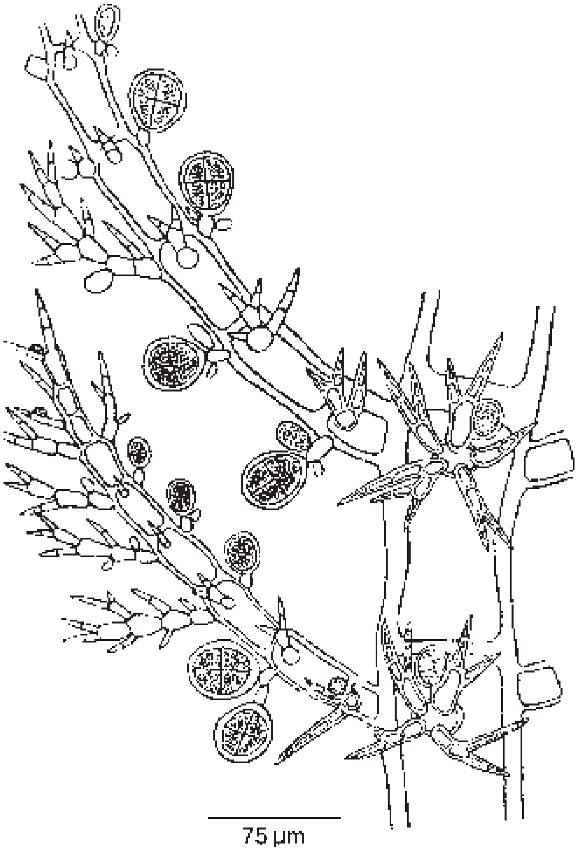


FIGURE 94. *Pterothamnion orbignianum:* Portion of axis showing heteromorphic opposite pairs of whorl branches, bearing tetrasporangia and gland cells (from Kylin, 1925: fig. 34f).

Platythamnion reversum (Setchell et N. L. Gardner) Kylin, 1925:54, fig. 34d–f; Dawson, 1961b:439; 1962a:8, pl. 1: fig. 4d–f; Wollaston, 1972b:48, figs. 1, 7b, 10; Scagel et al., 1989:226; González-González et al., 1996:249.

Pterothamnion reversum (Setchell et N. L. Gardner) Athanasiadis et Kraft, 1994:130.

Algae are up to 2 cm long or more; axes ecorticate, branching to a greater extent basally; at intervals of 4–5 axial cells in distichous-alternate pattern; axial cells up to 600 µm long and to 300 µm in diameter in basal portions; becoming shorter in upper portions. Axial cells with 4 whorl branches of 2 different kinds: a pair of opposite major (long) branches and a pair of opposite minor (short) branches. Major whorl branches up to 650 µm long, and tetrastichously branched, i.e., with 4 branchlets of 2 kinds from each cell (or at least the more basal ones) similar to primary main axes. Each long whorl branchlet of a major whorl-branch with branchlets to either side (usually pectinate with most branches on the adaxial side in relation to branchlet axis) and transverse branchlets shorter and simpler, both types tapering to acute tips. Transverse minor whorl branches composed of a subspherical basal cell bearing a group of short, branched spinose branchlets that may be simple (a basal cell and a spine) or with 3 pronged spines from a basal cell; in some the spinose branchlets occasionally lacking. Gland cells occasional on cells of whorl branches and branchlets.

Tetrasporangia subspherical, cruciately divided, to 35 µm long, on 1-celled pedicels (mostly unbranched) replacing ultimate branchlets. Female gametophytes not known in Gulf of California. Spermatangial clusters with spermatia borne terminally on short branchlets, occurring in place of ultimate branchlets on major (long) whorl branches (after Wollaston, 1972b).

HABITAT. Epiphytic or entangled in larger algae; shallow subtidal, down to 40 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Isla San Esteban (Islas de la Cintura). Eastern Pacific: British Columbia to Oregon; Peru.

TYPE LOCALITY. [Puerto] Callao, Constitutional Province of Callao, Peru.

Pterothamnion pectinatum **(Kylin) Athanasiadis et Kraft**

FIGURE 95

Platythamnion pectinatum Kylin, 1925:53, figs. 32D, 33E, 34A–C; Smith, 1944:316, pl. 79: fig. 1; Dawson, 1961b:439; 1962a:6, pl. 1: fig. 4a–c, pl. 4: figs. 2, 3; 1966b:64; Wollaston, 1972b:51; 1976:588, fig. 528; Norris and Bucher, 1976:18; Stewart and Stewart, 1984:145; Scagel et al., 1989:226; González-González et al., 1996:249.

Pterothamnion pectinatum (Kylin) Athanasiadis et Kraft, 1994:130; Athanasiadis, 1996a:61; Spalding et al., 2003:277; Serviere-Zaragoza et al., 2007:11; Pacheco-Ruíz et al., 2008:211.

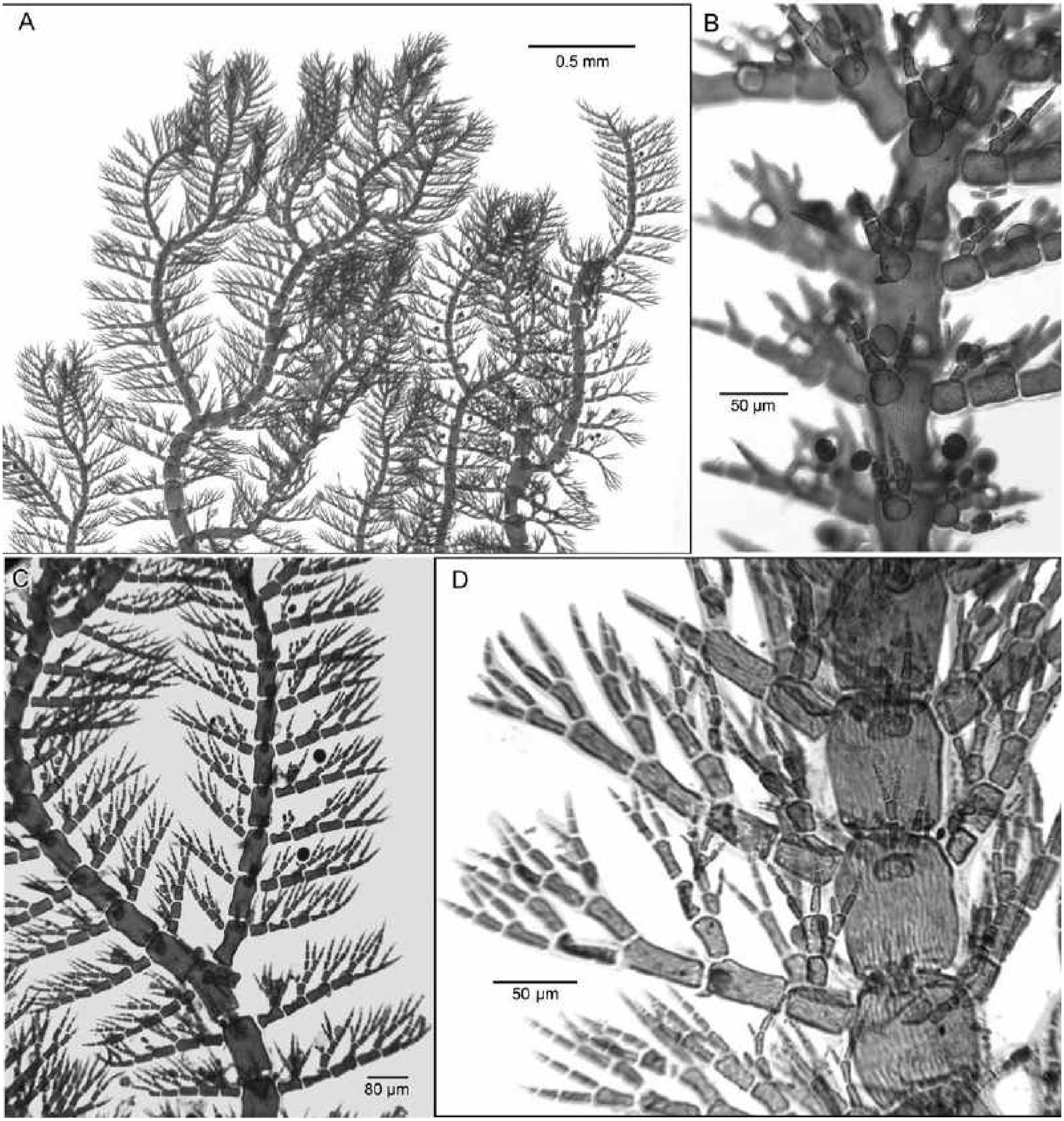


FIGURE 95. *Pterothamnion pectinatum*: A. Branching habit (*JN-5512*, US Alg. Coll. microscope slide 4706). B. Upper portion of an axis focused on plane to show minor whorl branches bearing gland cells (*JN-5263*, US Alg. Coll. microscope slide 4711). C. Tetrasporangia borne in branchlets of whorl branches (*JN-5512*, US Alg. Coll. microscope slide 4706). D. Each axial cell with dissimilar opposite pairs of whorl branches (*JN-5263*, US Alg. Coll. microscope slide 4710).

Platythamnion pectinatum var. *laxum* W. R. Taylor, 1945:266; Dawson, 1945c:57; 1961b:439; González-González et al., 1996:249.

Thalli up to 1.5(–3.5) cm high, with sinusoidal apices, axes up to120(–225) µm in diameter, axes completely uncorticated. Axial cells generally 1.0–1.7(–2.5) times as long as wide. Axial cells bearing 4 whorl branches, 2 pairs of two different types. Mature major whorl branches 6–8(–10) cells long, 250–430 µm in length, in basal portions of thallus; pectinately branched, with a series of branchlets on the adaxial side; sometimes with a pair of branchlets on periaxial cells and rarely the adjacent cell. Branchlets also pectinately branched, but abaxially as related to the rachis of the whorl branch. Branches and branchlets gradually diminish in diameter with each branch order, tapering to acute terminal cells. Pair of minor transverse whorl branches simple in young parts; when mature, transverse whorl branches composed of a basal cell with several 1–3(–7) upwardly directed independent short unbranched or branched branchlets; each up to 6 cells long, mostly up to 75 µm in length (can be longer, up to 180 µm, when on an axial cell that bears an indeterminate lateral branch). Gland cells 12–30 µm and abundantly scattered over the thallus, borne laterally on cells of both major and minor whorl branches, occasionally in a series.

Tetrasporangia cruciately divided, to 27–30(–45) µm long, and borne successively and usually abundantly on cells of proximal pectinate branchlets. Spermatangia terminal in clusters on short branchlets borne on cells of whorl branches (usually adaxial). Carposporangia in several rounded groups (3 gonimolobes), subtended by stout whorl branches from axial cells below, typically, 1 carposporophyte develops per indeterminate lateral.

HABITAT. On hard substrata or epiphytic on other algae; low intertidal to shallow subtidal down to 25 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Isla Las Ánimas (Isla San Lorenzo del Norte); Bahía de San Lucas. Eastern Pacific: Alaska to Isla Guadalupe, Baja California; Isla Clarión (Islas Revillagigedo).

LECTOTYPE LOCALITY. On piles at docks; Friday Harbor, San Juan Island, San Juan County, Washington (Athanasiadis, 1996a).

REMARKS. *Pterothamnion pectinatum* appears to be the most common species of *Pterothamnion* in the northern Gulf of California.

Pterothamnion tepocense (E. Y. Dawson) Athanasiadis et Kraft

Platythamnion tepocense E. Y. Dawson, 1944a:314, pl. 72: fig. 1 (as *P. tepocensis*); 1961b:439; 1962a:7, pl. 2; González-González et al., 1996:249.

Pterothamnion tepocense (E. Y. Dawson) Athanasiadis et Kraft, 1994:130; Athanasiadis, 1996a:53.

Algae up to 3 cm tall; of sparsely branched, main axes of large cells, (50–)70–105 µm long and 50–70 µm in diameter in upper portions, 150–225 µm long and 150 µm (or more) in diameter in lower portions. Axial cells with 4 whorl branches each; an opposite pair of compound longer lateral whorl branches and another pair of simpler minor whorl branches borne transversely. Most major whorl-branches to 500 µm long, curving and tapering upward; bearing opposite pinnate secondary branchlets, (30–)60–100 µm long, occasionally with third order of branchlets, tips acute. Gland cells frequent; borne on a single cell of whorl-branches or branchlets.

Tetrasporophyte and carposporophytes unknown. Spermatangia in clusters mostly on proximal cells of major whorl-branches.

HABITAT. Subtidal; known only from type collection dredged in 22 m depth.

DISTRIBUTION. Gulf of California: Bahía Tepoca (southeast side of Cabo Tepoca; *Hast Heeque Coopol* in the language of the Seri).

TYPE LOCALITY. Bahía Tepoca, Sonora, Gulf of California, Mexico.

REMARKS. *Pterothamnion tepocense* is known only from the northern Gulf type (Dawson, 1944a, as *Platythamnion tepocensis*) and possibly another specimen dredged from 38 m depth, Bahía Sebastián Vizcaíno (Pacific Baja California Sur) that was tentatively referred to this species (Dawson, 1962a).

DASYACEAE

Dasyaceae Kützing, 1843:413, 414.

Thalli are erect or partially prostrate and erect, composed of terete to compressed, branched polysiphonous axes that are ecorticate or corticated by compact descending rhizoid-like filaments. The major axes are polysiphonous, with 4–13 pericentral cells, and have determinate pseudolaterals that are either monosiphonous or monosiphonous only distally with proximal segments polysiphonous; the pseudolaterals may be free or united into a network. The leading axis is sympodial early in development, and branching may be radially or bilaterally or sometimes dorsiventrally organized.

Life histories are triphasic, where known, with isomorphic gametophytes and tetrasporophytes. Ultimate branches of the monosiphonous pseudolaterals are modified to become regenerated axes (polysiphonous with 4–5 pericentral cells) and the pericentral cells develop the reproductive structures. Procarps may also be formed on sympodial developed axes. Tetrasporangia are tetrahedrally divided, each with two to four cover cells, in cylindrical or compressed stichidia borne on the ultimate branches of the pseudolaterals, with several (4–6) tetrasporangia on each segment of a stichidium. Gametophytes are usually dioecious. Each procarp has a four-celled carpogonial branch and two groups of sterile cells. The fertilized carpogonium cuts off one or two connecting cells, one of which fuses with the auxiliary cell. A fusion cell and usually an ostiolate pericarp are formed after fertilization. Spermatangial stichidia cylindrical or lanceolate; spermatangial parent cells are divided off from pericentral cells of a modified ultimate branch of a pseudolateral; spermatangia form a dense colorless layer around it.

There are two genera, each in a different subfamily of the Dasyaceae, represented in the northern Gulf of California.

KEY TO THE GENERA OF DASYACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Pseudolaterals monosiphonous; pseudolaterals usually from every axial segment; usually radially (spirally) arranged; axial segments with (4–)5 pericentral cells; most northern Gulf species corticated . . . . *Dasya*
1b. Pseudolaterals monosiphonous distally, polysiphonous in proximal portions (at least basalmost segment); pseudolaterals not borne from every axial segment; usually bilaterally (distichously) branched; axial segments with 4–12 pericentral cells; northern Gulf species uncorticated . . . . *Heterosiphonia*

DASYACEAE SUBFAM. DASYOIDEAE

Dasyaceae subfam. Dasyoideae F. Schmitz et Falkenberg, 1897:471; H.-G. Choi et al., 2002:564.

The subfamily Dasyoideae is currently represented by one of its nine genera in the northern Gulf of California.

Dasya C. Agardh

Dasya C. Agardh, 1824:xxxiv, 211.

Algae are erect or partially prostrate, with sympodial apices, with main axes and branches terete and polysiphonous, with (4–)5 pericentral cells around the central axial filament cell, and often corticated by rhizoid-like filaments. Axes bear on every polysiphonous segment, radially placed pigmented, usually subdichotomously branched monosiphonous pseudolaterals of limited growth and sometimes adventitious monosiphonous filaments present. Cells are cut off by the pericentral cells that form corticating filaments that grow downward over lower pericentral cells. Monosiphonous filaments are sometimes corticated at their base or polysiphonous (this character not seen in species from the northern Gulf).

Tetrasporangia are tetrahedrally divided, with 2–4 cover cells, and borne in stichidia on pseudolaterals. Gametophytes are usually dioecious. Female reproductive structures are developed on polysiphonous segments of axes. The carposporophyte is surrounded by a well-developed pericarp, often with prominent elongated neck and ostiole. Spermatangial stichidia may be conical, subcylindrical, to linear-lanceolate, often with several sterile cells or filament at their tip; spermatangia are grouped in successive whorls that form colorless sheaths about branches of pseudolaterals.

There are five taxa including three species, one with two varieties and another with a subspecies and two varieties, in the northern Gulf of California.

KEY TO THE SPECIES, SUBSPECIES, AND VARIETIES OF *DASYA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Terminal cells of pseudolaterals acute . . . . *D. spinigera*
1b. Terminal cells of pseudolaterals blunt, rounded 2
2a. Pseudolaterals narrow near their base, 15–40 μm in diameter 3
2b. Pseudolaterals wider near their base, 40–110 μm in diameter 4
3a. Pseudolaterals sparse, axes nearly barren in lower portions; pseudolaterals short, mostly less than 500(–960) μm long . . . . **D. *pedicellata* subsp. *stanfordiana* var. *nudicaulis***
3b. Axes densely clothed with pseudolaterals; pseudolaterals longer, mostly 1–7 mm long . . . . **D. *pedicellata* subsp. *stanfordiana* var. *stanfordiana***
4a. Pseudolaterals narrower, mostly 60–85 μm in diameter, tending to be deciduous, leaving much of the axis bare . . . . **D. *sinicola* var. *sinicola***
4b. Pseudolaterals generally wider near their base, 80–110 μm in diameter, tending to persist, more densely covering upper branches . . . . **D. *sinicola* var. *californica***

Dasya pedicellata subsp. *stanfordiana* (Farlow) J. N. Norris et Bucher *comb. nov.*

FIGURE 96

Dasya stanfordiana Farlow, 1902:94; Setchell and Gardner, 1930:164; Taylor, 1945:287, pl. 97: fig. 2; Dawson, 1961b:448; Serviere-Zaragoza et al., 1993a:483.

Dasya baillouviana var. *stanfordiana* (Farlow) J. N. Norris et Bucher, 1976:19; Norris, 1985d:210; González-González et al., 1996:197; Cruz-Ayala et al., 2001:191; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:211.

Dasya pedicellata var. *stanfordiana* (Farlow) E. Y. Dawson, 1963b:407, pl. 128: fig. 3, pl. 130; 1966a:28; Huerta-Múzquiz, 1978:338; Stewart and Stewart, 1984:146; Huerta-Múzquiz and Mendoza-González, 1985:52; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:197; CONANP, 2002:138.

Dasya pedicellata sensu Dawson, 1944a:324; 1949c:237; 1951:56; 1957a:8; 1961b:448; Silva et al., 1996b:233 [non *Dasya pedicellata* (C. Agardh) C. Agardh, 1824:211].

Thalli erect, up to 25 cm tall, from a small discoid holdfast, axes polysiphonous, with 5 pericentral cells; completely but thinly corticated below the first 7–8 apical segments; sparingly to freely alternately branched, lateral branches infrequently redivided. Branches mostly 0.4–2.0 mm in diameter, densely covered with monosiphonous, repeated dichotomously branched pseudolaterals or sometimes lacking monosiphonous pseudolaterals in lower portions. Pseudolaterals 1–7 mm long and 15–40 μm

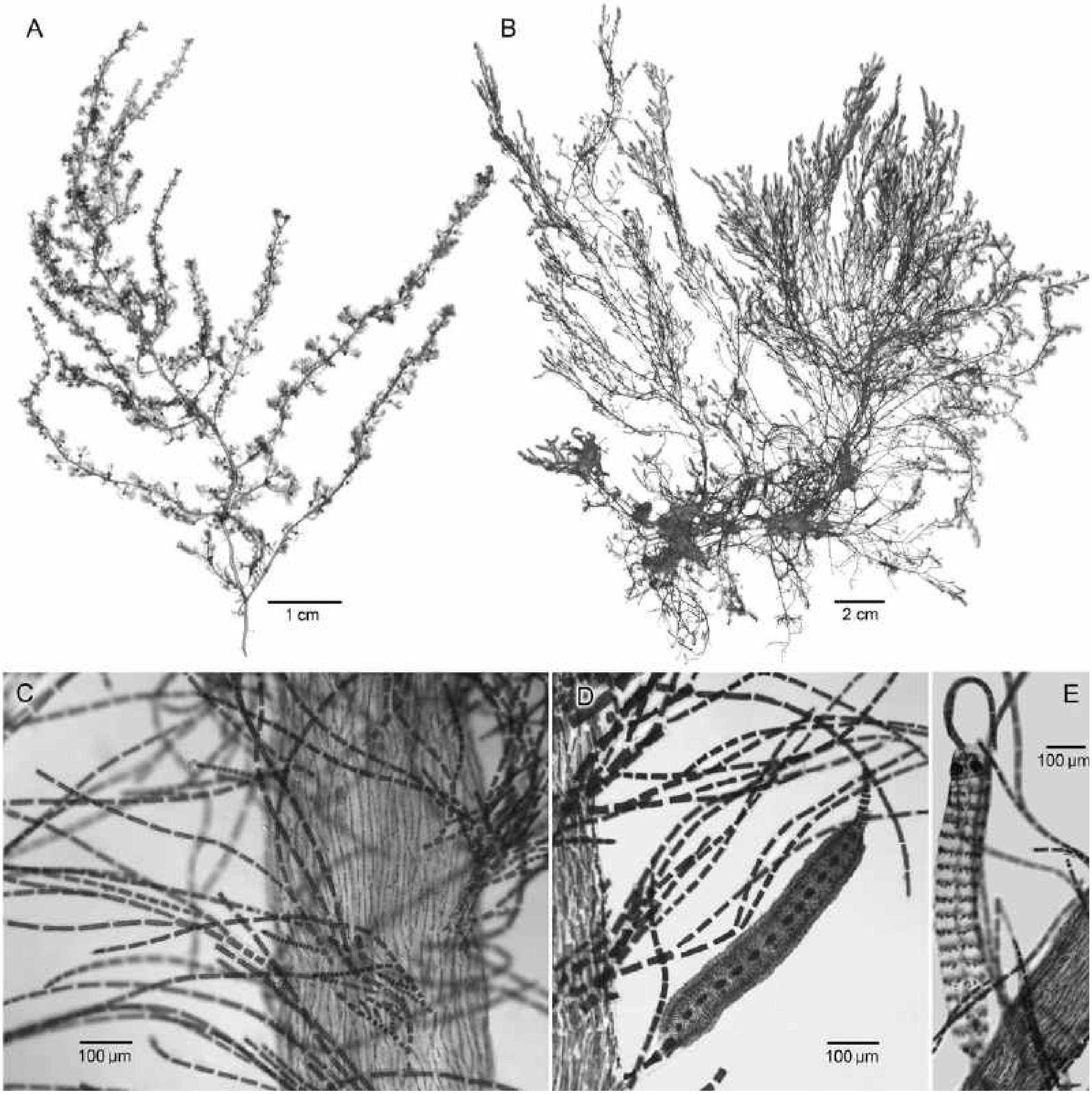


FIGURE 96. *Dasya pedicellata* subsp. *stanfordiana*: A. Cystocarpic thallus (*JN-4731*, US Alg. Coll.-159017). B. Habit of a tall, delicate specimen (*JN-4724*, US Alg. Coll.-159015). C. Corticated axis bearing slender long pseudolaterals. D. Spermatangial stichidium (*JN-5165*, US Alg. Coll. microscope slide 4852). E. Old nearly empty tetrasporangial stichidium showing cover cells and two tetrasporangia, with a terminal, sterile apical filament (C, E, *JN-4724*, US Alg. Coll. microscope slide 4855).

in diameter near their base, attenuated upward to 7–12 μm in diameter at their tips.

Tetrasporangial stichidia lanceolate to linear-lanceolate, 80–140 μm in diameter and to 800 μm long; tetrasporangia 40–50 μm in diameter. Cystocarps, 200–370 μm in diameter, usually borne laterally on slightly elongate ultimate branchlets, arising from indeterminate axes, apparently pedicellate when arising near end of a short lateral branch, urceolate, with narrow ostiolate neck. Spermatangial stichidia lanceolate to linear-lanceolate, 250–560 μm long, 60–90 μm in diameter, usually filament tipped.

Habitat. On rocks, or occasionally epiphytic; mid intertidal to subtidal, 5.0–22 m depths.

Distribution. Gulf of California: Playa Hermosa (vicinity of Puerto Peñasco) to Guaymas, Sonora; Puerto Refugio, Isla Ángel de la Guarda to Bahía Agua Dulce, Isla Tiburón; Caleta Santa María (north of Puerto Santa Rosalía) to La Paz, Baja California Sur; Topolobampo; Sinaloa to Nayarit; Isla María Magdalena, Islas Marías (Islas Tres Marías). Eastern Pacific: Bahía San Quintín to Punta Abreojos, Baja California; Isla Guadalupe; Rocas Alijos (about 299 km [186 miles] west of Cabo San Lázaro, Baja California Sur); Galápagos Islands.

Syntype Localities. Two localities in the Galápagos Islands, Ecuador, were listed for *Dasya stanfordiana* by Farlow (1902:94): Isla Wolf (Isla Wainman, usually misspelled "Wenman") and Punta Tortuga, Isla Isabela (Albemarle Island).

Remarks. *Dasya pedicellata* (C. Agardh) C. Agardh (1824; basionym: *Sphaerococcus pedicellatus* C. Agardh, 1822; type locality: New York, USA) is herein recognized as distinct species following others (e.g., Guiry and Guiry, 2010). Some have followed Montagne (1841) in considering *D. pedicellata* to be conspecific with *D. baillouviana* (S. G. Gmelin) Montagne (1841; basionym: *Fucus baillouviana* S. G. Gmelin, 1768; lectotype illustration Griselini, 1750: pl. 2, in Dixon and Irvine, 1970:480, fig. 2). Pena-Martín et al. (2007) also treated them as a single species and proposed to conserve a new type for *Fucus baillouviana*, but that was rejected by the "Nomenclature Committee for Algae" (Prud'homme van Reine, 2011; who also suggested the Mediterranean "*D. baillouviana*" may belong to different cryptic species then that of New York).

Dawson (1963b:408) recognized similarities between the Pacific *Dasya stanfordiana* Farlow (1902) and the western Atlantic *D. pedicellata* but considered differences in the position of the cystocarps as a character to support their taxonomic separation. Cystocarps are borne laterally on "somewhat elongate ultimate branchlets" of *D. stanfordiana* versus the terminal position on very short ultimate branchlets of *D. pedicellata*. Considering the similarities of the Gulf of California specimens to the Atlantic *D. pedicellata* and noting the differences pointed out by Dawson (1963b) and their apparent geographical isolation, at this time we propose to recognize them as a subspecies, *Dasya pedicellata* subsp. *stanfordiana*. Further comparative morphological and molecular testing of the Gulf of California specimens, with types and topotype materials of the eastern Pacific *D. stanfordiana* (syntype localities: Galápagos Islands), northwestern Atlantic *D. pedicellata* (lectotype locality: New York; Silva et al., 1996a), and *D. baillouviana* (S. G. Gmelin) Montagne (1841; type locality: Mediterranean Sea; Silva et al., 1996a; Lipkin and Silva, 2002) will help elucidate their taxonomic status and relationships.

Specimens of "*D.* cf. *pedicellata*" tentatively reported from Isla Monserrate in the southern Gulf by Dawson (1959a:42) need to be reexamined. Studies of the natural product chemistries of northern Gulf of California *D. pedicellata* subsp. *stanfordiana* revealed interesting secondary products, simple phenols of aromatic structure, that were shown to have antibiotic activity (Fenical and McConnell, 1976).

Dasya pedicellata subsp. *stanfordiana* var. *nudicaulis* (E. Y. Dawson) J. N. Norris et Bucher, *comb. nov.*

FIGURE 97

Dasya pedicellata var. *nudicaulis* E. Y. Dawson, 1963b:406, pl. 128: fig. 1, pl. 131: fig. 6; González-González et al., 1996:197.

Dasya baillouviana var. *nudicaulis* (E. Y. Dawson) J. N. Norris et Bucher, 1976:19; González-González et al., 1996:197; Pacheco-Ruíz and Zertuche-González, 2002:468.

Algae erect, up to 50 cm long or more, lower branched axes 3–4 mm in diameter; branching alternately to irregularly subdichotomously; holdfasts not observed. *Dasya pedicellata* subsp. *stanfordiana* var. *nudicaulis* differs from *D. pedicellata* subsp. *stanfordiana* var. *stanfordiana* in having heavily corticated, nearly barren axes and branches, with sparse, shorter pseudolaterals, mostly less than 500(–960) μm long.

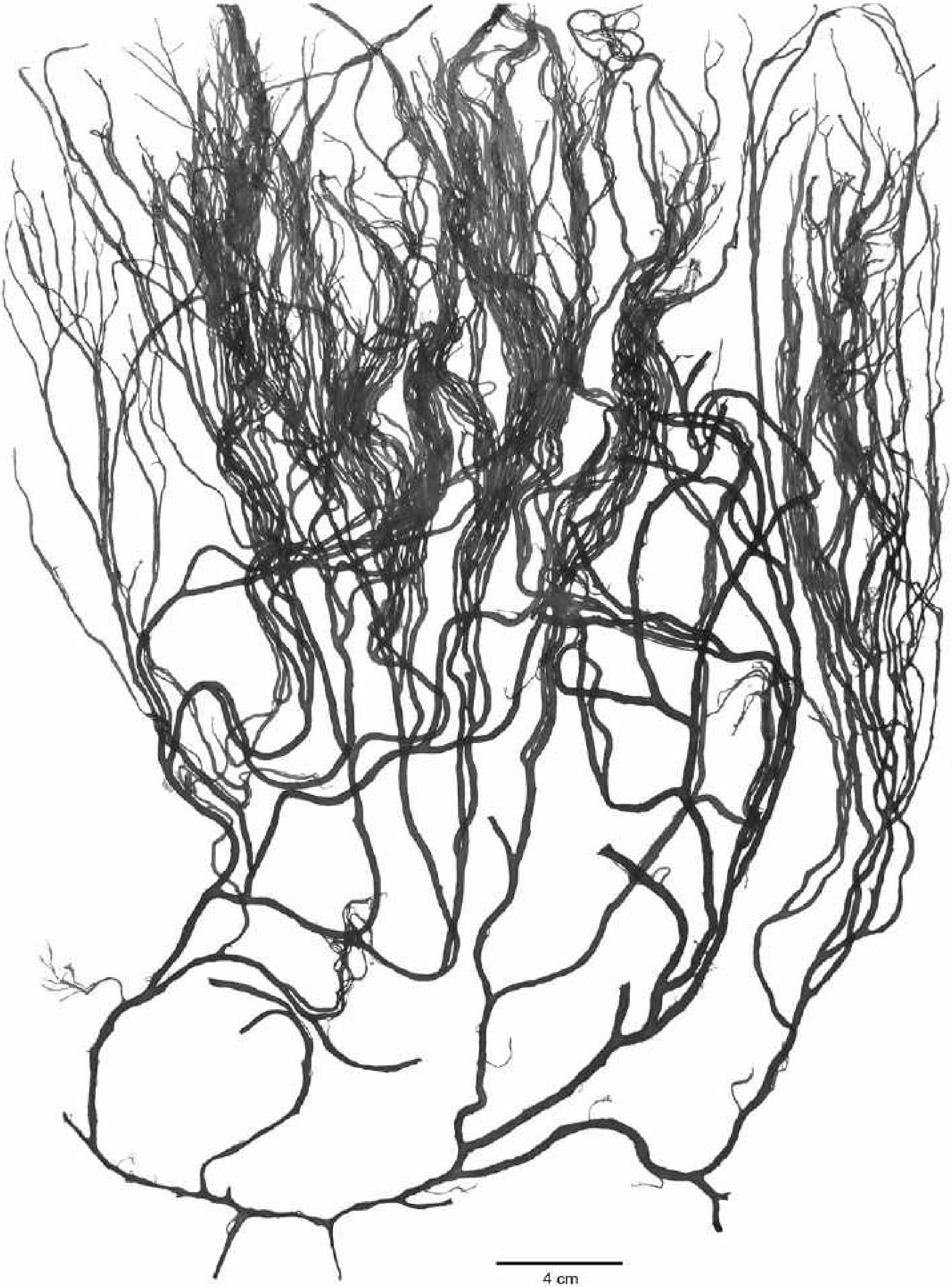
Habitat. On rocks; subtidal, 15–22 m depths.

Distribution. Gulf of California: Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda; Bahía de Los Ángeles; Puerto Escondido.

Type Locality. Bahía de Los Ángeles, Baja California, Gulf of California, Mexico.

Remarks. On the basis of the large size (to 50 cm—and probably longer, as only portions of noncomplete thalli have been collected) and marked lack of pseudolaterals of *Dasya pedicellata* subsp. *stanfordiana* var. *nudicaulis*, Dawson (1963b, as *D. pedicellata* var. *nudicaulis*) suggested that its habit represents a modification by its deepwater habitat. Our Puerto Refugio

FIGURE 97. (Opposite) *Dasya pedicellata* subsp. *stanfordiana* var. *nudicaulis:* Habit, showing mostly barren axes below, and an increasing number of pseudolaterals in upper thallus (*JN-5800*, US Alg. Coll.-159009).


4 cm

specimens collected by scuba at depths of 15–22 m (Norris and Bucher, 1976) were of similar habit but with much longer branches; some were more than 50 cm in length, with wide axes, 3–4 mm in diameter (*JN-5800*, US Alg. Coll.-159009).

Dasya sinicola (Setchell et N. L. Gardner) E. Y. Dawson var. *sinicola*

FIGURES 98D, 99B,C

Heterosiphonia sinicola Setchell et N. L. Gardner, 1924:770, pl. 28: figs. 59, 60, pl. 47b.

Dasya sinicola (Setchell et N. L. Gardner) E. Y. Dawson, 1959a:32, fig. 3B; 1961b:448; 1963b:408, pl. 128: fig. 4, pl. 158: fig. 3; 1966a:29; Norris, 1973:16; Abbott and Hollenberg, 1976:675, fig. 622; Huerta-Múzquiz, 1978:338; Stewart and Stewart, 1984:146; Huerta-Múzquiz and Mendoza-González, 1985:52; Sánchez-Rodríguez et al., 1989:45; Mateo-Cid et al., 1993:49; Mendoza-González et al., 1994:108; González-González et al., 1996:197; Mateo-Cid et al., 2000:67; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138; L. Aguilar-Rosas et al., 2002:235; Riosmena-Rodríguez et al., 2005a:33; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:211; Castañeda-Fernández de Lara et al., 2010:199.

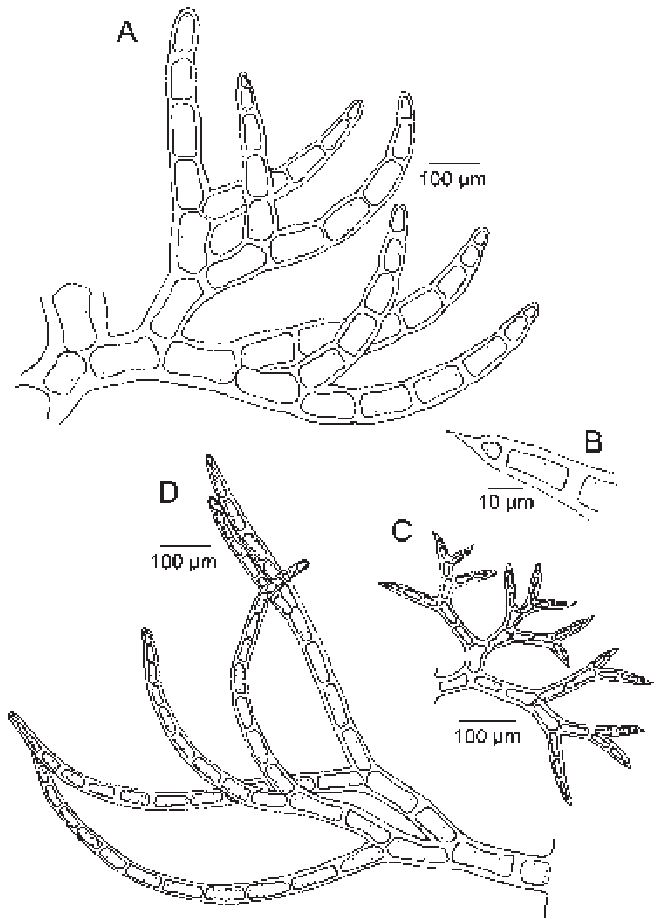


FIGURE 98. Diagrammatic comparisons of determinate monosiphonous pseudolaterals of *Dasya* species: A. *Dasya sinicola* var. *californica*, a coarse pseudolateral of comparatively wider cells. B, C. *Dasya spinigera*: B. Close-up showing acute terminal cell of a pseudolateral branch. C. Single pseudolateral (redrawn from type). D. *Dasya sinicola* var. *sinicola*, a thin pseudolateral (A–D, after Dawson, 1963a: pl. 128: figs. 2, 4–6).

Algae erect, 3–10 cm tall; of terete axes abundantly branched. Axes with 5 pericentral cells, heavily corticated (except at the tips). Monosiphonous pseudolaterals dichotomously branched, 2–4 orders. Axes more densely covered with tufts of monosiphonous pseudolaterals near apices. Determinate pseudolaterals, 0.6–1.5 mm long and (50–)60–80(–100) µm in diameter near base, upward becoming attenuated, with subacute to blunt tips; tending to be deciduous, often leaving much of the axis bare.

Tetrasporangial stichidia conical to cylindrical, 200–400 µm long; 1 to several borne off pseudolaterals or adventitious monosiphonous laterals. Cystocarps borne on the main axes, urceolate, 450–500 µm wide by 600 µm tall, with prominent beaked rostrum. Spermatangial stichidia short, mostly on lower fork of a pseudolateral, and usually with 1–3 sterile terminal cells.

HABITAT. On rocks or epiphytic on other algae; low intertidal to shallow subtidal, down to 7 m depths.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara); Bahía La Choya (Bahía Cholla), Puerto Peñasco to Cabo San Lucas; Mazátlan, Sinaloa. Eastern Pacific: Santa Catalina Island (California Channel Islands); Isla Guadalupe to Bahía Magdalena, Baja California Sur.

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. In addition to *Dasya sinicola* var. *sinicola* there are two other taxonomic varieties reported in the Gulf of California: *Dasya sinicola* var. *californica* (see description herein) and *D. sinicola* var. *abyssicola* (E. Y. Dawson) E. Y. Dawson (1963b) from the southern Gulf and Pacific Mexico from Islas Revillagigedo (Huerta-Múzquiz and Garza-Barrientos, 1975; Serviere-Zaragoza et al., 2007) and Oaxaca (Mateo-Cid and Mendoza-González, 1997).

Dasya sinicola var. *californica* (N. L. Gardner) E. Y. Dawson

FIGURES 98A, 99A

Dasya californica N. L. Gardner, 1927c:340, pl. 66: fig. 2; Dawson, 1951:53; 1952:431; 1954c:344; 1961b:448; González-González et al., 1996:197.

Dasya sinicola var. *californica* (N. L. Gardner) E. Y. Dawson, 1963b:409, pl. 127: fig. 2, pl. 128: fig. 2, pl. 158: figs. 1, 2; Abbott and Hollenberg, 1976:676, fig. 624; Stewart and Stewart, 1984:146; Mendoza-González and Mateo-Cid, 1985:28; Sánchez-Rodríguez et al., 1989:43; Stewart, 1991:151; Mateo-Cid et al., 1993:49; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:198.

Dasya eastwoodiae Setchell et N. L. Gardner, 1930:165; Dawson, 1961b:448; Stewart and Stewart, 1984:148; González-González et al., 1996:197.

Dasya sinicola var. *californica* shares similar-sized axes (400–1000 µm in diameter) with *D. sinicola* var. *sinicola*. It is generally not as tall but is usually coarser, with stiffer, wider incurved pseudolaterals (80–110 µm in diameter near their base)

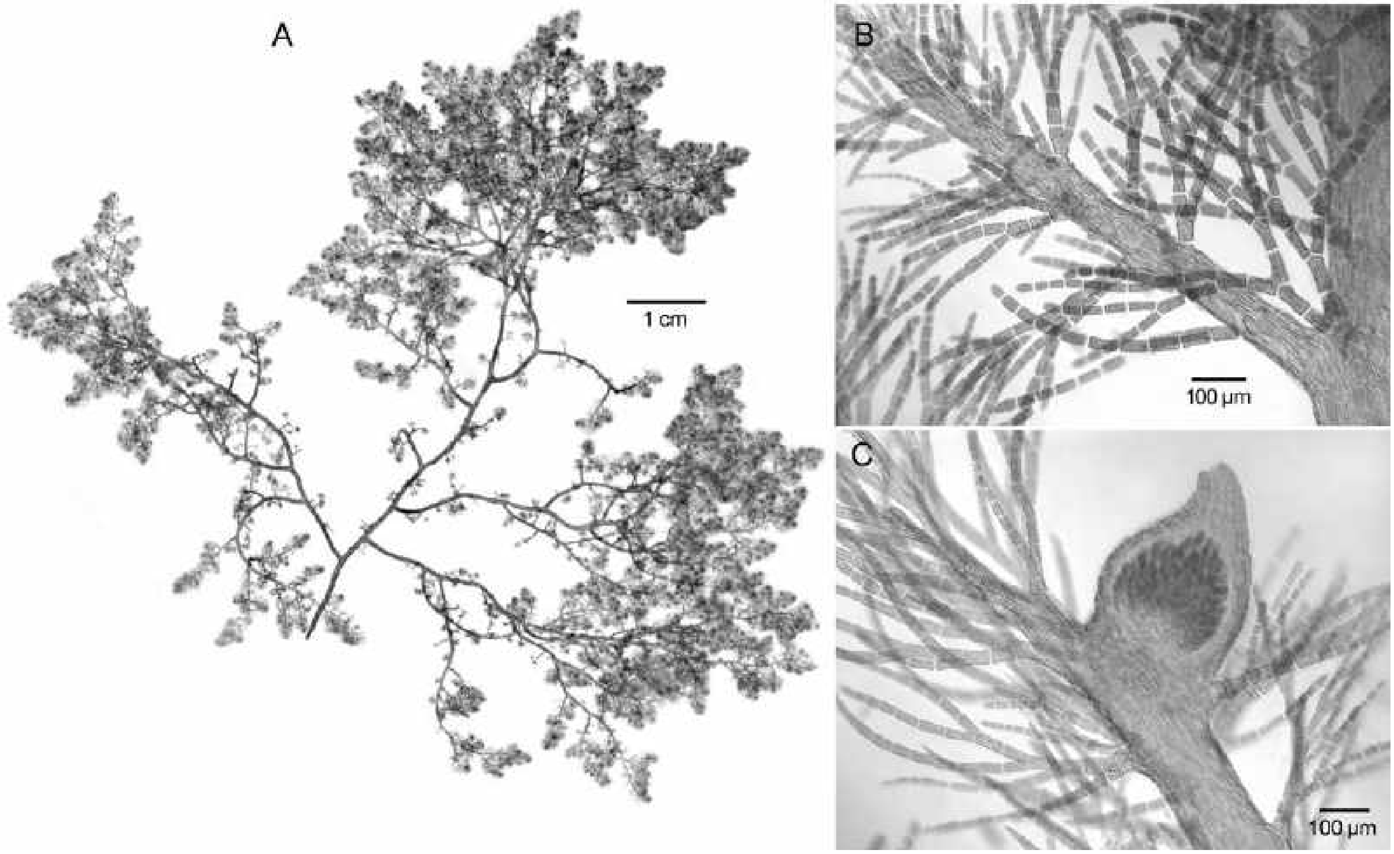


FIGURE 99. Varieties of *Dasya sinicola*. A. *Dasya sinicola* var. *californica*: Habit (*JN-3696*, US Alg. Coll.-159037). B, C. *Dasya sinicola* var. *sinicola:* B. Rhizoidally corticated polysiphonous axes with "straight" dichotomously branched pseudolaterals. C. Sessile broad-based cystocarp with ostiolate pericarp with distinct neck (B, C, *EYD-26119*, US Alg. Coll. microscope slide 792).

that tend to persist and thus more densely cover the branches, whereas the determinate pseudolaterals of *D. sinicola* var. *sinicola* are generally more lax, (60–80 µm in diameter near their base) and frequently deciduous.

HABITAT. On rocks; low intertidal.

TYPE LOCALITY. La Jolla, San Diego County, California, USA.

DISTRIBUTION. Gulf of California: Playa Hermosa, Puerto Peñasco to Bahía Concepción. Eastern Pacific: Santa Catalina Island (California Channel Islands); Newport Bay and La Jolla (southern California); Isla Guadalupe; Punta María to Punta Malarrimo, Baja California; Bahía Tortugas (inside southeast Bahía San Bartolomé) to Todos Santos, Baja California Sur.

REMARKS. *Dasya sinicola* var. *californica* is larger and usually has coarser pseudolaterals (80–110 µm in diameter at base) that generally persist, making the upper branches more densely covered than the other varieties, *D. sinicola* var. *sinicola* and *D sinicola* var. *abyssicola*. Described from the California Channel Islands, *D. sinicola* var. *abyssicola* (Dawson, 1963b; Dawson and Neushul, 1966) is apparently a subtidal species. It has been reported in the southern Gulf from 8 to 16 m depths, Punta Los Frailes, Baja California Sur (Dawson, 1963b). *Dasya sinicola* var. *abyssicola* can be distinguished primarily in being much smaller, only 10–13 mm tall, with axes 200–300 µm in diameter and pseudolaterals measuring 40–50 µm in diameter at their bases.

Dasya spinigera E. Y. Dawson

FIGURE 98B,C

Dasya spinigera E. Y. Dawson, 1963b:410, pl. 128: figs. 4, 5, pl. 158: fig. 4; Schnetter and Bula-Meyer, 1982:170, pl. 32: figs. B–D; González-González et al., 1996:198.

Algae 2.5–5 cm tall; of terete axes, 250–350 µm in diameter in lower to middle portions; sparsely branched at 2–10 mm intervals; main axis and branches similar, both covered with persistent, branched pseudolaterals, 400–500 µm long; attached by a small discoid holdfast (only partly seen in type specimens). Axis of 5 pericentral cells; partly corticated with short developing filaments produced from pericentral cells in younger portions, fully corticated in older portions. Determinate pseudolaterals, rigid, divaricate-dichotomously branched 4–5 times, with segments of 1–2 cells, 25–30 µm in diameter, and cells 50–60 µm in length, terminal cells sharply pointed.

Reproductive structures not known.

Habitat. On shell fragments in sand bottom; subtidal, dredged from 20–22 m depths.

Distribution. Gulf of California: Bahía Tepoca; Bahía de San Lucas. Eastern Pacific: Isla Gorgona, Colombia.

Type Locality. Sand bottom, dredged from 20 m depth; Bahía de San Lucas, Baja California Sur, Gulf of California, Mexico.

Remarks. A seemingly rare species, *Dasya spinigera* is only known from the two original Gulf of California collections (Dawson, 1963b) and a collection reported from Isla Gorgona, Pacific Colombia (Schnetter and Bula-Meyer, 1982).

DASYACEAE SUBFAM. HETEROSIPHONIOIDEAE

Dasyaceae subfam. Heterosiphonioideae H.-G. Choi, Kraft, I. K. Lee et G. W. Saunders, 2002:564.

The subfamily Heterosiphonioideae is represented by one of its seven known genera in the northern Gulf of California.

Heterosiphonia Montagne

Heterosiphonia Montagne, 1842d:4, *nom. cons.*

Algae are chiefly erect or decumbent, arising from prostrate axes or discoid holdfasts. Axes are terete to slightly compressed and either with or without rhizoidal cortication. They are branched alternately or subdichotomously and are distichously to subdistichously arranged or dorsiventrally organized. Thalli are polysiphonous, with 4 or 7–13 pericentral cells per segment. Determinate pseudolaterals are subdichotomously or alternately branched and distally monosiphonous and may be polysiphonous in proximal portions. Pseudolaterals or lateral branches arising 2–9 polysiphonous segments apart.

Tetrasporangia are tetrahedrally divided and in stichidia that occur as branches of pseudolaterals or on special monosiphonous or polysiphonous stalks. There are 4–6(–9) tetrasporangia whorled on each segment of the stichidium. Each sporangium is covered by 4 cover cells at maturity. Gametophytes are dioecious. The carpogonial branch is 4-celled with 2 groups of sterile cells. Cystocarps are conspicuous, ovoid to urn shaped, and generally develop near the bases of pseudolaterals near the apices of indeterminate axes. In some, the female reproductive structures may be formed on monosiphonous filaments. The cystocarps contain a fusion cell and well-developed corticated pericarp with ostiole. Spermatangial stichidia occur as branches of the pseudolaterals. Spermatangia are in successive whorled series that surround an ultimate–subultimate filament to form an elongate stichidia that is occasionally tipped by several sterile cells.

There are two taxa, one species and a variety of another species, known in the northern Gulf of California.

KEY TO THE SPECIES OF *HETEROSIPHONIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes 280–400 µm in diameter; determinate pseudolaterals polysiphonous in proximal portions, distally monosiphonous; tetrasporangial stichidia borne on polysiphonous base . . . . *H. erecta*

1b. Axes 80–185(–200) µm in diameter; determinate pseudolaterals with basal polysiphonous segment 1(–2) cells in length, thereafter monosiphonous; tetrasporangial stichidia with monosiphonous base . . . . *H. crispella* var. *laxa*

Heterosiphonia crispella var. _laxa_ (Børgesen) M. J. Wynne

FIGURE 100

Heterosiphonia wurdemannii (Bailey ex Harvey) Falkenberg var. *laxa* Børgesen, 1919:327, figs. 327, 328; Dawson, 1957c:22; 1959a:32; 1961b:448; 1963b:404, pl. 129: fig. 1; Schnetter and Bula-Meyer, 1982:171, pl. 32: fig. A; Stewart and Stewart, 1984:146; Mendoza-González et al., 1994:109; González-González et al., 1996:225.

Heterosiphonia crispella (C. Agardh) Wynne var. *laxa* (Børgesen) M. J. Wynne, 1985c:87; Mateo-Cid et al., 2000:67; Mateo-Cid et al., 2006:57; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:62.

Algae decumbent, plumose, composed of uncorticated axes and branches; up to 2 cm long and 80–185(–200) µm in diameter; creeping, entangled branched axes attached to host or substratum by rhizoids or modified tips at the ends of pseudolaterals (40–60 µm in diameter). Primary axes and indeterminate laterals polysiphonous, with 4 pericentral cells; determinate pseudolaterals monosiphonous except for single (rarely 2) polysiphonous basal segment(s), (55–)60–95(–110) µm in diameter. Determinate pseudolaterals, subdistichously arranged along the axes; developed alternately, mostly on every second axial segment; subdichotomously branched 3–5 times, up to 1.4 mm long; gradually attenuated upward, to 15–25 µm diameter at blunt tips. One filament at the first dichotomy of the determinate pseudolaterals often remains unbranched or may sometimes grow downward and is modified to attach to substratum; the other filament of the first dichotomy branches subdichotomously 3–4 times.

Tetrasporangial stichidia, somewhat conical, up to 250 µm in length, 75 µm in diameter; terminal on monosiphonous ultimate branchlets (on a 1–4-cell-long pedicel); tetrasporangia about 20 µm in diameter, overlaid by cover cells (Dawson, 1963a). Cystocarps not seen. Spermatangia develop as outer surface layer on a portion of ultimate branchlets of pseudolaterals, forming cylindrical to lanceolate stichidia.

Habitat. Epiphytic or entangled on larger algae, including *Dictyota*, *Padina*, and *Dictyopteris*; intertidal to shallow subtidal, down to 3.5 m depths.

Distribution. Gulf of California: Puerto Peñasco to Puerto Libertad; narrow channel between the northwestern end of Isla Espíritu Santo and southern end of Isla Partida Sur; Punta Arena (north of Cabo Pulmo) to Bahía de San Lucas;

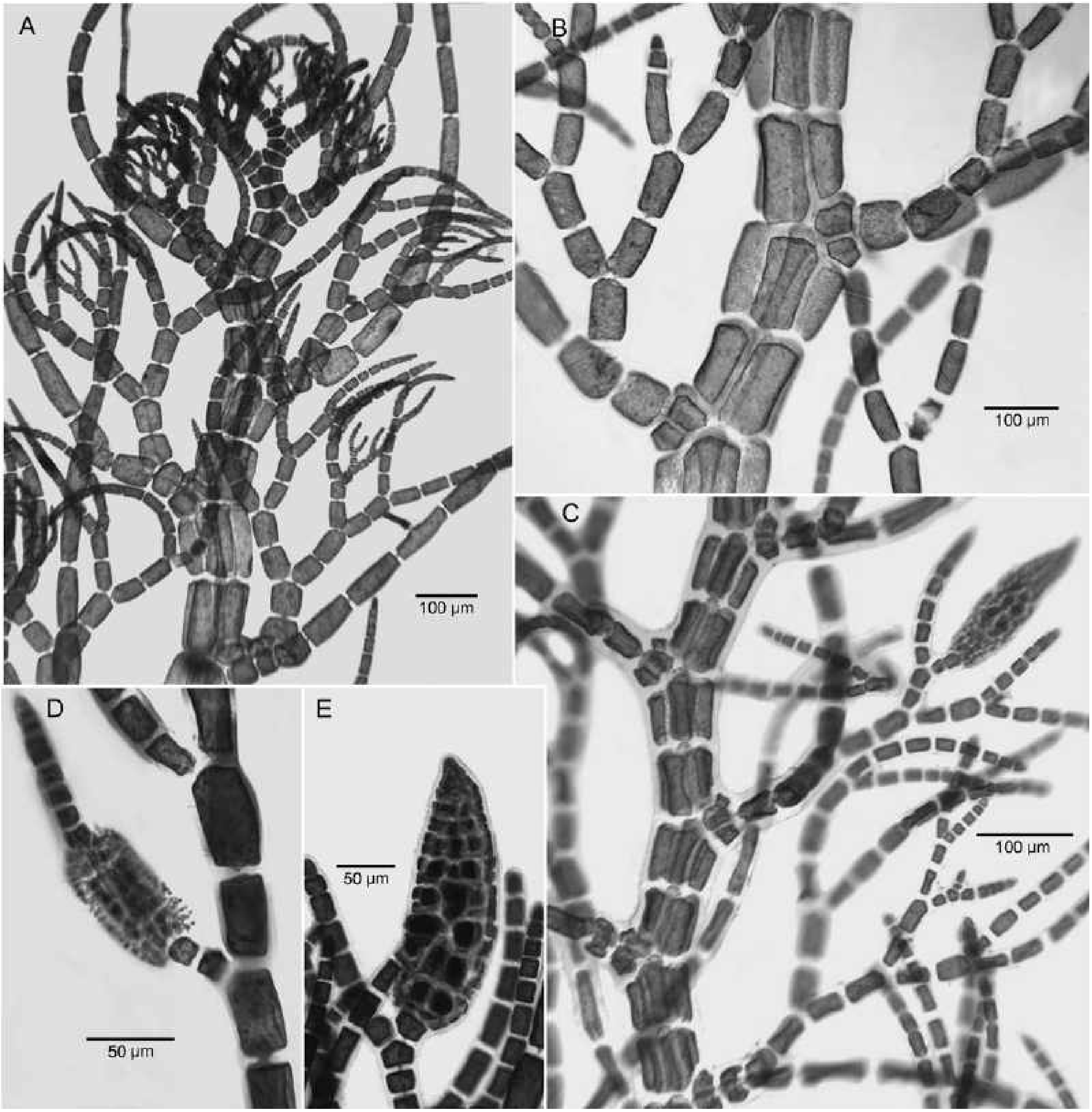


FIGURE 100. *Heterosiphonia crispella* var. *laxa*: A. Upper portion of alga showing determinate pseudolaterals, each composed of a branched group of incurved branches and a conspicuous abaxial uniseriate unbranched member (*JN-4898*, US Alg. Coll. Microscope slide 4889). B. Polysiphonous axis bearing on every other segment a determinate pseudolateral, monosiphonous except for a polysiphonous basal segment (*JN-4898*, US Alg. Coll. microscope slide 4889). C. Tetrasporangial stichidium terminal on a pseudolateral (note this is an unusual mixed-phase specimen with spermatangia on surface; *JN-4155*, US Alg. Coll. microscope slide 4883). D. Developing spermatangial stichidium (*JN-4898*, US Alg. Coll. microscope slide 4889). E. Detail of mixed-phase tetrasporangial stichidium with spermatangia on cover cells (JN-4155, US Alg. Coll. microscope slide 4884).

Mazátlan. Eastern Pacific: Isla Guadalupe; Costa Rica; Colombia; Galápagos Islands.

TYPE LOCALITY. St. Croix, U.S. Virgin Islands, Caribbean Sea.

REMARKS. In the northern Gulf, we only found specimens in agreement with *H. crispella* var. *laxa* sensu Dawson (1963b:405, as "*H. wurdemannii* var. *laxa* (J. Bailey ex Harvey) Falkenberg, in Schmitz and Falkenberg, 1897") and none that could be identified as *H. crispella* var. *crispella* (cf. Børgesen, 1919; Taylor, 1960, as "*H. wurdemannii* var. *wurdemannii*"; basionym: *Callithamnion crispellum* C. Agardh, 1828).

Dawson (1963b, as *H. wurdemannii* var. *laxa*) suggested this distinctive variety "is actually a separate species" from the Atlantic *H. wurdemannii*, reflecting the comments of Falkenberg (in Schmitz and Falkenberg, 1897, Falkenberg, 1901). The taxonomic status of Gulf of California *H. crispella* var. *laxa* and its relationship to those from the Caribbean type locality need to be tested.

An unusual mixed-phase specimen of *H. crispella* var. *laxa* bearing spermatangia on the tetrasporangial stichidia was discovered from San José del Cabo (*JN-4155*, US Alg. Coll. microscope slides 4883 and 4884; Figure 100C, E) in the southern Gulf. The reproductive structures with both tetrasporangia and spermatangia were similar in shape to tetrasporangial stichidia. Mixed-phase thalli have been reported in various other ceramialean algae (e.g., H.-G. Choi and Lee, 1996; Y. K. Lee et al., 1995).

Heterosiphonia erecta N. L. Gardner

FIGURE 101

Heterosiphonia erecta N. L. Gardner, 1927f:99, pl. 20: figs. 1, 2, pl. 21; Setchell and Gardner, 1937:84, pl. 21: figs. 42, 43, pl. 22: fig. 44, pl. 23: fig. 46; Taylor, 1945:288; Dawson, 1949b:26, pl. 7: fig. 43; 1951:53; 1957a:8; 1961b:448; 1963b:403, pl. 127: figs. 3, 4; Dawson and Neushul, 1966:182; Abbott and Hollenberg, 1976:676, fig. 625; Stewart and Stewart, 1984:146; Mendoza-González and Mateo-Cid, 1985:30; Sánchez-Rodríguez et al., 1989:45; Stewart, 1991:152; González-González et al., 1996:225; Silva et al., 1996b:233; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212; Castañeda-Fernández de Lara et al., 2010:199.

Algae erect or partly prostrate, up to 5 cm long; uncorticated throughout; polysiphonous main axes and branches with segments of 4 pericentral cells, 280–400 µm in diameter, attached to host by rhizoids. Growth sympodial. Pseudolaterals of limited growth alternate, from every second (to fourth) axial segment, distichously arranged; basally polysiphonous, similar to main axes but ending in monosiphonous ultimate branchlets, 8–12 cells in length, with acute apices.

Tetrasporangial stichidia cylindrical with conical apex, borne on polysiphonous base; tetrasporangia tetrahedrally divided. Cystocarps sessile, flask shaped, 600–700 µm in diameter at base, with long neck and ostiole; usually infrequent, near base of ultimate branchlets. Spermatangia dense, colorless clusters of small cells forming sheaths surrounding the lower part of ultimate monosiphonous branchlets, beginning 1–3 cells from the base (Dawson, 1949b: pl. 7: fig. 43).

HABITAT. Epiphytic on or entangled with various algae or sea grasses; low intertidal to shallow subtidal, down to 10 m depths.

DISTRIBUTION. Gulf of California: Isla Coronado (Isla Smith) to Islas de Los Gemelos, Bahía de Los Ángeles; Bahía de Loreto. Eastern Pacific: Santa Catalina Island and Anacapa Island (California Channel Islands) to La Jolla, California; Islas Todos Santos and Isla Guadalupe (Baja California) to Isla Magdalena, Bahía Magdalena and Rocas Alijos (Baja California Sur); Ecuador.

TYPE LOCALITY. Epiphytic on the sea grass, *Phyllospadix*; La Jolla, San Diego County, southern California, USA.

DELESSERIACEAE

Delesseriaceae Bory de Saint-Vincent, 1828:181.

Algae membranous, compressed to flat, many foliose, often with midribs and macroscopic or microscopic veins, a few genera small parasites. Thalli undivided, lobed, or much branched from midrib, blade margins, or surface or in a few genera forming a perforated blade or lattice-work. Blades monostromatic to polystromatic, attached by discoid, rhizoidal, and/or stoloniferous holdfasts. Algae initially uniaxial, but some genera later losing strictly apical growth, and growth appears to be from marginal meristems with intercalary cell divisions (diffuse growth) that constructs pseudoparenchymatous sheets, 1 or more cells thick. In some members, growth from apical cells continues through maturity, and in some of these an axial filament forms and issues 2 lateral pericentral cells to each side as well as 2 transverse pericentral cells that lie on top and beneath the axial filament cell, forming a polystromatic midrib. The lateral pericentral cells developing cell rows to several orders that form the blades; cells may be united laterally by secondary pit connections.

Tetrasporangia subspherical and tetrahedrally divided, aggregated in sori on blade or near margins of blade, some with sori in special leaflets or proliferations. Gametophytes dioecious. Carpogonial branches (3–)4-celled, bearing 1 or 2 groups of sterile branches composed of 1 to several cells. In some members, carpogonial branches develop from transverse pericentral cells along midline near apices; in others, carpogonial branches are scattered over the blades (developing from blade cells). The carposporophyte develops from the diploidized auxiliary cell, usually forming a basal fusion cell, branched gonimoblast filaments with carposporangia terminal, single or in chains. Carposporophytes surrounded by a pericarp with an ostiole. Spermatangia develop in patches or sori on the blade surface or near blade margins or on superficial proliferations.

REMARKS. Major subfamily separations are primarily based on (1) location of procarps, whether they are scattered over the surface of blades or restricted to primary cell rows (along midline), (2) presence or absence of midribs with rhizoidal cortication, and (3) presence or absence of intercalary cell divisions in primary cell rows (Lin et al., 2001). The ontogenetic development (i.e., patterns of development of cell rows in blade construction) and branching patterns are also valuable. Tribes

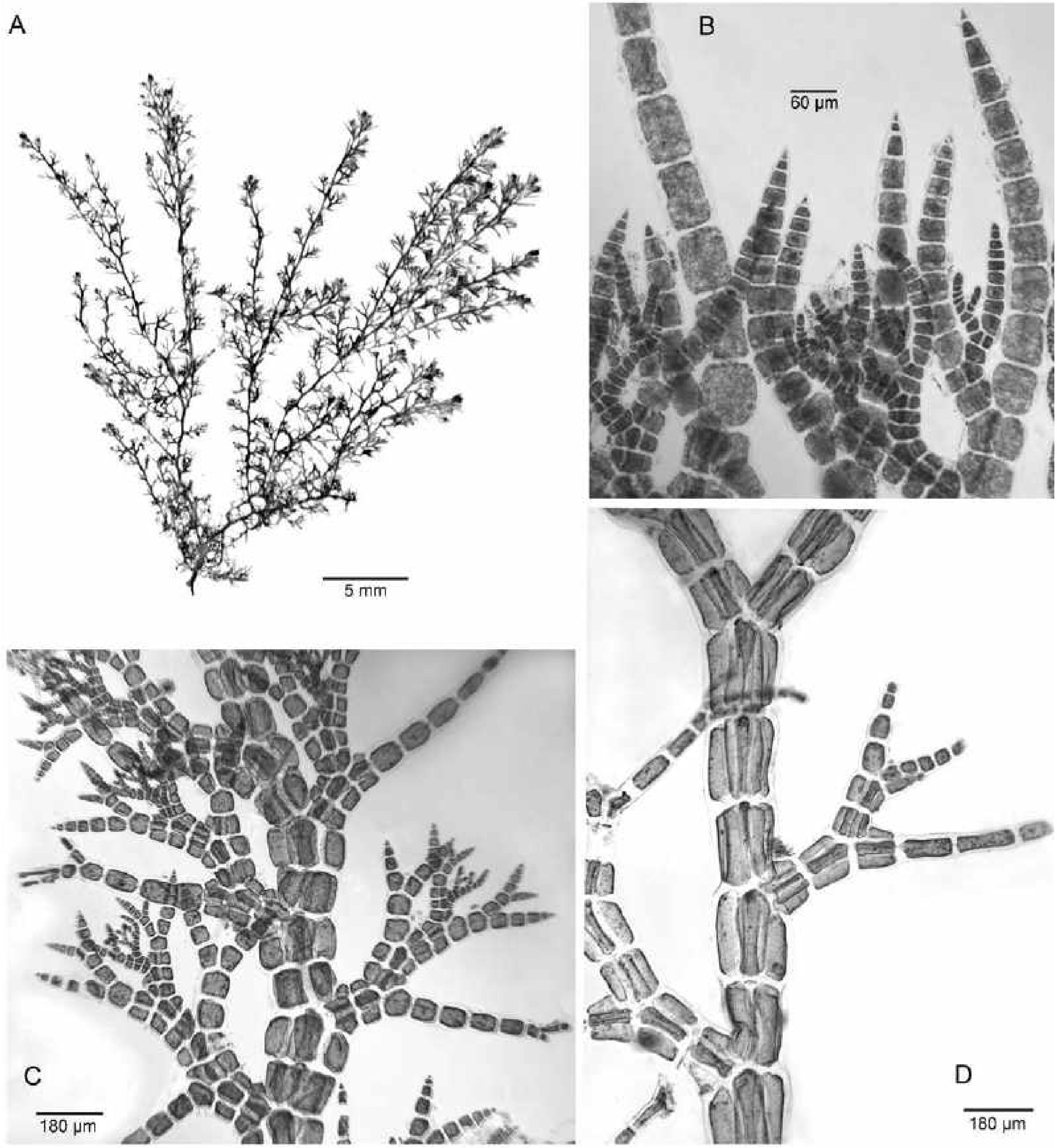


FIGURE 101. *Heterosiphonia erecta*: A. Habit (*JN-4746*, US Alg. Coll.-160012). B. Acute cells at the tips of pseudolaterals (*JN-4750,* US Alg. Coll. microscope slide 4879). C. Short determinate pseudolaterals alternately and distichously arranged along polysiphonous axis (*JN-4417*, US Alg. Coll. microscope slide 4885). D. Polysiphonous axis bearing pseudolaterals that are proximally polysiphonous and distally monosiphonous (*JN-4417,* US Alg. Coll. microscope slide 4886).

recognized within the family have been treated by Wynne (2001, 2014) and Lin et al. (2012).

Thirteen genera of the Delesseriaceae are known to occur in the northern Gulf of California.

KEY TO GENERA OF DELESSERIACEAE AND SARCOMENIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a.	Thalli narrow, up to 7 cells wide	2
1b.	Thalli more than 7 cells wide	3
2a.	Thallus composed of 2 different portions: terete axes (axial filament cells each surrounded by 4 pericentral cells); and distal flattened, determinate blades (mainly 5 cells wide) usually with free monosiphonous multicellular hairs at their apices	***Taenioma***
2b.	Thallus composed of flat, narrow blades of similar structure throughout, branching from midribs; blades usually 7 cells wide; free monosiphonous hairs absent from blade apices	***Platysiphonia***
3a.	Growth of blades from a primary apical cell; cell rows regularly arranged more or less “symmetrically” on each side of midrib; procarps/cystocarps restricted to primary cell row (midline)	4
3b.	Growth of blades from marginal initials, or if from primary apical cell, cell rows not obviously symmetrical, irregular in arrangement; procarps/cystocarps scattered over blade	8
4a.	Branches arising from midrib	5
4b.	Branches not arising from midrib	6
5a.	Thalli rarely branched in Gulf species; not all third-order cell row initials reach blade margins, with intercalary divisions occurring in second-order and higher cell rows	***Apoglossum***
5b.	Thalli occasionally to frequently branching; Gulf species with all second- and third-order cell row initials reaching blade margins, without intercalary cell divisions (some may have corticated midribs)	***Hypoglossum***
6a.	Thalli subdichotomously branched; living in brackish water to freshwater (mangroves, estuaries, lagoons); tetrasporangia in a single layer	***Caloglossa***
6b.	Thalli not subdichotomously branched; living in marine waters; tetrasporangia in 2 or more cell layers	7
7a.	Thallus branching from the margins in 1 plane; second-order cell rows of parent blade become first-order cell row (midrib) of lateral branches; all third-order cell row initials reach the thallus margin	***Branchioglossum***
7b.	Thallus often simple (unbranched) or sometimes irregularly branched or proliferous at base; not all third-order cell row initials reach the thallus margin	***Grinnellia***
8a.	Blade with an inconspicuous or a distinct midrib	10
8b.	Blade without a midrib, but micro- to macroscopic veins may be present	9
9a.	Monostromatic, except for micro- and macroscopic veins running irregularly and longitudinally; growth from apical cells	***Polyneurella***
9b.	Monostromatic to polystromatic; midrib and veins usually absent or rarely present; growth from marginal meristems and intercalary cell divisions	***Myriogramme*** **(in part)**
10a.	Midrib conspicuous; mature thallus with rounded apices; apical cells becoming indistinguishable from marginal row initials	12
10b.	Midrib inconspicuous (visible with hand lens or microscope); mature thallus apices abruptly tapering to single apical cell	11
11a.	Blades with irregular margins; tetrasporangia in series of longitudinal sori parallel to blade margin	***Erythroglossum***
11b.	Blades with smooth margins; tetrasporangia in median sori near blade tips	***Sorella***
12a.	Thallus monostromatic; midrib and veins usually absent	***Myriogramme*** **(in part)**
12b.	Thallus monostromatic, with polystromatic midrib and veins	13
13a.	Small blades, usually 3 cm or less high, with subdichotomously branched midribs (macroscopic veins)	***Schizoseris***
13b.	Larger foliose blades, mostly more than 3 cm high; central midrib with opposite, alternate or irregularly, branched lateral veins	***Phycodrys***

Apoglossum J. Agardh

Apoglossum J. Agardh, 1898:190.

Thalli are erect or decumbent, flat, membranous blades that may be simple to abundantly branched. Blades are monostromatic except for the percurrent midrib, may be with or without lateral microscopic veins, and are attached by a small discoid holdfast or stoloniferous basal portion. Growth is by a transversely dividing apical cell at the tip of each blade, along with intercalary divisions occurring in second- and higher-order cell rows. In intercalary cell divisions, the new cell is cut off distally only (so fourth-order cell rows are always on the adaxial side of third-order cell rows). Third- and fourth-order cell rows are often short. All second-order cell rows reach the thallus margin, not all of the initials from the tertiary row (or fourth or higher order) reach the blade margin. The midrib has lateral pericentral cells that do *not* undergo transverse divisions, leaving a median strip three cells across of long cells; however, this may be obscured in species with corticated midribs. Cortication is of small-celled descending "rhizoidal" filaments. Branching is rare to common depending on the species. In those that branch, branching is endogenous, with new blades arising from the midline.

Tetrasporangia are in linear sori lying parallel along both sides of blade midrib, formed on the lateral pericentral cells and second-order row cells; or circular to oval sori toward distal end of blade. Gametophytes are dioecious. Procarps are on the midline of fertile blades, carpogonial branches with two sterile groups, each composed of a single cell. Cystocarps are often only one per blade, but sometimes there may be more. Carposporangia are borne in branched terminal chains; pericarp 3–5 cells thick. Spermatangia are in superficial patches (sori) between the second- and third-order cell rows.

One species of *Apoglossum* occurs in the northern Gulf of California.

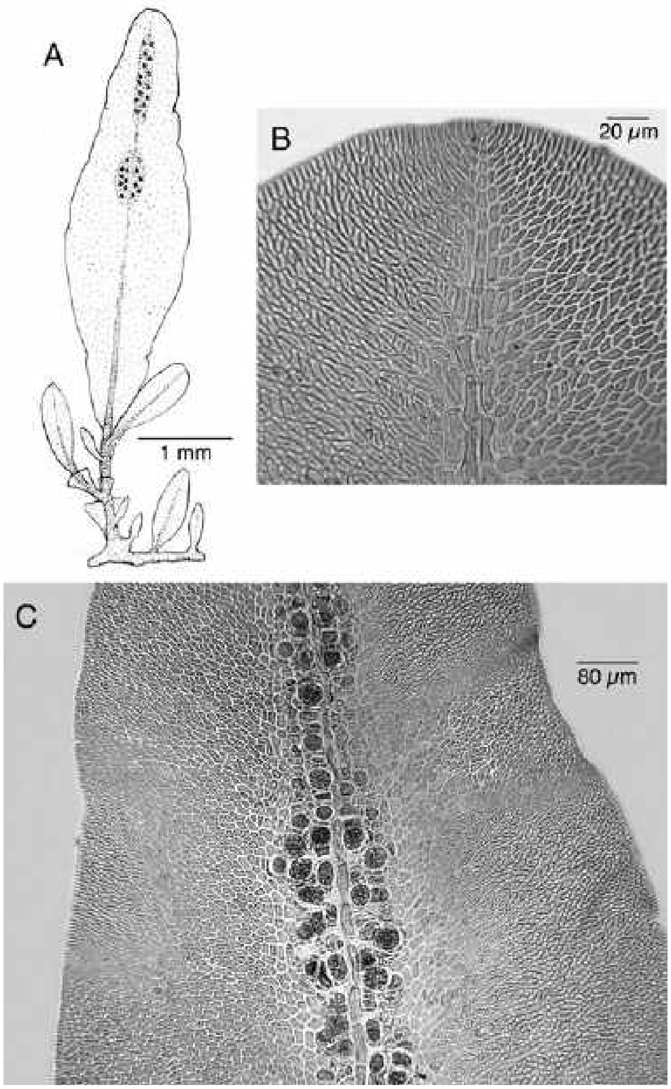


FIGURE 102. *Apoglossum gregarium*: A. Habit, frequently branched from stipe and midrib with additional blades arising from spreading base (after Dawson, 1966b: fig. 6C, as *Hypoglossum gregarium*). B. Apical region showing apical organization; note that lateral pericentral cells are not transversely divided. C. Tetrasporangial sori along both sides of midrib (A–C, *EYD-26123*, US Alg. Coll. microscope slide 791; type specimen of *Hypoglossum gregarium*).

***Apoglossum gregarium* (E. Y. Dawson) M. J. Wynne**

FIGURE 102

Hypoglossum gregarium E. Y. Dawson, 1966b:65, fig. 6C [type specimen]; González-González et al., 1996:228.

Apoglossum gregarium (E. Y. Dawson) M. J. Wynne, 1985a:169, figs. 1–6; Ballantine and Wynne, 1985:463, figs. 9–15; Stewart, 1991:139; González-González et al., 1996:175; Abbott, 1999:330, fig. 95A,B; Wynne, 2014:48.

Phrix gregarium (E. Y. Dawson) J. G. Stewart, 1974a:147, figs. 1–11; González-González et al., 1996:247.

Membranoptera spatulata E. Y. Dawson, 1950b:157, fig. 15; 1961b:445; 1962a:79, fig. 5; Wynne, 1985a:167, figs. 3–6 (holotype); Ballantine and Wynne, 1985:463, fig. 16 [type specimen]; González-González et al., 1996:243.

Algae of small, erect, delicate, membranous blades, single or in clumps; up to 6 mm tall, 1.0–2.5 mm wide; usually simple, more or less flattened or undulating; usually unbranched (or rarely branched from midline); oblanceolate to spatulate, with blunt apices. Blades monostromatic with prominent polystromatic midrib (of long, undivided lateral pericentral cells); on short, simple or branched stipe, with rhizomatous cortication on stipe, often also on basal region of midrib; attached below by a spreading basal disc or sometimes from cylindrical prostrate axis or decumbent blades in contact with substratum. Growth from transversely dividing apical cells; lateral cell rows initiated by the pericentral cells become obscured by frequent intercalary divisions (resulting irregularly shaped small cells make tracing the cell rows and their degree of branching difficult); not all tertiary cell row initials reach the blade margins.

Tetrasporangia irregularly tetrahedrally divided, up to 35 µm in diameter, with a surrounding hyaline envelope. Tetrasporangial sori long, paired, lining sides of blade midline, lateral pericentral cells and second-order row cells involved in tetrasporangial formation. Cystocarps (as reported in southern California): borne on the midline 1 to several per blade; prominent, protruding with large flared ostiole; carposporangia single, terminal on gonimoblast filaments. Spermatangial sori often numerous, forming small patches separated by sterile cells of second- and third-order cell rows (see Wynne, 1985a:167, figs. 5, 6, as *Membranoptera spatulata*).

DISTRIBUTION. Gulf of California: Isla Patos (off N end of Isla Tiburón) and Isla Las Ánimas. Eastern Pacific: southern California to Baja California; Islas San Benitos (east of Isla

Cedros); Galápagos Islands. Central Pacific: Hawaiian Islands. Western Pacific: Korea.

TYPE LOCALITY. Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. Wynne (1985a), in examining type material of two Gulf of California species, *Hypoglossum gregarium* and *Membranoptera spatulata*, concluded they were conspecific, representing a single taxon, *Apoglossum gregarium*.

Although *A. gregarium* is sparse where found and known only from two islands in the northern Gulf, it has been widely reported elsewhere: in the western Atlantic from Puerto Rico (Ballantine and Wynne, 1985) and Bermuda (Schneider, 2000), in the Mediterranean Sea (Sartoni and Boddi, 1993), and from South Africa (Wynne and Norris, 1991).

Branchioglossum Kylin

Branchioglossum Kylin, 1924:8.

Algae are membranous, symmetrical blades that may be entirely erect or with erect and prostrate portions. Blades can be simple or branched to several orders, entire or lobed, and are monostromatic apart from the percurrent polystromatic midrib (three cells thick), which may become corticated in some species. The branching is primarily developed from the margins of parent blades by conversion of a second-order cell row initial into a first-order initial that forms the midrib of the new blade. A few species are also known to produce endogenous branches from the midrib, although less frequently than marginal branches. Sometimes branches from the midrib may develop associated with wound regeneration from the cortical cells and not endogenously (Wynne and Norris, 1991; Millar and Wynne, 1992). Growth is from prominent apical cells. All or some cells of the second-order rows bear third-order rows, and all second-order and third-order cell row initials reach the blade margins. There are no intercalary cell divisions within cell rows.

Tetrasporangia are tetrahedrally divided, developing within two or more cell layers in longitudinal bands of sori that run parallel to the midrib of the blade. Carpogonial branches, with two groups of sterile cells, are borne along the blade midrib, issued from pericentral cells. Spermatangial parent cells develop from blade surface cortical cells. Spermatangial sori are arranged diagonally to the blade midrib, initially in discrete patches that later become confluent.

Two species of *Branchioglossum* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *BRANCHIOGLOSSUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli composed of narrow linear blades, 2(–3) mm wide, habit small to relatively large (–4 cm tall); branched irregularly pinnate-subboppositely, 2–3 or more orders; margins not undulate . . . . ***B. bipinnatifidum***

1b. Thalli of nonlinear blades, habit relatively small (–2 cm tall), but broader, up to 5 mm in width; upper portion of several broad lobes, with undulate or slightly ruffled margins . . . . ***B. undulatum***

Branchioglossum bipinnatifidum **(Montagne) M. J. Wynne**

FIGURE 103

Delesseria bipinnatifida Montagne, 1837:355; Montagne, 1846b:31, pl. 6: fig. 1; Howe, 1914:138; Mikami, 1979:35, fig. 1 [type specimen]; Wynne, 2014:20, fig. 5a (holotype).

Branchioglossum bipinnatifidum (Montagne) M. J. Wynne, 1983:442; 1988:53, figs. 1–14; Edding, 1988:153–161, figs. 2–10; Ramírez and Santelices, 1991:339; Silva et al., 1996b:233; Hoffman and Santelices, 1997:361, fig. 100; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:211; Wynne, 2014:20, fig. 5a–f.

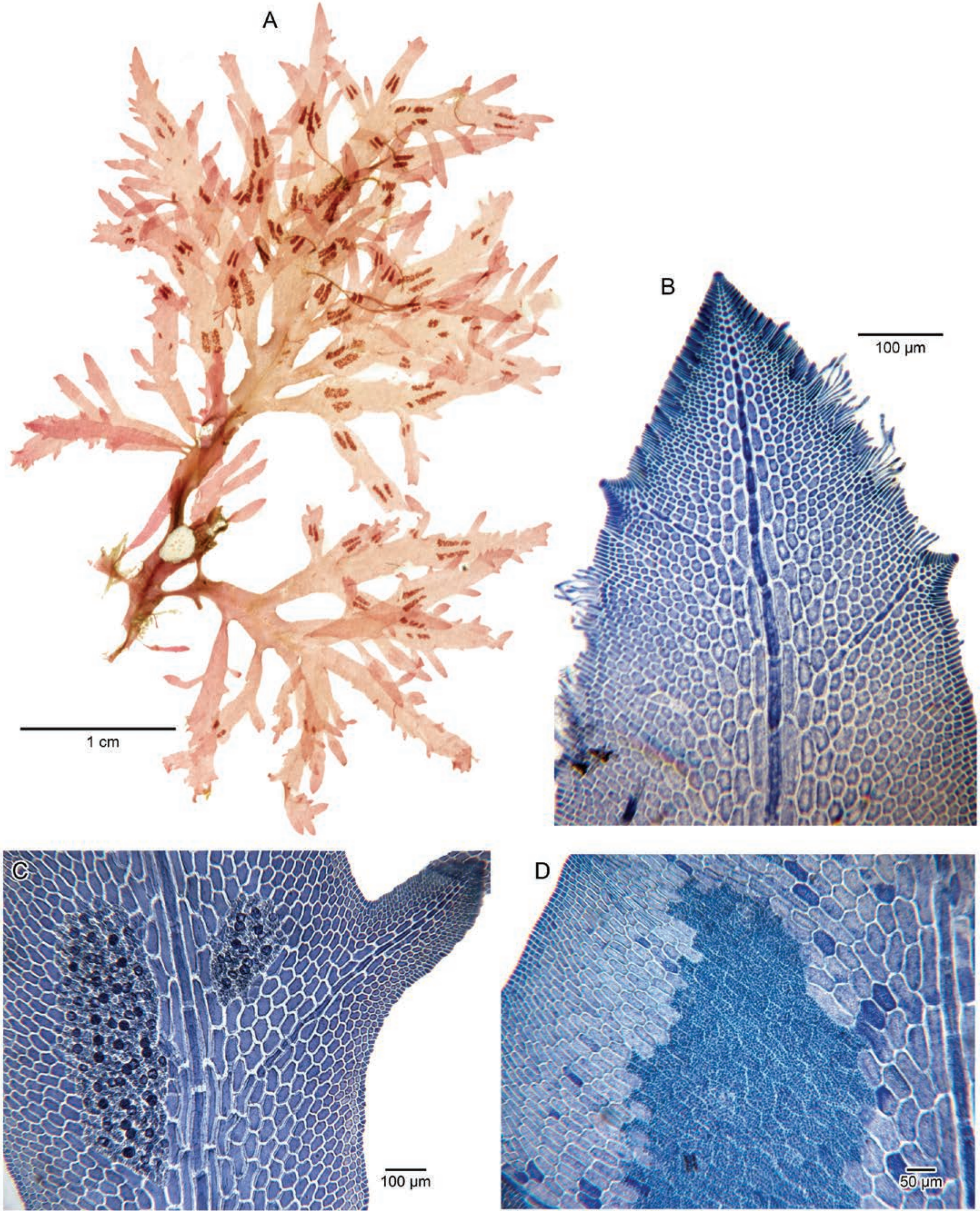
Hypoglossum bipinnatifidum (Montagne) Kützing, 1849:876; Kützing, 1866:6, pl. 15: figs. d–f.

Erythroglossum bipinnatifidum (Montagne) J. Agardh, 1898:176; Kylin, 1924:31, fig. 22E; Navas, 1966:113, pl. 9: fig.2; Mikami, 1979:35, figs. 1–15.

Delesseria woodii J. Agardh, 1872:54.

Branchioglossum woodii (J. Agardh) Kylin, 1924:8, fig. 2A; Kylin, 1941:30, pl. 10: figs. 25, 26; Dawson, 1944a:321; Smith, 1944:335, pl. 86: figs. 5–8; Dawson, 1954e:344; Wagner, 1954:283, figs. 1–19; Dawson, 1957a:8; 1959a:29; 1961b:444; 1962a:77, pl. 34: fig. 1, pl. 39: fig. 1; 1966a:28; Abbott and Hollenberg, 1976:637, fig. 577; Ramírez, 1982:22, figs. 14, 34, 35; Pacheco-Ruíz and Aguilar-Rosas, 1984:74; Stewart and Stewart, 1984:146; Stewart, 1991:140; González-González et al., 1996:180; Mateo-Cid et al., 2006:57.

FIGURE 103. (Opposite) *Branchioglossum bipinnatifidum*: A. Habit of tetrasporangial thallus (*JN-5036*, US Alg. Coll.-217354). B. Blade apex showing apical organization, lateral blades issued from blade margins, the second-order cell rows of parent blade becoming first-order cell rows (midribs) of branches, and rhizoids developing from cells at blade margins (*JN-5036*, US Alg. Coll. microscope slide 4615). C. Tetrasporangia in sori to both sides of midrib (*JN-4309*, US Alg. Coll. microscope slide 4619). D. Spermatangial sori in patches becoming confluent (*JN-3987,* US Alg. Coll. microscope slide 4625).


A
1 cm
B
100 µm
C
100 µm
D
50 µm

Branchioglossum macdougalii N. L. Gardner, 1927f:103, pl. 20: fig. 4; pls. 33–34; González-González et al., 1996:179.

Branchioglossum battstroemii Levring, 1960:65, fig. 16; Santelices and Abbott, 1978:219.

Algae erect, flat, branched linear blades, monostromatic, except at the midrib, tapering to subacute to acute apices; blades up to 4.0 cm high and 1–2(–3) mm wide; primary percurrent main blade, with secondary lateral blades formed from margins; blades usually abruptly attenuated distally, with an acute apex; branching irregularly pinnate, alternate or subopposite, up to 3–4 orders; attached by discoid holdfast and occasionally by groups of rhizoids along blade margins. Lateral branches develop along margin of parent blade by conversion of an initial of a second-order cell row into a first order initial (develops midrib of new blade). Blade margins entire, but may appear dentate in early stages as lateral blades initiate. Midrib usually uncorticated above; corticated near basal region. Apical organization with a single apical cell; all cells of second-order rows have third-order cell rows, and all third-order cell row initials reach the blade margins.

Tetrasporangia tetrahedrally divided, 54–65 µm in diameter; irregularly arranged in 2 or more layers within long narrow sori, parallel to and on opposite sides of midrib in ultimate and subultimate blades. Gametangial thalli dioecious. Procarps (and cystocarps) restricted to midrib region of erect blades. Spermatangia in superficial patches on blade to both sides of midrib.

Habitat. On rocks or occasionally epiphytic on other algae, in crevices and tide pools; low intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Ensenada de San Francisco; Isla Tiburón (Islas de la Cintura) to Isla San Ildefonso (NNE of Punta San Antonita, Baja California Sur). Eastern Pacific: British Columbia to Baja California; Rocas Alijos; Chile. Southern Ocean (subantarctic): Kerguelen (Papenfuss, 1964b).

Type Locality. Valparaíso, Valparaíso Province, central Chile.

Remarks. Northern Gulf of California specimens referred to *Branchioglossum bipinnatifidum* are up to 4.0 cm long by 1.0–3.0 mm wide and are closest to *B. macdougalii* N. L. Gardner, a species originally described from the northern Gulf that is now generally considered conspecific. Gulf *Branchioglossum bipinnatifidum* are generally smaller and grow in warmer subtropical waters, whereas the northeastern Pacific and Chilean *B. bipinnatifidum* are found in cooler temperate waters. California specimens of *B. bipinnatifidum* are 2.5–7.0 cm tall (Smith, 1944; Abbott and Hollenberg, 1976, both as *B. woodii*), and those from Chile are much larger and more robust, 13–18 cm tall and 4–8 mm wide (Mikami, 1979; Wynne, 1988; Ramírez and Santelices, 1991). Mikami (1979) suggested *Delesseria bipinnatifida* Montagne from Chile was a *Branchioglossum*. Wynne (1983) later transferred it to *B. bipinnatifidum* (Montagne) M. J. Wynne and also considered *B. woodii* and *B. battstroemii* Levring (type locality: Chile) as synonyms.

The molecular testing of type locality material of *B. bipinnatifidum* (Valparaíso, Chile), *B. woodii* (type locality: Vancouver Island, British Columbia), and northern Gulf *B. macdougalii* (type locality: Puerto Libertad, Sonora), all currently considered conspecific, should clarify their phylogenetic relationships as well as the taxonomic status of the northern Gulf specimens referred to *B. bipinnatifidum*.

Branchioglossum undulatum E. Y. Dawson

FIGURE 104

Branchioglossum undulatum E. Y. Dawson, 1949b:17, figs. 39–42; 1960a:51; Dawson et al., 1960a:50, pl. 33: fig. 2; 1960b:11, 24; Dawson, 1961b:444; 1962a:76, pl. 33: figs. 5, 6; 1966b:65; Abbott and Hollenberg, 1976:636, fig. 576; Wynne, 1988:63; Stewart, 1991:140; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:179; Wynne 2014:20.

Algae of small, erect, delicate, flat, oblanceolate blades with a precurrent midrib, 1–2 cm tall, 2–5 mm wide; pinnately branched 1–2 times; margins undulate or slightly ruffled, apices obtuse; blades monostromatic, except at the midrib; attached by a small discoid holdfast. Upper portion of blades broadened, somewhat lobed. Apical organization with all cells of second-order rows having third-order cell rows, and all third-order cell row initials reach the blade margins. Intercalary cell divisions are absent. Lateral "branches" (lobes) frequently developing along blade margin, giving the thallus an irregularly pinnate "webbed" appearance.

Tetrasporangia in irregular patches, sori between midrib and blade margin; of 2 or more cell layers. Tetrasporophyte blades narrower and more attenuated than cystocarpic or spermatangial blades. Gametangial thalli dioecious. Cystocarps projecting, hemispherical, 400–600 µm in diameter, ostiolate with flared rostrum (cf. Dawson, 1962a: pl. 33: fig. 5); restricted to midrib region of erect blades, 1 per blade. Spermatangial blades tending to be more undulate than cystocarpic blades. Spermatangia in elongated sori, diagonally oriented in relation to midrib; becoming partially confluent over blade.

Habitat. On rocks and tidal platform or epiphytic on *Sargassum*; low intertidal to shallow subtidal, down to 15 m depths.

Distribution. Gulf of California: Playa Hermosa, Puerto Peñasco to Punta Cirio; Isla San Ildefonso; Nayarit to Jalisco. Eastern Pacific: Carmel, central California to Todos Santos, Baja California Sur; Jalisco to Colima.

Type Locality. On a floating *Macrocystis* holdfast; San Miguel Passage, off NW end of Santa Rosa Island, California Channel Islands (Channel Islands National Park), southern California, USA.

Caloglossa (Harvey) G. Martens*

Delesseria subgen. *Caloglossa* Harvey, 1853:98.

Caloglossa (Harvey) G. Martens, 1869:234, 237, *nom. cons.*; King and Puttock, 1994:89; Krayesky et al., 2012:513.

Caloglossa (Harvey) J. Agardh, 1876:498.

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* Contributed by James N. Norris and David M. Krayesky. D. M. Krayesky: Department of Biology, Slippery Rock University, Slippery Rock, Pennsylvania 16057, USA.

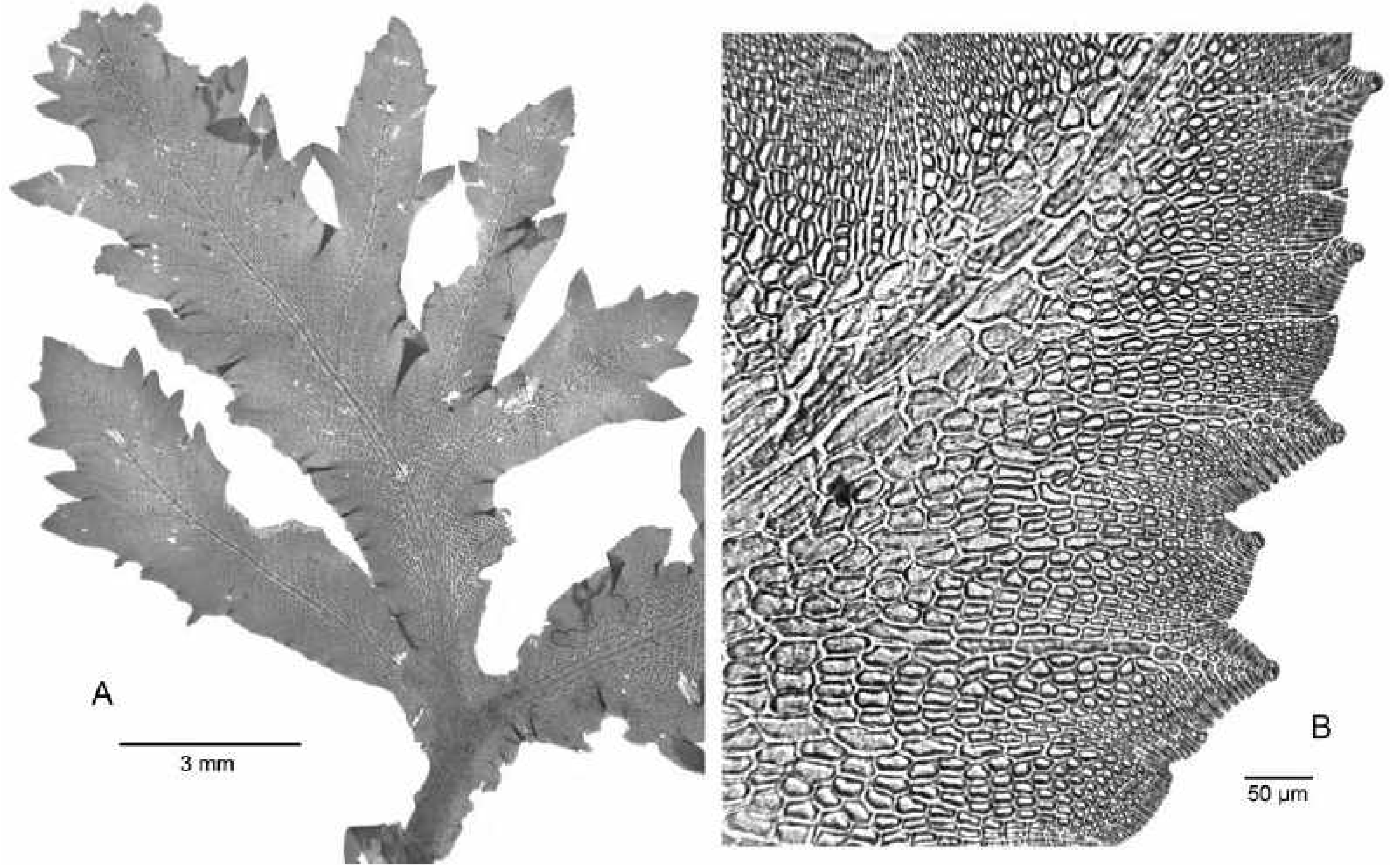


FIGURE 104. *Branchioglossum undulatum*: A. Habit. B. Closely spaced secondary blades initiating along margin of parent blade (A, B, *JN-4920*, US Alg. Coll. microscope slide 4617).

Apiarium Durant, 1850:18, *nom. rej.* (see Krayesky et al., 2011:51).

Algae are small, partially prostrate and erect, membranous, flat, narrow blades with a midrib, and usually regularly, subdichotomously branched. Thalli attached by rhizoidal filaments produced on ventral side of blades, and rhizoids either loosely arranged (not adhering to each other) or tightly compacted (strongly adhering to each other) into a peg-like attachment structure. Blades may be linear to obovate and slightly (sometimes just barely) to strongly constricted at the branching points (nodes) between comparatively long internodes. Main branches bearing exogenous indeterminate lateral branches, with endogenous and in some species also adventitious branches. The blade midrib is polystromatic, composed of elongated cells (lateral veins absent), and has single-layer (monostromatic) "wings" to each side of the midrib. Growth is apical, initially by transverse divisions of a wide apical cell, with all third-order cell row initials reaching the thallus margin; intercalary cell divisions absent in primary cell rows. The number of cell rows around the node are important characters for identifying *Caloglosssa* species.

Sporophytes develop tetrahedrally divided tetrasporangia, or in some bisporangia, in a series in the upper portions of branches, formed in a single layer outwards from lateral pericentral cells of the midrib (but not along blade margins). Asexual reproduction can also be apomictic. Gametangial thalli are monoecious or dioecious. Procarps with a 4-celled carpogonial branch and 1 group of sterile cells (and occasionally a second "group" of 1 cell occurs). Following fertilization, sessile cystocarps with a thin pericarp develop on the blade midribs. Spermatangia develop in superficial sori on blades between the midrib and blade margins in upper portions of terminal and subterminal blades.

REMARKS. Most species of *Caloglossa* are found in the intertidal habitats of brackish waters of lagoons, salt marshes, esteros, and shallow protected bays. A few species are also in freshwater of riverine habitats. They can grow on prop roots or pneumatophores of mangroves, on other aquatic plants, or on mud or hard substrata, such as wood or pilings. Species are often associated with other red algae: *Bostrychia* Montagne (1842c), *Catenella* Greville (1830), and *Murrayella* F. Schmitz (1893). The *Bostrychia–Caloglossa* ecological association was termed "Bostrychietum" by Post (1936).

Two species of *Caloglossa* are reported in the Gulf of California, one referred to with a taxonomic query.

KEY TO THE SPECIES OF *CALOGLOSSA* IN THE GULF OF CALIFORNIA

1a. Thallus generally broader, (0.9–)2.5–5.0 mm wide at median internode region; (1–)2–5 cell rows derived from the first axial cell of the main axis opposite a lateral branch . . . . *C. apomeiotica*

1b. Thallus usually narrower, 0.5–1.4 mm wide at median internode region; (2–)3–7 cell rows derived from the first axial cell of the main axis opposite a lateral branch . . . . *C. leprieurii*?

Caloglossa apomeiotica J. A. West et Zuccarello

FIGURE 105

Caloglossa apomeiotica J. A. West et Zuccarello in West, Zuccarello, Pedroche and Karsten, 1994:383, figs. 1–15; Pedroche et al., 1995:116; Kamiya et al., 1998:368, tbls. 1, 2; Krayesky et al., 2011:53, figs. 26–33; Zuccarello et al., 2012:107, figs. 7–8; Pérez-Estrada et al., 2012:190; Krayesky et al., 2012:525, figs. 1–2, tbls. 1–2; Wynne, 2014:73.

Caloglossa apomeiotica nom. prov. sensu Karsten and West, 1993:730, figs. 1–4, tbls. 1–2; West et al., 1993:148.

Caloglossa leprieurii sensu West and Zuccarello, 1990:236; González-González et al., 1996:303 (in part); Kamiya et al., 2003:478 (in part) [non *Caloglossa leprieurii* (Montagne) G. Martens, 1869:238; basionym: *Delesseria leprieurii* Montagne, 1840].

Algae small, prostrate to partially erect, 0.3–1.7 cm long; of flat, narrow, linear blades with a midrib, subdichotomously branched, slightly or occasionally strongly constricted at nodes (branching forks), 1.5–4.0 mm long, 0.9–2.5(–4.0) mm wide at median internode region; arising from a partially prostrate portion, attached by bundle of rhizoidal filaments issued from ventral surface and tightly appressed at base to form mound of compacted adhering cells, giving a holdfast-like appearance. Blade with a polystromatic midrib that consists of an axial cell filament with 2 transverse and 2 lateral periaxial cells and monostromatic "wings" to either side. Endogenous branching present; adventitious branching absent. Lacking adaxial cell rows derived from first axial cell of lateral axis. One to two cell rows derived from nodal axial cell opposite lateral branch. Number of cell rows derived from first axial cell at main axis opposite the lateral branch (1–)2–5.

Asexual reproduction by uninucleate, apomeiotic bisporangia and tetrasporangia, subspherical, 50–56(–60) µm tall, 40–49 µm in diameter. Sporangia formed in a single layer in regular rows. Other reproductive structures unknown in Gulf specimens.

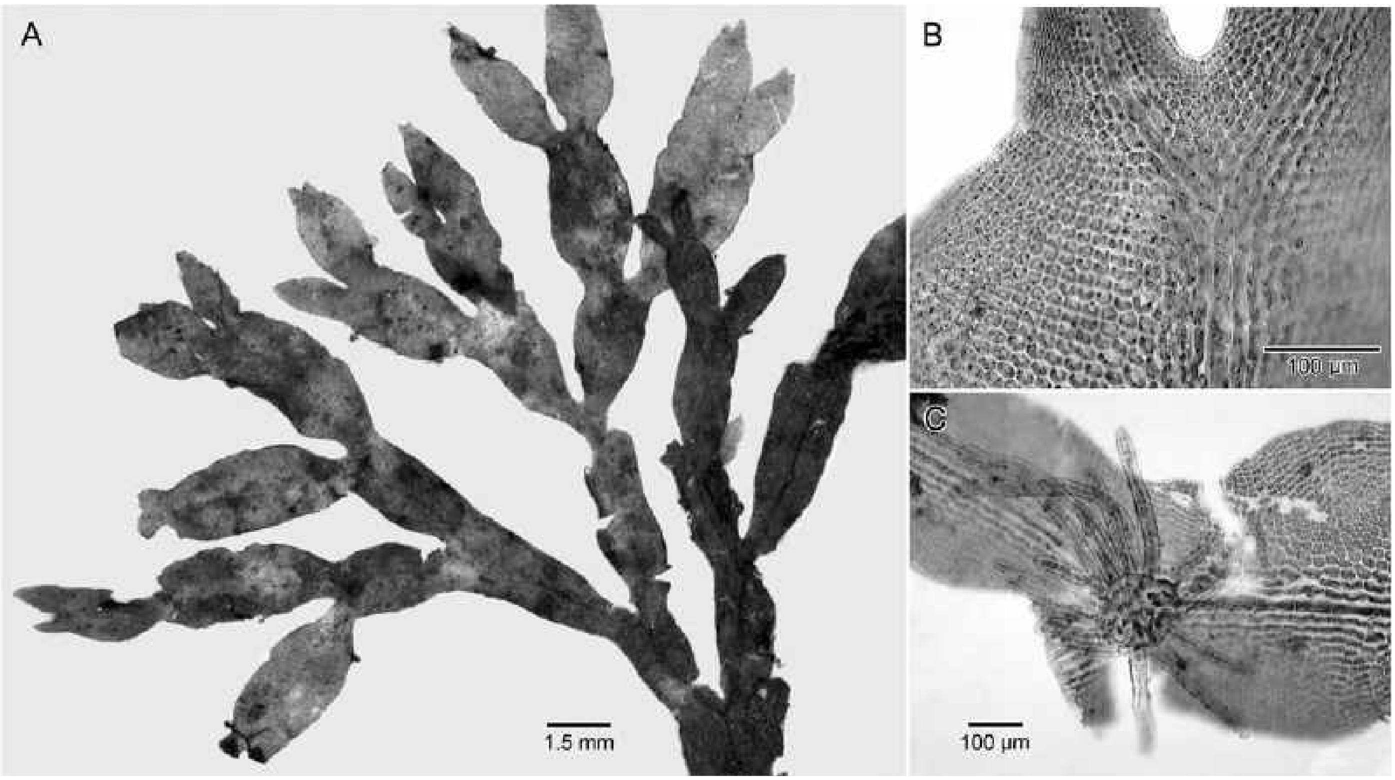


FIGURE 105. *Caloglossa apomeiotica*: A. Thallus constricted at branching nodes (forks) (specimen from Brazil; *Krayesky-73,* US Alg. Coll.). B. Constriction at branch node, showing main and lateral axis. C. Ventral view of free rhizoidal filaments at base of bundle of tightly appressed rhizoids forming peg-like attachment structure. (B, C, specimens from Pacific Panama; *Krayesky-64,* US Alg. Coll.).

Habitat. On mangrove prop roots of *Rhizophora mangle* Linnaeus, trunks and pneumatophores of *Avicennia germinans* (Linnaeus) Stearn and *Laguncularia racemosa* (Linnaeus) Gaertner f., and possibly on other aquatic vegetation in lagoons and estuaries; intertidal to very shallow subtidal.

Distribution. Gulf of California: Isla Espíritu Santo to Bahía Balandra and Estero Zacatecas, Ensenada de La Paz (vicinity of La Paz); Sinaloa to Jalisco. Eastern Pacific: Puerto San Carlos (Bahía Magdalena), Baja California Sur; Chiapas; Guatemala; El Salvador; Panama.

Type Locality. On prop roots of mangrove, *Rhizophora mangle* Linnaeus; Puerto San Carlos, within Bahía Magdalena, Baja California Sur, Pacific Mexico.

Remarks. Pacific Baja California Sur specimens referred to "*Caloglossa leprieurii*" by West and Zuccarello (1990) were later found to be a new species, C. *apomeiotica* J. A. West et Zuccarello, primarily because of their asexual mode of reproduction by apomictic bisporangia and tetrasporangia in cultured sporophytes (West et al., 1994). Kamiya et al. (2003) later concluded that the asexual *C. apomeiotica* was derived from *C. leprieurii* (Kamiya et al., 1998), and asexual reproduction alone was not considered sufficient to separate it from *C. leprieurii*. Subsequently, Krayesky et al. (2011) reestablished *C. apomeiotica* as a distinct species on the basis of morphological characters and new molecular data that placed it in a distinct clade.

Although *C. apomeiotica* is somewhat more robust, it is similar to *C. leprieurii*?. By examining the larger end of the range of the widths and the number of cell rows derived from the first axial cell of the main axis opposite a lateral branch, the two can be separated: *C. apomeiotica* has blades that are 2.5–5.0 mm wide with 2–5 cell rows, whereas *C. leprieurii* has blades that are 0.5–1.4 mm wide with 3–7 cell rows.

Caloglossa leprieurii? (Montagne) G. Martens

Delesseria leprieurii Montagne, 1840:196–197, pl. 5: fig. 1.

Caloglossa leprieurii (Montagne) G. Martens, 1869:234, 237; Krayesky et al., 2011:47, figs. 3–12; Krayesky et al., 2012:525; Wynne, 2014:71.

Caloglossa leprieurii (Montagne) J. Agardh, 1876:499; Ortega et al., 1987:75, pl. 8: figs. 37–38, pl. 9: fig. 39; González-González, 1993:442; Pedroche et al., 1995:115; González-González et al., 1996:303, 385; Dreckmann et al., 2006:155; Fernández-García et al., 2011:60.

Hypoglossum leprieurii (Montagne) Kützing, 1849:875.

Algae small, prostrate to partially erect, 0.8–2.0 cm long; of flat, narrow, linear blades with a midrib, subdichotomously branched, slightly or occasionally strongly constricted at branching nodes, 1.5–4.0 mm long, 0.5–1.4 mm wide at median internode region; arising from a partially prostrate portion, attached by tightly adhering rhizoidal filaments issued from base of blade to form a compact, peg-like mound; giving a holdfast-like appearance. Blade midrib of an axial cell filament with 2 transverse and 2 lateral periaxial cells and monostromatic "wings" to either side. Endogenous branching present; adventitious branching absent. Lacking adaxial cell rows derived from first axial cell from lateral axis. One to two cell rows derived from nodal axial cell opposite lateral branch. Number of cell rows from first axial cell at main axis opposite the lateral branch (2–)3–7 (description after Krayesky et al., 2011).

Tetrasporangia and bisporangia, 55–65(–80) µm tall, 35–56 µm in diameter, formed in a single layer in regular rows. Cystocarps forming near blade apices. Male reproductive structures not observed.

Habitat. Epiphytic on aquatic vegetation and mangrove (mangle) pneumatophores and prop roots; intertidal to very shallow subtidal.

Distribution. Gulf of California: Laguna Agiabampo, Sonora and Sinaloa. Eastern Pacific: Chiapas; Costa Rica.

Type Locality. Sinnamary, northwest of Cayenne, French Guiana.

Remarks. *Caloglossa leprieurii,* described from the western Atlantic, is probably widespread in tropical waters of the eastern Pacific, and Indian oceans (Krayesky et al., 2011, 2012). Specimens identified within a broadly defined "*C. leprieurii*" in the Americas by previous investigators were shown to actually encompass four distinct species that were morphologically and molecularly different from one another (Krayesky et al., 2011, 2012).

Caloglossa leprieurii has been reported in the southern Gulf from Laguna Agiabampo, Sonora and Sinaloa (Ortega et al., 1987). Gulf of California specimens are tentatively referred to "*C. leprieurii*?" with a taxonomic query until more collections from Laguna Agiabampo and elsewhere in the Gulf can be made to test if *C. leprieurii* is present by morphological and molecular comparisons to type locality *C. leprieurii* and *C. apomeiotica*. It is also possible there are other species to be found within a Gulf "*C. leprieurii* complex."

Erythroglossum J. Agardh

Erythroglossum J. Agardh, 1898:174.

Algae may be erect or decumbent and composed of 1 or more blades, with polystromatic midribs that are indistinct in some parts of the thallus. Lateral veins present or lacking, and margins may be dentate (toothed), especially in distal portions. Blades commonly stipitate and simple or branched from the margins. Growth is from single apical cells, with intercalary cell divisions in the primary and higher order cell rows.

Tetrasporangia arranged in sori, at maturity linear and parallel to margins. Gametophytes dioecious, procarps composed of two 4-celled carpogonial branches with a single group of sterile cells per supporting cell; carposporophyte with carposporangia in terminal branched chains. Cystocarps scattered over blade. Spermatangia in linear sori parallel to margins.

One species of *Erythroglossum* is reported in the northern Gulf of California.

Erythroglossum californicum (J. Agardh) J. Agardh

FIGURE 106

Delesseria californica J. Agardh, 1885:69.

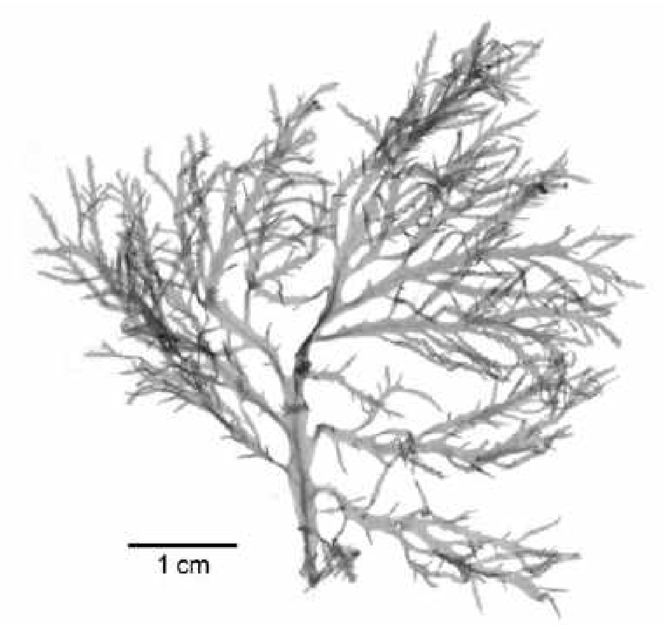


FIGURE 106. *Erythroglossum californicum:* Habit (*JN-6578a*, US Alg. Coll.-217358).

Erythroglossum californicum (J. Agardh) J. Agardh, 1898:176; Kylin, 1941:31, pl. 10: fig. 28; Dawson, 1962a:93, pl. 46: fig. 1; Abbott and Hollenberg, 1976:648, fig. 509; Stewart, 1991:143; González-González et al., 1996:199; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:191.

Psammophyllum californicum (J. Agardh) P. C. Silva et R. Moe in Silva, 1979:330, *nom. invalid.*

Erythroglossum obcordatum E. Y. Dawson et Neushul, 1966:183, pl. 43: figs. 4, 5; Scagel et al.,1989:293.

Algae erect, up to 4.0 cm tall, of ribbon-like, narrow, more or less linear, delicate blades, 2.5–3.0(–4.0) mm wide, subdichotomously to irregularly branched, up to 4(–6) orders, with an apparent, polystromatic midrib and without lateral veins; margins irregularly denticulate, often eroded; apical margins mostly irregular; apical cell inconspicuous; thalli attached below by a small, compact holdfast.

Tetrasporangial sori on both sides of midrib; initially discrete and circular to oval, later becoming confluent and more linear, mostly near the blade margins. Cystocarpic and spermatangial thalli not seen in Gulf specimens.

HABITAT. Shallow subtidal, down to 5 m depths.

DISTRIBUTION. Gulf of California: El Desemboque to Isla San Esteban. Eastern Pacific: Oregon (Hansen, 1997); Anacapa Island (California Channel Islands); Santa Barbara to San Diego, southern California.

TYPE LOCALITY. Santa Barbara, Santa Barbara County, southern California, USA.

REMARKS. The northern Gulf specimens are tentatively referred to *Erythroglossum californicum*. Their relationship to type locality material of *E. californicum* and to *Anisocladella pacifica* Kylin (1941) is in need of further investigation. The "*E. californicum*" as identified from Oregon (Doty, 1947) and central California (Smith, 1944, 1969) appear to be *A. pacifica* (Abbott and Hollenberg, 1976), a species that has been considered conspecific with *E. californicum* (Gabrielson et al., 2012).

In using the name *Psammophyllum californicum*, Silva and Moe (in Silva,1979) based it on *Anisocladella pacifica* and considered *Delesseria californica* an earlier synonym; unfortunately, the generic name *Psammophyllum* has not been validly published. The taxonomic status of the southern California *E. californicum* is in need of further study, and as Stewart (1991) indicated, its name and taxonomic position are likely to be changed.

Grinnellia Harvey

Grinnellia Harvey, 1853:91.

Algae are membranous blades, upper regions monostromatic, with a polystromatic midrib (conspicuous throughout or at least in lower portion of the blade). Blades are usually simple (unbranched) or sometimes have proliferous bladelets near base or are occasionally irregularly branched distally if wounded. Growth is from a prominent apical cell that divides transversely and later intercalary divisions within secondary and higher order cell rows. The lateral pericentral cells divide transversely, forming second-order cell rows that produce third-order rows; some, but not all, of the third-order row initials reach the thallus margin.

Tetrasporangia are tetrahedrally divided, cut off with small cortical cells toward both of the blade's surfaces in small sori, and scattered over the primary blade below the apices. Gametangial thalli are dioecious. Minute bladelets are scattered over the primary blade, with procarps produced from the midrib of the bladelets. Cystocarps are hemispherical, ostiolate, and project on either side of the bladelet (often appearing to be on a stalk) immersed in the surface of the parent blade. Spermatangia develop in small sori, scattered on one or both of the blade surfaces.

One species of *Grinnellia* occurs in the northern Gulf of California.

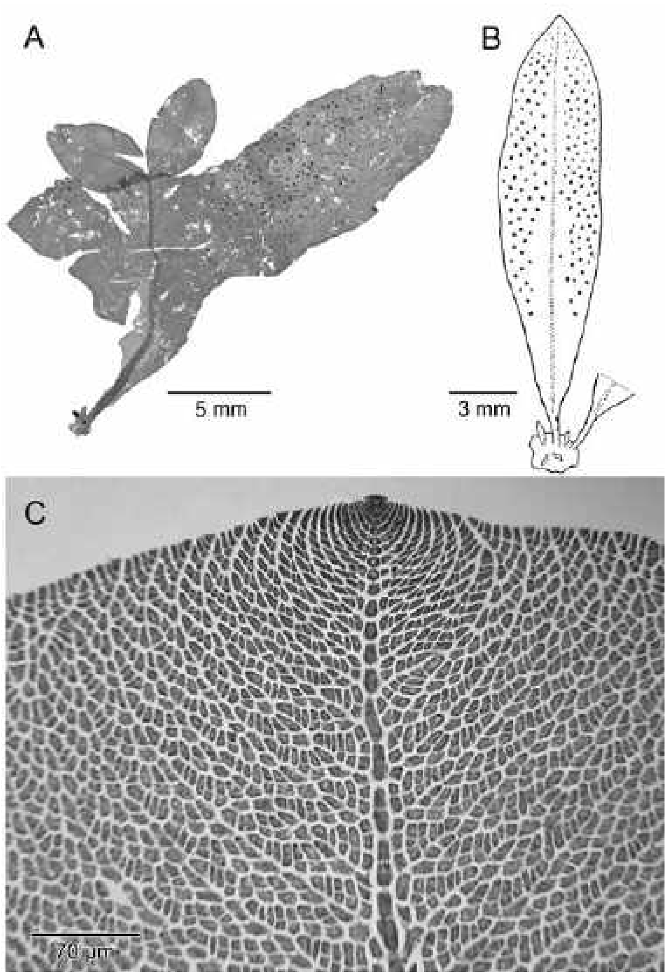
Grinnellia lanceolata E. Y. Dawson

FIGURE 107

Grinnellia lanceolata E. Y. Dawson, 1944a:322, pl. 47: fig.6; 1962a:84, pl. 39: fig. 5; Wynne, 1985a:169, figs. 7–12; Pacheco-Ruíz and Zertuche-González, 2002:468; Fernández-García et al., 2011:62; Wynne, 2014:105.

Apoglossum punctatum E. Y. Dawson, 1966b:65, fig. 6B.

Blades erect, 2.5–6.0 cm tall, narrowly cuneate above a short stipe, membranous, monostromatic except for percurrent, polystromatic midrib of larger elongated cells. Blades initially ovate-elliptical, then broadening up to 1.0–3.0 cm wide; with entire margins. Growth from an apical cell and also intercalary cell divisions in second-order and higher cell rows; intercalary divisions absent in first-order rows. Lateral pericentral cells divide transversely.



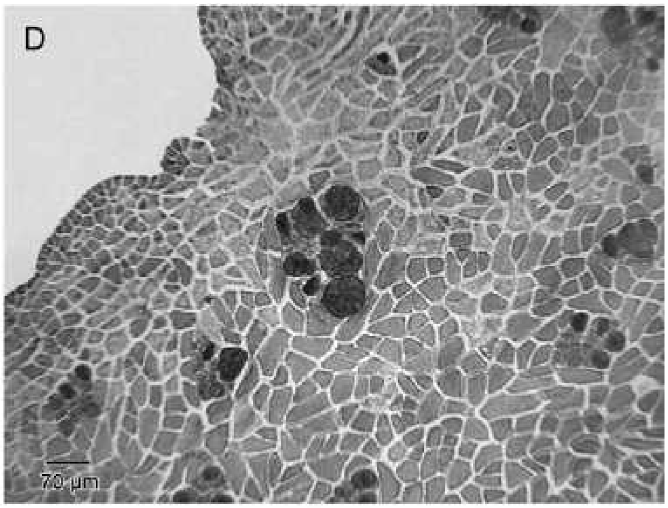


FIGURE 107. *Grinnellia lanceolata*: A. Habit of a damaged specimen that has regenerated some blades. B. Habit of narrow lanceolate blade with tetrasporangia (type specimen, after Dawson, 1944a, pl. 47: fig. 6). C. Blade apex showing apical organization; note that not all third-order cell rows reach blade margin and the lateral pericentral cells divide transversely. D. Small discrete tetrasporangial sori, with a limited number of tetrasporangia, distributed over blade (A, C, D, *EYD-26143*, US Alg. Coll. microscope slide 779, type of *Apoglossum punctatum*).

Tetrasporangia tetrahedrally divided, 60–70 µm long, 45–60 in diameter; in small, discrete sori scattered over the blade surface (punctate) on both sides of midrib. Procarps develop on midrib of fertile bladelets. Cystocarps up to 1 mm in diameter; appear to be scattered over blade, but actually borne on midline of very short, fertile bladelets that arise off main blade. Spermatangia in irregular, angular sori; scattered over blade.

Habitat. On rocks; shallow subtidal.

Distribution. Gulf of California: Bahía de Los Ángeles; Isla Salsipuedes (Islas de San Lorenzo); Puerto Escondido; Punta Gorda, Bahía San Jose del Cabo. Eastern Pacific: Panama.

Type Locality. Punta Gorda, NE end of Bahía San Jose del Cabo, Baja California Sur, Gulf of California, Mexico.

Remarks. Although previously *Grinnellia lanceolata* was considered endemic in the Gulf of California, it was recently reported in Pacific Panama (Littler and Littler, 2010). Two Gulf of California species, *G. lanceolata* and the endemic *Apoglossum punctatum*, were noted by Dawson (1966b) to be "related." Wynne (1985a) later observed both to have the same apical growth pattern and small discrete tetrasporangial sori, characteristics of *Grinnellia*, and considered them conspecific.

***Hypoglossum* Kützing**

Hypoglossum Kützing, 1843:444.

Thalli composed of flat blades, usually erect and attached by discoid holdfasts or secondarily by marginal rhizoids. Blades are membranous, monostromatic (except in midrib and fertile regions), and lack lateral veins. New blades are issued singularly or in pairs from the midrib (primary cell row) of older blades and are similar in structure to the supporting parent blade. The percurrent midrib can become corticated in some species and can form a thickened "stipe" basally if the blade erodes. Branching is endogenous, restricted to the midrib (except in *H. anomalus*). Most species are monopodially organized. Axial filament of cells with 2 lateral pericentral cells and 2 transverse pericentral cells. The lateral pericentral cells form second-order cell rows with one of two types of apical organization, either (1) all cells of second-order rows bear third-order rows or (2) not all cells of second-order rows bear third-order cell rows. All cell rows that are initiated reach blade margins. Almost all species are without intercalary cell divisions (only one species, *H. sagamianum* Yamada, 1941, has secondary cell rows with intercalary cell division).

Tetrasporangia can be borne in either (1) rows with cover cells not corticating the sori or (2) a random arrangement with cover cells corticating the sori. Tetrasporangia are in one or more cell layers, usually in sori along the sides of the blade midrib or extending over it. Gametophytes are dioecious. Procarps restricted to midrib. Cystocarps are borne along the midline and are emergent and prominent, with an ostiole that often has a rostrum. The rostrum in different species ranges from a slight collar to a long "neck." Spermatangia formed in small or large confluent sori between the midrib and blade margin. One species, *Hypoglossum attenuatum,* with two varieties, is reported in the northern Gulf of California.

KEY TO THE VARIETIES OF *HYPOGLOSSUM ATTENUATUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Lanceolate blades abundantly branched; blades slender 1–2(–2.5) mm wide . . . . ***H. attenuatum* var. *attenuatum***
1b. Lanceolate blades sparsely branched (usually without blades in lower portions); blades longer and wider, up to 6 mm wide . . . . ***H. attenuatum* var. *abyssicolum***

Hypoglossum attenuatum N. L. Gardner var. *attenuatum*

Hypoglossum attenuatum N. L. Gardner, 1927f:104, pl. 20: fig. 3, pls. 35, 36; Dawson, 1944a:321; 1960a:51; 1961b:445; 1962a:78; González-González et al., 1996:228; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212; Fernández-García et al., 2011:62; Wynne, 2014:29.

Blades erect, membranous, and lanceolate, dark pink to greenish in color, 2.5–7 cm tall and 1–2(–2.5) mm wide, mostly richly branched; arising from a small discoid holdfast. Blades monostromatic (except at the midrib), slender, linear-lanceolate, usually tapering to an acute apex; branched from midrib, up to 3(–4) orders. Blades of female thalli may be shorter and broader with more obtuse apices. Apical organization with second-order cells all issuing third-order cell rows, all third-order row initials reach the blade margins.

Tetrasporangia in sori; produced in 2 or more cell layers. Cystocarps prominent, protuberant, borne above midrib on blade surface; often a single cystocarp per blade, enclosed in a pericarp, ostioles with collar-like rostrum. Spermatangia unknown.

HABITAT. On rocks, epiphytic on or entangled with other algae; low intertidal to shallow subtidal, down to 8 m depths (also dredged from 12–80 m depths; Dawson, 1944a).

DISTRIBUTION. Gulf of California: Rocas Consag; Punta Pelicano to Guaymas; Cabo Pulmo-Los Frailes to Cabo San Lucas. Eastern Pacific: Isla Guadalupe; Bahía San Quintín, Baja California to Oaxaca; Panama; Colombia; Ecuador; Chile. Western Pacific: China; Vietnam.

TYPE LOCALITY. Puerto Libertad, Sonora, Gulf of California, Mexico (Gardner, 1927f).

Hypoglossum attenuatum var. *abyssicolum* (W. R. Taylor) E. Y. Dawson

FIGURE 108

Hypoglossum abyssicolum W. R. Taylor, 1945:277, pl. 89, figs. 1, 2; Bernecker, 2009:CD-Rom p. 66.

Hypoglossum attenuatum var. *abyssicolum* (W. R. Taylor) E. Y. Dawson, 1962a:77, pl. 34: fig. 3; Norris, 1973:15; Schnetter and Bula-Meyer, 1982:169, pl. 30: fig. 4; Stewart and Stewart, 1984:146; Huerta-Múzquiz and Mendoza-González, 1985:52; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:228; CONANP, 2002:138; Fernández-García et al., 2011:62; Wynne, 2014:29.

Hypoglossum attenuatum sensu Dawson, 1944a:321 [in part; non *Hypoglossum attenuatum* var. *attenuatum* N. L. Gardner, 1927f:104].

Algae of narrow delicate blades up to 12 cm long; sparingly branched from midrib; usually lacking branches in lower portions; to each side of polystromatic midrib blade 1 cell thick and without lateral veinlets, midrib becomes faint in ultimate branchlets; blades mostly 2.5–7.5 cm long and up to 6 mm wide; blades shorter and narrower with each successive order; tapering to base and apices. Blades of cystocarpic thalli shorter and wider, with broadly obtuse apices.

Tetrasporangia in oblong sori, up to 3 mm long, on both sides of midrib. Cystocarps usually singular on midrib of ultimate and subultimate blades; 0.9–1.2 mm in diameter. Spermatangia formed in small sori between the midrib and blade margin.

HABITAT. Subtidal; 10–40 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Isla San Esteban; Isla Tiburón; Bahía de Loreto to Punta Los Frailes; Sinaloa to Nayarit; Islas Marías (Islas Tres Marías). Eastern Pacific: Isla Guadalupe to Laguna de San Ignacio, Baja California; Oaxaca; Costa Rica; Isla Gorgona, Colombia; Galápagos Islands.

TYPE LOCALITY. Dredged from 56 m depth; off Post Office Bay, Isla Floreana (Isla Santa María), Galápagos Islands, Ecuador.

Myriogramme Kylin

FIGURE 109D

Myriogramme Kylin, 1924:55.

Blades may be foliose, simple, or lobed or variously branched, usually erect or with erect and prostrate portions, and are with or without midribs or macroscopic veins; microscopic veins absent. Some species have a compressed to cylindrical stipe; others lack a stipe; attached by small holdfasts or secondarily by ventral or marginal rhizoids. Blades are typically monostromatic above and may become tri- to polystromatic below, and have polystromatic veins, reproductive structures, and stipes

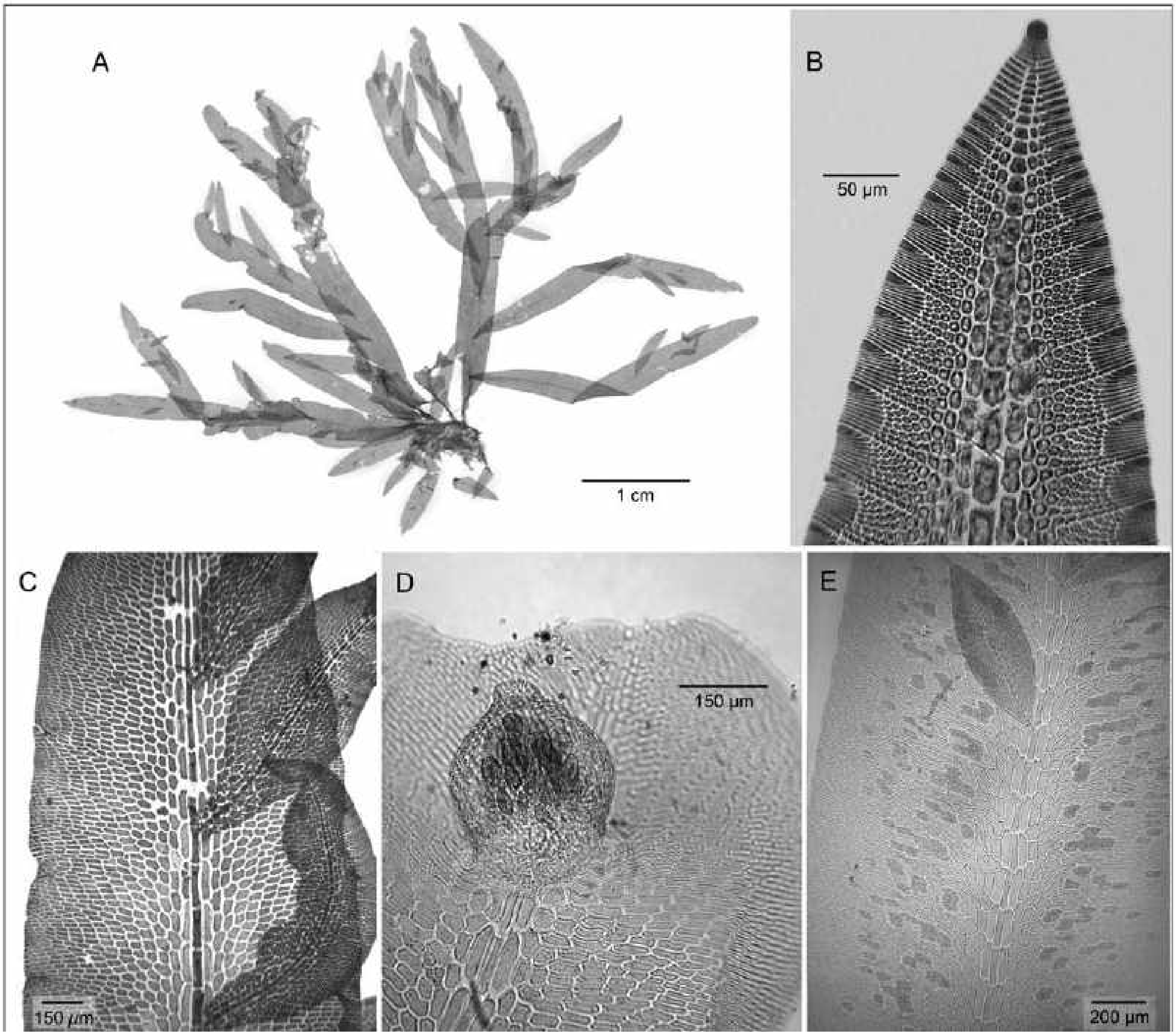


FIGURE 108. *Hypoglossum attenuatum* var. *abyssicolum*: A. Habit (*JN-4722*, US Alg. Coll.-160075). B. Blade apex showing all second-order row cells bear third-order cell rows and all third-order row initials reach the blade margin (in the photo second-order row initials are wedge-shaped at the blade margin, and third-order initials are elongated) (*EYD-26163*, US Alg. Coll. microscope slide 774). C. Several blades developing from midrib of parent blade (*JN-5156a*, US Alg. Coll. microscope slide 4609). D. Protuberant cystocarp borne on midline of blade with a short collar-like rostrum forming ostiole. E. Spermatangia in sori, with these in disjunct patches (D, E, *EYD-26117*, US Alg. Coll. microscope slide 793).

as well as near their base. Growth is diffuse, from marginal and intercalary meristems. Apical cells divide obliquely, becoming indistinguishable from marginal row initials. Cells of blade are polygonal in surface view; in transection arranged in vertical rows in polystromatic portions.

Tetrasporangia are tetrahedrally divided and borne in small circular, elliptical, linear or irregular sori grouped along the blade margins. Tetrasporangial sorus is covered by 2–3 layers of cortical cells, with tetrasporangia developed primarily from central cells and also from the inner cortical cells. Gametophytes are

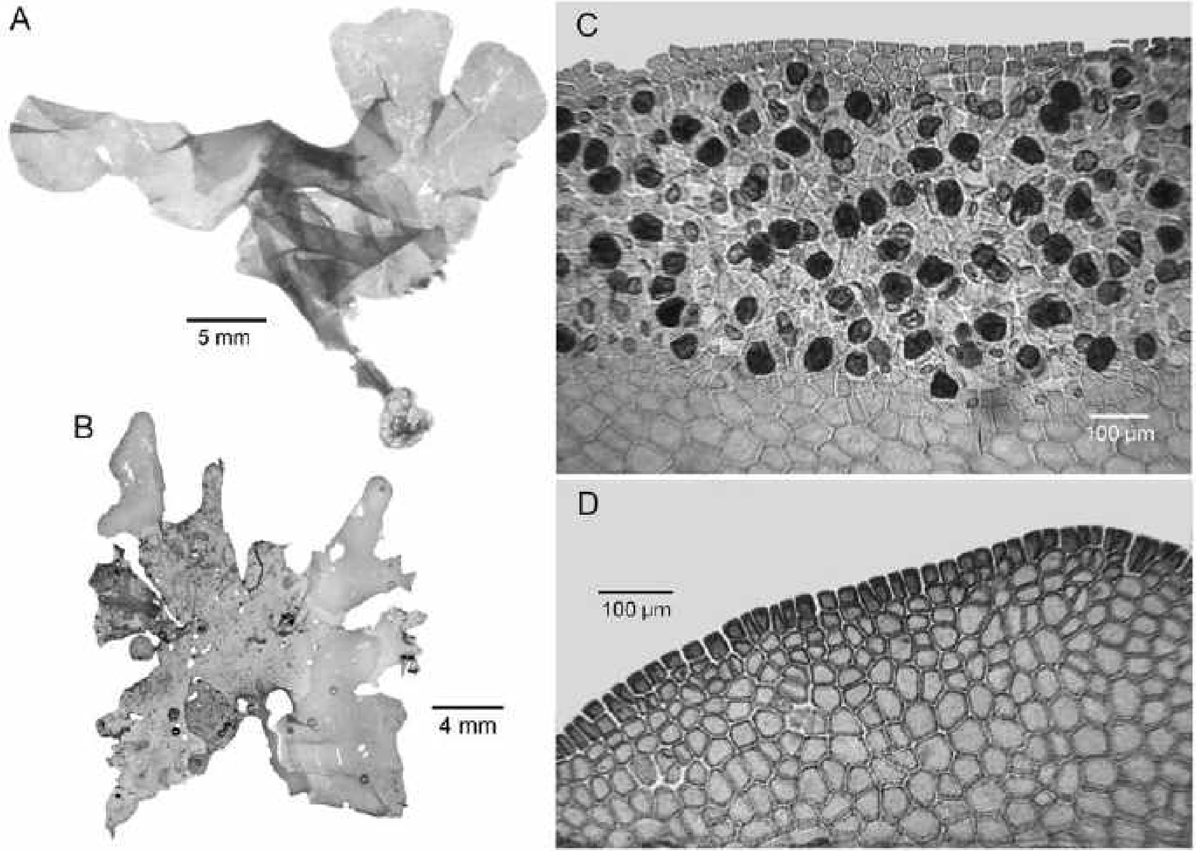


FIGURE 109. Species of *Myriogramme*: A. *Myriogramme divaricata:* Thallus dichotomously lobed with rounded apices (*JN-5583a*, US Alg. Coll.-217360). B, C. *Myriogramme auricularis*: B. Habit. C. Tetrasporangial sori near thallus margins (B, C, *EYD-26167*, US Alg. Coll. microscope slide 771, type of *M. auricularis*). D. *Myriogramme* sp.: Meristematic margin of blade (*JN-4901*, US Alg. Coll. microscope slide 5289).

dioecious. Procarps, a 4-celled carpogonial branch with 2 sterile-cell groups, are scattered on blades. Carposporophyte with extensive, branched basal fusion cell, carposporangia borne terminally in chains and occasionally also with lateral clusters. Cystocarps with ostiolate pericarp, several cells thick. Spermatangial sori small, produced in monostromatic areas, later enlarging as they become confluent. Spermatangial sori near blade margins on both sides of blade, with cells bearing layer of cortical initials that produce elongate spermatangia.

Three species of *Myriogramme* are known to occur in the northern Gulf of California.

KEY TO THE SPECIES OF *MYRIOGRAMME* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades simple, undivided; margins with rounded, “scalloped” lobes . . . . **M. caespitosa**
1b. Blades branched with a stipitate base 2
2a. Blades divaricately dichotomously branched . . . . **M. divaricata**
2b. Blades developed sympodially, somewhat auriculately “flared out” from top of stipe . . . . **M. auricularis**

Myriogramme auricularis E. Y. Dawson

FIGURE 109B,C

Myriogramme auricularis E. Y. Dawson, 1966b:66, fig. 6I [type specimen]; González-González et al., 1996:244; Wynne, 2014:178.

Blade membranous, mostly erect, up to 2.5 cm tall and to 2.5 cm wide; blades flared somewhat auriculately from top of stipe or secondary holdfasts; stipe initially short with a knobby holdfast, elongating up to 6 mm upon repeated grazing and branch regeneration, with successive blades tending to develop sympodially; secondary discoid or peg-like attachments may develop if appressed to hard substratum or solid objects or removed from stipe, also formed between overlapping blades. Blades deeply, irregularly palmately lobed, with undulate, entire margins; lacking midrib or veins; monostromatic throughout, except thickened immediately above stipe and polystromatic in basal region.

Tetrasporangia in oval to elongate tetrasporangial sori, just inside blade margins along outer lobes. Cystocarpic and spermatangial thalli unknown.

Habitat. Subtidal; dredged from 8–30 m depths.

Distribution. Gulf of California: Isla Rasa (Isla Raza) and Isla San Lorenzo (Islas de la Cintura).

Type Locality. Isla San Lorenzo ("Isla San Lorenzo del Sur"; southern island of Islas de San Lorenzo), off east coast of Baja California, Gulf of California, Mexico.

Myriogramme caespitosa E. Y. Dawson

Myriogramme caespitosa E. Y. Dawson, 1949b:19, fig. 8; Dawson et al., 1960a:68, pl. 33: fig. 5; 1960b:26; Dawson, 1961b:446; 1962a:96, pl. 47: fig. 4; Abbott and Hollenberg, 1976:654, fig. 597; González-González et al., 1996:244; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:178.

Myriogramme osorioi E. Y. Dawson, 1950b:158, figs. 18, 19; 1961b:447; 1962a:96, pl. 47: figs. 1, 2; 1966b:66; Abbott and North, 1972:76; González-González et al., 1996:244.

Blades small, delicate, rose pink, erect or repent, to 1.0 (-3.0) cm high and 5–8 mm wide; of several overlapping blades, forming clumps. Blades monostromatic, except in basal region, veins completely lacking. Blades undivided or palmately lobed, with rounded scalloped lobes, with smooth, ruffled, or undulate margins. Blades occasionally attached to each other by small accessory discs. Cells usually angular, 50–70 μm in diameter in mature portions of blade.

Tetrasporangia in circular to oval sori. Cystocarps scattered, with pericarp and conspicuous "beaked" ostiole. Spermatangial sori often becoming confluent.

Habitat. On rocks; low intertidal to shallow subtidal, down to 13 m depths.

Distribution. Gulf of California: Puerto Peñasco to Isla Coronado (Isla Smith), off north end of Bahía de Los Ángeles; Isla Estanque to Isla Las Ánimas (Isla San Lorenzo del Norte) and Isla San Lorenzo (both Islas de San Lorenzo); Isla Patos (off N end of Isla Tiburón); Isla Partida. Eastern Pacific: Santa Rosa Island and Santa Cruz Island (California Channel Islands), southern California to Isla Magdalena, Baja California Sur.

Type Locality. On a floating *Macrocystis* holdfast; in San Miguel Passage, off Santa Rosa Island, California Channel Islands (Channel Island National Park), southern California, USA.

Myriogramme divaricata E. Y. Dawson

FIGURE 109A

Myriogramme divaricata E. Y. Dawson, 1944a:323, pl. 47: fig. 5; 1962a:97, pl. 40: fig. 5, pl. 42: fig. 2; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:179.

Blades delicate, small (to 3 cm), from short stipe (1.0 mm), membranous, divaricately dichotomously branched, with more or less rounded or truncate tips. Blades monostromatic without midrib or veins.

Tetrasporangia in small sori. Carposporangial and spermatangial thalli unknown.

Habitat. On rock or entangled with other algae; shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Roca Consag; Puerto Refugio, Isla Ángel de la Guarda to Isla Estanque; Isla Coronado and Isla la Ventana, Bahía de Los Ángeles.

Type Locality. Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

Remarks. *Myriogramme divaricata,* a Gulf of California endemic species, was only known from the type (Dawson, 1962a). Additional subtidal collections extend its known distribution from Rocas Consag (*JN-3128*, US Alg. Coll. microscope slides 4637, 4638) to Isla Estanque, off the southern end of Isla Ángel de la Guarda (*JN-5583a,* US Alg. Coll.-217360).

***Phycodrys* Kützing**

Phycodrys Kützing, 1843:444.

Thallus leaf-like or foliose blades, arising from a discoid holdfast or creeping entangled stolons. Blades simple, lobed in upper portions, or producing secondary bladelets along margins. Blades monostromatic except for midrib regions, lateral veins, and holdfasts or some species tristromatic. Midribs conspicuous and lateral veins present, often paired and opposite, alternate or may be irregularly arranged; micropscopic veins lacking or faint. Midrib with or without cortication, without descending rhizoids; composed of more or less rectangular cells in cross section. Growth by means of a single transversely dividing apical cell, intercalary cell divisions in primary and higher-order cell rows.

Tetrasporangia in rounded sori on proliferous bladelets from margin or on main blade surface between lateral veins. Tetrasporangia in 2 layers, produced laterally from inner cortical cells, covered by layer of outer cortical cells. Gametophytes dioecious. Procarps with 4-celled carpogonial branch and 2 sterile-cell groups. Cystocarps with basal fusion cell, branched gonimoblast with terminal chains of carposporangia, surrounded by 3- to 8-cells-thick pericarp with ostiole. Cystocarps scattered over blade surfaces. Spermatangia in rounded sori scattered over blade.

Three species of *Phycodrys,* all endemic, are known in the northern Gulf of California.

KEY TO THE SPECIES OF *PHYCODRYS* IN THE NORTHERN GULF OF CALIFORNIA

1a.	Blades with lateral veins irregularly branched off midrib	***P. amplissima***
1b.	Blades with lateral veins regularly, oppositely branched off midrib	2
2a.	Blades usually simple with smooth margins	***P. simplex***
2b.	Blades often branched from margins with occasional rhizoidal bundles along blade margins	***P. lucasana***

Phycodrys amplissima E. Y. Dawson

FIGURE 110

Phycodrys amplissima E. Y. Dawson, 1962a:91, pl. 44, pl. 45:figs. 2, 3; González-González et al., 1996:247; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:208.

Thalli erect and membranous foliose blades, relatively large, mostly 10–13 cm (largest up to 27 cm) tall and to 16(–20) cm wide, symmetrical to asymmetrical, with conspicuous midrib and irregularly arranged lateral veins (becoming faint above), from a short stipe attached by a stoloniferous holdfast. Blades monostromatic, except for polystromatic region near midrib, veins, stipe, and holdfast; margins undulating and denticulate, with minute irregular proliferations (“teeth”) along margin. Growth from apical cell with intercalary divisions in all orders of cell rows. Lateral pericentral cells producing second-order rows that reach the blade margin, and further intercalary divisions form the blade.

Tetrasporangial sori start out small and rounded, then enlarge, some becoming confluent and somewhat elliptical in shape, over 1 mm long. Mature tetrasporangia 65–80 µm long. Gametophytes dioecious. Mature cystocarps up to 600–750 µm in diameter, ostiolate, scattered over the blade. Spermatangial sori forming rounded to irregularly shaped patches, 1–2 mm in diameter.

HABITAT. On rocks; intertidal to subtidal, 10–36 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco; El Desemboque to Isla San Esteban.

TYPE LOCALITY. Off Isla San Esteban (Islas de la Cintura) at 10–36 m depths, Gulf of California, Mexico.

REMARKS. The endemic *Phycodrys amplissima* is apparently restricted in distribution to the northern Gulf of California.

Phycodrys lucasana E. Y. Dawson

Phycodrys lucasana E. Y. Dawson, 1962a:88, pl. 37: figs. 7, 8, pl. 43: fig. 1; 1966b:66; González-González et al., 1996:247; Wynne, 2014:208.

Blades membranous, erect, up to 5 cm tall and to 13 mm wide, monostromatic apart from midrib and slender opposite lateral veins. Blade usually single and branched above a short terete stipe (2 mm); attached by discoid holdfast. Branches arise from blade margins, branches similar to primary blade. Margins at first denticulate, these “teeth” later developing into terete, simple or branched rhizoidal bundles. Tetrasporangial sori small, scattered on blades. Sexual reproduction unknown.

HABITAT. On rocks; subtidal, dredged 12 to 36 m depths.

DISTRIBUTION. Gulf of California: Isla Salsipuedes; Bahía de San Lucas.

TYPE LOCALITY. Dredged, 36 m depth, Bahía de San Lucas, Baja California Sur, Gulf of California, Mexico.

Phycodrys simplex E. Y. Dawson

FIGURE 111

Phycodrys simplex E. Y. Dawson, 1962a:90, pl. 38: figs. 2, 3; 1966b:66; González-González et al., 1996:248; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:209.

Algae upright, mostly 4–5.5 cm tall, consisting of several stipitate blades (each with a short stipe 3–5(–10) mm long), that arise from a basal, terete, common stipe 5–10 mm long. Blades simple and lanceolate with evident midrib and faint slender opposite lateral veins. Older blades 1.0–2.5 cm wide, gently tapering to apex, with midrib to 1 mm wide at base of blade; margins smooth, slightly undulate.

Reproduction not observed.

HABITAT. On rocks; subtidal, dredged 20 to 44 m depths.

DISTRIBUTION. Gulf of California: channel between Islas Mejia and Isla División (NW end of Isla Ángel de la Guarda); Puerto Refugio, Isla Ángel de la Guarda; Isla San Lorenzo (Isla San Lorenzo del Sur).

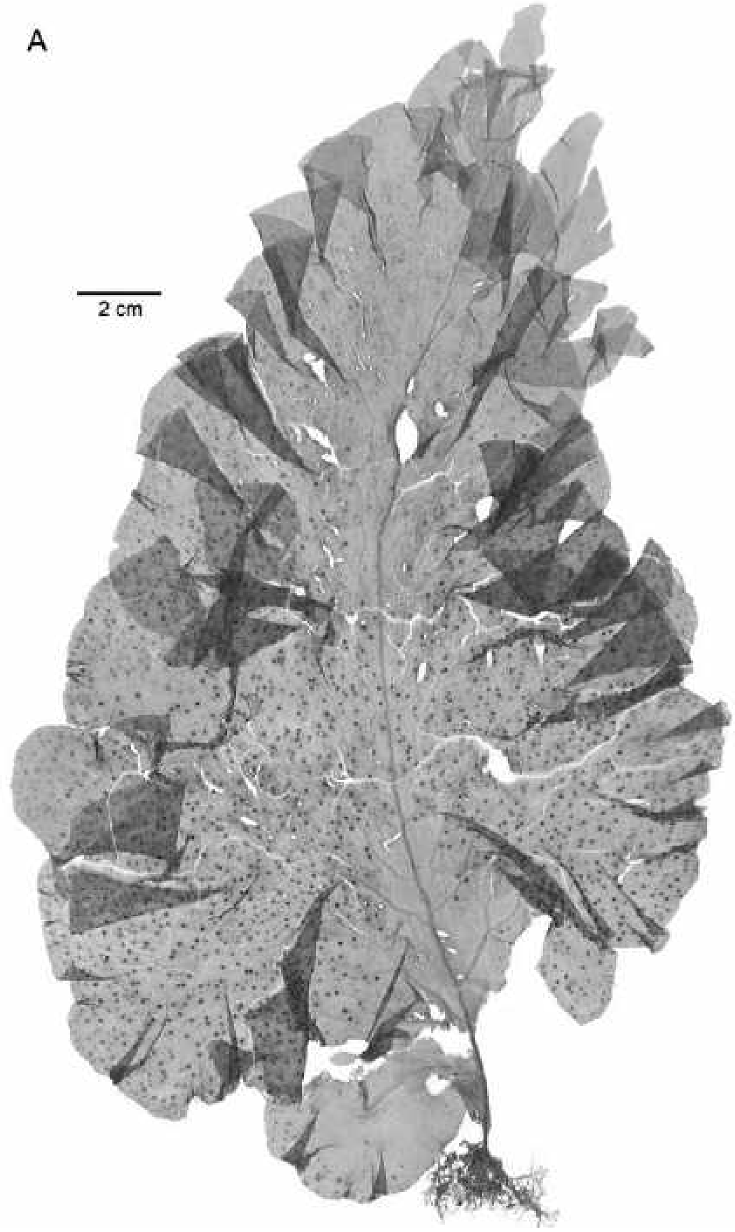
TYPE LOCALITY. Dredged from 22–44 m depths; Puerto Refugio, Isla Ángel de la Guarda (Las Islas de la Cintura), Gulf of California, Mexico.

REMARKS. *Phycodrys simplex* is an endemic species, thus far only known in the northern Gulf of California. Although its reproduction remains unconfirmed, Dawson (1966b:66) noted numerous minute bladelets (to 350 µm long) that were “sterile” but similar to sporangial bladelets.

Polyneurella E. Y. Dawson

Polyneurella E. Y. Dawson, 1944a:322.

Blades membranous, from branched stipe, with entire margins; attached by a small discoid holdfast. Blades mostly monostromatic; midribs lacking but with longitudinal veins and veinlets, inconspicuous (microscopic) above, more visible (macroscopic) in lower portion of mature blades. Veins indistinctly anastomosing in basal portion of blade; in upper portions veins



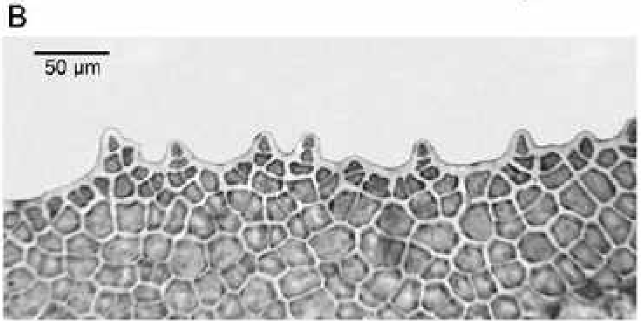


FIGURE 110. (Left, above) *Phycodrys amplissima*: A. Large, somewhat asymmetrical blade with stoloniferous holdfast, midrib with lateral, irregularly opposite veins, and numerous scattered cystocarps (*JN-6578b*, US Alg. Coll.-217347). B. Denticulate margin, showing short teeth along blade margin (isotype, *EYD-21580*, US Alg. Coll. microscope slide 635).

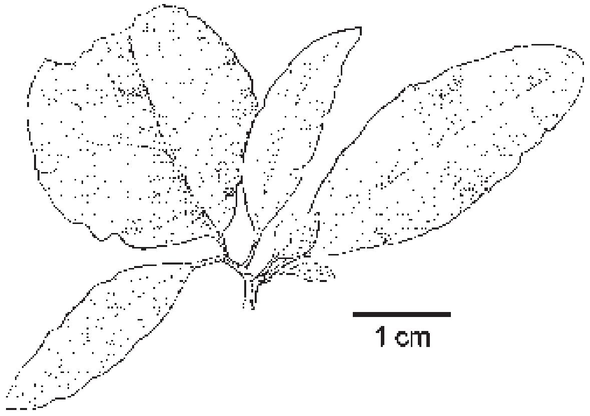


FIGURE 111. *Phycodrys simplex*: Habit of lanceolate blades borne off terete stipes (holotype: *EYD-183-40*, AHFH, now UC).

somewhat parallel; veins not always connected (discontinuous). Blades arising from subcylindrical stipe-like lower portion. Growth by means of an apical cell, with intercalary divisions in primary cell row.

Tetrasporangial sori small, scattered on blades. Cystocarps scattered over blade surface. Spermatangia unknown.

A monotypic genus, its one species, with two varieties, is known in the northern Gulf of California.

KEY TO THE VARIETIES OF *POLYNEURELLA* IN THE GULF OF CALIFORNIA

1a. Blades above a short, branched stipe, attached by a small discoid holdfast; blade margins smooth .... *P. hancockii* var. *hancockii*

1b. Blade above a prostrate, fleshy basal structure; with groups of rhizoids and proliferous branchlets along blade margins .... *P. hancockii* var. *rhizoidea*

Polyneurella hancockii E. Y. Dawson var. *hancockii*

FIGURE 112

Polyneurella hancockii E. Y. Dawson, 1944a:323, pl. 47: figs. 1 [type specimen], 2; 1961a:446; 1962a:85, pl. 40; figs. 3, 4; 1966b:66; Abbott and Hollenberg, 1976:651, fig. 594; González-González et al., 1996:252; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1 [as "*Polyneura hancockii*"]; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:149, fig. 69.

Blades erect, usually in a clump from branched stipe, rosy to pink, ovate, 2.0–7.5 cm tall and to (2–)3–6 cm wide, margins usually entire, with gentle taper to apices; some blades may become lacerated and then regrow, appearing lobed near top. Thallus usually 1 larger primary blade, and smaller blades developed along semiterete to compressed stipe-like portion that arises from discoid holdfast. Blades monostromatic with longitudinal veins and veinlets (distromatic), these microscopic in upper portions of blade and macroscopic in mature portions. Abundant secondary pit connections among adjacent vegetative cells.

Tetrasporangia in small, more or less circular to irregular sori (enlarging as blades mature), distributed in mid- to upper parts of blade toward margins. Gametophytes apparently dioecious. Single female blade observed slightly wider than tetrasporic blades, veins visible with slightly greenish cast against pink-purplish blade. Cystocarps 500–600 μm in diameter, scattered on blade; protruding on both sides of blade. Carposporangia elongate, to 100 μm long by 40 μm wide.

HABITAT. On rocks; subtidal, 15–40 m depths.

DISTRIBUTION. Gulf of California: Isla Ángel de la Guarda; Canal de Infiernillo (midway between Isla Tiburón and Campo Viboras, Sonora); Punta Los Frailes. Eastern Pacific: Carmel Submarine Canyon (south of Monterey Canyon), Monterey Bay National Marine Sanctuary, central California.

TYPE LOCALITY. Dredged from 22–44 m depths; Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

REMARKS. Dawson (1966b: 66) noted that cystocarps on *Polyneurella hancockii* from Isla San Lorenzo were "mainly in submarginal regions," whereas they were scattered on the blade from Canal de Infiernillo (*JN-4727*; Figure 112B).

Polyneurella hancockii var. *rhizoidea* E. Y. Dawson

Polyneurella hancockii var. *rhizoidea* E. Y. Dawson, 1962a:86, pl. 37: fig. 2; González-González et al., 1996:252; Wynne, 2014:149.

Blades similar to. *P. hancockii* var. *hancockii*; differing primarily in having a prostrate, adherent basal structure and blade margins that are somewhat proliferous with groups of branched, spreading rhizoidal outgrowths.

Tetrasporangial sori very small, mostly less than 300 μm in diameter. Cystocarps and spermatangia unknown.

HABITAT. On rocks; subtidal, dredged from 18.3–36.6 m depths.

DISTRIBUTION. Gulf of California: Bahía de San Lucas.

TYPE LOCALITY. Dredged from 20 fathoms (about 36.6 m) depth, Bahía de San Lucas, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Polyneurella hancockii* var. *rhizoidea* is known only from the type specimens. More collections are needed to evaluate its taxonomic status.

Schizoseris Kylin

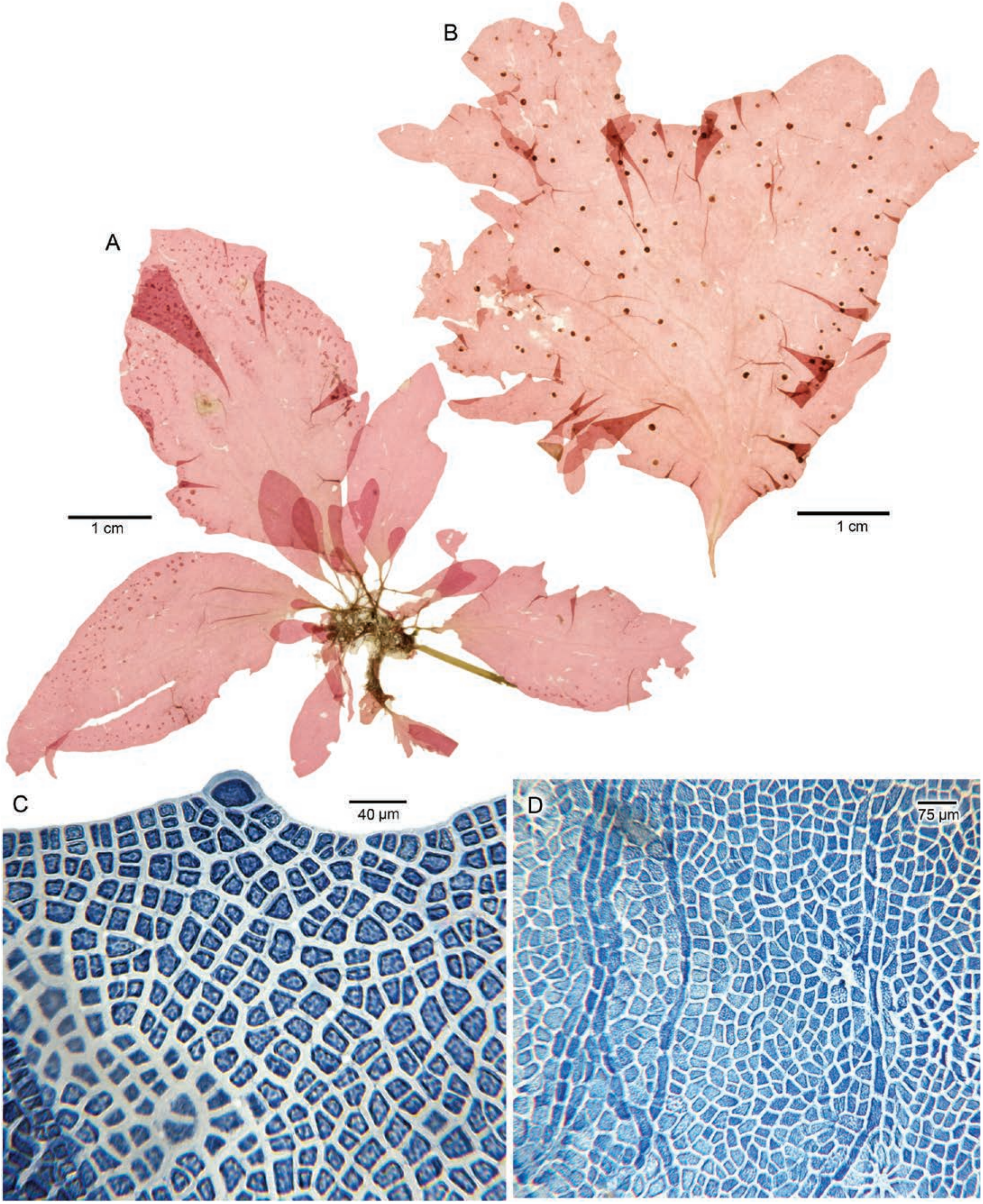
Schizoseris Kylin, 1924:67.

Blades erect, simple, lobed, irregularly divided or laciniate, arising from a stipe. Blades are branched in 1 plane. Macroscopic veins are present, basal and simple, or subdichotomously branched and extending through most of blade but are not percurrent and do not reach the thallus margins. Macroscopic veins increase in thickness with age; microscopic veins are absent. Growth is diffuse, from marginal and intercalary meristems. Thalli are initially and primarily monostromatic and may become polystromatic in basal areas, stipes, and the macroscopic veins. In surface view, blades are an irregular mixture of cells of various shapes and sizes, a result of intercalary cell divisions.

Tetrasporangial sori are small and discrete or can become confluent, forming large sori. Tetrasporangia are tetrahedrally divided, borne in 2 layers, primarily originating from subsurface cortical cells. Gametophytes are usually dioecious. Procarps are formed singly, with 2 sterile groups (each composed of 1–2 cells), off a 4-celled, strongly curved, carpogonial branch. Cystocarps are borne near blade margins, with extensive branched fusion cell, pericarp 4–6 cell layers thick, with an ostiole. Carposporangia are borne in simple or branched chains. Spermatangial sori are produced in both monostromatic and polystromatic areas of the blade, with spermatangia cut off from cortical cell initials on both sides of the blade.

One species of *Schizoseris* is known in the northern Gulf of California.

FIGURE 112. (Opposite) *Polyneurella hancockii*: A. Habit, small group of blades with barely visible longitudinal veins, and tetrasporangial sori (*JN-4720*, US Alg. Coll.-217356). B. Cystocarps scattered over blade, veins discernable to some extent (*JN-4727*, US Alg. Coll.-217357). C. Apex of blade with an apical cell (*JN-4725*, US Alg. Coll. microscope slide 5283). D. Slender longitudinal veins in blade (US Alg. Coll. microscope slide 5285).


B
A
1 cm
1 cm
C
40 µm
D
75 µm

Schizoseris pygmaea E. Y. Dawson

FIGURE 113

Schizoseris pygmaea E. Y. Dawson, 1950b:157, figs. 16, 17; 1959a:29; 1961b:445; 1962a:80, pl. 35: figs. 3, 4; 1966a:28; Dawson and Neushul, 1966:183 [with a query]; Stewart and Stewart, 1984:146; González-González et al., 1996:252; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468.

Myriogramme bombayensis sensu Pacheco-Ruíz et al., 2008:212 [non *Myriogramme bombayensis* Børgesen, 1931:23, which is now *Schizoseris bombayensis* (Børgesen) S.-M. Lin, 2002:39; =*Schizoseris bombayensis* (Børgesen) Womersley, 2003:112, *nom. illeg.*)].

Blades erect, membranous, small, up to 2(–3) cm tall and 2.5–3.5 mm wide, with short, terete, stipe-like portions at base of blades. Stipes thickness extends into blade as conspicuous broad midvein, to about 200 μm wide, and divides subdichotomously; midveins gradually tapering, not extending to blade tips or margins. Vegetative blades monostromatic apart from polystromatic midveins and stipes. New blades can develop along stipe or on short "secondary" stipes from the macroscopic veins in basal portion of a blade. Blades orangish brown, simple or lobed to sparsely irregularly subdichotomously divided. Tips of blades rounded, margins entire, smooth to ruffled. Tufts of rhizoids can grow out from blade margins for secondary attachment. In surface view, cells of blade of various shapes, 6.0–12 μm in diameter.

Tetrasporangial sori typically a single broadly rounded patch in middle and distal portions of a blade, covering most of the blade's width.

HABITAT. On rock and epizoic on sponges; low intertidal to shallow subtidal, 0.75–2.0 m depths.

DISTRIBUTION. Gulf of California: Playa Tucson and Playa Las Conches (Playa Estación), Puerto Peñasco to Puertecitos; Isla la Ventana (Bahía de Los Ángeles); Isla Partida Norte; Isla San Pedro Nolasco; Bahía Agua Verde to Isla Cholla (off northern end of Isla Carmén). Eastern Pacific: California Channel Islands to Punta Eugenia ("San Eugenio"); Bahía Sebastián Vizcaíno, Baja California Sur; Isla Guadalupe. Western Pacific: Korea (Y.-P. Lee and Kang, 2001).

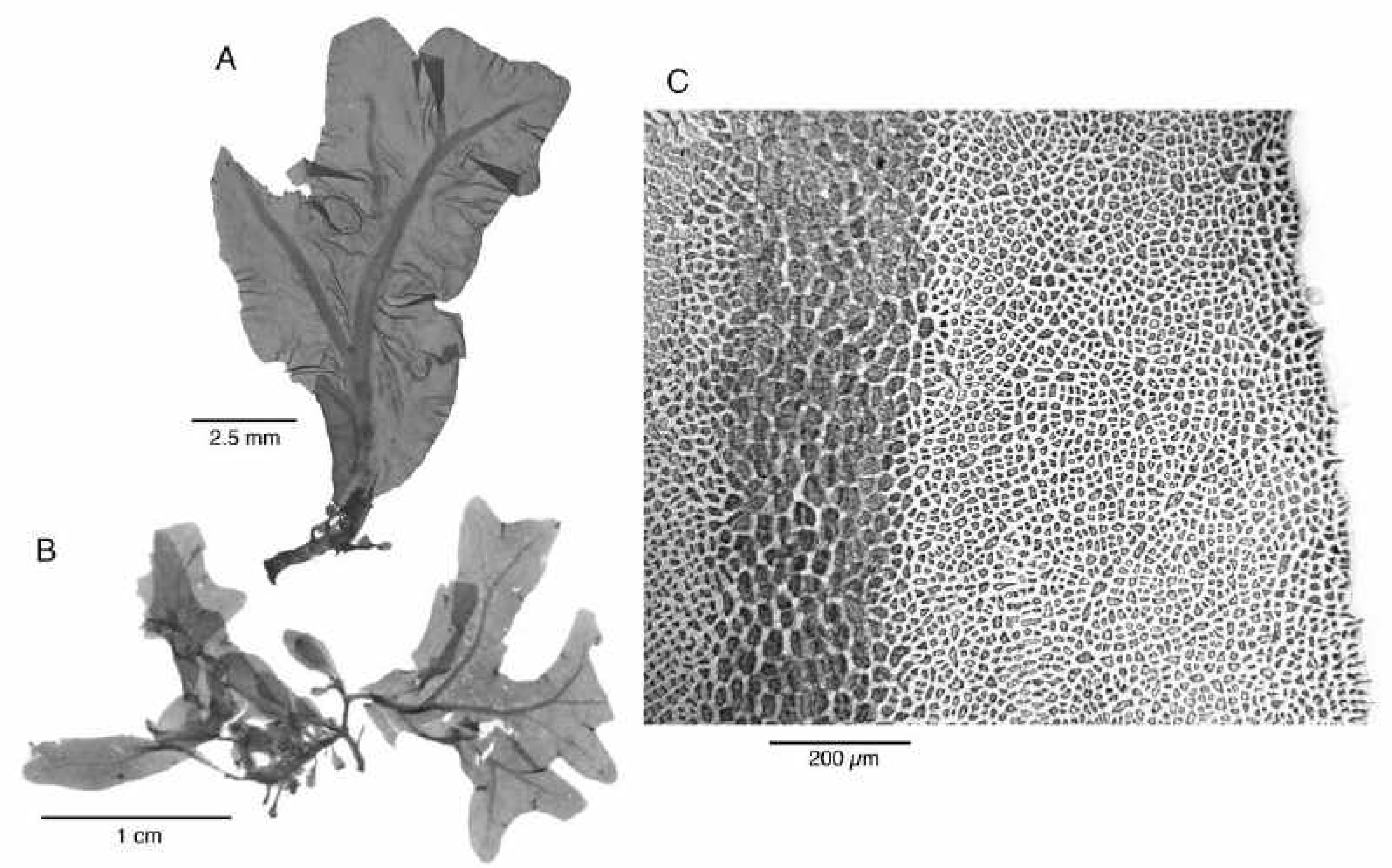


FIGURE 113. *Schizoseris pygmaea*: A. Blade with subdichotomously branching midvein (*JN-3823*, US Alg. Coll. microscope slide 5282). B. Habit (*JN-3823*, US Alg. Coll.-160889). C. Close-up of polystromatic midrib region and monostromatic blade, with cells of various sizes and shapes, the result of intercalary cell divisions (*JN-3902*, US Alg. Coll. microscope slide 5286).

Type Locality. Intertidal rocks; Isla Partida Norte, Islas de la Cintura, Gulf of California, Mexico.

Remarks. *Schizoseris pygmaea* is apparently rare but occurs sparsely at scattered localities in the Gulf of California. Noting a lack of female material, Dawson (1959a) commented that on the basis of vegetative morphology it was similar to the Japanese *Myriogramme subdichotoma* Segawa (1941; now *Schizoseris subdichotoma* (Sewaga) Yamada, 1944; =*Schizoseris minima* Kaneko et Masaki, 1973), but Dawson (1962a) later observed that *S. pygmaea* differed in its less extensive dichotomy and its large, usually solitary, tetrasporangial sori. Following Segawa (1941), Dawson (1959a) also noted its resemblance to *Myriogramme bombayensis* Børgesen (1931), and later Abbott (1999) tentatively placed *S. pygmaea* in synonymy with *M. bombayensis* (see also Millar and Kraft, 1993; Wynne, 2014). Lin (2002) and Womersley (2003) thought features of *M. bombayensis* better fit the genus S*chizoseris* with the earliest combination being *S. bombayensis* (Børgesen) S.-M. Lin.

Although observing similarities to the Gulf of California *Schizoseris pygmaea*, Dawson and Neushul (1966) tentatively referred their Anacapa Island (California Channel Islands) specimens to *S. pygmaea* but noted they were probably an undescribed species. Until reproductive gametophytes are found and described for Gulf of California *S. pygmaea* (especially from the type locality), and it can be tested by comparative morphology and molecular analyses with other taxa, including *S. bombayensis*, the Gulf specimens are retained as *Schizoseris pygmaea*.

***Sorella* Hollenberg**

Sorella Hollenberg, 1943:577.

Algae erect, small membranous fronds that are uniformly narrow and much branched (up to 4–8 orders) from the blade margins. Some of lowermost basal branches are more or less prostrate, attaching the frond by hapterous bundles of rhizoids produced adventitiously near blade margins. Axes and branches are slender, generally of similar width and with smooth margins, monostromatic, except in the inconspicuous midrib regions, and lack lateral veins. Apical cells are prominent, and intercalary divisions occur in primary cell row; secondary and tertiary cell rows indistinct.

Tetrasporangial sori are oval and typically singular in the center of blades, most developing near the apices. Cystocarps are found on 1 side of the midrib, with an ostiole. Spermatangia are in oval to oblong sori, single or in pairs toward the distal region of branches.

Two species of *Sorella* are reported in the northern Gulf of California.

KEY TO THE SPECIES OF *SORELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Narrow fronds, 0.2–0.5(–0.6) mm wide; repeatedly dichotomously to subdichotomously branched, up to 8 orders, with comparatively long intervals between branches . . . . **S. delicatula**

1b. Fronds generally broader, mostly (0.5–)0.8–2.0 mm wide; pinnately branched, up to 4 orders . . . . **S. pinnata**

***Sorella delicatula* (N. L. Gardner) Hollenberg**

Erythroglossum delicatulum N. L. Gardner, 1926:208, pl. 18.

Sorella delicatula (N. L. Gardner) Hollenberg, 1943:577; Dawson, 1961b:446; 1962a:83, pl. 34: fig. 2; Dawson and Neushul, 1966:183; Abbott and Hollenberg, 1976:648, fig. 591; Stewart and Stewart, 1984:146; Stewart, 1991:149, fig. 14; González-González et al., 1996:270; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:212, fig. 102.

Sorella delicatula var. *californica* Hollenberg, 1943:577, figs. 13, 14; Dawson, 1961b:446; Stewart, 1977:5–15, fig. 1A–C,F; Pacheco-Ruíz and Zertuche-González, 2002:468.

Erythroglossum divaricatum Setchell et N. L. Gardner in Gardner, 1926:207, pl. 17: fig. 2; Smith, 1944:340, pl. 87: fig. 7.

Sorella divaricata (Setchell et N. L. Gardner) Hollenberg, 1943:578; Dawson, 1961b:446; Hollenberg and Abbott, 1966:105.

Erythroglossum californicum sensu Dawson, 1962a:93 [in part; Isla Magdalena specimens only; see Abbott and Hollenberg, 1976:648; non *Erythroglossum californicum* (J. Agardh) J. Agardh, 1898:176; basionym: *Delesseria californica* J. Agardh, 1885:69].

Blades mostly 1–2(–10) cm tall; of delicate, narrow, ribbon-like axes and branches, 200–500(–600) µm wide, mostly with entire margins; dichotomous to subdichotomously branched, up to 8 orders; relatively long intervals between branches. Blades monostromatic, with an inconspicuous, polystromatic midrib (distinct with magnification).

Tetrasporangia in more or less oval sori, 200–400 µm wide; sori solitary in upper portion of branches toward the tips. Cystocarps 400–450 µm in diameter (nearly the entire width of the blade). Spermatangia in irregular oval sori near branch apices.

Habitat. On rocks or in tidal channels; also reported to be occasionally epiphytic on other red algae or epizoic on worm tubes or sponges (Stewart, 1991); low intertidal to shallow subtidal, down to 20 m depths.

Distribution. Gulf of California: Isla Coronado (Isla Smith), Bahía de Los Ángeles. Eastern Pacific: Santa Cruz to San Diego, California; California Channel Islands; Isla Coronado Norte (Islas Los Coronados), and Isla Guadalupe off northern Baja California; Isla Magdalena (NNW side of Bahía Magdalena), Baja California Sur. Western Pacific: Japan.

Type Locality. Cast ashore; San Pedro, Los Angeles County, southern California, USA.

***Sorella pinnata* Hollenberg**

FIGURE 114

Sorella pinnata Hollenberg, 1943:578, figs. 15, 16; Dawson, 1944a:321, pl. 47: figs. 3, 4; 1951:53; 1961b:446; 1962a:84, pl. 38: fig. 1; pl. 40: fig. 6; Dawson and Neushul, 1966:183; Abbott and Hollenberg, 1976:650, fig. 592; Stewart, 1977:5–15, fig. 1D, E, G; 1991:150, fig.

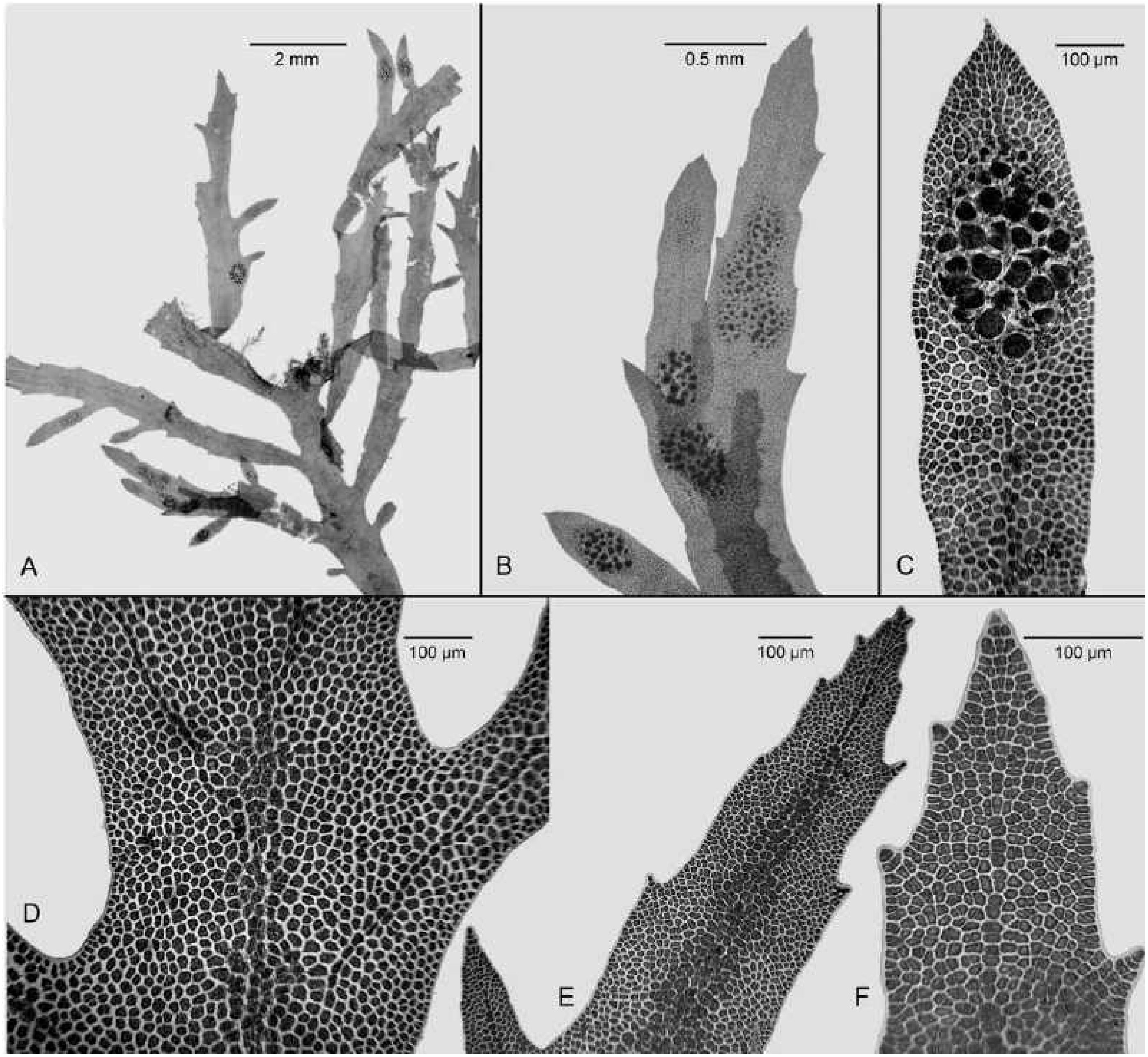


FIGURE 114. *Sorella pinnata:* A. Branching habit, median tetrasporangial sori mostly in distal regions. B. Median tetrasporangial sori. C. Tetrasporangial sorus covering distal and central portion of blade (A–C, *JN-4749*, US Alg. Coll. microscope slide 4642). D. Portion of blade showing midrib of main axis and developing midribs of branches (*JN-5154*, US Alg. Coll. microscope slide 4643). E. Upper portion of blade showing monostromatic blade with thickened midrib region (*JN-3131*, US Alg. Coll. microscope slide 4645). F. Upper portion of blade with conspicuous apical cells and developing midrib (*JN-5154*, US Alg. Coll. microscope slide 4643).

14; González-González et al., 1996:270; Pacheco-Ruíz et al., 2008:212; Wynne, 2014:213.

Blades small, semierect to partly repent, mostly 1–2(–7) cm tall and (0.5–)0.8–2.0(–3.5) mm wide, peach to rose pink in color; of thin, lanceolate blades, pinnately branched from margins, up to 3(–4) orders. Blades monostromatic, except for basal portions and indistinct midribs (distinct under magnification); attached by filamentous rhizoids that develop in groups along blade margin where in contact with substrate. Growth from an apical cell, primary cell row with intercalary cell divisions. Blades with smooth margins, except for protruding apical cells (branch initials), giving a widely spaced, dentate appearance under a microscope (Figure 114B, E). Blades usually tapering to acute tip with apical cell.

Tetrasporangial sori oval, 300–600(–800) µm long, mostly 200–300 µm wide; single in middle of blades near apices; tetrasporangia about 45–50 µm in diameter. Cystocarps 400–500 µm in diameter, with an ostiole; on one side of midrib. Spermatangia in oblong sori; mostly in pairs, one to each side of midrib region; often several pairs of sori on one branch.

Habitat. On rocks; shallow subtidal, down to 20 m depths.

Distribution. Gulf of California: Rocas Consag; Puerto Libertad to Guaymas; Puerto Refugio, Isla Ángel de la Guarda. Eastern Pacific: Laguna Beach to Cortez Bank, California Channel Islands (about 188 km west of San Diego, 82 km SW of San Clemente Island), southern California; Islas San Benito and Isla Cedros, Baja California.

Type Locality. On intertidal rocks; Laguna Beach, Orange County, southern California, USA.

Taenioma J. Agardh

Taenioma J. Agardh, 1863:1256.

Thalli are small, often growing in turf-like mats, with erect and prostrate portions and determinate and indeterminate branches. Thalli uniaxial in structure with growth of branches from a single apical cell, branching exogenous at branch apices, often endogenous or adventitious below. Primary prostrate axes are terete (to compressed), ecorticate, rhizomatous, and spreading, attached to substrate by uniseriate rhizoids. Prostrate axes give rise to erect and ascending tufted branch systems composed of secondary axes with determinate flattened laterals. These secondary axes are terete to compressed and bear both additional axes and erect, alternately or radially arranged determinate flattened laterals. The determinate flattened laterals are monostromatic blades, except for their polystromatic midrib (3 cells thick). Midrib with axial cells each surrounded by 4 pericentral cells. The lateral pericentral cells of determinate blades each issue 2 flanking cells, which remain undivided or in some species divide to form 2–3 (or more) cell chains (monostromatic). Apices of determinate blades nearing maturity typically terminate in 0–5 (or more) persistent, unpigmented, unbranched multicellular "hairs" (filaments), each with a meristem at its base.

Tetrasporangia are tetrahedrally divided and produced in a single layer, 2 per segment, forming 2 longitudinal rows along sides of the midrib of determinate blades. Tetrasporangia are issued 1 per fertile lateral pericentral cell, before the rudimentary cover cells are formed. Gametophytes are usually dioecious, but fertile specimens are apparently rarely encountered. Procarps and cystocarps are borne on indeterminate axes. Procarps composed of a 4-celled carpogonial branch and 2 sterile-cell groups. Cystocarps have a basal fusion cell and carposporangia in short chains enclosed in an urceolate pericarp with ostiole. Spermatangia are borne in sori on both surfaces of determinate blades between midrib and blade margin.

One species of *Taenioma* is known in the northern Gulf of California.

Taenioma perpusillum (J. Agardh) J. Agardh

FIGURE 115

Polysiphonia perpusilla J. Agardh, 1847:16.

Taenioma perpusillum (J. Agardh) J. Agardh, 1863:1257; Okamura, 1930:26, pl. 264: figs. 17–19, pl. 265: figs. 5–9; Dawson, 1944a:324; Tseng, 1944:223, pl. 25: figs. 1–6; Papenfuss, 1944b:193, pl. 23: figs. 1–4, pl. 24: figs. 5–16; Dawson, 1962a:82, pl. 37: fig. 1, pl. 47: fig. 3; Papenfuss, 1964a:159, figs. 1–10; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Santelices and Abbott, 1987:9; Ramírez and Santelices, 1991:358; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:326, 408; Yoshida, 1998:997; Abbott, 1999:348 [in part; not including *Taenioma dotyi* Hollenberg, 1967:1202, fig. 101C]; CONANP, 2002:138; Zheng et al., 2001:134, fig. 81(1–6) ; Abbott et al., 2002:314, figs. 28–29; Pacheco-Ruíz et al., 2008:212; Fernández-García et al., 2011:65; Wynne, 2014:74, fig. 35.

Thalli short, to 3 mm high, with creeping, terete indeterminate axes, 65–90(–200) µm in diameter, and erect and ascending branches. Prostrate axes polysiphonous, with 4 pericentral cells, attached to the substrate by long nonseptate rhizoids issued from ventral pericentral cells. Indeterminate prostrate axes bear terete secondary axes that bear both additional indeterminate axes and are abundantly alternately branched with determinate flat blade-like laterals. The determinate branches start off terete for several segments, then flatten above as lateral pericentral cells each give rise to 2 flanking cells, each about half the length of a pericentral cell, forming the monostromatic "wings" of the blade. Determinate blades unbranched, composed of a midrib (three cells thick, the axial filament with 2 transverse pericentral cells above and below), lateral pericentrals, and flanking cells along blade margins. Determinate blades up to 1 mm long and usually 5 cells across (to 100 µm wide). Up to 3 persistent unpigmented, uniseriate filaments ("hairs") develop terminally on most determinate blades near maturity; these apical filaments each have a basal meristem with elongated cells above.

Tetrasporangia in a single layer, in consecutive segments forming 2 longitudinal rows of tetrasporangia, on both sides of the midrib of determinate blades. A single tetrasporangium arises from a fertile lateral pericentral cell, and later 2 small rudimentary cover cells are cut off. Gametophytes unknown in Gulf material (apparently rarely encountered elsewhere). Gametophytes reported elsewhere usually dioecious (Papenfuss, 1964a). Procarps usually solitary on erect terete secondary axes (Papenfuss, 1964a; Abbott, 1999). Cystocarps urceolate and ostiolate. Spermatangia borne on determinate blades.

Habitat. On rocks, entangled or epiphytic on other algae, or in algal turfs; mid to low intertidal.

Distribution. Gulf of California: Bahía de San Luis Gonzága; Isla Tiburón to Topolobampo; Sinaloa to Jalisco. Eastern Pacific: Golfo de Tehuantepec, Oaxaca; El Salvador; Panama; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: China; Korea; Japan; Vietnam.

Type Locality. San Agustín (San Augustin), "presumably in the Isthmus of Tehuantepec along the coast of Oaxaca" (Dawson, 1962a:83), Pacific Mexico.

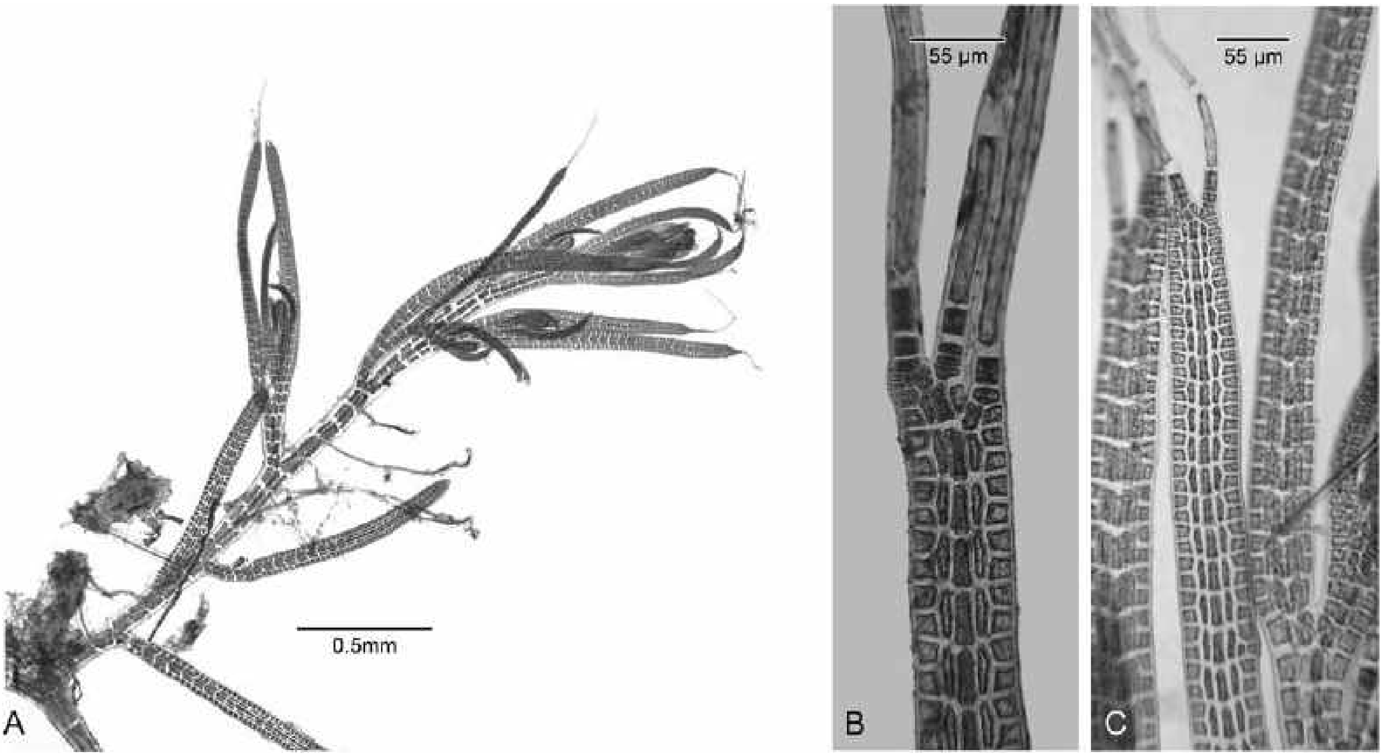


FIGURE 115. *Taenioma perpusillum*: A. Habit showing creeping indeterminate terete axes giving rise to determinate flat blades and additional indeterminate axes. B, C. Upper portions of mature determinate blades with 2–3 monosiphonous "hairs" at their tips (A, C, *EYD-10891*, US Alg. Coll. microscope slide 569; B. *EYD-10908*, US Alg. Coll. microscope slide 570).

REMARKS. *Taenioma perpusillum* is reported to be widespread in tropical and subtropical seas and into temperate regions. Apparently, *T. perpusillum* is rare or uncommon in the northern Gulf; probably because of its small size and usual entanglement with other algae, it may be easily overlooked. C. F. Puttock (National Museum of Natural History, Department of Botany, personal communication) observed there is likely more than one species included within the *T. perpusillum* complex.

SARCOMENIACEAE

Sarcomeniaceae Womersley, 2003:148–150.

Algae are erect, cylindrical or compressed, branched thalli. The apical cell is prominent, with axial filament cells cutting off four pericentral cells, two transverse pericentral cells and two slightly larger lateral pericentral cells. The lateral pericentral cells each cut off two flanking cells that are about half the length of a pericentral cell. The flanking cells produce additional rows of cells in some genera. Intercalary divisions are absent in primary cell rows. Branching is endogenous.

Tetrasporangia are cut off from the lateral pericentral cells in two longitudinal rows, forming in a single layer, with post-sporangial cover cells. Gametophytes are dioecious. Procarps are borne on the transverse pericentral cells. The carpogonial branch is four-celled with two groups of sterile cells. Carposporophytes have a basal fusion cell and branched gonimoblasts that bear clavate carposporangia terminally. Cystocarps protruding from blade; ovoid to urceolate, with post-fertilization pericarp and ostiole. Spermatangia are borne in sori on surface of blades.

The Sarcomeniaceae is represented by one genus in the northern Gulf of California.

Platysiphonia Børgesen

Platysiphonia Børgesen, 1931:28.

Thalli of erect, branched, blades and prostrate portions that are morphologically similar in structure and width. Blades are delicate, narrow, flattened, and monostromatic, apart from the midrib, and taper to a single apical cell at apices. Intercalary cell divisions absent. Midrib is percurrent with 4 pericentral cells. Endogenous branches usually arise from the midline of a parent blade. Lateral pericentral cells issue flanking cells, and in some species these produce flanking cell derivatives that increase the number of cells and width of the blades. Blades are ecorticate in some species but heavily corticated in others. All vegetative axes are potentially indeterminate. Monosiphonous filaments are absent.

Tetrasporangia are produced in stichidium-like ultimate blades, in a single layer, and paired, each fertile lateral pericentral cell cutting off a tetrasporangium, subsequently forming 2 longitudinal rows, with sterile cells lining blade margins. Gametophytes are dioecious. Procarps and cystocarps are restricted to midline of fertile blades, carposporangia terminal. Spermatangial blades have sterile bases and tips and sterile transverse pericentral cells and cells along margins. Spermatangia formed mostly from lateral pericentral cells.

There is one species of *Platysiphonia* known in the northern Gulf of California.

Platysiphonia decumbens M. J. Wynne

FIGURE 116

Platysiphonia decumbens M. J. Wynne, 1969:190, figs. 1–36; Abbott and Hollenberg, 1976:644, fig. 585; Scagel et al., 1989:225; Stewart, 1991:148, fig. 13 [left illustration]; Wynne, 2014:240, figs. 116b–c (type collection).

Platysiphonia clevelandii sensu Dawson, 1966b:66; González-González et al., 1996:248 [in part]; Pacheco-Ruíz et al., 2008:212 [non *Platysiphonia clevelandii* (Farlow) Papenfuss, 1944a:206; basionym: *Taenioma clevelandii* Farlow, 1877:236].

Thalli small, usually less than 2 cm high, with both erect and prostrate portions. Blades slender, ribbon-like, usually to 7 cells wide (200–400 µm wide). Blades taper to an acute apex, and growth is from a single apical cell, midribs with central axial cell surrounded by 4 pericentral cells, the midline is 3 cells thick (axial cell and a transverse pericentral cell above and below), blades monostromatic away from the midline. Blades flat, ecorticate, the lateral pericentral cells cut off flanking cells, each of which cuts off flanking cell derivatives that form the blade's margin and are laterally elongated. Attachment rhizoids develop from several contiguous marginal cells, and abutting flanking cells also sometimes involved in producing a holdfast. Branches originating at irregular intervals from midrib of parent blade, only from the adaxial surface. Branch blades more slender at attachment point as the lowest several segments may be missing flanking cells and flanking cell derivatives. Erect branches may later become prostrate by developing marginal rhizoids and attaching to substrate or host.

Reproduction not seen in Gulf material. Tetrasporangia cruciately divided, borne in single cell layer in short, stichidium-like ultimate blades. Each lateral pericentral cell producing a single tetrasporangium with a cover cell; 2 in each segment, resulting in

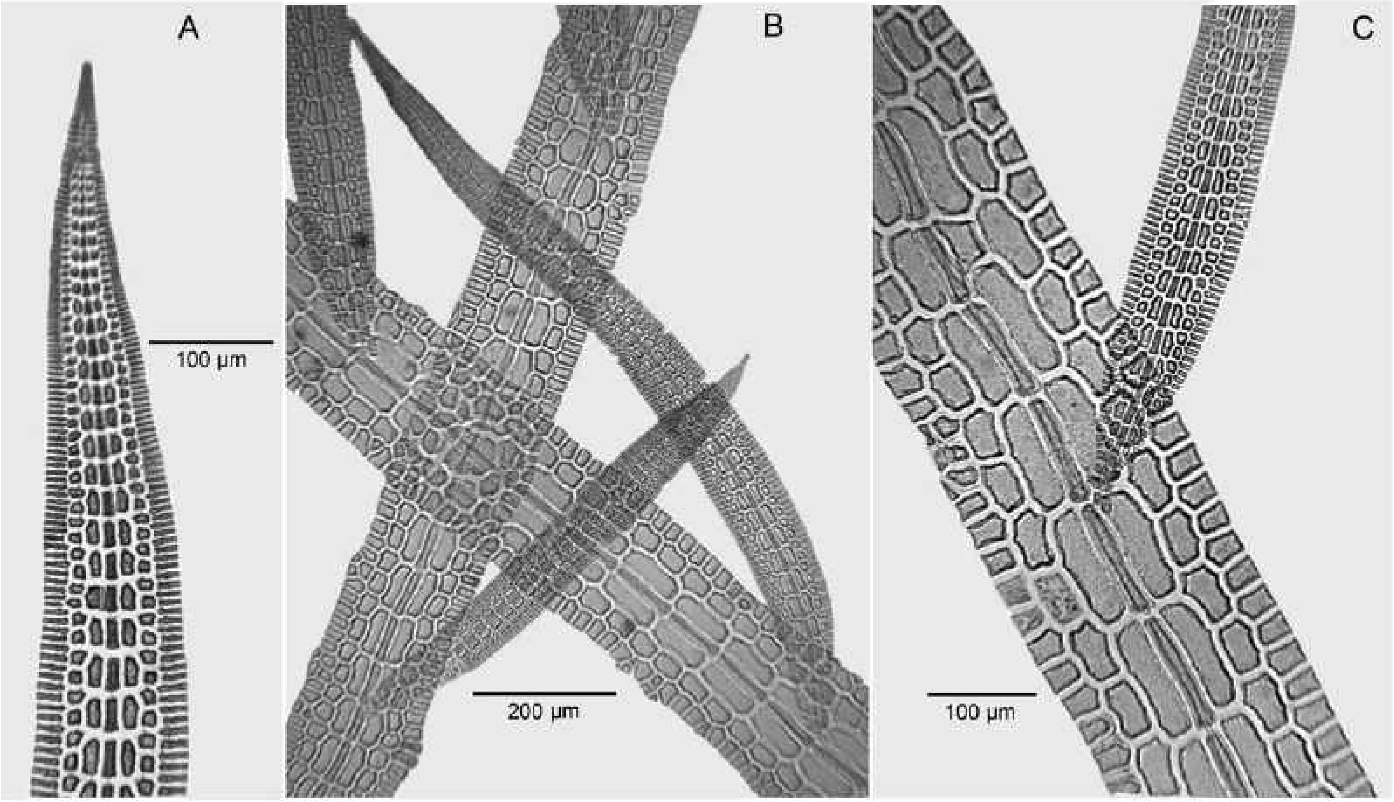


FIGURE 116. *Platysiphonia decumbens*: A. Surface view of blade apex of specimen from the northern Gulf of California (*JN-5324*, US Alg. Coll. microscope slide 5290). B, C. Blades 7 cells wide, new blades originating from midrib of parent blade (specimen from the southern Gulf ; *EYD-26116*, US Alg. Coll. microscope slide 794).

2 paired longitudinal rows, bordered by sterile cells along blade edges (after Wynne, 1969).

HABITAT. Often epiphytic or entangled on larger algae or growing on hard substratum; low intertidal to subtidal, 8–16 m depths (Dawson, 1966b, as "*P. clevelandii*").

DISTRIBUTION. Gulf of California: Isla Ángel de la Guarda; Isla Las Ánimas (Isla San Lorenzo del Norte). Eastern Pacific: southern Alaska to northern Baja California.

TYPE LOCALITY. West Beach, Whidbey ("Whidby") Island, Island County, Puget Sound, Washington, USA.

REMARKS. *Platysiphonia decumbens* was described from the cool, temperate waters of Whidbey Island, Washington. It was surprising to find it in the warmer waters of the northern Gulf (Norris, 2010). In Pacific Mexico, *P. decumbens* from Isla Guadalupe (Stewart and Stewart, 1984) and northern Baja California (Dawson, 1962a) can also occur with *P. clevelandii* (Farlow) Papenfuss (1944a) and *P. parva* P. C. Silva et Cleary (1954).

RHODOMELACEAE

Rhodomelaceae Areschoug, 1847:260.

Thalli are usually erect or partially to entirely prostrate and may be terete, compressed, or flat and sparsely to abundantly branched. All species are polysiphonous and either ecorticate or faintly to fully corticated. Growth is uniaxial from large apical cells. Two or more pericentral cells are cut off in an alternating sequence around each central axial cell. Erect species have branches of similar structure or indeterminate branches and determinate branches of limited growth with different structures. Apices are radially or dorsiventrally organized. Monosiphonous trichoblasts, commonly present in certain genera, are branched or unbranched and colorless in most genera, but in a few they can be pigmented.

Tetrasporangia are generally tetrahedrally divided and are usually developed from pericentral cells or, in a few, from the outer cortical cells. Tetrasporangia borne in specialized branchlets, stichidia, or within main axes or lateral branches, and may be (1) one per segment, sometimes in a series in a straight row or spirally arranged; (2) two per segment and distichously or decussately arranged; or (3) 4–6 per segment when verticillate in arrangement. Gametophytes are usually dioecious. Gametangia in many are developed from or usually associated with the trichoblasts. Procarps borne on lower cells of trichoblast or directly on thallus branches. Cystocarps are prominent, with carposporangia in short chains and an ostiolate pericarp. Spermatangia may be borne in modified trichoblasts or replace a whole trichoblast; in discoid plate-like structures with sterile marginal cells, usually near apices; on special spermatangial branchlets; or less frequently on ordinary axes and branches.

Fifteen genera of the family Rhodomelaceae are represented in the northern Gulf of California.

KEY TO THE GENERA OF RHODOMELACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Algae flattened, mostly prostrate, lobed blades; composed of polysiphonous branches congenitally fused to adjacent branches to form blades . . . . **Amplisiphonia**

1b. Algae not a membranous blade; thalli terete, compressed, or flattened; erect or partly prostrate axes with at least some erect branches; polysiphonous axes not congenitally fused (or only 1 to few basal segments of laterals fused) 2

2a. Thallus polysiphonous, not corticated throughout; segments of pericentral cells easily seen below the apices 3

2b. Thallus either polysiphonous and partly to entirely corticated, obscuring segments of pericentral cells below apex; or terete to flattened with a pseudoparenchymatous medulla and cortex 10

3a. Pericentral cells divided transversely to form 2 tiers of cells within the length of a single axial filament cell; growing in brackish water . . . . **Bostrychia**

3b. Pericentral cells not transversely divided, same length as axial filament cell they surround; growing in marine waters . . . 4

4a. Thallus with pigmented trichoblasts (ultimate monosiphonous branchlets) . . . . **Veleroa**

4b. Thallus without trichoblasts (ultimate monosiphonous branchlets), or if present, trichoblasts unpigmented (colorless) 5

5a. Thalli radially or spirally arranged 6

5b. Thalli either bilaterally arranged (at least in older portions) or dorsiventrally arranged 7

6a. Trichoblasts rare or absent; rhizoids (nonseptate) remaining open in connection with bearing pericentral cell; spermatangial branches arising from lateral branch initials without trichoblasts; tetrasporangia arranged in straight series; carpogonial branch 4-celled . . . . **Polysiphonia**

6b. Trichoblasts abundant; rhizoids separated from bearing pericentral cells by a cell wall (pit-connected); spermatangial branches on a branch of a trichoblast; tetrasporangia in a spiral series; carpogonial branch 3-celled . . . . . **Neosiphonia**

7a. Determinate and indeterminate laterals in regular defined sequence; axes with 3 simple determinate laterals between each indeterminate compound lateral; primary indeterminate axis prostrate . . . . **Herposiphonia**

7b. Determinate and indeterminate laterals not arranged in regular defined sequence; primary indeterminate axis not prostrate 8

8a. Branch segments at base of lateral branches with little or no fusion (coalescing) with the bearing axis . . . . . **Tayloriella**

8b. Branch segments at base of lateral branches fused (coalescing) with bearing axis for 1 to a few segments 9

9a. Distichous branching; determinate laterals alternate, with 2–4 axial segments between them; trichoblasts absent on nonreproductive thalli . . . . *Pterosiphonia*
9b. Determinate laterals initially multifariously arranged at tips of erect axes, then becoming more distichous below; trichoblasts few to common on nonreproductive thalli . . . . *Pterosiphoniella*
10a. Axes and branches, usually densely surrounded by short, stiff, simple corticated branchlets . . . . *Digenea*
10b. Axes not as above; without numerous, dense stiff lateral branchlets 11
11a. Spermatangial structure a flat, oval disc, with a margin of sterile cells; borne on trichoblast; in cross section of axes, 5 pericentral cells and central axial cell discernible in most species . . . . *Chondria*
11b. Spermatangial structure not discoid or plate-like; in cross section of axes, central axial cell and pericentral cells only clearly discernible near apices 12
12a. Thalli of species in Gulf compressed to flattened, tetrasporangia develop from random epidermal cells; filament-type spermatangial development . . . . *Osmundea*
12b. Thalli terete to only slightly compressed, tetrasporangia produced from specific pericentral cells; trichoblast-type spermatangial development 13
13a. Vegetative segments with axial cell bearing 2 pericentral cells 14
13b. Vegetative segments with axial cell bearing 4 pericentral cells . . . . *Laurencia*
14a. Tetrasporangial axial segments in first and second pericentral cells sterile, and additional fertile pericentral cells issued to produce tetrasporangia . . . . *Chondrophycus*
14b. Outer cortical cells longitudinally elongated, and in a distinctive palisade-like arrangement in transection; in tetrasporangial axial segments only first pericentral cell is sterile, second is fertile with an additional third fertile pericentral cell to produce tetrasporangia . . . . *Palisada*

RHODOMELACEAE TRIBUS BOSTRYCHIEAE

Rhodomelaceae tribus Bostrychieae Falkenberg, 1901:504.

REMARKS. Phylogenetic analyses of Zuccarello and West (2006: fig. 2) found the Baja California Sur *Bostrychia radicans* grouped with others within the "Cladohapteron clade" of the subfamily Bostrychioideae. Further, their analyses did not support continued recognition of two genera within the tribe, with *Stictosiphonia* J. D. Hooker et Harvey (in Harvey and Hooker, 1847:483; King and Puttock, 1989) being considered congeneric with *Bostrychia*.

The tribe is represented by one genus, *Bostrychia*, in the Gulf of California. It usually occurs in brackish water habitats with some freshwater influences.

Bostrychia Montagne

Bostrychia Montagne, 1842b:39; Montagne, 1842c:600.

Stictosiphonia J. D. Hooker et Harvey in Harvey and Hooker, 1847:483; Zuccarello and West, 2006:31.

Algae are dorsiventrally organized, with narrow terete to compressed polysiphonous axes and branches that usually form dense turfs, clumps, patches, or spreading mats. They are often epiphytic on mangroves or other aquatic vegetation, entangled with other algae, or may grow on hard or soft substrata. Thalli are composed of prostrate and erect indeterminate polysiphonous axes and branches of 4–10 pericentral cells that are uncorticated or corticated by up to 5 layers of cortical cells. Each pericentral cell transversely divides into 2–5 tiers, with the basal cell pit connected to the axial cell. Prostrate axes give rise to creeping or erect lateral branches alternately to irregularly arranged and attached by bundles of rhizoids developed from pericentral or cortical cells (peripherohaptera), or by terminal rhizoidal haptera on specialized branches (cladohaptera). Branches are simple or branched up to 3(–4) orders. Trichoblasts are absent. Ultimate branches may be entirely or partly monosiphonous.

Tetrasporangia tetrahedrally divided, borne 2–6 per segment in polysiphonous branches or in stichidia up to 25 segments in length. Gametophytes are usually dioecious, but some may be monoecious. Procarps develop in a series of 1–4 per segment on polysiphonous determinate branches. Each procarp is a single sterile group and a 3– to 4–celled carpogonial branch. Carposporophytes are sessile and usually borne 1–2 per branch, with a short, branched gonimoblast that bears terminal carposporangia within ovoid to subspherical pericarp. Spermatangia are superficial on determinate laterals that lack or may have sterile tips.

REMARKS. West et al. (2013) noted that the taxonomy and molecular phylogeny of *Bostrychia*, while well studied, is not yet completely resolved. One species, *Bostrychia moritziana* (Sonder ex Kützing) J. Agardh (1863; including *B. radicans* f. *moniliforme* E. Post, 1936, as a synonym), has been reported in the southern Gulf of California from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985), from Nayarit and Jalisco (Dawson, 1963b; Serviere-Zaragoza et al., 1993a), and in Pacific Mexico from Chiapas (Dreckmann et al., 2006).

One species of *Bostrychia* is known in the northern Gulf of California.

Bostrychia radicans (Montagne) Montagne

Rhodomela radicans Montagne, 1840:198, pl. 5: fig. 3.

Bostrychia radicans (Montagne) Montagne, 1842c:661; Kützing, 1847:4; Montagne, 1850:286; Howe, 1914:145; Post, 1936:13; Tseng, 1943:173, pl. 2: figs. 6, 7; Dawson, 1944a:336, pl. 49: figs. 3, 4; Taylor, 1945:306; Post, 1955:354, 377, pl. 15: fig. 2; Post, 1957:85; Dawson, 1957c:23; 1961b:451; 1963b:419, pl. 136: fig. 3; Dawson et al., 1964:84, pl. 34: fig. D; Tanaka and Chihara, 1984:172, fig. 2; Huerta-Múzquiz and Mendoza-González, 1985:54; Tanaka, 1991:6, figs. 1–14; Ramírez and Santelices, 1991:359; Serviere-Zaragoza et al., 1993a:483; Pedroche et al., 1995:115; González-González et al., 1996:303, 385; Yoshida, 1998:1011, fig. 3-102M–O; Dreckmann et al., 2006:155; Zuccarello and West, 2006:26, tbl. 1, fig. 3; G.-H. Kim et al., 2008:1519; Bernecker, 2009:CD-Rom p. 66; Pérez-Estrada et al., 2012:190.

Bostrychia rivularis Harvey, 1853:57, pl. 14D; Santelices and Abbott, 1987:219; Ramírez and Santelices, 1991:360.

Algae forming dense mats, reddish brown, up to 1.5 cm tall; thallus distichously branched (somewhat feather-like appearance), with incurved apices; growing from creeping prostrate axes, 150–200 µm in diameter; attached by small trunk-like holdfasts and secondary basal branches with rhizoid-like attachments. Erect branches, 75–125 µm in diameter, uncorticated, polysiphonous, of 4–8 pericentral cells; each pericentral cell transversely divided once into 2 tiers.

Tetrasporangia in whorled series within mid to upper portions of swollen, ultimate branchlets. Gametophytes not known in the northern Gulf.

HABITAT. On mangroves (prop roots of *Rhizophora mangle* Linnaeus and pneumatophores of *Avicennia germinans* Linnaeus), other aquatic vegetation or sometimes on mud, in fresh to brackish waters of river mouths, esteros, and lagoons; intertidal to shallow water.

DISTRIBUTION. Gulf of California: Río Mayo, on north side of Yavaros (about 26 km southwest of Huatabampo, Sonora); Estero Coyote, Bahía San Ignacio (Baja California Sur); Bahía de La Paz; Nayarit to Jalisco. Eastern Pacific: Chiapas; Guatemala to El Salvador; Costa Rica to Panama; Colombia to Chile; Galápagos Islands. Western Pacific: Japan; Korea; Vietnam.

TYPE LOCALITY. Probably an estuary of the Cayenne River; near Cayenne, French Guiana.

REMARKS. *Bostrychia radicans* is widely reported in warm temperate to tropical regions. Zuccarello and West (2003) found several cryptic species within a *Bostrychia radicans–B. moritziana* species complex (Zuccarello et al., 1999), and more recently, West et al. (2013) recognized this complex to be of seven molecular lineages that were not reproductively intercompatible. Although there was considerable genetic divergence, taxonomic resolution of the species lineages remains problematic (e.g., Zuccarello and West, 2006; West et al., 2013). G.-H. Kim et al. (2008) found that using proteomic analyses of species of *Bostrychia* made it possible to discern genetic differentiation and may be a useful technique for taxonomic studies.

RHODOMELACEAE TRIBUS CHONDRIEAE

Rhodomelaceae tribus Chondrieae F. Schmitz et Falkenberg, 1897:432.

The tribe is represented by one genus in the northern Gulf of California.

Chondria C. Agardh

Chondria C. Agardh, 1817:xviii, 443.

Algae usually erect, rarely prostrate, composed of one to several axes arising from a common base. Axes are polysiphonous with 5 pericentral cells, but these are obscured from surface view by surrounding cortical layers of cells. Branches are mostly terete and irregularly and radially alternate; occasionally opposite or whorled. In those with several orders of branching, the smaller branches are reduced in diameter at their base. Apices have a terminal tuft of branched trichoblasts. Growth is from an apical cell that may be seen on or protrude from the apices or may be sunken in a terminal pit.

Tetrasporangia develop from pericentral cells and are tetrahedrally divided and formed in whorls of 1–3(–4), embedded beneath the cortical surface in the ultimate branches. Gametophytes are dioecious. Cystocarps are lateral on ultimate branches, covered by cortical layer. Spermatangial structures are generally a colorless flat disc with a sterile margin, discs borne in clusters at the branch apices (develop from trichoblasts).

REMARKS. *Chondria arcuata* Hollenberg (1945) has been reported in the southern Gulf of California from Mazátlan, Sinaloa (Mendoza-González et al., 1994), and Jalisco (Mendoza-González and Mateo-Cid, 1992), and in Pacific Mexico from Michoacán (Dreckmann et al., 1990; Sentíes-G. et al., 1990), and Oaxaca (León-Tejera et al., 1993).

Currently, three species of *Chondria* are recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *CHONDRIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Branch apices without a terminal depression; apices attenuate with protruding apical cell usually surrounded by trichoblasts; thalli usually epiphytic and iridescent . . . . *C. acrorhizophora*

1b. Apices of branches with apical cell of central axis sunken within a terminal depression from which tufts of trichoblasts may protrude 2

2a. Thalli 5–15 cm tall, mostly 500–1000 µm in diameter; irregularly alternately branched; outer cortical cells in surface view narrow-oblong and arranged in more or less longitudinal rows . . . . **C. species A**

2b. Thalli low growing, in part creeping; mostly less than 1 cm tall and 200–300(–400) µm in diameter; outer cortical cells in surface view rounded to polygonal . . . . *C. repens*

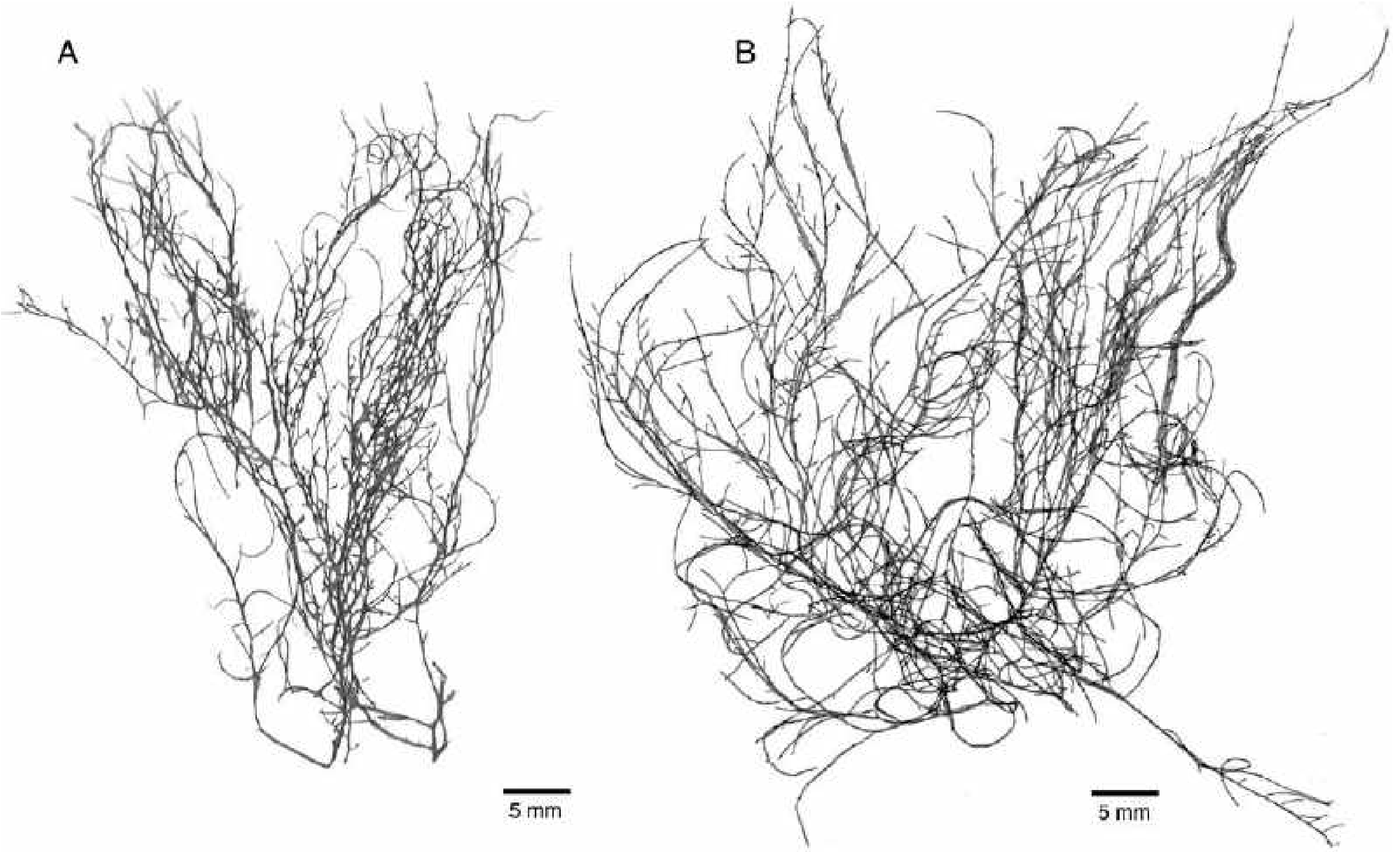


FIGURE 117. *Chondria acrorhizophora*: A. Habit of isotype (*Marchant-44*, US Alg. Coll.-56205). B. Habit (*JN-6577*, US Alg. Coll.-158967).

Chondria acrorhizophora Setchell et N. L. Gardner

FIGURES 117, 118B

Chondria acrorhizophora Setchell et N. L. Gardner, 1924:766, pl. 40: fig. b; Silva, 1991:465; González-González et al., 1996:190; Mateo-Cid et al., 2000:67; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:212; Castañeda-Fernández de Lara et al., 2010:199.

Chondria tenuissima f. *californica* F. S. Collins, in Collins, Holden and Setchell, 1899:*P.B.-A.* No. 636.

Chondria californica (F. S. Collins) Kylin, 1941:41, pl. 12: fig. 35; Dawson, 1944a:325; Taylor, 1945:294; Dawson, 1959a:36; 1963b:443, pl. 138: figs. 1, 2, pl. 139: figs. 1, 2, pl. 140: fig. 3; Abbott and North, 1972:75; Abbott and Hollenberg, 1976:724, fig. 673; Devinny, 1978:359; Huerta-Múzquiz, 1978:335; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:28; Santelices and Abbott, 1987:9; Salcedo-Martínez et al., 1988:83; Sánchez-Rodríguez et al., 1989:46; Santelices, 1989:364, pl. Ñ: fig. 5; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Stewart, 1991:155; Ramírez and Santelices, 1991:363; Mateo-Cid and Mendoza-González, 1992:22; Mendoza-González and Mateo-Cid, 1992:20; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:49; González-González et al., 1996:190; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:26; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:468; Fernández-García et al., 2011:61.

Chondria clarionensis Setchell et N. L. Gardner, 1930:158; González-González et al., 1996:190; Serviere-Zaragoza et al., 2007:9.

Algae erect, often bushy, of slender, mostly cylindrical, iridescent, densely branched axes, (1–)4–5(–8) cm high; occasionally on hard substratum, usually epiphytic, often attached to hosts by entangled tendril-like branchlets or by more or less prostrate lower axes with numerous discoid holdfasts. Branching irregularly alternate, multifarious, or somewhat distichous. Branches cylindrical, 185–225 µm in diameter, to compressed, 350–550(–700) µm wide and 150–200 µm thick (flattening most prominent in young or low, basally attached thalli). Branch apices attenuate, with protruding apical cell of central axis surrounded by short tufts of trichoblasts; surfaces of axes and branches with few to many minute depressions throughout (representing branch primordia). Branchlets reduced in diameter at base. Pericentral cells 5 (not easily seen; more evident in young growing apices). Cortical cells variable, roundish to elongate (sometimes

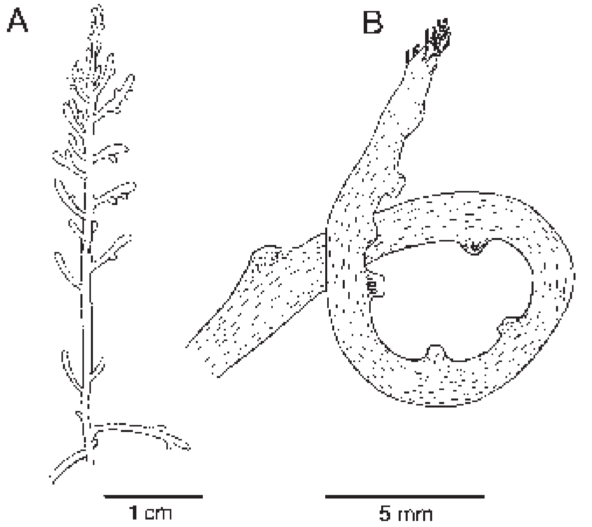


FIGURE 118. Species of *Chondria*: A. *Chondria* species A: Small portion of alga to show branching habit (after Dawson, 1963b: pl. 140: fig. 4, as "*Chondria dasyphylla*"). B. *Chondria acrorhizophora:* Detail of a branch tip to show papillate attachment structures (redrawn after Dawson 1963b: pl. 140: fig. 3, as "*Chondria californica* f. *cuscutoides*") .

up to 8 times longer than wide); lenticular thickenings usually present in walls of inner cortical cells.

Tetrasporangia borne in swollen ultimate branchlets; tetrasporangia up to 110 µm in diameter. Cystocarps scattered, subspherical to urceolate, 500–600 µm in diameter. Spermatangia unknown.

Habitat. Common from spring to summer, usually epiphytic on various algae, particularly on *Sargassum*, *Digenea*, and articulated corallines; low intertidal to shallow subtidal, down to 8 m depths (also dredged from 4–32 m depths; Dawson, 1944a).

Distribution. Gulf of California: Puerto Peñasco to Bahía de San Lucas; Nayarit to Jalisco. Eastern Pacific: Santa Cruz Island (California Channel Islands); southern California to Bahía Magdalena, Baja California Sur; Isla Guadalupe; Isla Clarión (Islas Revillagigedo); El Salvador; Costa Rica; Panama; Chile.

Type Locality. Eureka, near La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. *Chondria acrorhizophora* was considered to be a highly polymorphic species by Dawson (1959a, 1963b, as "*Chondria californica*"), who also included *C. clarionensis* and several other taxa as synonyms. Two of these were recognized as subspecific taxa, *C. californica* f. *concrescens* (E. Y. Dawson) E. Y. Dawson (1963b:444; basionym: *C. concrescens* E. Y. Dawson, 1961c:422) and *C. californica* f. *cuscutoides* (E. Y. Dawson) E. Y. Dawson (1963b:444; basionym: *C. cuscutoides* E. Y. Dawson, 1945c:79). This northeastern Pacific *Chondria acrorhizophora-californica-clarionensis* complex likely includes more than one taxa and is in need of critical morphological and molecular study.

Chondria repens Børgesen

Chondria repens Børgesen, 1924:299, figs. 40, 41; Dawson, 1957c:24; 1963b:448, pl. 168: fig. 2; Tanaka, 1963:66, fig. 4; Dawson, 1966a:30; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Santelices and Abbott, 1987:9; Ramírez and Santelices, 1991:363; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:191; Yoshida, 1998:1019; Fernández-García et al., 2011:61; Pérez-Estrada et al., 2012:191.

Algae terete, branched axes, forming low-growing turfs, up to 1 cm tall; of creeping and semi-erect axes and branches 200–300(–400) µm in diameter; lowermost axes attached to substratum by small discs or haptera formed by bundles of rhizoids. Branches short, moderately constricted at base, with blunt apices; apical cell within terminal depression. Cortical cells rounded to polygonal with thick cell walls; central axis and pericentral cells not distinct.

Tetrasporangia in upper portions of slightly swollen ultimate tetrasporangial branchlets; tetrasporangia elliptical, 80–90 µm in diameter. Cystocarps and spermatangia not observed in Gulf specimens.

Habitat. Attached to shells, coralline algae, mangroves, and other substrata; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía de La Paz; Nayarit to Jalisco. Eastern Pacific: Isla Guadalupe to Laguna de Ojo de Libre (Scammon's Lagoon), Baja California Sur; El Salvador; Costa Rica; Rapa Nui (Easter Island; Isla de Pascua). Western Pacific: Japan; Vietnam.

Type Locality. Rapa Nui (Easter Island; Isla de Pascua), Valparaiso Region, Chile.

Chondria species A

FIGURE 118A

Chondria dasyphylla [in part, only Gulf of California] sensu Dawson, 1944a:325; 1959a:37; 1963b:444, pl. 140: fig. 4, pl. 163; Hollenberg, 1970:70, fig. 22; Abbott and Hollenberg, 1976:726, fig. 674; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1986:425; González-González et al., 1996:306; CONANP, 2002:139; L. Aguilar-Rosas et al., 2000:132; Cruz-Ayala et al., 2001:191; L. Aguilar-Rosas et al., 2002:235; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212; Pérez-Estrada et al., 2012:191 [non *Chondria dasyphylla* (Woodward) C. Agardh, 1817:xviii; basionym: *Fucus dasyphyllus* Woodward, 1794:239, pl. 23: figs. 1–3].

Algae 5.0–15 cm tall; of slender, flaccid, cylindrical axes and branches, 300–750(–1000) µm in diameter; branching multifariously in irregularly alternate arrangement, up to 3(–4) orders. Main axis usually not distinct; sometimes second- and third-order branches more or less percurrent. Ultimate branchlets simple, constricted at their base, with obtuse to truncate apices.

Apical cell of central filament sunken in terminal pit, with a protruding tuft of short trichoblasts. Outer cortical cells in surface view, narrow-oblong, arranged in more or less longitudinal rows. Medulla in transection of large, thin-walled cells, 75–300 µm.

Tetrasporangia borne abundantly in upper portions of ultimate branches; tetrasporangia 140–165 µm in diameter. Cystocarps subspherical to ovoid; borne lateral on branchlets. Spermatangia not observed in Gulf specimens. On the basis of Pacific Baja California specimens (Dawson, 1963b): spermatangial structures flat, colorless discs, circular to cordate, 500–600 µm broad, each with a margin of large sterile cells and a system of branched veins; discs clustered at the branch tip; arising from the basal cell of a trichoblast.

HABITAT. On rocks, low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara); El Coloradito to Bahía San Luis Gonzága; Bahía Coyote (vicinity of Mulege) to Bahía de La Paz; Bahía San Carlos to Bahía Topolobampo.

REMARKS. The northern Gulf of California "*Chondria* species A" are typically more delicate, slender, and diffusely branched than the coarser, erect forms of southern California (cf. Abbott and Hollenberg, 1976, as "*C. dasyphylla*"). Although both forms were referred to "*C. dasyphylla*" by Dawson (1944a, 1963b), Gordon-Mills (1987) has suggested that the identification of all non-European records identified as *Chondria dasyphylla* are suspect. In the western Pacific, specimens from Korea identified as "*C. dasyphylla*" were found to differ and described as *C. pellucida* Y.-P. Lee (in Y.-P. Lee and Yoon, 1996). Thus, critical studies are needed of Gulf of California *Chondria* species A (including Gulf specimens referred to "*C. dasyphylla*") in order to resolve its taxonomic status and phylogenetic relationship to other species. Comparative morphological and molecular studies should include the Atlantic *C. dasyphylla* (type locality: Yarmouth, Norfolk, England; Maggs and Hommersand, 1993) *C. pellucida* (type locality: Hansu, Jeju, Korea; Y.-P. Lee and Yoon, 1996; Y.-P. Lee, 2008), and two others from Pacific Mexico, *C. pacifica* Setchell et N. L. Gardner (1937; type locality: Bahía San Bartolomé, Baja California Sur) and *C. telmoensis* E. Y. Dawson (1946a; type locality: reef, Río San Telmo, Baja California). The latter two were earlier considered to be conspecific with "*C. dasyphylla*" by Dawson (1963b); however, the Gulf specimens of *Chondria* species A appear to be closest to *C. pacifica*.

***Digenea* C. Agardh**

Digenea C. Agardh, 1822:388.

Algae are erect, often bushy, and composed of cartilaginous axes that are widely, dichotomously, subdichotomously or irregular laterally branched. The axes and branches are mostly densely covered by spirally arranged short, slender, stiff, simple to branched, determinate branchlets; they can sometimes be denuded in lower portions, probably from aging or possibly by grazing. The 5–12 pericentral cells are more apparent in the upper portions and branchlets but become obscured by the thickening pseudoparenchymatous cortex of mature portions. The inner cortical cells are large; the cells decreasing in size toward the outer cortical cell layers. The apical cell and small deciduous trichoblasts (usually observed on determinate branchlets) are at the tips of the branchlets. Branchlets develop 6-8 pericentral cells surrounded by a thin pseudoparenchymatous cortex.

Tetrasporangia in upper region of determinate branchlets; 1 per swollen segment, with 3 cover cells. Cystocarps are ovoid, borne lateral or terminal on determinate branchlets. Spermatangia in flat, oval discs that replace the trichoblasts in the upper portion of the determinate branchlets.

***Digenea simplex* (Wulfen) C. Agardh**

FIGURE 119

Conferva simplex Wulfen, 1803:17.

Digenea simplex (Wulfen) C. Agardh, 1822:389; Setchell and Gardner, 1924:769; Dawson, 1944a:326; Taylor, 1945:297; Dawson, 1959a:32; 1963b:418, pl. 140: fig. 5, pl. 159: fig. 1; 1966a:29; Norris, 1973:16; Huerta-Múzquiz and Garza-Barrientos, 1975:11; Tseng, 1983:146, pl. 76: fig. 4; Norris, 1985d:211; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1986:425; Mateo-Cid et al., 1993:49; Dreckmann and Sentiés G., 1994:443; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:308; Riosmena-Rodríguez et al., 1998:26; Yoshida, 1998:1021, fig. 3-106E; Mateo-Cid et al., 2000:67; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Cruz-Ayala et al., 2001:191; Mateo-Cid et al., 2006:57; Serviere-Zaragoza et al., 2007:9; Berneckner, 2009:CD-Rom p. 67; Fernández-García et al., 2011:61.

Algae bushy, 3–15(–25) cm high, tough and cartilaginous; axes widely dichotomous or irregularly laterally branched; axes and branches usually densely (or occasionally sparsely) clothed with slender, stiff, usually simple determinate branchlets, 3–5(–15) mm long; primary axes sometimes denuded in lower portions; attached by a discoid holdfast, that often spreads and may possibly coalesce with other holdfasts.

Tetrasporangia borne in distal, mostly uncorticated, portions of determinate branchlets. Cystocarps ovoid; terminal and lateral on the determinate branchlets. Spermatangia in small ovoid discs clustered at the apices of determinate branchlets.

HABITAT. On rocks, often sand covered; mid to low intertidal, occasionally shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo. Eastern Pacific: Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Socorro (Islas Revillagigedo); Costa Rica. Western Pacific: China; Japan.

TYPE LOCALITY. Trieste, Gulf of Trieste, northeast Italy, Adriatic Sea.

REMARKS. In the Gulf of California *Digenea simplex* can seasonally become heavily epiphytized by various other algae, particularly *Jania* and crustose corallines, and also by some sessile invertebrates, such as bryozoans. Gulf *D. simplex* sometimes can be found growing on sand-covered substrate, and in areas where it is heavily grazed, it appears to persist by its

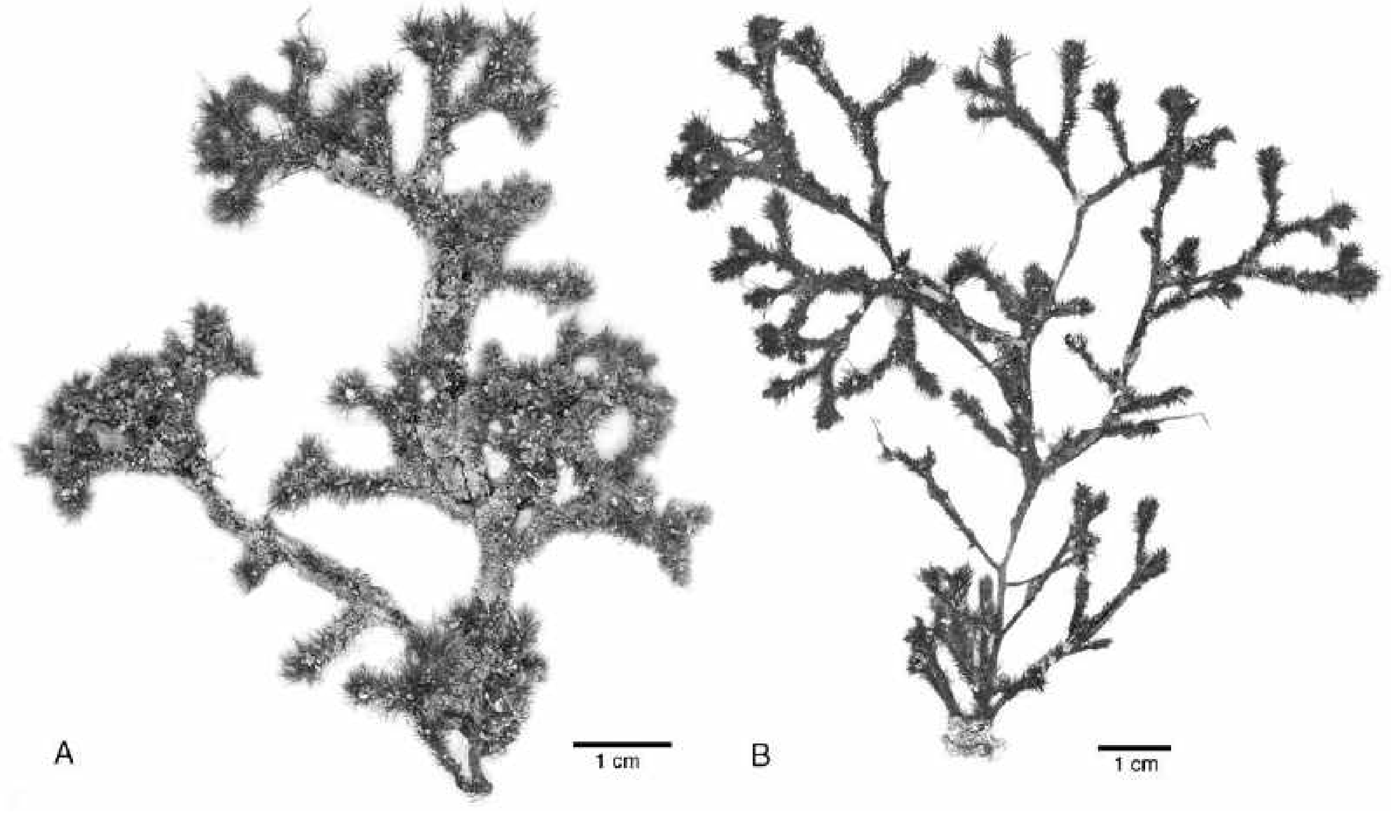


FIGURE 119. *Digenea simplex*: A. Habit of a specimen dense with slender, stiff branchlets; lowermost portion was partly buried in sand (*JN-4204*, US Alg. Coll.-159105). B. Axes with many branchlets missing, probably removed by grazing herbivores (*JN-4204*, US Alg. Coll.-159104).

spreading crustose base (a morphological form resistant to grazing; cf. Lewis et al., 1987).

The natural products of this alga have long been used in medicine as an anthelmintic agent (vermifuge) (e.g., Michanek, 1975, Tseng, 1983; Kimura et al., 1996). Studies of Pakker et al. (1996) found ecological and evolutionary differentiation between disjunct populations of *Digenea simplex,* with Pacific isolates having a wider temperature range than those of the Atlantic. It will be interesting to similarly investigate those of the northern and southern Gulf of California to test their origins and relationships with those of the Indo-Pacific and type locality.

RHODOMELACEAE TRIBUS HERPOSIPHONIEAE

Rhodomelaceae tribus Herposiphonieae F. Schmitz et Falkenberg, 1897:457.

Thalli are composed of an erect upper portion and a lower prostrate portion or may be entirely prostrate. Members are polysiphonous, ranging from 4 to 18 pericentral cells, and usually not corticated. Indeterminate and determinate branches are exogenous and in a regular (defined) sequence. Determinate laterals are usually unbranched or sometimes slightly to regularly branched. Indeterminate axes are subcylindrical to compressed, and bilateral or radially arranged. Apices are usually dorsiventrally developed, and often curved upward. Axes are attached by rhizoids produced from the ventral or lateral pericentral cells. Trichoblasts are usually present on determinate laterals, although they may be rare.

Tetrasporangia with 2–3 cover cells, are 1 per segment within straight to curved determinate laterals. Gametophytes are mostly dioecious but a few are monoecious. Procarps develop on lower cells of trichoblasts, with the fertile axial cells becoming polysiphonous. Cystocarps are globose, ovate to urn-like, with an ostiolate pericarp. Spermatangial structures ovoid to lanceolate on modified trichoblasts.

The tribe of seven known genera is represented by one genus in the northern Gulf of California.

Herposiphonia Nägeli

Herposiphonia Nägeli, 1846:238.

Algae are polysiphonous and completely ecorticate, with each species having a characteristic number of pericentral cells. Thalli consist of indeterminate creeping axes that bear distichous or erect and parallel determinate and indeterminate branches in a regular sequence, and are attached by numerous rhizoids cut off from the distal end of the ventral pericentral cells. Determinate branches are usually unbranched, and sometimes may have subterminal trichoblasts. Thalli are often epiphytes or in algal turfs.

Tetrasporangia are tetrahedrally or obliquely cruciately divided, and 1 per segment in a series, within central portions of determinate branches. Cystocarps are ovoid to urceolate, and lateral or subterminal on determinate branches. Spermatangial stichidia are cylindrical to ovoid, borne on branches of the trichoblasts on determinate branches, and may end in a terminal sterile cell or cells.

REMARKS. Two species are reported in the southern Gulf: *Herposiphonia hollenbergii* E. Y. Dawson (1963b) from Cabo San Lucas (Dawson, 1963b), Bahía Concepción (Mateo-Cid et al., 1993) and Cabo Pulmo (Mateo-Cid et al., 2000), and *H. verticillata* (Harvey) Kylin (1925; basionym: *Polysiphonia verticillata* Harvey, 1833) from Bahía Concepción (Mateo-Cid et al., 1993).

Three species of *Herposiphonia,* one with two taxonomic varieties, occur in the northern Gulf.

KEY TO THE SPECIES OF *HERPOSIPHONIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Determinate branches ending in a colorless spine of several cells . . . . ***H. spinosa***
1b. Determinate branches ending in blunt cell 2
2a. Determinate branches from alternate sides of successive segments of axes, distichously arranged (in 1 plane) 3
2b. Determinate branches not alternate, nor distichously arranged,erect from prostrate axes, unbranched and parallel to each other . . . . ***H. littoralis***
3a. Indeterminate branches long in lower portions, becoming shorter above, strictly distichous . . . . ***H. plumula* var. *plumula***
3b. Indeterminate branches mostly remaining rudimentary throughout, slightly offset from distichous; generally smaller . . . . ***H. plumula* var. *parva***

Herposiphonia littoralis Hollenberg

FIGURE 120

Herposiphonia littoralis Hollenberg, 1970:69, figs. 16–18; Abbott and Hollenberg, 1976:718, fig. 666; Pedroche and González-González, 1981:68; Pacheco-Ruíz and Aguilar-Rosas, 1984:74; Dreckmann et al., 1990:32; Sentíes-G. et al., 1990:103, pl. 6; Stewart, 1991:157; Serviere-Zaragoza et al., 1993a:483; Stout and Dreckmann, 1993:16; González-González et al., 1996:223; Riosmena-Rodríguez et al., 1998:26; Hernández-Herrera et al., 2005:147; Fernández-García et al., 2011:62.

Herposiphonia secunda sensu Huerta-Múzquiz and Garza-Barrientos, 1975:9; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30 [non *Herposiphonia secunda* (C. Agardh) Ambronn, 1880:197; basionym: *Hutchinsia secunda* C. Agardh, 1824:149].

Herposiphonia tenella sensu Setchell and Gardner, 1930:164; Hollenberg, 1948:159; Dawson, 1944a:334, pl. 49: fig. 1; 1959a:34; 1961b:452; 1963b:435, pl. 140: fig. 1; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-

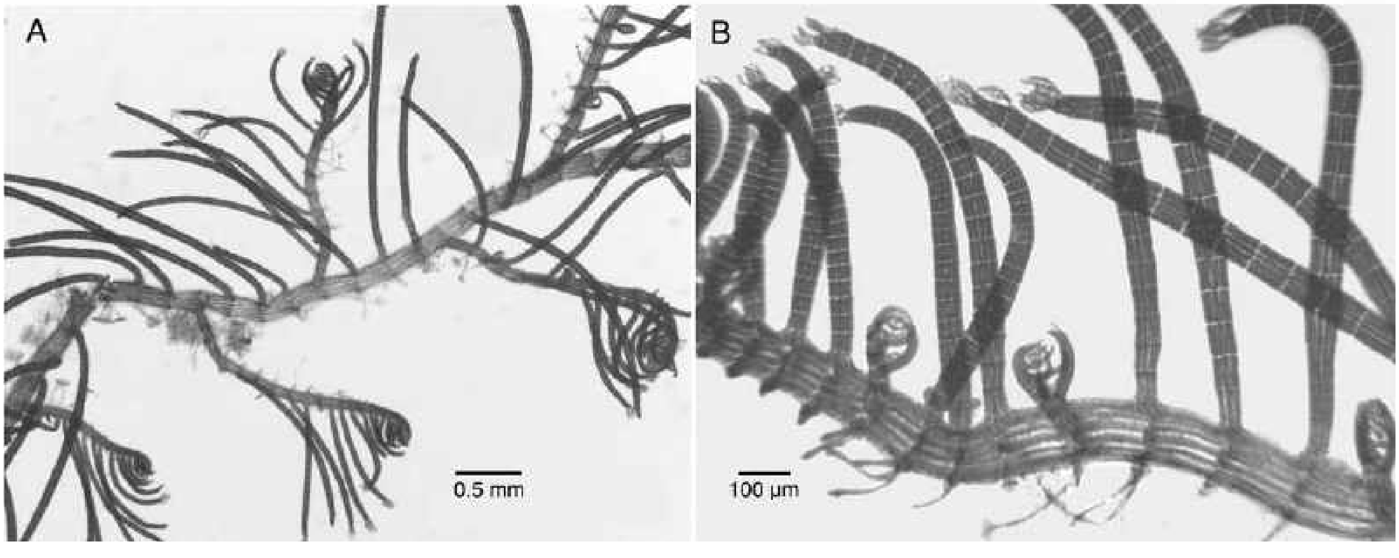


FIGURE 120. *Herposiphonia littoralis*: A. Portion of thallus showing pattern of three determinate branches between indeterminate branches. B. Portion near apex showing young indeterminate branches slightly offset from determinate branches, one branch per segment with rhizoids (A, B, *JN-5153*, US Alg. Coll. microscope slide 4946).

Barrientos, 1975:9; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30; Mendoza-González and Mateo-Cid, 1986:425; Dreckmann et al., 1990:32; Sentíes-G. et al., 1990:106, pl. 8; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:42 [non *Herposiphonia tenella* (C. Agardh) Ambronn, 1880:197; basionym: *Hutchinsia tenella* C. Agardh, 1828:105; which is now *Herposiphonia secunda* f. *tenella* (C. Agardh) M. J. Wynne, 1985e:173].

Herposiphonia secunda f. *tenella* sensu Stout and Dreckmann, 1993:16; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:26; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Mateo-Cid et al., 2006:57; Serviere-Zaragoza et al., 2007:10 [non *Herposiphonia secunda* f. *tenella* (C. Agardh) Wynne, 1985e:173].

Algae dorsiventrally organized with creeping, prostrate axes of unlimited growth (indeterminate), (40–)80–175 µm in diameter, and simple, erect branches of limited growth (determinate) often arching distally. Prostrate axes attached by numerous, unicellular rhizoids, 1 or more per segment, cut off from the distal ends of ventral pericentral cells. Axes polysiphonous, of 9–10(–12) pericentral cells. Branches 1 per segment, in a regular pattern of 3 consecutive determinate branches between each indeterminate branch. Determinate branches arising dorsally, unbranched, 20–27(–40) segments long; middle portions 30–80 µm in diameter; narrowed at their base, with subacute to blunt tips. Indeterminate branches often developing from alternate sides of prostrate axes slightly offset from determinate branches, indeterminate axes relatively rudimentary near growing apices of prostrate axes, apices ascending, often inrolled. As growth continues, the indeterminate branches subsequently grow out to become prostrate axes and repeat this branching pattern. Short trichoblasts sometimes present, abundantly branched; subterminal or terminal on both determinate and indeterminate branches.

Tetrasporangia about 40–45 µm in diameter; borne in a series, 1 per segment in determinate branches. Gametophytes dioecious. Cystocarps usually terminal, sometimes subterminal, on determinate branches. Spermatangial thalli occasionally with an irregular pattern of determinate and indeterminate branches, and not as regularly 1 per segment; spermatangial structures cylindrical, slightly incurved, about 200 µm long, 30–40 µm in diameter, with 1–2 terminal sterile cells; borne above a 1-celled pedicel on modified trichoblasts of determinate or indeterminate branches (after Dawson, 1963a).

HABITAT. Growing on rocks, in algal turfs, or epiphytic; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo San Lucas; Nayarit to Jalisco; Isla María Magdalena (Islas Marías; =Islas Tres Marías). Eastern Pacific: Santa Catalina Island (California Channel Islands); Conora del Mar, southern California to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Socorro, Isla Clarión and Isla San Benedicto (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador.

TYPE LOCALITY. Corona del Mar, Orange County, southern California, USA.

Herposiphonia plumula (J. Agardh) Hollenberg var. *plumula*

FIGURE 121

Polysiphonia plumula J. Agardh, 1885:99; Falkenberg, 1901:317.

Herposiphonia plumula (J. Agardh) Hollenberg, 1970:68, fig. 21 [type specimen]; Abbott and Hollenberg, 1976:718, fig. 667; Pacheco-Ruíz and Aguilar-Rosas, 1984:74; Sánchez-Rodríguez et al., 1989:46; Scagel et al., 1989:194; R. Aguilar-Rosas et al., 1990:126; Sentíes-G. et al., 1990:103, pl. 7; Stewart, 1991:157; González-González et al., 1996:223; CONANP, 2002:139; Riosmena-Rodríguez et al., 2005a:33; Pacheco-Ruíz et al., 2008:212.

Herposiphonia rigida N. L. Gardner, 1927f:100, pl. 23: figs. 1, 2 [type specimen], pl. 21; Smith, 1944:369, pl. 95: fig. 5, pl. 96: fig. 3.

Herposiphonia subdisticha sensu Dawson, 1944a:334 [in part], pl. 49, fig. 2; 1953c:3; 1959a:32; 1963b:433, pl. 141: figs. 4, 5 [in part]; Stewart and Stewart, 1984:147 [non *Herposiphonia subdisticha* Okamura, 1899:37; see Hollenberg, 1968c:555].

Thalli of uncorticated, terete, polysiphonous, creeping and erect portions, 5–20(–30) mm tall, main axes with 8–12(–14) pericentral cells, up to 300 µm in diameter. Distichously branched on every segment, with 3 (rarely 4) alternate determinate branches between successive alternate indeterminate branches. Indeterminate branches on same side of axes as determinate branch on segment below it. Determinate branches unbranched, polysiphonous with (6–)7–10(–12) pericentral cells, 150–190 µm in diameter at their base, curved toward the branch tip, short, mostly 0.5–1.0(–2) mm long, tapering to acuminate or blunt tip. Indeterminate branches 10–17 segments long or more, branched similar to main axis; progressively shorter in length toward the thallus apex. Trichoblasts frequently absent.

Tetrasporangia spherical, about 60 µm diameter, obliquely cruciately divided, borne in straight series in the determinate branches. Cystocarps sessile, ovoid, 300–450 µm in diameter and up to 600 µm long, borne singly on the adaxial side of determinate branches. Spermatangial stichidia cylindrical and incurved, 1 to several on the adaxial side of determinate branches.

HABITAT. Epiphytic on various algae, especially on articulated corallines; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to San José del Cabo. Eastern Pacific: Alaska to Bahía Magdalena, Baja California Sur; Islas Todos Santos and Isla Guadalupe, off Baja California; Colima to Oaxaca.

TYPE LOCALITY. Santa Barbara, Santa Barbara County, southern California, USA.

Herposiphonia plumula var. *parva* (Hollenberg) Hollenberg

FIGURE 122

Herposiphonia parva Hollenberg, 1943:575, figs. 8, 9; Dawson, 1945d:65; Hollenberg and Abbott, 1966:116; Smith, 1969:726; Stewart, 1991:158.

Herposiphonia plumula var. *parva* (Hollenberg) Hollenberg, 1970:69; González-González et al., 1996:223.

Herposiphonia pygmaea Hollenberg in G. M. Smith, 1944:369, pl. 96: fig. 2, *nom. invalid*.

Herposiphonia subdisticha [in part] sensu Dawson, 1944a:334, pl. 49: fig.2; 1959a:32; 1960a:51; 1961a:452; 1963b:433, pl. 141: figs. 4, 5;

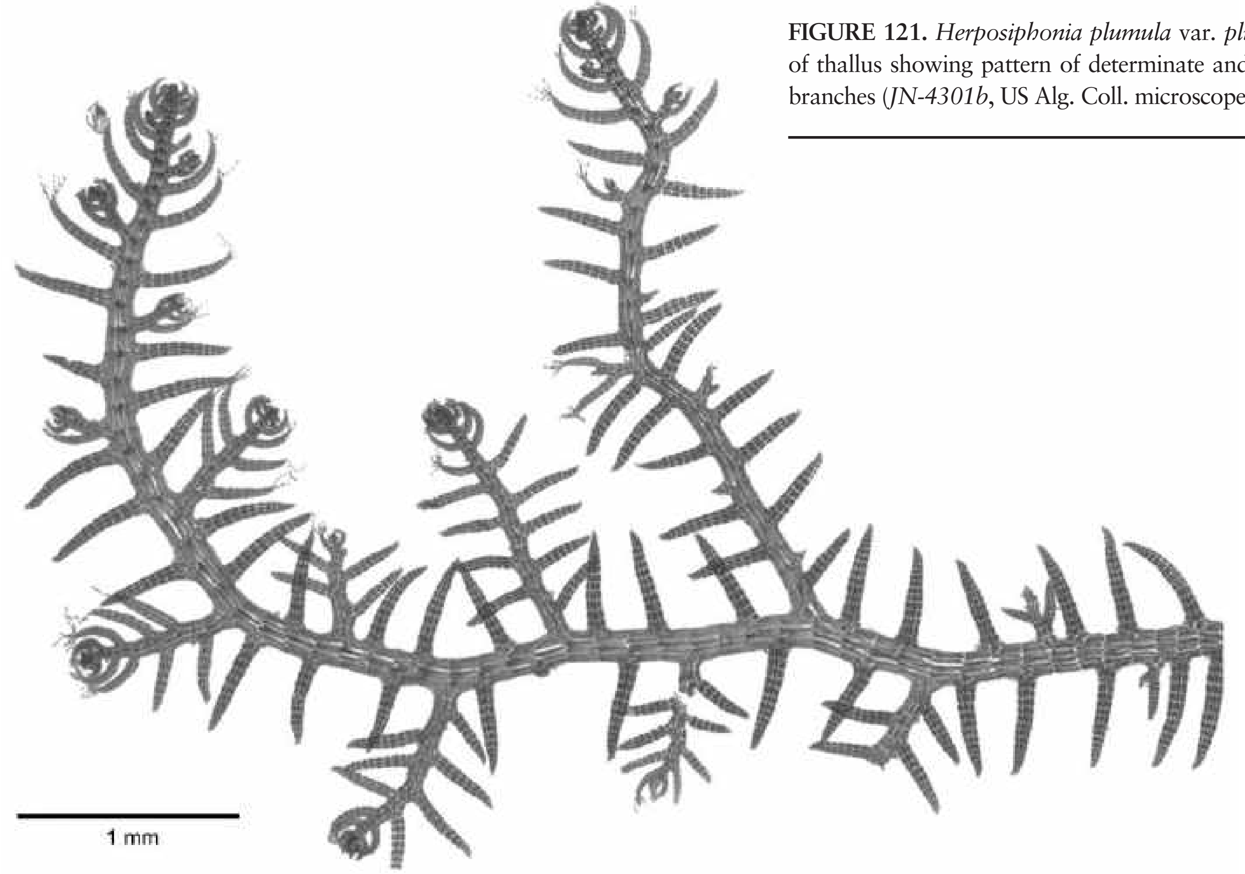


FIGURE 121. *Herposiphonia plumula* var. *plumula*: Portion of thallus showing pattern of determinate and indeterminate branches (*JN-4301b*, US Alg. Coll. microscope slide 4913).

1966a:30; González-González et al., 1996:224 [non *Herposiphonia subdisticha* Okamura, 1899:37].

Although similar to *Herposiphonia plumula* var. *plumula*, *H. plumula* var. *parva* is distinguished in being smaller, with indeterminate branches that mostly remain rudimentary.

HABITAT. Usually epiphytic on other algae; in tide pools and low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco. Eastern Pacific: Oregon; central California to Santa Cruz Island, off southern California; Punta Banda, Baja California.

TYPE LOCALITY. Lady's Harbor, Santa Cruz Island, California Channel Islands (Channel Islands Marine Park), southern California, USA.

Herposiphonia spinosa E. Y. Dawson

FIGURE 123

Herposiphonia spinosa E. Y. Dawson, 1959a:34, fig. 7B; 1961b:452; 1963b:432, pl. 129: fig. 2; 1966a:30; 1966b:66; Schnetter and

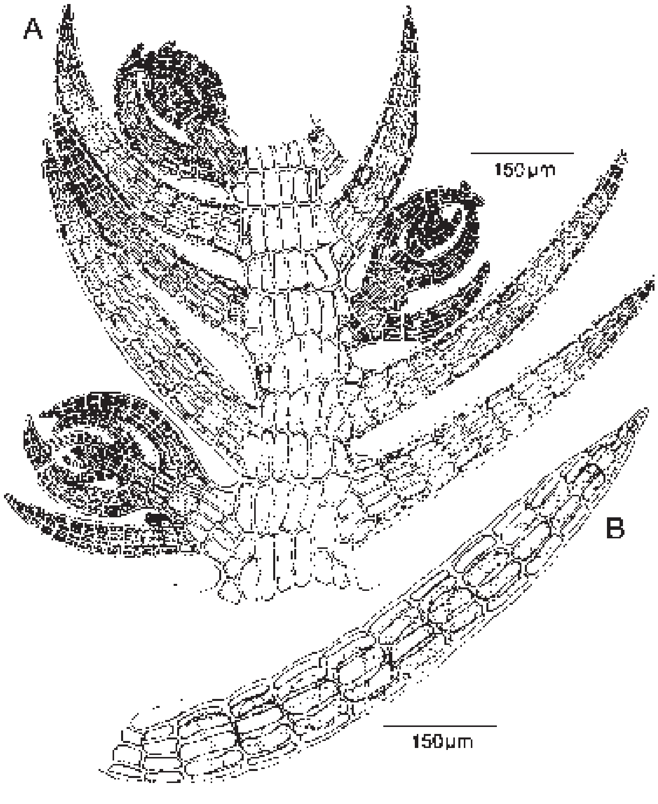


FIGURE 122. (Left) *Herposiphonia plumula* var. *parva*: A. Portion showing arrangement of determinate and indeterminate branches. B. Determinate branch with tetrasporangia in straight series (A, B, after Hollenberg, 1943: figs. 9, 8).

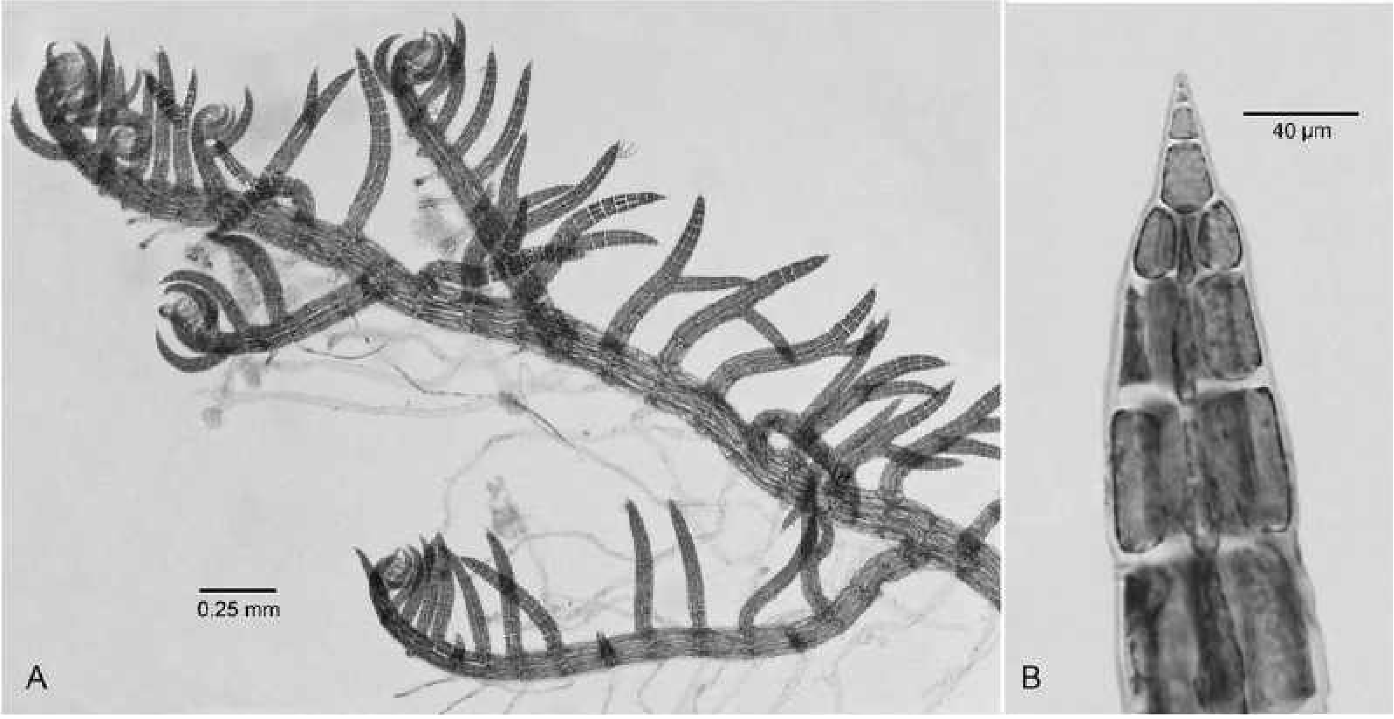


FIGURE 123. *Herposiphonia spinosa*: A. Habit (*JN-4390*, US Alg. Coll. microscope slide 4912). B. Colorless 3-celled spine at tip of determinate branch (*JN-3175*, US Alg. Coll. microscope slide 4907).

Bula-Meyer, 1982:187, pl. 36: fig. I; Bula-Meyer, 1995:39; González-González et al., 1996:224; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212.

Thalli of creeping, polysiphonous main axes of (8–)10–12 pericentral cells (130–240 µm in diameter) and erect determinate branches of 6–8 pericentral cells (120–150 µm in diameter at base, narrowing above); attached by numerous unicellular rhizoids issued from ventral pericentral cells, occasionally terminating with a digitate disc. Indeterminate branches at every fourth segment, separated by 3 determinate branches. Determinate branches arising from dorsal side of prostrate axes, once or twice forked, rigid, divaricate, and slightly recurved, acuminate with a series of colorless cells (usually 3) forming a point (spine). Trichoblasts occasionally present, compound, usually on the fourth or fifth segment back from the spine at tip of branches.

Reproductive structures not observed.

Habitat. On rocks and in tide pools, found creeping among other algae or epiphytic on *Sargassum* and *Amphiroa* and probably other larger algae as well; mid intertidal to very shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía de Los Ángeles; Isla Tiburón; Isla Partida (east of Bahía de La Paz) to Punta Los Frailes; Cabo San Lucas. Eastern Pacific: Isla Gorgona, Colombia.

Type Locality. Isla Partida (off the north end of Isla Espíritu Santo), Baja California Sur, Gulf of California, Mexico.

Rhodomelaceae tribus Laurencieae

Rhodomelaceae tribus Laurencieae F. Schmitz, 1889:447; Womersley, 2003:452.

The tribe includes members that are (1) erect and branched macrophytes; branchlets with an apical cell sunk within an apical depression with a cluster of trichoblasts; axial and pericentral cells more readily observed in uppermost developing branchlets (becoming obscured within extensive cortex below apices); and (2) minute, subspherical to cushion-shaped parasites (e.g., *Janczewskia* Solms-Laubach, 1877).

Tetrasporangia subspherical to ovoid, mostly tetrahedrally divided; in outer cortex; developed on upper end of elongated pericentral cells or cut off from outer cortical cells, with 2 cover cells. Gametophytes are dioecious. Procarps develop on lower cells of trichoblasts; carpogonium of 4 cells and 2 sterile groups of cells. Cystocarps pedicellate, partly immersed, or sessile; with ostiolate pericarp, corticated, 3–6 cell layers thick. Spermatangia develop within cup-shaped receptacles in apical pits of branchlets to deep urn-shaped pockets in branchlets, either on modified trichoblasts formed by axial cells in apical pits (“trichoblast type”) or from filaments formed by apical and epidermal cells (“filament type”).

REMARKS. *Laurencia* had long been recognized as a broadly defined genus. Saito (1967) divided the genus *Laurencia* into two subgenera, *Laurencia* subgen. *Laurencia* and *L.* subgen. *Chondrophycus* J. Tokida et Saito. Within the last 20 years, morphological, anatomical, molecular and genetic data have supported its separation into several genera (see Nam and Sohn, 1994; Garbary and Harper, 1998; Nam et al., 2000; McIvor et al., 2002; Lewis et al., 2008; Martin-Lescanne et al., 2010; Nam, 2011). A reinterpreted *Laurencia, Chondrophycus* (J. Tokida et Saito) Garbary et J. Harper (1998), and *Osmundea* Stackhouse (1809) were recognized within the "*Laurencia*-complex" (Garbary and Harper, 1998; Nam et al., 2000; McIvor et al., 2002; Fujii et al., 2006). More recently described are the genera *Palisada* K. W. Nam (2007), and *Yuzurua* Martin-Lescanne (in Martin-Lescanne et al., 2010). A sixth genus, *Laurenciella* Cassano, Gil-Rodríguez, Sentíes, Díaz-Larrea, M. C. Oliveira et M. T. Fujii (in Cassano et al., 2012), was separated by molecular sequence data, but the genus apparently cannot be distinguished from *Laurencia* solely on morphological characters. There is the possibility that *Corynecladia* J. Agardh (1876), currently treated as a synonym of *Laurencia,* might also be a separate genus (see Nam, 2006). The proposed subgenus *Saitoa* G. Furnari et Serio, 1993, *nom. illeg.* (McIvor et al., 2002), if found to be distinct could not be used for a genus name since it would be a later homonym of *Saitoa* C. Rajendran et B. Muthappa (1980).

There are some overlapping morphological characters as well as exceptions to the diagnostic characters used for separation of both generic and subgeneric taxa. To accommodate the differences within *Chondrophycus,* Nam (1999) proposed other subgenera. Two of these have secondary pit connections between the outer cortical cells and two sterile pericentral cells in tetrasporangial axial segments but differ in the arrangement of tetrasporangia; that is, in *C.* subgen. *Chondrophycus* tetrasporangia are in a right-angle pattern, whereas in *C.* subgen. *Kangjaewonia* K. W. Nam (1999) they are in a parallel pattern. The third, *C.* subgen. *Yuzurua* K. W. Nam (1999), is now a genus, *Yuzurua*, and also has a right-angle arrangement of tetrasporangia, a character shared with some species of *Chondrophycus*. *Yuzurua* differs from *Chondrophycus* (which has two sterile pericentral cells in tetrasporangial axial segments) in having only one sterile pericentral cell in its tetrasporangial axial segments. The presence or absence of secondary pit connections in the outer cortical cells separates two of the genera: *Yuzurua* has secondary pit connections between epidermal cells, whereas *Palisada* lacks them.

Whereas only one genus, *Laurencia*, was once known in the Gulf of California, currently four of the six genera of the tribe Laurencieae—*Laurencia, Chondrophycus*, *Osmundea,* and *Palisada*—are recognized in the northern Gulf of California.

KEY TO THE GENERA OF LAURENCIEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli of Gulf species compressed to flattened; 2 pericentral cells per axial segment in vegetative axes; *corp en cerise* (gland cells) absent; tetrasporangia produced from random epidermal (cortical) cells; "filament type" spermatangial development . . . . **_Osmundea_**
1b. Thalli terete to subterete; either with 2 or 4 pericentral cells per axial segment in vegetative axes; *corp en cerise* absent or present; tetrasporangia produced from particular pericentral cells; "trichoblast-type" spermatangial development 2
2a. Vegetative axial cell with 2 pericentral cells (seen only near branchlet apices) 3
2b. Vegetative axial cell with 4 pericentral cells (seen only near branchlet apices); *corps en cerise* often present within cortical cells and trichoblasts . . . . **_Laurencia_**
3a. Tetrasporangial axial segments with 1 sterile pericentral cell (1st pericentral cell); spermatangial branches develop from 1 of 2 laterals on the suprabasal cell of trichoblasts . . . . **_Palisada_**
3b. Tetrasporangial axial segments with 2 sterile pericentral cells (1st and 2nd); spermatangial branches produced from 2 laterals on the suprabasal cell of a trichoblast but one remains partly sterile . . . . **_Chondrophycus_**

Laurencia J. V. Lamouroux

Laurencia J. V. Lamouroux, 1813:130, *nom. cons.* (see Papenfuss, 1947b:15).

Thalli cylindrical to subcylindrical, mostly radial, bilateral, or irregularly branched and attached by discoid, stoloniferous, or encrusting holdfasts. Apical cell always sunk in small terminal apical pit of branchlet and surrounded by branched, colorless deciduous trichoblasts. Central axial cell row (filament) with 4 pericentral cells per axial segment in vegetative axes; first pericentral cell is under a trichoblast (usually only distinguishable near apical cell, becoming obscured by formation of an extensive pseudoparenchymatous cortex). Secondary pit connections are present between adjacent epidermal cells. Spherical refractive inclusions, the *corps en cerise* (gland cells), are often present in cortical cells and trichoblast cells; they are thought to be the site of synthesis and/or storage of halogenated secondary metabolites (Young et al., 1980). Medullary cells are with or without lenticular thickenings, their abundance varying from sparse to frequent. Quantitative differences in the amount of lenticular thickenings (seen in sections) can vary between those in cells of the main axis, each order of branches, and the ultimate branchlets within thalli of the same species and sometimes in the same individual thallus.

Tetrasporangia axial segments develop near the apical cells of branchlets, with tetrasporangia produced from particular pericentral cells. Each tetrasporangial axial segment has two sterile pericentral cells, including the second pericentral cell.

Procarps are borne on lower cells of modified trichoblasts with segments of five pericental cells in the apical pits. Cystocarps are ostiolate, noticeably protruding above branchlet and sometimes branch surfaces. Spermatangial branches develop in cup-shaped depressions that are lateral or terminal on ultimate branchlets. Spermatangial branches are produced from one of the two laterals on the suprabasal cell of the trichoblasts; the other lateral remains sterile.

REMARKS. Species of *Laurencia* are found worldwide in tropical to temperate habitats from the intertidal to subtidal. Most species of *Laurencia* synthesize at least one specific secondary metabolite that is not found in other *Laurencia* species (Fenical, 1975; Fenical and Norris, 1975; Norris and Fenical, 1982; Faulkner, 1984; Norris and Fenical, 1985). Howard et al. (1980a, 1980b) found the unique natural chemistry of several species of *Laurencia* remained constant under varying conditions in the field and in culture. The chemotaxonomic value of these compounds has been supported in several studies (e.g., Howard et al., 1980b; McDermid, 1988a; Masuda et al., 1996; Gil-Rodríguez et al., 2009).

Agar has been described in the cell wall polysaccharides from a few of the species—for example, *Laurencia flexilis* Setchell (1926) from China, where it is commercially harvested (Tseng, 1983; Wu and Zeng, 1985), and *Laurencia* sp. from Hawaii (Zablackis and McDermid, 1988). It would be interesting to investigate the polysaccharide chemistries of species from the northern Gulf of California.

The southern Gulf of California endemic *Laurencia subcorymbosa* E. Y. Dawson (1963a) described from Cabo Pulmo has also been reported from Punta Palmilla and Punta Los Frailes (Dawson, 1963) and Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985). Four others, originally described from Pacific Mexico, have also been recorded in the southern Gulf: *L. masonii* Setchell et N. L. Gardner (1930) and *L. decidua* E. Y. Dawson (1954a) from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985), *L. voragina* W. R. Taylor (1945) from Punta Arena (Mateo-Cid et al., 2000), and *L. richardsii* E. Y. Dawson (1954a) from Mazátlan (Mendoza-González et al., 1994).

Currently there are six species of *Laurencia* in the northern Gulf of California, including three new species described herein.

KEY TO THE SPECIES OF *LAURENCIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Alga of terete axes; distinctly bright to dark green (sometimes almost blackish green) . . . . *L. johnstonii*
1b. Alga of terete axes; not green, usually reddish to blackish 2
2a. Algae semierect, low-growing clumps, less than 3 cm tall; in spreading low turfs or mats 3
2b. Algae erect, larger and taller, individuals or clumps up to 15 cm tall 4
3a. Loose clumps, comparatively shorter and thinner, 1.5–2.5 cm tall; branches narrow, 300–500 μm in diameter; ultimate branchlets contracted at base . . . . *L. hancockii*
3b. Dense clumps, up to 3 cm tall, often forming turfs; branches wider, 700–850 μm in diameter . . . . *L. lajolla*
4a. Thalli very lax, axes (700–)1000 μm in diameter, branches mostly 300–500 μm in diameter; branching irregularly alternate; ultimate branches densely crowded; contain the brominated diterpene iriediol . . . . *L. iriei*
4b. Thalli not lax; ultimate branches not densely crowded; do not contain iriediol 5
5a. Algae bright red, main axis 700–1000 μm in diameter, with branches mostly 500–700 μm in diameter; branching irregularly alternate, with long intervals between branches in lower portions, intervals become shorter upwards; with small ultimate branches; contains halogenated sesquiterpenes similar to elatol . . . . *L. aguilar-rosasorum*
5b. Algae dark red to blackish, thin and rigid; axes and branches of more or less uniform diameter, mostly about 500 μm in diameter; branching mostly opposite (occasionally alternate), with fewer ultimate branchlets; has acetylene-containing compound chondriol . . . . *L. fenicalii*

Laurencia aguilar-rosasorum J. N. Norris, *sp. nov.*

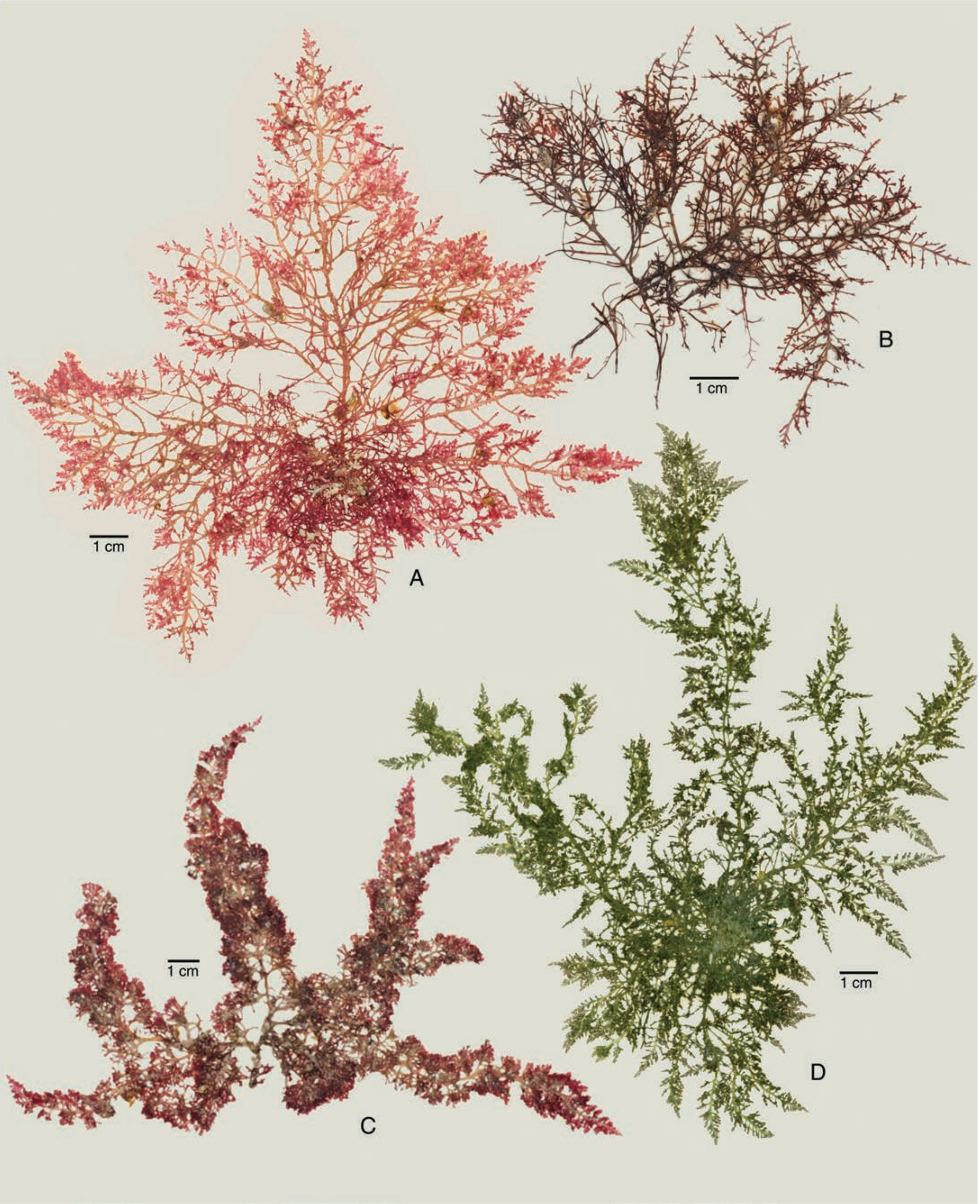
FIGURE 124A

Laurencia pacifica sensu Dawson, 1963b:457 [in part; only among Gulf of California specimens; non *Laurencia pacifica* Kylin, 1941:42].

Laurencia sp. III of Fenical and Norris, 1975:106, figs. 2, 3.

LATIN DESCRIPTION. Thalli ruborem rosae purpureus, laxa, usque cm 15, unius plures, ramosi teretes, axes plus minus pyamidal habitu prima 0.7–1.0 mm axes diametro, irregulariter alterne ramosae usque 4(–6) iussione intervalla iam in inferiora rami, ramo breviores spatio sursum ramos 500–700 μm

FIGURE 124. (Opposite) Species of *Laurencia*. A. *Laurencia aguilar-rosasorum, sp. nov.*: Holotype specimen (*JN-4369*, US Alg. Coll.-217740). B. *Laurencia fenicalii, sp. nov.*: Holotype specimen (*JN-4515*, US Alg. Coll.-217741). C. *Laurencia iriei, sp. nov.*: Holotype specimen (*JN-4519*, US Alg. Coll.-217742). D. *Laurencia johnstonii*: Habit (*JN-4068*, US Alg. Coll.-160140).


B
1 cm
1 cm
A
1 cm
1 cm
D
C

diametro, basi leviter angustata plerumque ramum origine ultima denique ramulis plerumque 250–500 µm longae, apices rotundatos, de similis diametro ramulis magis rotundato; circumdederunt securibus ramis brevibus numerosis, ramulis papillosis; appensa stolonifera holdfast pronus implicuit brachia; distinguitur chemica *L. fenicalii* e *L. iriei* secunda sua naturali product praedominantis, similiter apud halogenated elatol sesquiterpenes.

Algae rose red to bright red, lax, up to 15 cm tall; of 1 to several terete multifariously branched axes, more or less pyramidal in appearance; primary axes 700–1000 µm in diameter, irregularly alternately branched up to 4(–6) orders, with longer intervals between branches in lower portions, branch interval shorter upward; branches 500–700 µm in diameter, basally usually slightly narrowed at branch origin; ultimate branchlets short, mostly 250–500 µm long, with rounded apices, of similar diameter; axes and branches beset with numerous short, papillate branchlets; attached by holdfast and entangled stoloniferous prostrate branches.

Reproductive structures not observed.

Habitat. On rocks and tidal platform and in tide pools; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco and vicinity.

Holotype. *JN-4369* (US Alg. Coll.-217740).

Type Locality. Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Gulf of California, Mexico.

Etymology. *Laurencia aguilar-rosasorum* is named for two marine botanists, brothers Luis Ernesto Aguilar-Rosas (Instituto de Investigaciones Oceanológicas, Universidad de Baja California, Ensenada) and Raúl Aguilar-Rosas (Facultad de Ciencias Marinas, Universidad de Baja California, Ensenada), in recognition of their contributions to our knowledge of the marine algae of Baja California and the Gulf of California (many of their publications are cited herein).

Remarks. Three separate morphological forms were found within a broadly defined concept of "*Laurencia pacifica*" sensu Dawson (1963b) in the upper Gulf of California. Each of these was recognized to be distinct from *Laurencia pacifica* Kylin (see Fenical and Norris, 1975: figs. 2, 3; Howard et al., 1980b) on the basis of differences in their unique natural product chemistries and morphologies. The three of the upper Gulf can be distinguished from each other by their own characteristic secondary metabolites. Chemically, *Laurencia aguilar-rosasorum* is distinguished from the other two, *L. fenicalii* and *L. iriei*, by its predominant secondary natural product, a halogenated sesquiterpene similar to elatol (Sims et al., 1974). (See also Remarks under *L. fenicalii* and *L. iriei*.)

Laurencia fenicalii J. N. Norris, *sp. nov.*

FIGURE 124B

Laurencia pacifica sensu Dawson, 1963b:457 [in part; only among Gulf of California specimens; non *Laurencia pacifica* Kylin, 1941:42].

Laurencia sp. I of Fenical and Norris, 1975:106, figs. 2, 3; Howard and Fenical, 1975:1687.

Chondria oppositiclada sensu Sims et al., 1974:3774; Fenical et al., 1974:1507 [non *Chondria oppositiclada* E. Y. Dawson, 1945d:78].

Latin Description. Thalli fasciculus, ad cm 10, brunneo-rufa of nigricantes rubent comparative teretes rigidi axibus 500 µm diametro, plerumque opposite ramosae usque 4(–6) iubet (uel ramis interdum alternis) plus quam planum de ramis 350–500 µm diametro attachiatus est per holdfast discoidea, secundario prostrata ramis parvis; rami leviter constrictum basi rotundatis apicibus; segmenta fere longiores inter ramos basi angustata ramulis ultimis sensim ad apices antice, 200–350 µm. Medulla cellulis hyalinis magna, lenticellis inspissato nulla, cortical cells videtur exteriora sine hospitibus secunda lacum. Subsperical tetrasporangiis, 72–96 µm longa, 70–85 µm diametro, ramulis ultimis in. Cystocarpic subglobosa, sessilia, 500–600 µm diametro, ostiolo in, ferme 1–2, plerumque in ramis lateralibus ramulis ultimis et. Spermatangia puteos in vado plures in ultimas superne ramulis; racemis spermatangial magna sterilis terminalis cellula apicalis subglobosa 10–15 µm longa, 8–10 µm diametro. Distinguitur chemica *L. iriei* e *L. aguilar-rosasorum* praedominantis secunda sua naturalia, et chondrin chondriol et alia sesquiterpenoid plicia etiam cycloeudesmene.

Algae in clumps, up to 10 cm tall; of brownish red to blackish red, comparatively rigid terete axes, thin, 500 µm in diameter, mostly oppositely branched up to 4(–6) orders (or only occasionally with alternate branches) in more than 1 plane; branches about 350–500 µm in diameter; attached by a discoid holdfast and secondarily by short prostrate branches. Branches slightly narrower at base, with rounded apices; most with long intervals between branches; ultimate branchlets narrowed basally, gradually widening toward apices, 200–350 µm in diameter. Medulla of large colorless cells; lenticular thickenings absent. Outer cortical cells apparently without secondary pit connections.

Tetrasporangia subspherical, 72–96 µm long, 70–85 µm in diameter, in ultimate branchlets. Cystocarps subglobose, sessile, 500–600 µm in diameter, with an ostiole; usually 1–2, mostly lateral on branches and ultimate branchlets. Spermatangia clustered in shallow cup-shaped pits, several on upper ends of spermatangial ultimate branchlets; spermatangia on whorled branchlets, each with a large, subglobose, sterile terminal cell, 10–15 µm tall, 8–10 µm in diameter.

Habitat. On rocks, in tide pools, and on tidal platforms; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco and vicinity to Punta Cirio (south of Puerto Libertad), and Bahía San Carlos, northwest of Guaymas, Sonora.

Holotype. *JN-4515* (US Alg. Coll.-217741), Coll. J. N. Norris and K. E. Bucher, 9 November 1973.

Paratypes. Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco (all coll. J. N. Norris and K. E. Bucher): *JN-4314* (spermatangial) (US Alg. Coll.-160355); microscope slide *5092 & JN-4320* (spermatangial) in tidal runoff from Cumpleaños Tide Pool, 24 October 1973, and *JN-4513*, 9 November 1973; and tidal platform, Playa Las Conchas (Playa Estación), *JN-4372*. Punta Cirio (south of Puerto Libertad): *JN-4876*, Coll. J. N. Norris, K. E. Bucher & D. Moore, 19 November 1973.

Type Locality. Cumpleaños Tide Pool, on intertidal platform; Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Gulf of California, Mexico.

ETYMOLOGY. *Laurencia fenicalii* is named for Bill Fenical (Professor William H. Fenical, Center for Marine Biotechnology and Biomedicine, Scripps Institution of Oceanography, University of California, San Diego), a long-time friend, research collaborator, fellow diver, and "Baja aficionado" and Chief-Scientist on our Gulf of California and Pacific Mexico ship expeditions on the R/V *Dolphin* and ORV *Alpha Helix*. This is in recognition of not only his contributions to our knowledge of the natural product chemistry of marine algae and marine chemical ecology, including numerous studies on Gulf of California macroalgae, but also his early and continued emphasis on the importance of critical taxonomic identifications and voucher specimens.

REMARKS. Chemically, *Laurencia fenicalii* (Fenical and Norris, 1975: figs. 2, 3, as "*L.* sp. I") is distinguished from *L. iriei* and *L. aguilar-rosasorum* by its predominant secondary natural products, chondriol and chondrin, and other sesquiterpenoid derivatives, including cycloeudesmene (Fenical and Sims, 1974; Fenical et al., 1974, as "*Chondria oppositiclada*"; Howard and Fenical, 1975; Howard et al., 1980a, as "*Laurencia* sp."). (See also Remarks under *Laurencia aguilar-rosasorum* and *L. iriei*.)

Laurencia hancockii E. Y. Dawson

Laurencia hancockii E. Y. Dawson, 1944a:328, pl. 50: fig. 1 [part of type specimen]; 1961b:454; 1963b:452, pl. 149: fig. 1; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:9; Schnetter and Bula-Meyer, 1982:190, pl. 30: fig. H; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30; Dreckmann et al., 1990:32, pl. 6: figs. 3, 4; Sentíes-G. et al., 1990:111, pl. 12; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:484; Stout and Dreckmann, 1993:17; Mendoza-González et al., 1994:109; Bula-Meyer, 1995:39; González-González et al., 1996:321; Mateo-Cid et al., 2000:67; Hernández-Herrera et al., 2005:148; Serviere-Zaragoza et al., 2007:10.

Algae forming loose clumps, mostly 1.5–2.5 cm tall; erect, branched, nondistinct main axis, cylindrical, 300–500 μm in diameter, up to 600 μm in lowermost portions; sometimes attached to each other by rhizoidal outgrowths; attached below by rhizoids from lower portions of erect branches and by prostrate branched axes. Branching irregular, multifarious or often more or less unilateral on convex side of curving or arching branches; ultimate branchlets short, up to 3 mm long, contracted at base. Outer cortex in surface view of isodiametrical cells near apices. In transection, medulla of large colorless cells without lenticular thickenings. Cortex of 3–4 cell layers; surface smooth; outer cells not protruding, not in palisade arrangement, secondary pit connections present; inner cortical cells elongated.

Tetrasporangia 80–100 μm in diameter; abundant in upper portion of unmodified ultimate branchlets; parallel arrangement. Gametangial specimens not observed.

HABITAT. On rocks and tidal platforms, in tide pools, and epiphytic on *Sargassum* and possibly other algae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Ensenada de San Francisco (near Puerto San Carlos); Bahía Agua Verde to Cabeza Ballena; Mazátlan, Sinaloa to Jalisco. Eastern Pacific: Baja California; Isla Socorro (Islas Revillagigedo); Colima to Guerrero; Isla Gorgona, Colombia.

TYPE LOCALITY. Rocky low intertidal; Bahía Agua Verde, Baja California Sur, Gulf of California, Mexico.

Laurencia iriei J. N. Norris et Fenical, *sp. nov.*

FIGURE 124C

Laurencia pacifica sensu Dawson, 1963b:457 [in part; only among Gulf of California specimens; non *Laurencia pacifica* Kylin, 1941:42].

Laurencia sp. II of Fenical and Norris, 1975:106, figs. 2, 3; Fenical et al., 1975:3983.

Laurencia iriei, nom. nud., sensu Howard and Fenical, 1978:4401; Fenical, 1978:245; Erickson, 1983:195.

LATIN DESCRIPTION. Thalli rubra surrexit fortissimi laxa, usque 10 cm, ramosis teretibus secures 0.7–1.0 mm diametro, irregulariter alterne ramosae, usque III ordinibus axium plerumque dense numerosis ramis lateral 300–500(–700) μm diametro, angustata basin; rami usque 4 rebranched ordines formandi corymbosa dense aggregati ramulis unusquisque de ramulus 250–300 μm diametro ramulis ultimis minoribus, apices rotundatos, per filo infra holdfast discoidea, nunc prostratus inseruerunt posterius rami. Medulla cellulis hyalinis magna, lenticellis inspissato nulla. Cortical cells exteriores aspectu superficiali, sphaericae vel irregulariter elongatae angulis rotundatis, plerumque 20–50 μm longa, 15–20 μm latae, in transection, 20–30 μm longa, 30–50 μm crassa; nexus-secunda lacum quidam observatur inter cortical cells exteriores. Subsperical tetrasporangiis, 85–105 μm longa, 80–100 μm diametro in superiore parte ramulis ultimi; cystocarpiis et spermatangia clavatae. Distinguitur chemica *L. fenicalii* et *L. aguilar-rosasorum* ceterum secunda per naturalia, iriedol, iriediol et irieols A-G, nova diterpenes brominated.

Algae rose to red; very lax; up to 10 cm tall; of branched terete axes, 700–1,000 μm in diameter, irregularly alternately branched; axes usually densely covered with numerous lateral branches 300–500(–700) μm in diameter, narrowed at base; branches multifariously rebranched up to 4 orders, forming dense clusters of corymbose branchlets; each branchlet about 250–300 μm in diameter; ultimate branchlets smaller, with rounded apices; attached below by a discoid holdfast and sometimes secondarily by entangled prostrate branches. Medulla of large colorless cells; lenticular thickenings absent. Outer cortical cells in surface view, subspherical to irregularly elongated with rounded corners, mostly 20–50 μm long, 15–20 μm wide; in transection, 20–30 μm tall, 30–50 μm wide; secondary pit connections observed between some outer cortical cells.

Tetrasporangia subspherical, 85–105 μm long, 80–100 μm in diameter; in upper portion of ultimate branchlets (*JN-4286,* US Alg. Coll. microscope slide 5062). Cystocarps and spermatangia not observed.

HABITAT. On tidal platforms, in crevices, and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco and vicinity; Bahía Concepcíon.

HOLOTYPE. *JN-4519* (US Alg. Coll.-217747); Coll. J. N. Norris and K. E. Bucher, 9 November 1973.

Type Locality. Attached to sides of Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Gulf of California, Mexico.

Paratypes. Sonora: on tidal platform, vicinity of Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Coll. W. Fenical and K. Robertson, 23 October 1973, *JN-4286* (tetrasporophyte), US Alg. Coll. microscope slide 5062.

Etymology. *Laurencia iriei* is named in honor of Toshi Irie (Professor Emeritus, Department of Chemistry, Faculty of Science, Hokkaido University, Sapporo, Japan) in recognition of his pioneering contributions to our knowledge of the natural product chemistry of marine algae of Japan and the western Pacific. Professor Irie, who is now deceased, was the "father" of *Laurencia* chemistry.

Remarks. Natural product chemistries that distinguish *Laurencia iriei* (see Fenical and Norris, 1975: figs. 2, 3, as "*L.* sp. II") from *L. fenicalii* and *L. aguilar-rosasorum* are the predominant secondary metabolities, iriediol and irieols A–G, novel brominated diterpenes (Fenical, 1975, 1978; Fenical et al., 1975; Howard and Fenical, 1978), and the dipterpenoid neoirieone (Howard et al., 1982). (See also Remarks under *Laurencia aguilar-rosasorum* and *L. fenicalii*.)

Laurencia johnstonii Setchell et N. L. Gardner

FIGURE 124D

Laurencia johnstonii Setchell et N. L. Gardner, 1924:764, pl. 52: fig. A, pl. 53; Dawson, 1944a:328; 1959a:36; 1963b:453, pl. 156: figs. 1, 2; 1966a:30; Norris, 1973:17; Huerta-Múzquiz, 1978:338; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30; Norris, 1985d:213; González-González et al., 1996:232; Riosmena-Rodríguez et al., 1998:26; L. Aguilar-Rosas et al., 2000:132; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:212.

Laurencia obtusiuscula Setchell et N. L. Gardner, 1924:760, pl. 23: fig. 17, pl. 55; Dawson, 1944a:327 [in part]; 1949c:244; 1959a:36.

Algae usually 10–20 cm tall; bright green and dark green to greenish purple when fresh (upon drying, often very dark to blackish green); of 1 or more erect, cylindrical main axes up to 1.5 mm in diameter, abundantly, multifariously branched; branches mostly 500–1000 μm in diameter, usually crowded with branchlets; ultimate branchlets 300–400(–600) μm in diameter, somewhat constricted at base; attached below by a discoid holdfast and sometimes secondarily by stoloniferous prostrate branches. Outer cortex in surface view of isodiametrical cells near apices, below becoming elongated; not protruding, surface smooth. In transection: medulla of large colorless cells; lenticular thickenings, small in size, occasionally to frequently present in some, apparently lacking in others; cortex of 3–4 cells; outer cortical cells of surface layer not in palisade arrangement.

Tetrasporangia mostly about 70 μm in diameter; abundant in upper portion of elongated, subcylindrical ultimate branchlets. Cystocarps urceolate, sessile, 500–600 μm in diameter; usually 1–2 on ultimate branchlets. Spermatangia in whorls on spermatangial branch of trichoblast terminating with a tear-shaped sterile cell (10–14 μm long by 6–8 μm in diameter); spermatangial branches among sterile long, branched trichoblasts (up to 600 μm long) within broad cup-shaped pit of ultimate branchlets clustered on upper branches (*JN-4304*, US Alg. Coll. microscope slide 5063).

Habitat. On rocks; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Punta Palmilla; Bahía Topolobampo. Eastern Pacific: Punta Morro (vicinity of Ensenada), Baja California, to "Campito," 19.3 km east of Punta Eugenia ("San Eugenio"), on southern shore of Bahía Sebastián Vizcaíno, Baja California Sur.

Type Locality. Isla San Marcos (southeast of Santa Rosalía), Baja California Sur, Gulf of California, Mexico.

Remarks. Studies of the natural product chemistry of *Laurencia johnstonii* resulted in two halogenated sesquiterpenes being described (Fenical, 1975), johnstonol (Sims et al., 1972) and prepacifenol epoxide (Faulkner et al., 1974). Two others, the cyclolauranes laurinterol and debromolaurinterol, which were described by Irie et al. (1970, as *Laurencia intermedia* Yamada, 1931) from the Japanese *Palisada intermedia* (Yamada) K. W. Nam (2007), have been also reported in *Laurencia johnstonii* (Erickson, 1983).

The red alga hemiparasite *Erythrocystis saccata* (J. Agardh) P. C. Silva (1952), although not observed in the northern Gulf of California, has been reported in the southern Gulf on *L. johnstonii* from Cabeza Ballena (Dawson, 1963b:441, pl.156: fig. 1).

Laurencia lajolla E. Y. Dawson

Laurencia lajolla E. Y. Dawson, 1958:77, pl. 24: fig. 12; 1963b:455, pl. 154: fig. 2; 1966a:31; Abbott and Hollenberg, 1976:731, fig. 682; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1986:425; Stewart, 1991:159; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:49; Mateo-Cid and Mendoza-González, 1994b:42; Mendoza-González et al., 1994:109; González-González et al., 1996:232; Mateo-Cid et al., 2000:67; L. Aguilar-Rosas et al., 2000:132; Fernández-García et al., 2011:62.

Algae small, dense, dark red clumps, often forming spreading turfs; of erect terete branched axes, up to 3 cm tall; primary axes sparse with branches, up to 1.5 cm long, that bear short branchlets in upper portions, (600–)700–850 μm in diameter; above a complex entangled system of prostrate, basal branches that attach at several places to substratum by small discs. Cortical cells not in a palisade layer; not projecting terminally; medullary cells without lenticular thickenings.

Tetrasporangia within simple, unmodified, short ultimate branchlets. Cystocarps and spermatangia not known.

Habitat. On rocks and tidal platform; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Isla Bargo, Bahía Concepción; Punta Arena to Cabo Pulmo; Mazátlan. Eastern Pacific: La Jolla (southern California) to Laguna Ojo de Liebre (Scammon's Lagoon); Todos Santos, Baja California Sur; Oaxaca; El Salvador.

Type Locality. Growing among coralline algal turf on reef flat, below the north end of Neptune Place, Wind-and-Sea Beach, La Jolla, San Diego County, southern California, USA.

Remarks. *Laurencia lajolla* is not a well-known species. The collection of reproductive thalli and morphological and molecular DNA testing will help elucidate its taxonomic status. Dawson (1963b) also suggested some of the *Laurencia* collected from Puerto Escondido may also be *L. lajolla*.

Excluded Species:
***Laurencia pacifica* Kylin**

Laurencia pacifica sensu Dawson, 1963b:457 [in part: only Gulf of California specimens; non *Laurencia pacifica* Kylin, 1941:42].

Remarks. Studies have shown that the Pacific Coast *Laurencia pacifica* Kylin is a distinct species (Fenical and Norris, 1975; Howard et al., 1980b). Those in the northern Gulf of California identified as "*L. pacifica*" following Dawson's (1963b) broadly defined species concept are not *L. pacifica* Kylin but are actually three different species that are described herein as new species, *L. aguilar-rosasorum*, *L. fenicalii*, and *L. iriei*. Each of these species has its own unique natural product chemistries and morphologies, which are chemically and morphologically distinct from *L. pacifica* Kylin (lectotype locality: La Jolla, California; Smith, 1944).

Chondrophycus (J. Tokida et Y. Saito) Garbary et J. Harper

Chondrophycus (J. Tokida et Y. Saito) Garbary et J. Harper, 1998:194.

Laurencia subgen. *Chondrophycus* J. Tokida et Y. Saito in Saito, 1967:72.

Algae are erect, terete to strongly compressed, radially or distichously branched up to five orders, and attached by a discoid holdfast or stoloniferous branches. The apices of ultimate branchlets have depressed pits with numerous inconspicuous trichoblasts. Structurally, there is a central axial filament that bears the apical trichoblasts. Each vegetative axial segment has two pericentral cells, with the first pericentral cell developing lateral to the trichoblast (seen only near apical cell). However as the axis continues to develop, this soon becomes obscured and axes appear pseudoparenchymatous in structure. Inner cortical cells are ovoid and comparatively large. Medullary cells are without lenticular thickenings, and may or may not have internal rhizoids among them (Nam, 2011). The outer pigmented epidermal cells are smaller, with a single nucleus or multiple nuclei and mostly without secondary pit connections between them. Epidermal and cortical cells and trichoblasts are without *corps en cerise*.

Tetrasporangial axial segments have 2 sterile pericentral cells (first and second pericentral cells are sterile), and additional fertile pericentral cells are produced that develop tetrasporangia in right-angle arrangement. Gametophytes are dioecious. Procarps developed in segments of five pericentral cells are a four-celled carpogonial branch and a basal sterile group of cells developed on the basal cell of trichoblasts. Cystocarps, with an ostiolate pericarp, are sessile and borne laterally on branches; internally, there is a basal fusion cell and branched gonimoblast that produces terminal carposporangia. Spermatangial branches are produced within cup-shaped pits from two laterals on the suprabasal cell of a trichoblast that remains partly sterile. Spermatangia are in lateral whorls around spermatangial branches that terminate with a large, sterile globose cell.

Remarks. Garbary and Harper (1998), in recognizing *Chondrophycus* as a distinct genus, noted that there is a delay in the formation of auxiliary cells after presumed fertilization (Nam and Sohn, 1994) and that the larger spermatangia (greater than 10 μm long) may also be useful diagnostic characters.

There is one species of *Chondrophycus* reported in the northern Gulf of California.

Chondrophycus glanduliferus (Kützing) Lipkin et P. C. Silva

Chondria glandulifera Kützing, 1845:329.

Chondrophycus glanduliferus (Kützing) Lipkin et P. C. Silva, 2002:35.

Laurencia glandulifera (Kützing) Kützing, 1849:855; Abbott, 1999:386, pl. 112C,D; Mateo-Cid et al., 2006:57.

Chondria obtusa var. *paniculata* C. Agardh, 1822:342.

Laurencia paniculata sensu Saito, 1969b:158; Mendoza-González and Mateo-Cid, 1986:425; McDermid, 1988b:236, fig. 21 [non *Laurencia paniculata* Kützing, 1849:855; non *L. paniculata* (C. Agardh) J. Agardh, 1852b:755, *nom illeg*.].

Algae of several axes, up to 12 cm tall; arising from a discoid holdfast. Primary axes divided 2–3 times; lower portions bare; upper portions branched up to 4 orders, uppermost dense with small alternate to opposite short lateral branchlets. Medullary cells with thick cell walls (evident in older thalli), but without lenticular thickenings. Outer cortical cells radially elongate (description after Abbott, 1999).

Reproduction not described for Gulf of California specimens (Mateo-Cid et al., 2006).

Habitat. Intertidal.

Distribution. Gulf of California: Puerto Peñasco; Isla Tiburón (Islas de la Cintura). Central Pacific: Hawaiian Islands. Western Pacific: Korea; Hong Kong.

Type Locality. Trieste, Gulf of Trieste, Adriatic Sea, northeastern Italy.

Remarks. The report of *Chondrophycus glanduliferus* in the upper Gulf of California is based on the record of Mateo-Cid et al. (2006) and from Isla Tiburon (Mendoza-González and Mateo-Cid, 1986, as "*Laurencia paniculata*"). Since I have not seen their specimens, the description is based on Abbott (1999). *Laurencia paniculata* (C. Agardh) J. Agardh (1852b) has been considered conspecific with *C. glanduliferus* (e.g., Abbott, 1999; John et al., 2004). (Note that this is a different species than *Laurencia paniculata* Kützing (1849), which is recognized to be a *Palisada* herein.) The Puerto Peñasco *C. glanduliferus* (Mateo-Cid et al., 2006) should be compared with type locality *C. glanduliferus* of the Adriatic Sea and the northern Gulf *Palisada paniculata* and *P. pedrochei* to elucidate their relationships.

Osmundea Stackhouse

Osmundea Stackhouse, 1809:56, 79; Nam et al., 1994:384.

Thalli of the Gulf of California species are usually compressed to flattened, and branching is distichous, rarely radial.

Ultimate branchlets with apical pit or depression with a tuft of inconspicuous, deciduous trichoblasts. The apical cell is always sunken in the apical pit of branchlets, and the central axial filament with its 2 pericentral cells per axial cell (vegetative segment), can be distinguished only near the apical cell, being obscured below by the formation of an extensive cortex. Secondary pit connections between epidermal cells are absent in some or, if present, are variable, frequent to rare. *Corps en cerise* (gland cells) are apparently absent in the known species.

Tetrasporangia develop from random, outer cortical (epidermal) cells with longitudinal cover cells in parallel arrangement. Female gametophytes form 5 pericentral cells in the procarp-bearing segment of the female trichoblast. Cystocarps lack or may have ostioles that are usually protuberant. Spermatangia develop on filaments formed by apical and epidermal cells ("filament type") that either lack or may terminate with 1 to a cluster of enlarged sterile cells. Spermatangial filaments develop in urn-shaped (pocket) spermatangial depressions (North Pacific species); in cup-shaped spermatangial depressions (European species); or rarely in slightly sunken cup-shaped depressions.

REMARKS. *Laurencia* sect. *Pinnatifidae* J. Agardh (1876) as defined by Saito (1982) was later emended and merged into *L.* subgen. *Saitoa* G. Furnari et Serio, 1993, *nom. illeg.,* a group now recognized to contain many members of *Osmundea* (McIvor et al., 2002). Although spermatangial development in urn-shaped receptacles (pocket; depressions) was reported to be only in the genus *Osmundea* (Nam et al., 1994), further studies showed that not all of the species of *Osmundea* have this character (Garbary and Harper, 1998; Serio et al., 1999; Nam et al., 2000; McIvor et al., 2002). Comparative morphological and molecular phylogenetic studies found three clades from three different geographical regions (McIvor et al., 2002). The North American (California) clade had a fixed, urn-shaped spermatangial receptacle, and the number of secondary pit connections in the surface cortical cells was variable. In contrast, the two European clades showed character reversals: spermatangial receptacles were cup-shaped in both, and the two were distinguishable by the presence or absence of secondary pit connections between epidermal cells. However, McIvor et al. (2002) also question the sole use of morphological characters in infrageneric subdivision of *Osmundea*.

Agar has been found to be a component in at least one of the species, *Osmundea pinnatifida* (Hudson) Stackhouse (1809), by Bowker and Turvey (1968a, 1968b, as "*Laurencia pinnatifida*"). It is not known at this time whether any of the species from the northern Gulf of California produce agar. Apparently the species of *Osmundea* have not evolved antiherbivore secondary metabolites (Hommersand, 1990; McIvor et al., 2002) as found in *Laurencia* (e.g., Fenical, 1975; Norris and Fenical, 1982, 1985).

Species of *Osmundea* mostly occur in temperate waters and are known only on the coasts of Pacific North America and the Atlantic and Mediterranean coasts of Europe (Serio et al., 1999, Nam et al., 2000; McIvor et al., 2002). A tropical Pacific Mexico species, *O. purepecha* Sentíes, Mendoza-González et Mateo-Cid, described from Michoacán (Sentíes et al., 2014) is distinguished from those in the Gulf by its unique stoloniferous holdfast and genetic analyses.

There are three species of *Osmundea* occurring in the northern Gulf of California.

KEY TO THE SPECIES OF *OSMUNDEA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus usually large, 5–10 cm tall, with relatively wide flat branches, mostly 3–4 mm wide, with short, blunt subterete branchlets on flattened distal portions of branches; initial branching distichous to subdistichous, alternate; attached by a small discoid holdfast; medullary cells without lenticular thickenings . . . . **O. estebaniana**

1b. Thalli comparatively shorter, mostly less than 4.0(–9) cm tall; branching open or dense, flat branches 1–4 mm wide; medullary cells with or without lenticular thickenings 2

2a. Thalli epiphytic, somewhat lax; flat branches up to 2(–4) mm wide; branching distichous throughout, irregularly alternate-pinnate; medullary cells without or sometimes with lenticular thickenings (especially in large specimens) . . . **O. sinicola**

2b. Thalli growing on rocks (not epiphytic), rigid, crisp, compact; flat branches wider, 3–4 mm in width; branching alternately distichous, obscured by dense crowding of branches; attached by spreading basal crust; medullary cells without lenticular thickenings . . . . **O. blinksii**

Osmundea blinksii (Hollenberg et I. A. Abbott) K. W. Nam

Laurencia blinksii Hollenberg et I. A. Abbott, 1965:1186, pl. 2: fig. 5; Hollenberg and Abbott, 1966:117, fig. 52; Smith, 1969:727, fig. 52; Saito, 1969a:87; Abbott and Hollenberg, 1976:728, fig. 678; Riosmena-Rodríguez et al., 1998:26.

Osmundea blinksii (Hollenberg et I. A. Abbott) K. W. Nam in Nam, Maggs and Garbary, 1994:393; Pacheco-Ruíz et al., 2008:213.

Algae erect, forming dense, expanding tufts, 4–7 cm tall and nearly as wide; of cartilaginous, crisp flattened axes (except near the base), more or less alternately distichously branched (distichous branching becoming obscure by divergent growth and crowding of branches); branches lanceolate–conical, pyramidal in outline, 3–4 mm in width (see Abbott and Hollenberg, 1976: fig. 678); axes arising from spreading basal crust, about 3–4 cm wide. Medulla of large cells, 300–400 μm long, 60–150 μm in diameter, without lenticular thickenings. Cortex in surface view of pigmented cortical cells, 25–45 μm long, 13–15 μm wide; cortical cells in transection, slightly radially elongated to deeply anticlinal in smaller branches, 15–30 μm deep; secondary pit connections between epidermal cells very rare. Epidermal cells nonpalisade in arrangement; secondary pit connections between epidermal cells very rare.

Reproductive branches irregularly lobed or divided. Tetrasporangial branches fungiform or alternately branched; tetrasporangia in parallel arrangement (see Saito, 1969a: fig. 4A). Cystocarps unknown. Male gametophyte with spermatangial filaments in deep ovoid cavities (urn-shaped); following formation of initial spermatangial cavity, subsequent cavities formed upwards; more or less irregularly arranged on short subultimate branchlets (see Saito, 1969a: fig. 5A, B).

HABITAT. On rocks; low intertidal.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles. Eastern Pacific: central California.

TYPE LOCALITY. Exposed rocky shores; just south of Malpaso Creek, Monterey County, central California, USA.

REMARKS. A California species, *Osmundea blinksii* has also been reported in the northern Gulf by Riosmena-Rodríguez et al. (1998). Since I have not seen their material, the description is based on Abbott and Hollenberg (1976) and Saito (1969a), both as *Laurencia blinksii*.

Osmundea estebaniana (Setchell et N. L. Gardner) J. N. Norris, *comb. nov.*

FIGURE 125A,B

Laurencia estebaniana Setchell et N. L. Gardner, 1924:763, pl. 24: fig. 34, pl. 45: fig. a [type specimen]; Dawson, 1944a:328; 1963b:451, pl.

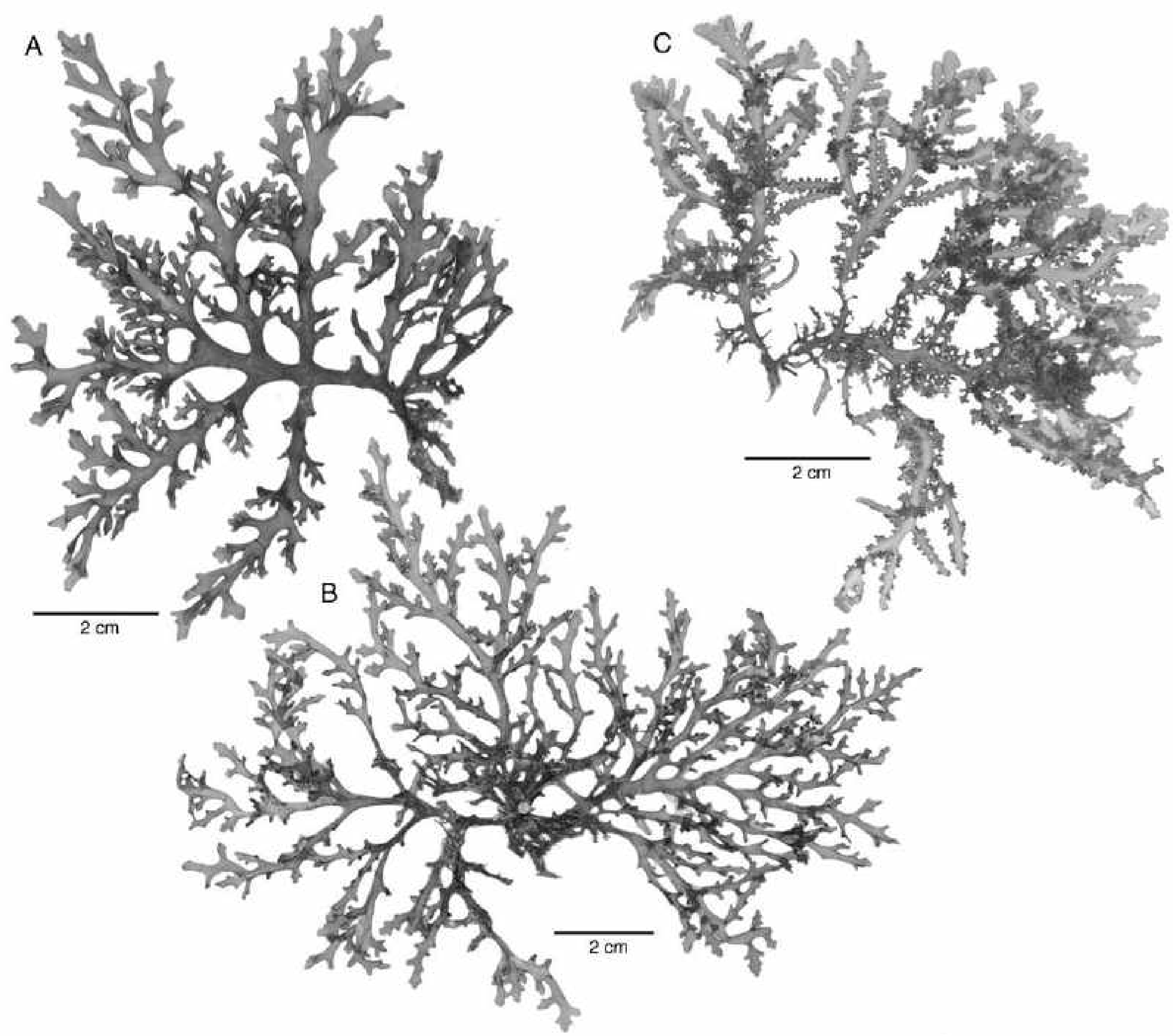


FIGURE 125. Species of *Osmundea*. A, B. *Osmundea estebaniana*: A. Habit (*JN-5832*, US Alg. Coll.-160119). B. Habit (*JN-5273*, US Alg. Coll.-160111). C. *Osmundea sinicola:* Habit of large robust specimen (*D. Bean, s.n.*, US Alg. Coll.-30106).

146: fig. 2; Norris, 1973:17; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:232; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:212.

Algae up to 10 cm tall; of distinctly compressed axes, 2.0–4.0 mm wide, branched up to 4(–5) orders; attached by small discoid holdfast. Branching distichous to subdistichous, mostly alternately from primary and secondary axes; later, shorter blunt subterete branchlets may develop from flattened surfaces of distal branches. Medullary cells large, colorless, without lenticular thickenings. Cortical cells, isodiametrical, 12–25 µm in diameter. *Corps en cerise* absent.

Ultimate branchlets with reproductive structures; short, subcylindrical to rounded (wart-like), few to several subdistichous to subverticillately arranged. Tetrasporangia in short nearly cylindrical branchlets. Cystocarps on short nearly cylindrical branchlets. Spermatangial branchlets turbinate; spermatangia in dense, short clusters, surrounding simple spermatangial filament that terminates with a distinctive, large, subglobose sterile cell, 20–25 µm long, 16–20 µm in diameter (see Setchell and Gardner, 1924: pl. 24: fig. 34, "filament type"); spermatia 2–3 µm in diameter.

Habitat. On rocks; low intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía Agua Dulce, Isla Tiburón and Isla San Esteban (Islas de la Cintura); Isla Coronado (Isla Smith) to Bahía San Francisquito; Bahía de Loreto; Bahía de Banderas, Nayarit-Jalisco.

Type Locality. On rocks; Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

Remarks. A Gulf of California endemic, the largest specimens of *Osmundea estebaniana* have been found in Las Islas de la Cintura. The slender, subcylindrical southern Gulf specimens referred to "*O. estebaniana*" from Puerto Escondido by Dawson (1963b, as "*L. estebaniana*") may be another species.

Osmundea sinicola (Setchell et N. L. Gardner) K. W. Nam

FIGURE 125C

Laurencia sinicola Setchell et N. L. Gardner, 1924:764, pl. 29: figs. 65, 66, pl. 50: fig. a [type specimens]; Dawson, 1944a:328; 1959a:36; 1961b:455; 1963b:461, pl. 146: fig. 1, pl. 166: figs.1, 2; 1966a:31; Abbott and Hollenberg, 1976:732, fig. 685; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30; Mendoza-González and Mateo-Cid, 1986:425; Sánchez-Rodríguez et al., 1989:47; R. Aguilar-Rosas et al., 1990:126; R. Aguilar-Rosas and Machado-Galindo, 1990:188 ; Stewart, 1991:160; Mateo-Cid et al., 1993:49; R. Aguilar-Rosas and Aguilar-Rosas, 1994:525; González-González et al., 1996:234; Riosmena-Rodríguez et al., 1998:26; Cruz-Ayala et al., 2001:191; Pacheco-Ruíz and Zertuche-González, 2002:469.

Osmundea sinicola (Setchell et N. L. Gardner) K. W. Nam in Nam et al., 1994:393; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2006:57; Serviere-Zaragoza et al., 2007:11; Pacheco-Ruíz et al., 2008:213; Castañeda-Fernández de Lara et al., 2010:200; Fernández-García et al., 2011:62.

Laurencia scrippsensis E. Y. Dawson, 1944b:234, pl. 26: fig. 3, pl. 27: figs. 1, 2, 4; 1945d:68; 1951:53; 1952:431; 1961b:454; González-González et al., 1996:234.

Algae epiphytic; caespitose, compressed, dark reddish brown, (1.0–)4.0–9.0 cm high, 1.0–2.0 (–4.0) mm wide, and 400–500 µm thick; branching irregularly alternate-pinnate in 1 plane (tetrasporophytes more regularly pinnate). Secondary pit connections between surface cortical cells rare. Medullary cells 70–90 µm in diameter, thin walled; lenticular thickenings absent, or rare to abundant (mostly seen in larger thalli; generally absent in smaller ones). Cortical cells 20–30(–50) µm in diameter. Arrangement of epidermal cells nonpalisade.

Tetrasporangia in short, simple to digitate branchlets. Cystocarps ovoid to hemispherical, 600–800 µm in diameter; scattered, on margins and surfaces of irregularly branched ultimate branchlets. Spermatangial filaments within urn-shaped receptacles; receptacles solitary or in series; embedded in subterminal portions of ultimate branchlets.

Habitat. Usually epiphytic on other algae; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía San José del Cabo. Eastern Pacific: Santa Cruz Island (California Channel Islands); Islas Todos Santos (Baja California); La Jolla, southern California to Isla Magdalena (Bahía Magdalena), Baja California Sur; Isla San Benedicto (Islas Revillagigedo); Panama.

Type Locality. Epiphytic on *Sargassum*; Eureka (vicinity of La Paz: 23°36′N, 109°36′W), Baja California Sur, Gulf of California, Mexico.

Remarks. Dawson (1963a, as *Laurencia sinicola*) observed that during fall–winter, the smaller thalli of *Osmundea sinicola* had thin-walled medullary cells without lenticular thickenings, whereas during summer the thalli he referred to this species were larger and had developed abundant lenticular thickenings. Season and growth may play a role in the development of lenticular thickenings, at least for this species. The range of thallus size and variability of anatomical characters suggests this is either a single, broadly defined species or possibly a complex of more than one species.

Palisada K. W. Nam

Palisada K. W. Nam, 2007:53.

Palisada K. W. Nam, 2006:693, *nom. illeg.*

Laurencia sect. *Palisadae* Yamada, 1931:190.

Chondrophycus subgen. *Palisada* (Yamada) K. W. Nam, 1999:467.

Algae are mostly terete to subterete. Ultimate branchlets have an apical pit or depression with a tuft of inconspicuous trichoblasts. The apical cell is also sunken within the apical pit, and the central axis can only be seen near the apical cell (becoming obscured by formation of an extensive cortex). The vegetative axial segments have two pericentral cells, with the first pericentral cell developed underneath the basal cell of the trichoblast. The cortical (epidermal) cells, as seen in transection, are in a palisade-like arrangement (most evident in branches), with secondary pit connections mostly absent between adjacent cells. Medullary cell walls can be wide, but are without lenticular thickenings. *Corps en cerise* are apparently absent or rare.

Tetrasporangia develop on specific pericentral cells; the first pericentral cell remains sterile and the second pericentral cell is fertile, and an additional third pericentral cell (and in some species a fourth) is issued that also develop tetrasporangia. Procarps are borne on fertile segments of four or five pericentral cells on a female trichoblast. Auxiliary cells are normally developed after presumed fertilization. Spermatangial branches are produced from one of two laterals on the suprabasal cells of the trichoblasts, "trichoblast-type development" (reproduction after Nam, 2006, 2007, 2011; Cassano et al., 2009).

REMARKS. Agar has been reported in the cell wall polysaccharides from a few of the species, e. g., *Palisada perforata* (Bory Saint-Vincent) K. W. Nam (2007) in Tanzania (Mshigeni and Nzalalila, 1977, as "*Laurencia papillosa*"), and *P. flagellifera* (J. Agardh) K. W. Nam (2007) from Brazil (Ferreira et al., 2012). The polysaccharide chemistries of species from the northern Gulf of California have not yet been investigated.

Palisada perforata (Bory de Saint-Vincent) K. W. Nam (2007) has been reported in the southern Gulf from Bahía de La Paz (Cruz-Ayala et al., 2001, as "*Laurencia papillosa*"). These Gulf specimens should be reexamined and compared to *Palisada pedochei* and *P. papillosa* (C. Agardh) K. W. Nam (2007, 2011).

Currently, two species of *Palisada* are recognized in the northern Gulf of California. In the field, *Palisada paniculata* and *P. pedrochei* are the coarsest, widest in diameter, and sometimes the largest among the cylindrical species of the tribe Laurencieae known in the Gulf of California.

KEY TO THE SPECIES OF *PALISADA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Ultimate branchlets not dense, but loosely disposed, mostly peg-like (some may be partly wart-like) . . . . . ***Palisada paniculata***
1b. All branches densely covered with very short, wart-like ultimate branchlets . . . . ***Palisada pedrochei***

Palisada paniculata* (Kützing) J. N. Norris, *comb. nov.

FIGURES 8E, 126A–D

Laurencia paniculata Kützing, 1849:855; Kützing, 1865:22, pl. 63: figs. a-b [illustrations designated as lectotype herein; non *Laurencia paniculata* (C. Agardh) J. Agardh, 1852b:755; basionym: *Chondria obtusa* var. *paniculata* C. Agardh, 1822:343; Yamada, 1931:192, pl. 3a (type specimen); see Remarks below].

Laurencia paniculata sensu Howe, 1911:508; Setchell and Gardner, 1924:762; Dawson, 1944a:326; 1963b:459, pl. 145: fig. 5, pl. 155: figs. 1, 2; 1966a:31; Saito, 1969b:158; Norris, 1973:17; Huerta-Múzquiz, 1978:337; Stewart and Stewart, 1984:147; Mendoza-González and Mateo-Cid, 1986:425; González-González et al., 1996:233; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:469; Pacheco-Ruíz et al., 2008:213 [non *Laurencia paniculata* (C. Agardh) J. Agardh, 1852b:755, *nom. illeg.* (see Furnari et al., 1999:44); =*Chondrophycus paniculatus* (C. Agardh) G. Furnari in Boisset et al., 2000:393, *nom. illeg.*, which is now *Palisada thuyoides* (Kützing) Cassano, Sentíes-Granados, Gil-Rodriguez et M. T. Fujii (in Cassano et al., 2009:95); basionym: *Laurencia thuyoides* Kützing, 1865:26].

Algae up to 12 cm tall, somewhat coarse and bushy, usually dark reddish; of a single main axis, often abundantly branched up to 5 orders; axis and branches, cylindrical, up to 1.5 mm in diameter in upper portions and up to 2.5 mm in diameter in lower portions; secondary branches tending to percurrent and pyramidal; attached by a coarse, discoid holdfast. Branch intervals somewhat variable, usually 3–10 mm in lower thallus; branches with wart-like to peg-like ultimate branchlets, not dense or crowded, giving an open appearance. Medulla of larger cells, without lenticular thickenings. In transaction, epidermal cells are rectangular, 25–35 µm long and about 10–16 µm in diameter, in palisade-like arrangement.

Tetrasporangia embedded in upper portion of short, turbinate branchlets. Cystocarps urceolate or hemispherical, 600–800 µm in diameter on ultimate branchlets. Spermatangia not seen in Gulf of California specimens.

HABITAT. On rocks and tidal platforms and in tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Isla San Jorge (Bird Island); Puerto Peñasco to Guaymas; Puerto Refugio, Isla Ángel de la Guarda; Bahía de Los Ángeles to Cabeza Ballena. Eastern Pacific: Isla Guadalupe (off Baja California); Islas San Benito (west of Isla Cedros).

TYPE LOCALITY. Syntype localities: in Adriatic and Mediterranean Seas (Kützing, 1849:855); lectotype locality: "mari mediterraneo" (Kützing, 1865:22).

REMARKS. Morphologically, *Laurencia paniculata* Kützing (1849) has the characteristics of *Palisada*, and the new combination is proposed. In the absence of a known type specimen, the illustration of Kützing (1865: pl. 63: figs. a, b; herein Figure 126A) of *Laurencia paniculata* Kützing (1849) are selected as the lectotype.

The epithet "*paniculata*" has been used for more than one taxa. First, the name was used to describe a variety, *Chondria obtusa* var. *paniculata* C. Agardh (1822), which was then transferred to *Laurencia,* as *L. paniculata* (C. Agardh) J. Agardh (1852b); that name and those authors have long been used in the literature (e.g., De Toni, 1903; Yamada, 1931; Dawson, 1963b; McDermid, 1988b; Abbott, 1999, as *Laurencia glandulifera*). Unfortunately, as noted by Furnari et al. (1999), J. Agardh's (1852b) use of that name created a later homonym of *Laurencia paniculata* Kützing (1849). Furnari et al. (1999) also suggested *L. paniculata* Kützing (1849) may taxonomically be conspecific with *Osmundea ramosissima* (Oeder) Athanasiadis (1996b; basionym: *Fucus ramosissimus* Oeder, 1766), and Boisset et al. (2000) noted that according to Ardissone (1883), *L. paniculata* Kützing may be conspecific with "*Laurencia pinnatifida*" (probably *L. pinnatifida* (Hudson) J. V. Lamouroux (1813); basionym: *Fucus pinnatifidus* Hudson, 1762, which is now *Osmundea pinnatifida* (Hudson) Stackhouse, 1809). Thus, there is confusion on its taxonomic status, and it is suggested

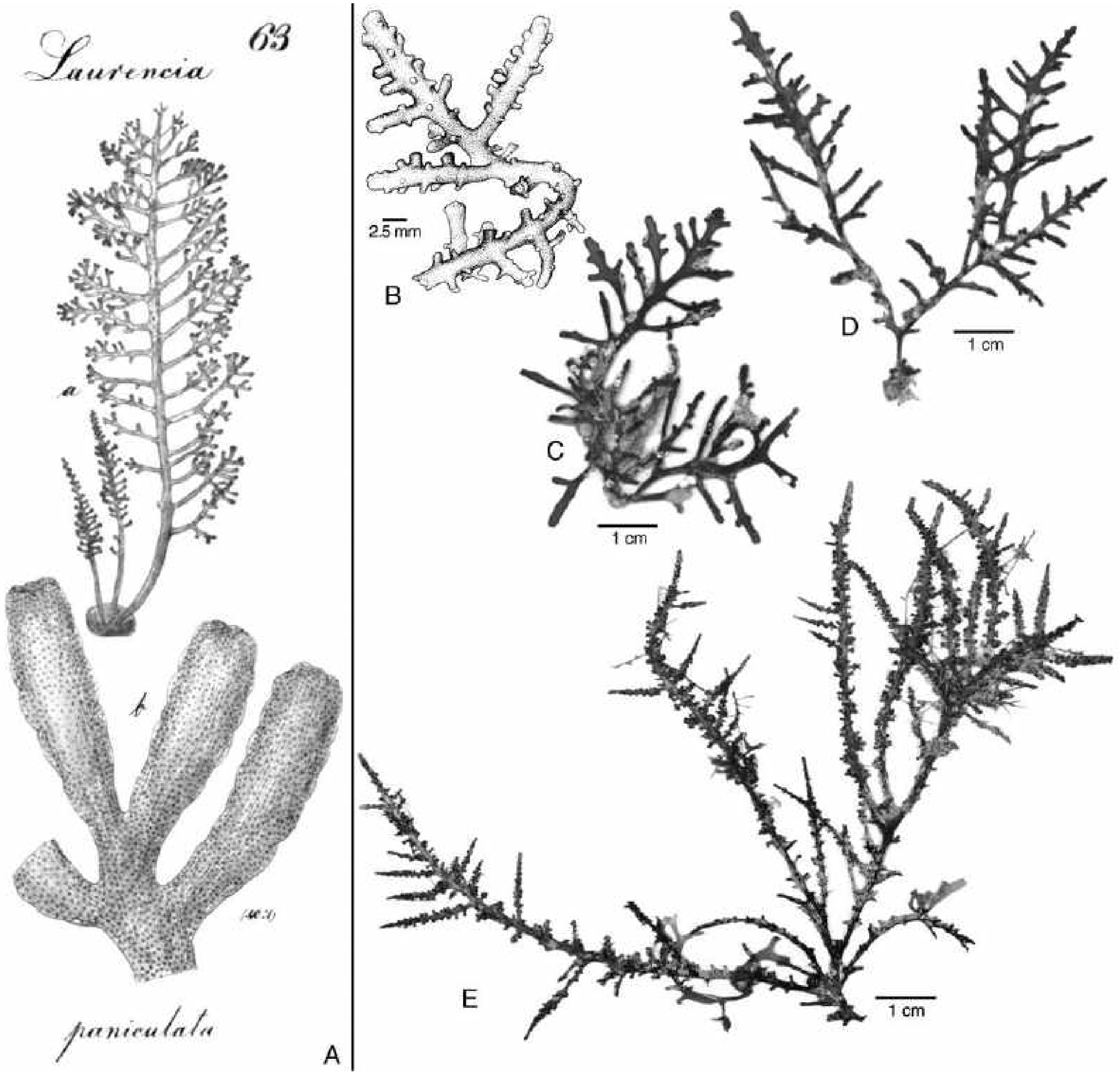


FIGURE 126. Species of *Palisada*: A–D. *Palisada paniculata*: A. Lectotype illustration selected of *Laurencia paniculata* Kützing (from Kützing, 1865: pl. 63a,b). B. Habit of a small part of a slender form (from Dawson, 1963b: pl. 145: fig. 5). C, D. Habits (*JN-5006*, US Alg. Coll.-160223).E. *Palisada pedrochei*: Habit (holotype, *JN-5879*, US Alg. Coll.-160250).

that *L. paniculata* Kützing (1849) sensu stricto be based on its lectotype illustrations (Figure 126A) until molecular analyses on its type locality material can be performed to compare it with other taxa.

Another similar-looking species, *Laurencia thuyoides* Kützing (1865:26, pl. 74: figs. a, b) was considered to be conspecific with "*L. paniculata* (C. Agardh) J. Agardh" by Yamada (1931), a conclusion followed by Boisset et al. (2000, as *Chondrophycus paniculatus* (C. Agardh) G. Furnari). Since that combination was illegitimate, Furnari et al. (2001) subsequently proposed another name for the taxon, *C. thuyoides* (Kützing) G. Furnari (basionym: *L. thuyoides* Kützing, 1856). More recently, it was transferred to *Palisada*, as *P. thuyoides* (Kützing) Cassano, Sentíes-Granados, Gil-Rodriguez et M. T. Fujii (in Cassano et al., 2009; =*P. thuyoides* (Kützing) Serio, Cormaci, G. Furnari et Boisset, 2010:14, *nom. illeg.*).

The northern Gulf of California specimens referred to *Palisada paniculata* (Kützing) J. N. Norris need to be tested in comparative molecular studies with *L. paniculata* Kützing (lectotype locality: Mediterranean Sea), the Adriatic "*L. paniculata* (C. Agardh) J. Agardh" (type locality: Trieste, Italy), *L. pinnatifida* (Hudson) J. V. Lamouroux (type locality: Harwick, Essex, England), *Chondrophycus glanduliferus* (Kützing) Lipkin et P. C. Silva (type locality: Trieste, Italy), the South Pacific *Palisada thuyoides* (type locality: New Caledonia), and the eastern and western Atlantic *P. thuyoides* (Cassano et al., 2009) to further elucidate the relationships and taxonomic status of these geographically widespread but somewhat similarly looking species.

Palisada pedrochei J. N. Norris, *sp. nov.*

FIGURE 126E

Laurencia papillosa var. *pacifica* Setchell et N. L. Gardner, 1924:765, pl. 23: fig. 18, pl. 24: fig. 34, pl. 43a,b, pl. 54 [type specimen: *Marchant-38*, CAS, now UC]; Dawson, 1944a:327; 1959a:36; 1961b:454; 1963b:460, pl. 166: fig. 3; Norris, 1973:16; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:30; Sánchez-Rodríguez et al., 1989:47; Mateo-Cid and Mendoza-González, 1992:22; Mendoza-González and Mateo-Cid, 1992:20; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid and Mendoza-González, 1994b:42; González-González et al., 1996:233; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:26; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:469; Mateo-Cid et al., 2006:57; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:213.

LATIN DESCRIPTION. Thalli ad 13 cm altus; plus minus forma pyramidalis, purpureo brunneo ad atro-rubio colore, axes principales teres percurrentes, ramosae 3–4 ad ordines, ramulis lateralis primam ad 6.5 cm longis, 1.5 ad 2.5 mm diametro, inter breviores aliquot quae ramis plerumque dense ramosae brevibus ramulis ultimis ut turbinata. Cortex in transection de radialiter rectangulae cells, ordinate in vallumque-amolayer; cortical cells, aspectu superficiali, polygoniis, tenui-membranis, 18–22 µm in diametro. Sine cellulis lenticellis medullare inspissato. Tetrasporangial sphaerica circa 100 µm diametro infra circa ramulis ultimi depression terminali. Cystocarpiis non describet. Verticillis in spermatangia in axial fiament cessat in uno terminari, large cell pyriformis.

Algae erect, up to 13 cm tall, somewhat pyramidal in shape; dark red, brownish to purplish (drying blackish brown); terete main axes percurrent, branched to 3–4 orders; with primary lateral branches up to 6.5 cm long, 1.5–2.5 mm in diameter, each with several shorter branches; covered, usually densely, with short, subspherical to turbinate, ultimate branchlets. In transection the outer cortical cells are elongated and rectangular, arranged in a palisade-like layer; cortical cells in surface view, polygonal, thin walled, 18–22 µm in diameter. Medullary cells without lenticular thickenings.

Tetrasporangia spherical, about 100 µm in diameter; within the ultimate branchlets around their apical depression. Cystocarps not observed. Spermatangia in whorls around dense spermatangial branches borne off one lateral of trichoblast, each spermatangial branch terminated by a single, large pyriform cell.

HABITAT. On rocks, tidal platforms, and sides of tide pools; high to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Kino (Sonora); El Coloradito (Baja California) to Punta Palmilla (Baja California Sur); Nayarit to Jalisco. Eastern Pacific: Bahía Magdalena to Todos Santos, Baja California Sur; Isla Clarión (Islas Revillagigedo).

HOLOTYPE. *JN-5879* (US Alg. Coll.-160250).

TYPE LOCALITY. On tidal platform; Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Gulf of California, Mexico.

ETYMOLOGY. *Palisada pedrochei* is named for Francisco F. Pedroche (Rector de la Unidad Lerma and Professor, Departamento de Ciencias Ambientales, División de Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana-Lerma, Lerma de Villada, Mexico) in recognition of his continuing contributions to our knowledge of the marine algae of Pacific Mexico, including the Gulf of California.

REMARKS. Morphologically, *Palisada pedrochei* is the same as the variety *Laurencia papillosa* var. *pacifica* Setchell et N. L. Gardner (1924) described from Eureka (near La Paz, Baja California Sur) in the southern Gulf. Since there is no priority outside of rank (International Code of Botanical Nomenclature [ICBN]; McNeill et al., 2006; 2012), I chose to describe it as a new species to avoid any confusion that might be created by using the name "*pacifica,*" an epithet already used for both *L. papillosa* var. *pacifica* and *L. pacifica* Kylin (1941).

Specimens of Setchell and Gardner (1930, as "*L. papillosa* var. *pacifica*") from Isla Guadalupe (Pacific Baja California) appear to be a different species and need to be further studied.

RHODOMELACEAE TRIBUS POLYSIPHONIEAE

Rhodomelaceae tribus Polysiphonieae F. Schmitz, 1889:147.

REMARKS. The tribe Polysiphonieae is represented by two of its genera in the northern Gulf of California.

Neosiphonia M.-S. Kim et I. K. Lee

Neosiphonia M.-S. Kim et I. K. Lee, 1999:272.

Algae composed of terete, polysiphonous axes and branches of 4–9 pericentral cells per segment that may be corticated or uncorticated and are attached at irregular intervals by mostly unicellular rhizoids cut off from basal pericentral cells or cortical cells by a cross wall. Branching is mostly alternate to several orders and sometimes profuse or dense. Branches and ultimate branchlets are basically similar to main axes and primary branches, and most develop exogenously but sometimes may be formed in connection with a trichoblast or rarely cicatrigenous (lateral branches originating from scar cells). Trichoblasts are colorless, slender, simple or forked filaments formed at regular intervals, 1 per segment, and spirally arranged, most common near branch apices; deciduous, often leaving conspicuous scar cells.

Tetrasporangia tetrahedrally divided; borne in spiral series, one per segment, developed on the second pericentral cell next to the basal cell of a trichoblast on indeterminate branches. Procarps bearing a 3-celled carpogonial branch. Cystocarps are subglobose to ovate, borne on a short pedicel, and scattered on the upper branches. Spermatangial branchlets (stichidia) develop on 1 branch fork of a fertile trichoblast;cylindrical in shape, some may have 1(–2) short sterile cell(s) at tip.

Remarks. In describing *Neosiphonia,* M.-S. Kim and Lee (1999) noted that the genus differs from the similar *Polysiphonia* in vegetative and reproductive characters. These have long been used by Hollenberg (e. g., 1942a, 1942b, 1944, 1961, 1968a, 1968b; Abbott and Hollenberg, 1976; Hollenberg and Norris, 1977) as species characters to distinguish taxa of a broadly defined *Polysiphonia*. As currently recognized, *Neosiphonia* has lateral branch initials and trichoblast initials produced on successive segments; determinate branches that develop from the main axes; attachment rhizoids are cut off from pericentral cell by a cross wall; trichoblasts are spirally arranged and usually abundant; tetrasporangia are in spiral series; carpogonial branch is three-celled; and spermatangia develop on one fork of a trichoblast.

The relationship of *Neosiphonia* to another genus, *Carradoriella* P. C. Silva (in Silva et al., 1996a, generitype *C. virgata* (C. Agardh) P. C. Silva, a replacement name for *Carradoria* Kylin, 1956 [non *Carradoria* C. Martius, 1833]) needs to be investigated. Although noting that *Neosiphonia* shares some generic characters with *Polysiphonia* sensu stricto, H.-G. Choi et al. (2001a) also suggested that *Carradoriella*, on the basis of their molecular analyses, may be the same as *Neosiphonia* or possibly a sister taxon. Until critical comparative morphological studies, particularly of reproductive structures, and further DNA genetic comparisons that include the respective generitypes are carried out, *Neosiphonia* is recognized herein.

Species of *Neosiphonia* are found growing as epiphytes on other algae or seagrasses, epizoic on sea turtles, or on rocks or other hard substrata. There are three species reported in the southern Gulf: *Neosiphonia bajacali* (Hollenberg) Mamoozadeh et Freshwater (2011; basionym: *Polysiphonia bajacali* Hollenberg, 1961) from Laguna Agiabampo (Ortega et al., 1987, as *P. bajacali*) and Jalisco (Hernández-Herrera et al., 2005, as *P. bajacali*); *N. sphaerocarpa* (Børgesen) M.-S. Kim et I. K. Lee (1999) from Nayarit (Sentíes-G., 1995, as *P. sphaerocarpa*; see also Remarks under *N. savatieri*); and *N. beaudettei* (Hollenberg) M.-S. Kim et I. A. Abbott (2006; basionym: *Polysiphonia beaudettei* Hollenberg, 1961) from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985, as *P. beaudettei*).

There are 11 species of *Neosiphonia* in the northern Gulf of California.

KEY TO THE SPECIES OF *NEOSIPHONIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Polysiphonous filaments with 4 pericentral cells per segment; *Neosiphonia* sect. *Neosiphonia* 2
1b. Polysiphonous filaments with 5 or more pericentral cells per segment; *Neosiphonia* sect. *Multisiphonia* 7
2a. Branching dichotomous throughout . . . . ***N. masonii***
2b. Branching subdichotomous (not strictly dichotomous) 3
3a. Epizoic; only known growing on sea turtle carapace . . . . ***N. cheloniae***
3b. Either epiphytic or saxicolous; not growing on sea turtles 4
4a. Branches arising from a primary branch of a trichoblast (axillary to a trichoblast) . . . . ***N. flaccidissima***
4b. Branches arising from an entire trichoblast primordium 5
5a. Thalli mostly less than 2 cm high; epiphytic . . . . ***N. savatieri***
5b. Thalli mostly more than 2 cm tall; usually not epiphytic 6
6a. Segments in main branches mostly shorter, not as long as diameter or sometimes as long as wide . . . . ***N. simplex***
6b. Segments in main branches longer than wide; mostly 1.5 times longer (or occasionally longer) than diameter . . . ***N. eastwoodae***
7a. Pericentral cells 5 per segment; segments shorter in length than diameter . . . . ***N. concinna***
7b. Pericentral cells 5 or more per segment; segments of similar length and diameter or longer 8
8a. Pericentral cells 5–6 per segment; segments 1.5 times longer or more than diameter . . . . ***N. johnstonii***
8b. Pericentral cells 6 or more per segment; segments of similar length and diameter or slightly longer or up to about 2.0–4.0 times longer than diameter 9
9a. Thalli minute, up to 2 mm tall; prostrate axes and lower portion of erect branches mostly of 6 pericentral cells per segment; upward in erect portions the 6 pericentral cells divide to 12 pericentral cells per segment . . . . ***N. mexicana***
9b. Thalli much larger, more than 1 cm tall; prostrate and erect axes and branches with similar number of pericentral cells, 8 or more per segment 10
10a. Thalli mostly less than 2 cm high; segments more or less equal in length and diameter to only slightly longer in length than diameter . . . . ***N. confusa***
10b. Thalli usually much larger, up to 20 cm tall; segments 2.0–2.5(–4.0) times longer than diameter . . . . . . ***N. paniculata***

Neosiphonia M.-S. Kim et I. K. Lee sect. *Neosiphonia*

Members of *Neosiphonia* sect. *Neosiphonia* have four pericentral cells per polysiphonous segment, thus differing from members of *N.* sect. *Multisiphonia,* which have five or more pericentral cells per segment.

TYPE. *Neosiphonia flavimarina* M.-S. Kim et I. K. Lee, 1999:272.

There are six species of this section currently known in the northern Gulf of California.

Neosiphonia cheloniae* (Hollenberg et J. N. Norris) J. N. Norris, *comb. nov.

FIGURE 127

Polysiphonia sphaerocarpa var. *cheloniae* Hollenberg et J. N. Norris, 1977:16, figs. 4A–C, 6A; Norris, 1985d:213; González-González et al., 1996:257.

Algae up to 3.5 cm high; main branches up to 300 µm in diameter, uncorticated; polysiphonous segments of 4 pericentral cells, segments 1.0–2.5(–3.0) times as long as the diameter; branching subdichotomous; attached by a basal tuft of rhizoids, augmented by rhizoids from assurgent branches. Each rhizoid cut off as separate cell from the proximal end of its pericentral cell. Branches narrowed toward their base; developed from an entire trichoblast primordium at intervals of mostly 5–12 segments. Trichoblasts 1 per segment, up to 400 µm long, dichotomously divided 1–3 times, tapering to delicate apices.

Tetrasporangia unknown. Cystocarps globular, up to 370 µm in diameter. Spermatangial stichidia cylindrical to fusiform, 160–175 µm long by 40–48 µm in diameter, mostly without sterile apices at maturity; arising as a primary fork of a trichoblast.

HABITAT. On carapace of a living black sea turtle, *Chelonia mydas agassizii* (Bocourt, 1868; see Cliffton et al., 1995; Parham and Zug, 1996), found overwintering subtidally on the bottom; surface to subtidal.

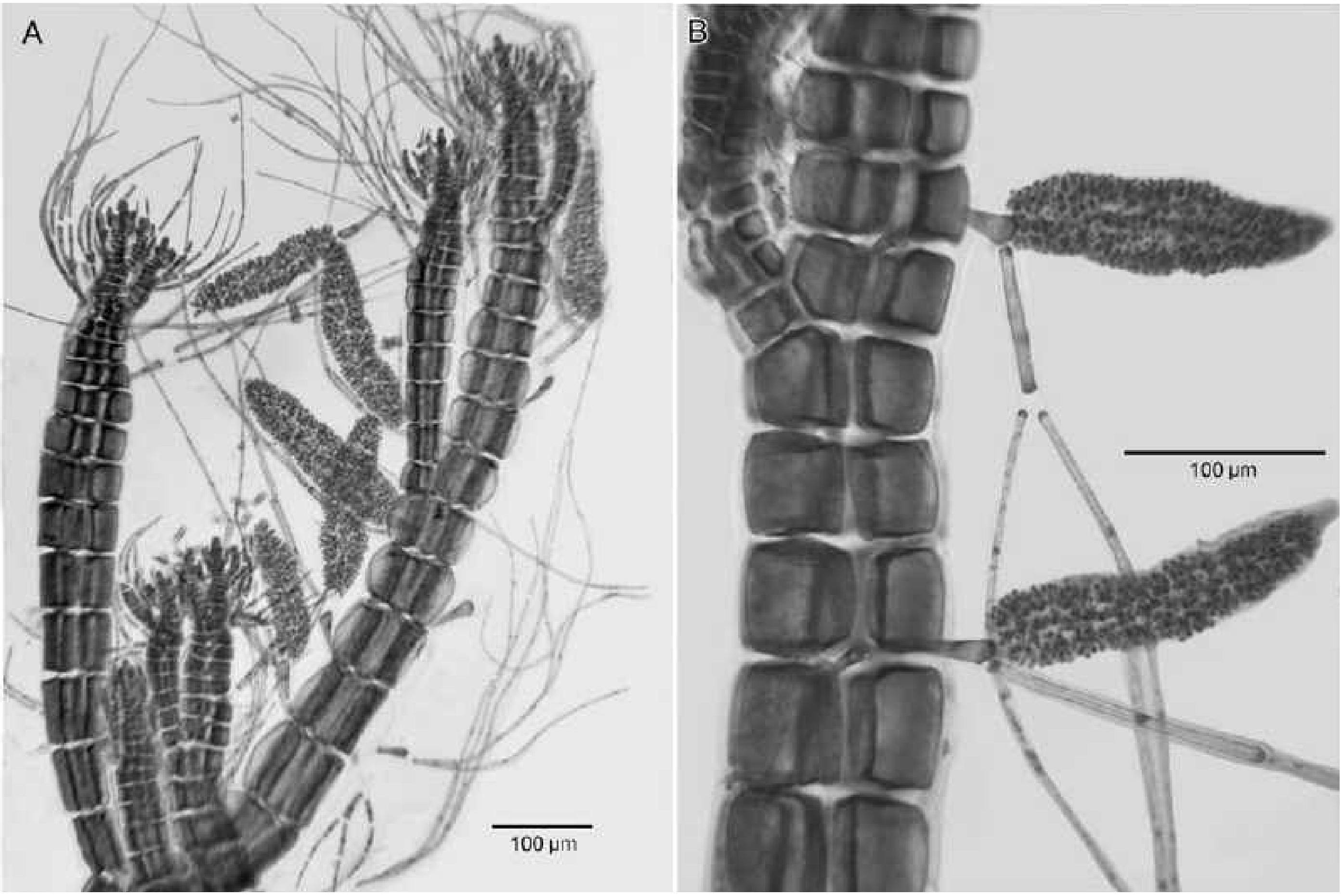


FIGURE 127. *Neosiphonia cheloniae*: A. Upper region with numerous trichoblasts at apices and spermatangial stichidia. B. Spermatangial stichidia arising as a primary fork of a fertile trichoblast (A, B, *JN-4765.5*, US Alg. Coll. microscope slide 5046).

Distribution. Gulf of California: Canal de Infiernillo, between coast of Sonora and east coast of Isla Tiburón (Islas de la Cintura).

Type Locality. Epizoic on a black sea turtle, *Chelonia mydas agassizii*; in Canal de Infiernillo, off the mainland coast of Sonora between Campo Ona and Campo Viboras, opposite the east coast of Isla Tiburón, Sonora, Gulf of California, Mexico.

Remarks. *Neosiphonia cheloniae* is thus far known only on the black sea turtles in the Gulf of California (Hollenberg and Norris, 1977), which are known to overwinter in this region (Felger et al., 1976). It is one of several epizoic algae known on sea turtles (Sentíes-G. et al., 1999; Báez et al., 2002), including *Polysiphonia carettia* Hollenberg (1971a), a species found on loggerhead sea turtles, *Caretta caretta* (Linnaeus), in the eastern Pacific, Atlantic, and Mediterranean Sea (Abbott and Hollenberg, 1976; Báez et al., 2001).

Neosiphonia eastwoodae (Setchell et N. L. Gardner)
J. N. Norris, _comb. nov._

FIGURE 128D

Polysiphonia eastwoodae Setchell et N. L. Gardner, 1930:161; Dawson, 1954b:160; Kapraun et al., 1983:881, figs. 25–29; Stewart and Stewart, 1984:147; Young and Kapraun, 1985:107, figs. 11–16; R. Aguilar-Rosas and Machado-Galindo, 1990:188; González-González et al., 1996:323.

Polysiphonia mollis sensu Dawson, 1957a:8; 1957c:22; 1959a:32; Dawson et al., 1960a:72, pl. 41: figs. 7, 8; Hollenberg, 1961:359, pl. 4: fig. 2; Dawson, 1961b:450; 1962b:216, fig. 127; 1966a:29; Chávez-Barrear, 1972b:269; Abbott and Hollenberg, 1976:688, fig. 636; Hollenberg and Norris, 1977:9, fig. 5b; Huerta-Múzquiz, 1978:336; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1986:425; Ortega et al., 1987:75, pl. 10: fig. 43, pl. 11: figs. 44–46 ; Stewart, 1991:166; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:49; Mendoza-González et al., 1994:109; Sentíes-G., 1995:42, figs. 13–17; González-González et al., 1996:255; Silva et al., 1996b:233; Hoffman and Santelices, 1997:388, fig. 109:1–6; L. Aguilar-Rosas et al., 2000:132; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; López et al., 2004:12; Dreckmann et al., 2006:155; Pérez-Estrada et al., 2012:191 [non *Polysiphonia mollis* J. D. Hooker et Harvey in Harvey, 1848a:43].

Polysiphonia senticulosa sensu Snyder in Collins et al., 1899: Fasciculus 8, No. 638 [type of *Polysiphonia snyderae* Kylin, 1941:35; non *Polysiphonia senticulosa* Harvey, 1862:160].

Polysiphonia snyderae Kylin, 1941:35, pl. 12: fig. 34 [type specimen]; Hollenberg, 1942a:784, fig. 9; Dawson, 1944a:330; 1951:56; 1954b:160; Stewart and Stewart, 1984:147; González-González et al., 1996:257.

Polysiphonia tongatensis sensu Setchell and Gardner, 1930:160; Segi, 1951:207 [in part; only Pacific Mexico material; non *Polysiphonia tongatensis* Harvey ex Kützing, 1864:14, which is now *Neosiphonia tongatensis* (Harvey ex Kützing) M.-S. Kim et I. K. Lee, 1999:280; =*P. mollis* var. *tongatensis* (Harvey ex Kützing) Hollenberg ex P. C. Silva, Meñez et Moe, 1987:70; =*P. mollis* var. *tongatensis* (Harvey ex Kützing) Hollenberg, 1968a:69, *nom. illeg.*].

Neosiphonia tongatensis sensu Pacheco-Ruíz et al., 2008:213 [non *Neosiphonia tongatensis* (Harvey ex Kützing) M.-S. Kim et I. K. Lee, 1999:280].

Algae erect, mostly 5–12 cm long; main branches repeatedly subdichotomously branched above, lower portions usually without branches; polysiphonous segments of 4 pericentral cells; uncorticated; dull reddish brown; arising above prostrate branches of limited extent or sometimes from a discoid base; attached by unicellular rhizoids frequently with digitate ends; rhizoids 1–2(–5) per segment cut off by a curving wall from the proximal ends of pericentral cells. Erect branches 300–400 μm in diameter below, mostly 60–180 μm in diameter in upper parts; segments in main branches mostly 1–2 times as long as the diameter but sometimes considerably longer. Trichoblasts 1 per segment in spiral sequence, with ¼ divergence; deciduous, leaving persistent scar cells; branch replacing a trichoblast in the spiral sequence at irregular intervals; usually 6–10 segments apart.

Tetrasporangia 60–70 μm in diameter; in spiral series in the ultimate and subultimate branches. Cystocarps ovoid to nearly globular, 300–350 μm in diameter. Spermatangial stichidia constitute a primary branch of a trichoblast.

Habitat. Epiphytic on other algae or growing on rock, wood, or shells or epizoic on hydroids; intertidal.

Distribution. Gulf of California: El Tornillal to Bahía de San Lucas; Mazátlan; Sinaloa to Nayarit. Eastern Pacific: Alaska to northern Baja California; Santa Catalina Island (California Channel Islands); Rocas Alijos; Guerrero; Chiapas.

Type Locality. On rocks; South Anchorage, Isla Guadalupe (off Baja California), Pacific Mexico.

Remarks. The new combination *N. eastwoodae* is proposed on the basis of characteristics that are in general agreement with *Neosiphonia*—rhizoids that are cut off from the pericentral cells, numerous trichoblasts and scar cells in spiral sequence, tetrasporangia arranged in spiral series, and spermatangia developed on primary branch of trichoblast.

Hollenberg (1961, 1968a) observed that the branches of *N. eastwoodae* replaced the trichoblasts in development, thus differing from *P. mollis* where the branches developed in the axils of trichoblasts (see also Womersley, 1979; Young and Kapraun, 1985, as *P. eastwoodae*). M.-S. Kim and Lee (1999, as *P. eastwoodae*) considered the Pacific Mexico *N. eastwoodae* to be a synonym of the South Pacific *N. tongatensis* (Harvey ex Kützing) M.-S. Kim et I. K. Lee (1999; basionym: *P. tongatensis* Harvey ex Kützing, 1864). However, primarily on the basis of the disjunct distribution of the two, they are retained as separate species herein, with *Neosiphonia eastwoodae* being a cold temperate to subtropical species and *N. tongatensis* being a tropical species. Records of Pacific Mexico material referred to "*P. mollis*" should be reexamined. The relationship of the Gulf of California *N. eastwoodae* to the Pacific Mexico *N. eastwoodae* (type locality Isla Guadalupe, Baja California), California type locality *P. snyderae*, and the tropical western Pacific *N. tongatensis* (type

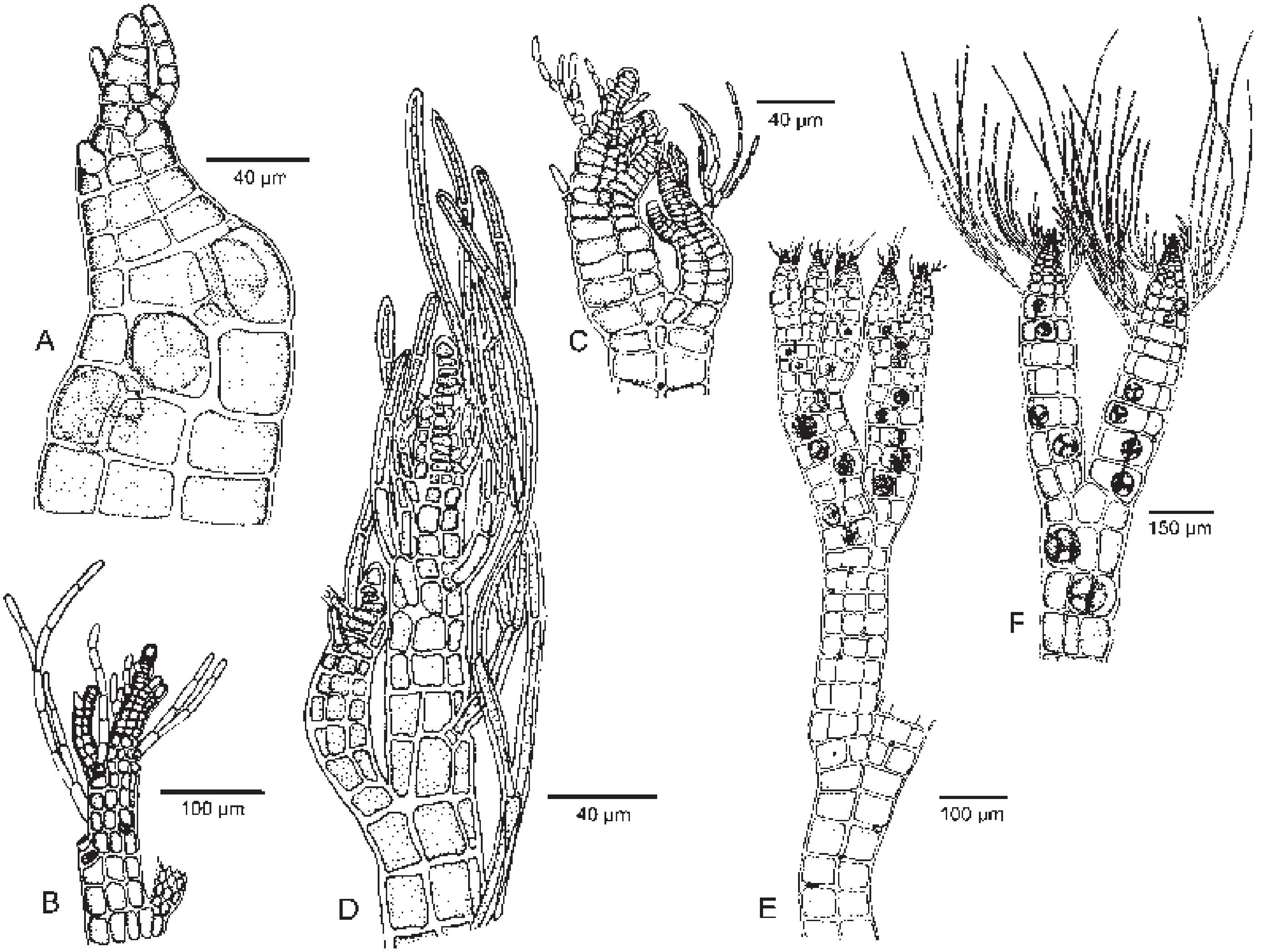


FIGURE 128. Species of *Neosiphonia*. A. *Neosiphonia concinna*: Apical portion of a branch (after Hollenberg, 1944: fig 10, as *Polysiphonia concinna*). B. *Neosiphonia confusa*: Apical portion of a branch showing trichoblasts, scar cells, and a branch arising exogenously in connection with a trichoblast (after Hollenberg, 1961: pl. 1: fig. 5, as *Polysiphonia confusa*). C. *Neosiphonia johnstonii* var. *johnstonii*: Apical portion of an axis showing trichoblasts and incurved tips (after Hollenberg and Norris, 1977: fig. 2B, as *Polysiphonia johnstonii*). D. *Neosiphonia eastwoodae*: Branch tip (after Hollenberg and Norris, 1977: fig. 5B, as "*Polysiphonia mollis*"). E, F. *Neosiphonia masonii*: Terminal portion of axes, tetrasporangia in spiral series (after Hollenberg, 1961: pl. 6: figs. 2, 3, as *Polysiphonia masonii*).

locality: Tonga) should be further compared and tested using molecular analyses.

Neosiphonia flaccidissima (Hollenberg) M.-S. Kim et I. K. Lee

FIGURE 129

Polysiphonia flaccidissima Hollenberg, 1942b:783, figs. 8, 19; Hollenberg, 1961:351, pl. 2: fig. 2; Dawson, 1961b:449; 1962b:217, fig. 128; Dawson et al., 1964:88, pl. 78: fig. b; Hollenberg, 1968a:63, figs. 2A, 11; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Huerta-Múzquiz and Garza-Barrientos, 1975:9; Abbott and Hollenberg, 1976:688, fig. 634; Hollenberg and Norris, 1977:4, fig. 2e; Kapraun and Norris, 1982:231, fig. 110a–d; Schnetter and Bula-Meyer, 1982:172, pl. 32: figs. E–H; Young and Kapraun, 1985:108, figs. 17–22; Stewart and Stewart, 1984:146; Stewart, 1991:164; Ramírez and Santelices, 1991:376; Mateo-Cid and Mendoza-González, 1992:22; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:49; Mateo-Cid and Mendoza-González, 1994b:42; Sentíes-G., 1995:42, figs. 8–12; González-González et al., 1996:324; Mendoza-González and Mateo-Cid, 1996b:69, pl. 13: figs. 49–55; M.-S. Kim and Lee, 1996:143, fig. 5; Abbott, 1999:414, fig. 121A–D; Masuda et al., 2000:575, figs. 24–31; Fernández-García et al., 2011:63.

Neosiphonia flaccidissima (Hollenberg) M.-S. Kim et I. K. Lee, 1999:279.

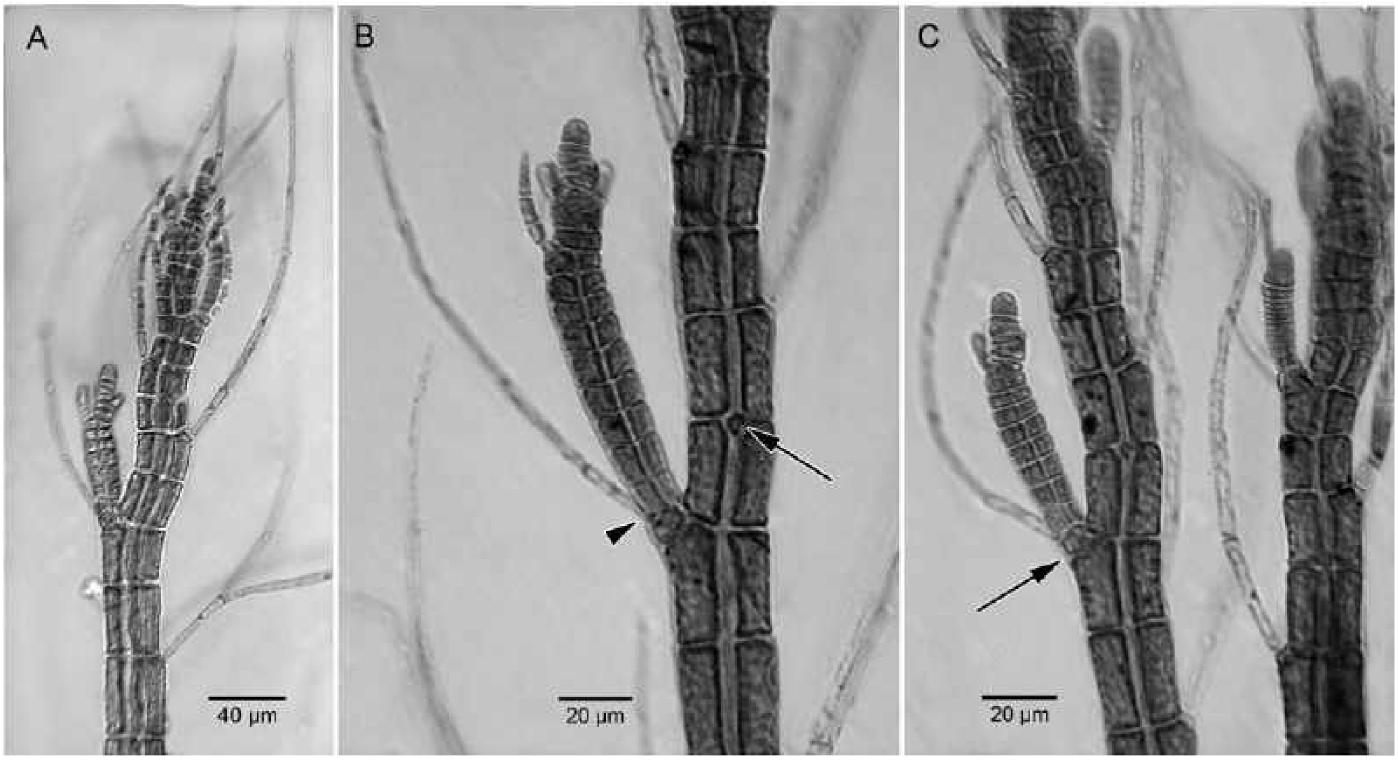


FIGURE 129. *Neosiphonia flaccidissima*: A. Branch tip with abundant trichoblasts (*JN-4266*, US Alg. Coll. microscope slide 5029). B. Lateral branch and trichoblast arising from same primordium (arrowhead), scar cell (arrow). C. Apical region showing lateral branch and trichoblast from same primordium (arrow), trichoblasts one per segment, spirally arranged (B, C, *JN-4270*, US Alg. Coll. microscope slide 5031).

Polysiphonia sertularioides sensu L. Aguilar-Rosas et al., 2000:1341; L. Aguilar-Rosas et al., 2002:235; Serviere-Zaragoza et al., 2007:11; Bernecker, 2009:CD-Rom p. 67; [non *Polysiphonia sertularioides* (Grateloup) J. Agardh, 1863:969; basionym: *Ceramium sertularioides* Grateloup, 1806:[1], fig. IV].

Algae 10–25 mm high, erect, axes and branches uncorticated, with thin hyaline walls; polysiphonous segments of 4 pericentral cells; branching to many orders, arising from creeping basal branches attached by numerous unicellular rhizoids, each cut off as separate cell from the proximal end of pericentral cells. Main erect axes (50–)70–80 µm in diameter, with segments mostly (50–)70–160 µm long (1–2 times as long as the diameter). Branches gradually narrowed at both ends (base and apex); at first usually curving toward the parent branch; up to 2.5 mm long, 35–55 µm in diameter, segments mostly 35–100 µm long; branches arising exogenously at base of trichoblasts from common primordium, mostly at irregular intervals of 5–6 (rarely 12) segments. Trichoblasts mostly with a single dichotomy or occasionally simple, arising 1 per segment with ¼ divergence in spiral sequence; trichoblasts tapering to slender apices; deciduous, leaving persistent scar cells.

Tetrasporangia 50–70 µm in diameter; in spiral series, somewhat distending the segments in smaller branches. Cystocarps globular. Spermatangial stichidia originating as a primary branch of a trichoblast with apices of 1–2 sterile cells.

HABITAT. On rocks or occasionally epiphytic; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara); Bahía San Carlos (north of Guaymas) to Canal de San Lorenzo (off southern end of Isla Espíritu Santo); Nayarit to Jalisco. Eastern Pacific: Santa Catalina Island (California Channel Islands); southern California to Todos Santos, Baja California Sur; Isla Guadalupe; Isla Socorro (Islas Revillagigedo); Colima to Chiapas; El Salvador; Costa Rica; Panama; Colombia; Peru. Central Pacific: Hawaiian Islands.

TYPE LOCALITY. On a coralline alga; rocky point, Laguna Beach, Orange County, California, USA.

REMARKS. Womersley (1979:478, with a taxonomic query), although noting “no apparent differences,” tentatively suggested the southern California *P. flaccidissima* may be a synonym of *P. sertularioides* (Grateloup) J. Agardh (1863; basionym: type locality: Cette, Golfe du Lion, France). Subsequently, Silva et al. (1996a) considered the two conspecific. However, others have observed differences between the two (e.g., Young and Kapraun, 1985; M.-S. Kim and Lee, 1996, 1999; Masuda et al., 2000; Dreckmann et al., 2006). To test the taxonomic status of the Gulf specimens referred to *Neosiphonia flaccidissima*, molecular analyses and morphological comparisons of newly collected Gulf specimens with the type locality specimens of southern California *P. flaccidissima* and the French Mediterranean *P. sertularioides* need to be performed.

Neosiphonia masonii (Setchell et N. L. Gardner) J. N. Norris, _comb. nov._

FIGURE 128E,F

Polysiphonia masonii Setchell et N. L. Gardner, 1930:160; Hollenberg, 1942b:783; Dawson, 1954d:160; 1961b:450; Hollenberg, 1961:358, pl. 6: figs. 2, 3; Hollenberg and Norris, 1977:8, fig. 2d; Stewart and Stewart, 1984:147; Sánchez-Rodríguez et al., 1989:45; González-González et al., 1996:255.

Algae 2–3 cm high, flaccid; uncorticated, of polysiphonous segments of 4 pericentral cells; segments mostly as long as wide (diameter); main axis 350–400 μm in diameter in lower portions, branched repeatedly and regularly dichotomously above; attached by bundle of short unicellular rhizoids, with digitate ends, issued from the lower segments of the erect primary axis. Branches arising from an entire trichoblast primordium; more or less of same size as main axis at the point of insertion. Trichoblasts 1 per segment in spiral sequence with ¼ divergence; up to 480 μm long, dichotomously branched 2–3 times; tapering to very slender apices; deciduous, leaving persistent scar cells.

Tetrasporangia 85–95 μm in diameter; in spiral series in the ultimate branches, barely distending the segments. Cystocarps subspherical, 300–325 μm diameter, nearly sessile on branches. Spermatangial stichidia broadly fusiform; arising from a primary branch of a trichoblast.

HABITAT. Epiphyte on sea grass and probably on marine algae; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco. Eastern Pacific: Isla Guadalupe; Bahía Magdalena, Baja California Sur.

TYPE LOCALITY. Epiphytic on *Zostera*; Isla Guadalupe, off Baja California, Pacific Mexico.

REMARKS. Apparently rare, *Neosiphonia masonii* is known only from Puerto Peñasco in the upper Gulf of California and in Pacific Mexico from Isla Guadalupe and Bahía Magdalena.

Neosiphonia savatieri (Hariot) M.-S. Kim et I. K. Lee

FIGURE 130

Polysiphonia savatieri Hariot, 1891:226; Segi, 1951:202, figs. 10, 11, pl. 3: fig. 8; Dawson, 1954d:160; Hollenberg, 1961:363, pl. 7: fig. 4; Dawson, 1961b:450; Hollenberg, 1968a:77, figs. 37, 38; Abbott and

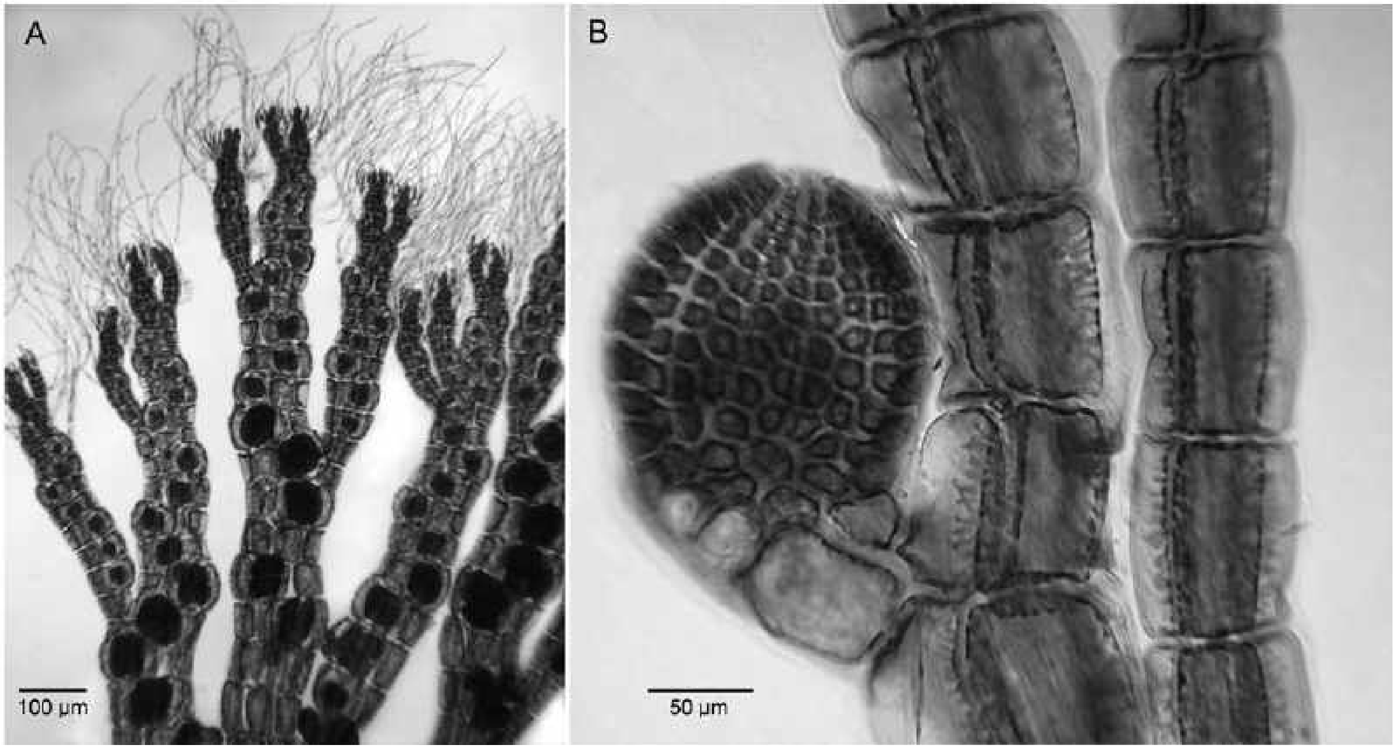


FIGURE 130. *Neosiphonia savatieri*: A. Upper portion of thallus with tetrasporangia arranged in spiral series, distending segments a little; apices with abundant trichoblasts that are soon deciduous (*JN-4195*, US Alg. Coll. microscope slide 5027). B. Maturing cystocarp and scar cell left behind by deciduous trichoblast (*JN-4266*, US Alg. Coll. microscope slide 5030).

Hollenberg, 1976:692, fig. 639; Hollenberg and Norris, 1977:12, fig. 8a; Young and Kapraun, 1985:112, figs. 29–34; Stewart and Stewart, 1984:147; Santelices and Abbott, 1987:9; Stewart, 1991:167; Ramírez and Santelices, 1991:378; González-González et al., 1996:256; Yoshida, 1998:1070; Abbott, 1999:424, fig. 125B.

Neosiphonia savatieri (Hariot) M.-S. Kim et I. K. Lee, 1999:279; Masuda et al., 2001:474, figs. 24–31; Lobban and Tsuda, 2003:78; M.-S. Kim, 2005:164, figs.1–4[lectotype: *Polysiphonia savatieri* Hariot], figs. 5–20; Y.-P. Lee, 2008:315, figs. A–F.

Polysiphonia japonica var. *savatieri* (Hariot) H. S.Yoon, 1986:34, figs. 20, 21, pl. 9E–J [non *Polysiphonia japonica* Harvey, 1857:331; see M.-S. Kim, 2005:172].

Polysiphonia minutissima Hollenberg, 1942b:781, fig. 21; González-González et al., 1996:255.

Algae dull reddish brown, erect, 3–10 mm high; polysiphonous segments of 4 pericentral cells, uncorticated; main axes indistinct, to 150 µm diameter, branching dichotomously to several orders; axes arising from a basal attachment tuft (or cushion) of rhizoids that usually penetrates the host tissue. Basal rhizoids up to 1 mm long, cut off by a curving wall from the proximal end of the pericentral cells. Branches exogenous (not associated with trichoblasts in origin), at variable intervals. Trichoblasts relatively short, 1 per segment in spiral sequence, with ¼ divergence; deciduous, leaving persistent scar cells.

Tetrasporangia up to 80 µm in diameter; in spiral series, somewhat distending the segments, in upper portions of axes. Cystocarps slightly urceolate or mostly globular, 225–290 µm in diameter. Spermatangial stichidia about 135 µm long and 40 µm in diameter, without a sterile apex; forming 1 primary branch of a trichoblast.

Habitat. Epiphytic on various algae, including *Codium*, *Dictyota*, *Sargassum*, *Gracilaria*, *Gelidium,* and *Sarcodiotheca*, or growing on rocks or in tide pools; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía de Las Ánimas; Guaymas. Eastern Pacific: central California to northern Baja California; Santa Catalina Island (California Channel Islands); Isla Guadalupe (off Baja California); Chile. Western Pacific: Japan; Korea.

Type Locality. Epiphytic on larger algae; Yokosuka, on Tokyo Bay, Kanagawa Prefecture, Honshū, Japan.

Remarks. The taxonomic interpretation of *Polysiphonia savatieri* has been somewhat unclear, and the species concept may involve more than one species. Yoon (1986, as *P. japonica* var. *savatieri*) reduced *P. savatieri* to varietal status of the Japanese *P. japonica*. Later, Abbott (1999, as *P. savatieri*) retained the Hawaiian material as a species but noted that it may not be the same as the Japanese and Korean species. M.-S. Kim and Lee (1999) considered that the western Pacific *P. savatieri* belonged to the genus *Neosiphonia*, and M.-S. Kim (2005, as *N. savatieri*), studying the types, concluded that *P. savatieri* was a species distinct from *P. japonica*.

Earlier, Hollenberg (1968b) noted that Hawaiian and other tropical specimens of *P. savatieri* may be variants of *P. sphaerocarpa* Børgesen (1918; now *Neosiphonia sphaerocarpa* (Børgesen) M.-S. Kim et I. K. Lee, 1999) but separated the two on the tendency of *P. savatieri* to be erect from a basal tuft of rhizoids versus *P. sphaerocarpa*, which is decumbent and has rhizoids distributed along its prostrate segments (characters also emphasized by M.-S. Kim, 2005).

For now, on the basis of characters observed in Gulf of California *N. savatieri*, they are retained in *Neosiphonia*. Culture, genetic, and comparative reproductive developmental studies are needed to test the status of the Gulf *N. savatieri* and its relationship to the type of *N. savatieri* (Japan) as well as other geographically widespread specimens referred to "*P. savatieri*" to see if the complex involves more than one taxa.

Neosiphonia simplex (Hollenberg) Y.-P. Lee

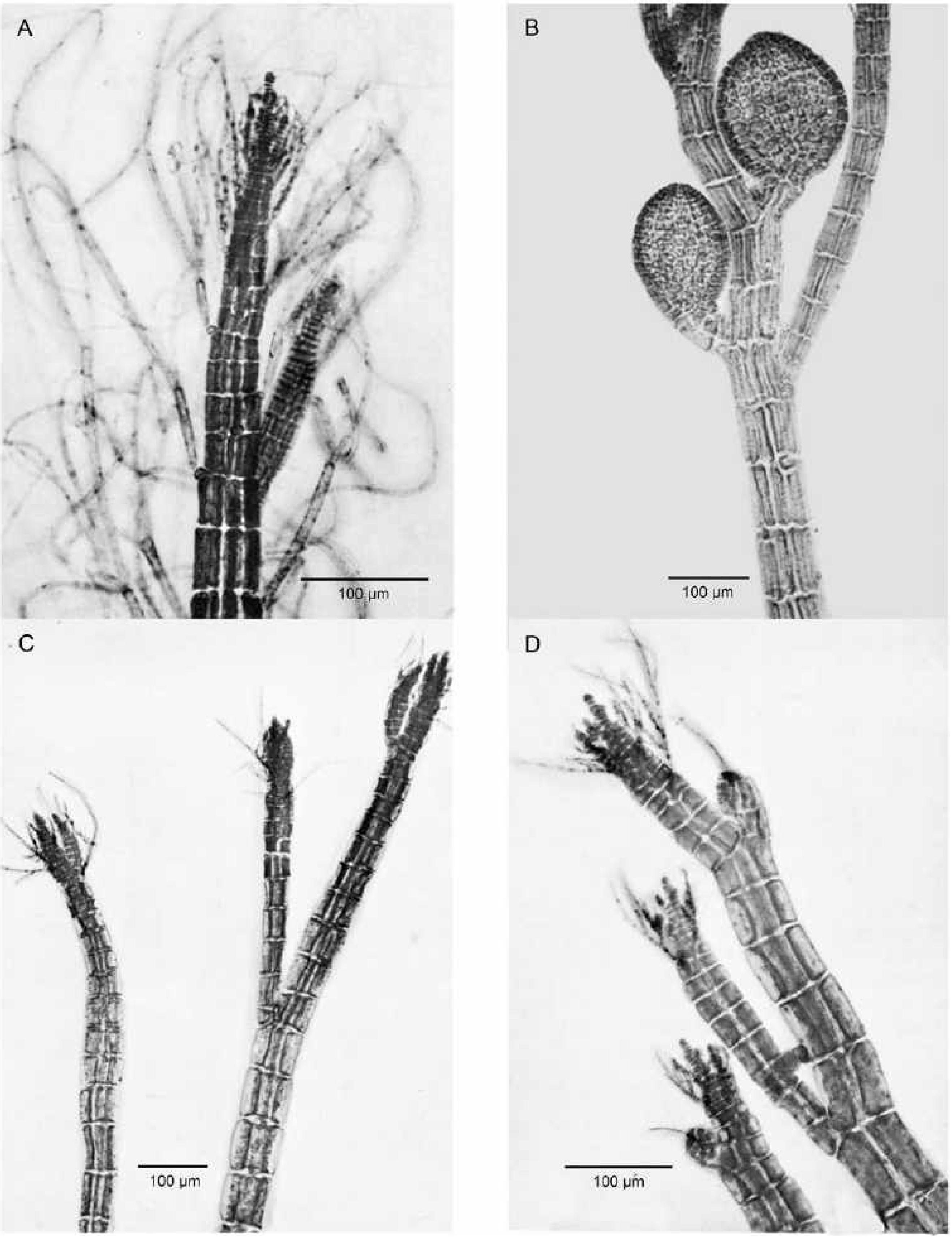
FIGURE 131C,D

Polysiphonia simplex Hollenberg, 1942b:782, fig. 18; Dawson, 1944a:331; 1951:53; 1954b:160; Hollenberg, 1961:364, pl. 5: fig. 1; Dawson, 1961b:450; 1966a:29; Abbott and Hollenberg, 1976:694, fig. 641; Huerta-Múzquiz and Garza-Barrientos, 1975:9, 12 ; Hollenberg and Norris, 1977:14, fig. 9; Young and Kapraun, 1985:113, figs. 41–44; Huerta-Múzquiz and Mendoza-González, 1985:54; Sánchez-Rodríguez et al., 1989:46; Mateo-Cid and Mendoza-González, 1992:23; Mendoza-González and Mateo-Cid, 1992:21; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:49; Mateo-Cid and Mendoza-González, 1994b:42; Mendoza-González et al., 1994:109; Sentíes-G., 1995:47: figs. 25–29; González-González et al., 1996:256; Riosmena-Rodríguez et al., 1998:26; Abbott, 1999:426, fig. 126D; Mateo-Cid et al., 2000:67; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:469; López et al., 2004:12; Mateo-Cid et al., 2006:57, 62; Dreckmann et al., 2006:155; Serviere-Zaragoza et al., 2007:11; Pacheco-Ruíz et al., 2008:213; Bernecker, 2009:CD-Rom p. 68; Fernández-García et al., 2011:63; Pérez-Estrada et al., 2012:191.

Neosiphonia simplex (Hollenberg) Y.-P. Lee, 2008:316, figs. A–F.

Algae composed of polysiphonous filaments of 4 pericentral cells per segment; often spreading, forming mats; medium to dark brownish red (drying nearly black). Erect branches 1–3(–7) cm

FIGURE 131. (Opposite) Species of *Neosiphonia*. A, B. *Neosiphonia confusa*: A. Apical portion of thallus showing trichoblasts and some of its 8 pericentral cells per segment (*JN-5577*, US Alg. Coll. microscope slide 5052). B. Cystocarps (*JN-3835*, US Alg. Coll. microscope slide 5000). C, D. *Neosiphonia simplex*: C. Upper portion of thallus showing delicate trichoblasts (*JN-5098b*, US Alg. Coll. microscope slide 4996). D. Upper portion of a thallus with young cystocarps (*JN-5038*, US Alg. Coll. microscope slide 4994).


A
100 µm
B
100 µm
C
100 µm
D
100 µm

high and 160–250 µm in diameter near the base; developed in an exogenous assurgent manner; main axes usually distinct (but not prominent), sparingly branched, arising from creeping basal branches of short segments, 250–360 µm in diameter; attached by numerous unicellular rhizoids cut off as a separate cell from the proximal end of a pericentral cell, often digitate at their end. Branches exogenous, radially directed, of several orders. Trichoblasts up to 730 µm long, with 1 or 2 dichotomies; 1 per segment in spiral sequence with ¼ divergence; delicate, deciduous, leaving persistent scar cells; branches replacing trichoblasts in the spiral (arising from an entire trichoblast primordium).

Tetrasporangia mostly about 70 µm in diameter; in spiral series within the ultimate branches, more or less distending the segments. Cystocarps ovoid to globular, 300–350 µm in diameter. Spermatangial stichidia, elongate, 100–170 µm long, 35–40 µm in diameter, apex without sterile cells; comprising 1 primary branch fork of a trichoblast.

HABITAT. Solitary or mixed with other turf algae, sometimes forming spreading mats; usually on rocks and tidal platforms and in tide pools or occasionally epiphytic on other algae, such as *Gastroclonium* or *Amphiroa*; mid intertidal to shallow subtidal, down to 8 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena; Mazatlán; Sinaloa to Nayarit. Eastern Pacific: Santa Catalina Island (California Channel Islands); southern California to Todos Santos, Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Colima; Guerrero to Chiapas; Costa Rica. Central Pacific: French Frigate Shoals, Northwestern Hawaiian Islands. Western Pacific: Korea.

TYPE LOCALITY. On intertidal rocks; Laguna Beach, Orange County, southern California, USA.

REMARKS. McIvor et al. (2001) found that "*Neosiphonia simplex,*" as identified from San Diego, California (e.g., Stewart, 1991, as *Polysiphonia simplex*), was actually an introduced species, *Neosiphonia harveyi* (J. W. Bailey) M.-S. Kim, H.-G. Choi, Guiry et G. W. Saunders (in Choi et al, 2001a; basionym: *Polysiphonia harveyi* J. W. Bailey, 1848) from the Western Atlantic. More recently, *N. harveryi* was discovered in Humbolt Bay, northern California (Hughey et al., 2009; Miller at al., 2011). To determine whether one or both of these species occur southward, specimens identified as "*N. simplex*" in Pacific Mexico and in the Gulf of California should be reexamined and molecularly compared with type locality specimens of *N. simplex* and *N. harveryi* (lectotype locality: Connecticut, northwest Atlantic; Maggs and Hommersand, 1993).

Neosiphonia sect. *Multisiphonia* J. N. Norris, *sect. nov.*

LATIN DIAGNOSIS. Algae huius sectionis cellulis pericentralibus quinque vel plus per segmentum; differt *N.* sect. *Neosiphonia* cellulis pericentralibus quaterni per segmentum.

Members of *Neosiphonia* sect. *Multisiphonia* are characterized by having five or more pericentral cells per polysiphonous segment, thus differing from members of *N.* sect. *Neosiphonia,* which has species with 4 pericentral cells per segment grouped around each axial filament cell.

TYPE. *Neosiphonia johnstonii* (Setchell et N. L. Gardner) J. N. Norris, herein (basionym: *Polysiphonia johnstonii* Setchell et N. L. Gardner, 1924:767).

There are five species of this taxonomic section currently known in the northern Gulf of California.

Neosiphonia concinna (Hollenberg) J. N. Norris, *comb. nov.*

FIGURE 128A

Polysiphonia concinna Hollenberg, 1944:474, fig. 10; Dawson, 1951:53, 56; 1954d:159; 1959a:32; González-González et al., 1996:253.

Polysiphonia johnstonii var. *concinna* (Hollenberg) Hollenberg, 1961:358, pl. 3: fig. 4; Dawson, 1961b:450; Abbott and Hollenberg, 1976:699, fig. 650; Hollenberg and Norris, 1977:7, figs. 2a, 4d; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:32; Sánchez-Rodríguez et al., 1989:45; Stewart, 1991:165; González-González et al., 1996:254; L. Aguilar-Rosas et al., 2000:132; Pacheco-Ruíz and Zertuche-González, 2002:469; Hernández-Herrera et al., 2005:148; Castañeda-Fernández de Lara et al., 2010:200.

Algae up to 2(–4) cm tall; branching axes, uncorticated, of polysiphonous segments of 5 pericentral cells; segments short (usually about half as long as wide), 300–400 µm in diameter, about 150–200 µm tall; attached by basal tuft of unicellular rhizoids. Trichoblasts short and simple (unbranched) or lacking; scar cells regular, 1 per segment in spiral arrangement.

Tetrasporangia 1 per segment; spirally arranged in ultimate branchlets. Cystocarps observed in northern Gulf specimens: immature about 65–120 µm in diameter, mature to 360 µm in diameter. Spermatangia arising as a primary branch of a trichoblast in Gulf material.

HABITAT. Epiphytic on various algae, including *Codium*, *Padina*, and *Tacanoosca*; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Agua Verde; Isla Venado, off Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Santa Catalina Island (California Channel Islands), southern California to Bahía Magdalena, Baja California Sur; Isla Guadalupe.

TYPE LOCALITY. Epiphytic on other algae; near Scripps Institution of Oceanography (University of California, San Diego), La Jolla, San Diego County, southern California, USA.

REMARKS. *Neosiphonia concinna* has spirally arranged tetrasporangia, a character of *Neosiphonia*. Although similar to *N. johnstonii*, *N. concinna* differs in being smaller and in having five very short pericentral cells per segment. Further vegetative and reproductive comparisons, along with genetic testing, with type locality materials are needed to clarify the taxonomic status of this species.

A Bahía de Los Angeles specimen (Islas de Los Gemelos, *JN-3011*; US Alg. Coll. microscope slide 5009), tentatively referred to "*P. johnstonii* var. *concinna*" by Hollenberg and Norris (1977:7), was unusal in that its branches arise in pairs, one segment apart—a feature not observed in other northern Gulf *N. concinna*. Also there were several immature cystocarps, possibly in arrested development (Hollenberg and Norris, 1977: fig. 4D). Further collections are needed to elucidate its identity.

Neosiphonia confusa **(Hollenberg) J. N. Norris,** ***comb. nov.***

FIGURES 128B, 131A,B

Polysiphonia confusa Hollenberg, 1961:350, pl. 1: fig. 5; Dawson, 1961b:449; Dawson et al., 1964:87, pl. 33: fig. d; Abbott and Hollenberg, 1976:696, fig. 643; Hollenberg and Norris, 1977:2, fig. 1; Dreckmann et al., 1990:32; Sentíes-G. et al., 1990:95, pl. 1: figs. 1–4; Stewart, 1991:164; Ramírez and Santelices, 1991:375; Stout and Dreckmann, 1993:16; Sentíes-G., 1995:40, figs. 1–7; González-González et al., 1996:253; López et al., 2004:12; Hernández-Herrera et al., 2005:148; R. Aguilar-Rosas et al., 2006b:1, figs.1–7; Castañeda-Fernández de Lara et al., 2010:200.

Polysiphonia inconspicua Hollenberg, 1944:479, *nom. illeg.*; González-González et al., 1996:254 [non *Polysiphonia inconspicua* Reinsch, 1888:146].

Algae erect, branched axes, 0.8–1.5(–3.0) cm high, and prostrate, basal branches composed of polysiphonous segments of 8–10 pericentral cells; uncorticated; arising from prostrate branches 100–175 µm in diameter, of segments about as long as the diameter or somewhat longer; attached by numerous unicellular rhizoids, 1 to several per segment; rhizoids cut off from the proximal ends of the pericentral cells, frequently ending with digitate disc. Erect branches 60–150 µm in diameter, of segments 1.0–2.5 times as long; lateral branches arising exogenously in connection with trichoblasts at irregular intervals. Trichoblasts up to 1 mm long, with 1–2 dichotomies; 1 per segment in spiral sequence with ¼ divergence; deciduous, leaving persistent scar cells.

Tetrasporangia, 60–80 µm in diameter; in spiral series in slightly swollen segments of ultimate and subultimate branches. Cystocarps globular, up to 225 µm in diameter. Spermatangial thalli unknown in northern Gulf.

HABITAT. Epizoic on sand dollars, epiphytic on *Codium,* and growing near surface on a floating buoy and probably on other hard substrata as well; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to El Desemboque de San Ignacio; Jalisco. Eastern Pacific: Corona del Mar, southern California, to Bahía Tortugas (inside southeast Bahía San Bartolomé), Baja California Sur; Michoacán to Oaxaca; Peru.

TYPE LOCALITY. Mid intertidal rocks; Corona del Mar, Orange County, southern California, USA.

REMARKS. Characters of northern Gulf specimens referred to *Neosiphonia confusa* are in general agreement with the genus *Neosiphonia*. However, spermatangial thalli are not yet known in the northern Gulf. Pacific Mexico specimens from northern Baja California had both tetraspores and cystocarps on the same individual (R. Aguilar-Rosas et al., 2006b:2, fig. 6, as *Polysiphonia confusa*). Finding northern Gulf spermatangial specimens is needed to confirm its identification and for molecular comparisons with type locality specimens to elucidate their phylogenetic relationship.

Neosiphonia johnstonii **(Setchell et N. L. Gardner) J. N. Norris,** ***comb. nov.***

FIGURE 128C

Polysiphonia johnstonii Setchell et N. L. Gardner, 1924:767; Hollenberg, 1944:475, figs. 4, 5; Dawson, 1944a:329; 1949c:237; 1951:53, 57; 1954d:160; 1959b:32; 1960a:72, pl. 41: figs. 5, 6; Dawson et al., 1960b:26; Hollenberg, 1961:357, pl. 2: figs. 4, 5; Dawson, 1966a:29; Norris, 1973:16; Abbott and Hollenberg, 1976:699, fig. 649; Hollenberg and Norris, 1977:4, figs. 2b, 3; Huerta-Múzquiz, 1978:338; Huerta-Múzquiz and Mendoza-González, 1985:52; Sánchez-Rodríguez et al., 1989:45; Stewart, 1991:165; González-González et al., 1996:254; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:26;; León-Tejera and González-González, 2000:328; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:469; Pacheco-Ruíz et al., 2008:213; Pérez-Estrada et al., 2012:191.

Polysiphonia marchantae Setchell et N. L. Gardner, 1924:768, pl. 49a.

Polysiphonia sinicola Setchell et N. L. Gardner, 1924:769.

Polysiphonia acuminata sensu Dawson, 1950a:68; 1954d:159 [non *Polysiphonia acuminata* N. L. Gardner, 1927f:100].

Polysiphonia richardsoni sensu Segi, 1951:253; Dawson, 1954b:160 [in part; with reference only to Gulf of California specimens cited by Setchell and Gardner, 1924:768, as "*P. marchantae*"; non *Polysiphonia richardsoni* W. J. Hooker ex Harvey in W. J. Hooker, 1833:333, which is now *Polysiphonia fibrillosa* (Dillwyn) Sprengel, 1827:349].

Algae of several erect, repeatedly branched primary axes, 5–8(–12) cm high and up to 1.0 mm in diameter (near base); uncorticated; polysiphonous segments of (5–)6 pericentral cells, 1.5 times or more longer than diameter (up to 1 mm in length near base); attached by numerous unicellular rhizoids, each cut off as separate cells from pericentral cells of the prostrate basal axes. Branches replacing trichoblasts in origin at irregular intervals, spirally arranged, initially at narrow angle, angle becoming wider with growth; ultimate branches usually relatively close and dense. Trichoblasts unbranched, or 1–2 times forked; 1 per segment in spiral sequence, with ⅕ or ⅙ divergence; deciduous, leaving persistent scar cells.

Tetrasporangia 70–90 µm in diameter; 1(–2) per segment in spiral series in branchlets. Cystocarps globular, 450–500 µm in diameter, nearly sessile on branches. Spermatangial stichidia 100–140 long, 30–40 µm in diameter; arising as a primary branch of a trichoblast.

HABITAT. Usually epiphytic on other algae such as *Sargassum*, *Gracilaria*, and *Osmundea sinicola* or sometimes on rocks; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes; Sinaloa. Eastern Pacific: Santa Catalina Island (California Channel Islands) to Bahía Magdalena, Baja California Sur.

TYPE LOCALITY. On *Gracilaria* sp.; Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

Neosiphonia mexicana **(E. Y. Dawson) J. N. Norris, *comb. nov.***

FIGURE 132A–D

Lophosiphonia mexicana E. Y. Dawson, 1944a:333, pl. 48: figs. 7–10; 1954b:347; 1954d:161; 1961b:451; Dawson and Hollenberg, 1963:420, pl. 169: figs. 4–7; González-González et al., 1996:242; Serviere-Zaragoza et al., 2007:11; Pacheco-Ruíz et al., 2008:213.

Algae small tufts, 1–2 mm tall; of polysiphonous erect and prostrate portions. Erect branches 1–2 mm long; lower portions of 6 pericentral cells, 50–60 μm in diameter; branches becoming wider in middle to upper portions, 70–80 μm in diameter, after 6 pericentral cell segments divided to 12 pericentral cells; branch apices with only a few unbranched trichoblasts. Prostrate axes about 55 μm in diameter, attached by rhizoids in series, each rhizoid cut off from the middle of a pericentral cell (Figure 132D).

Tetrasporangia about 30–35 μm in diameter; in slightly irregular rows of 5–10 (tending toward spiral arrangement; cf. Figure 132A) in the upper segments of erect branches. Cystocarpic and spermatangial thalli not known.

HABITAT. On rocks; low intertidal.

DISTRIBUTION. Gulf of California: Isla Estanque, off Isla Ángel de la Guarda. Eastern Pacific: Isla Cedros (off Baja California); Bahía Sulphur, Isla Clarión (Islas Revillagigedo).

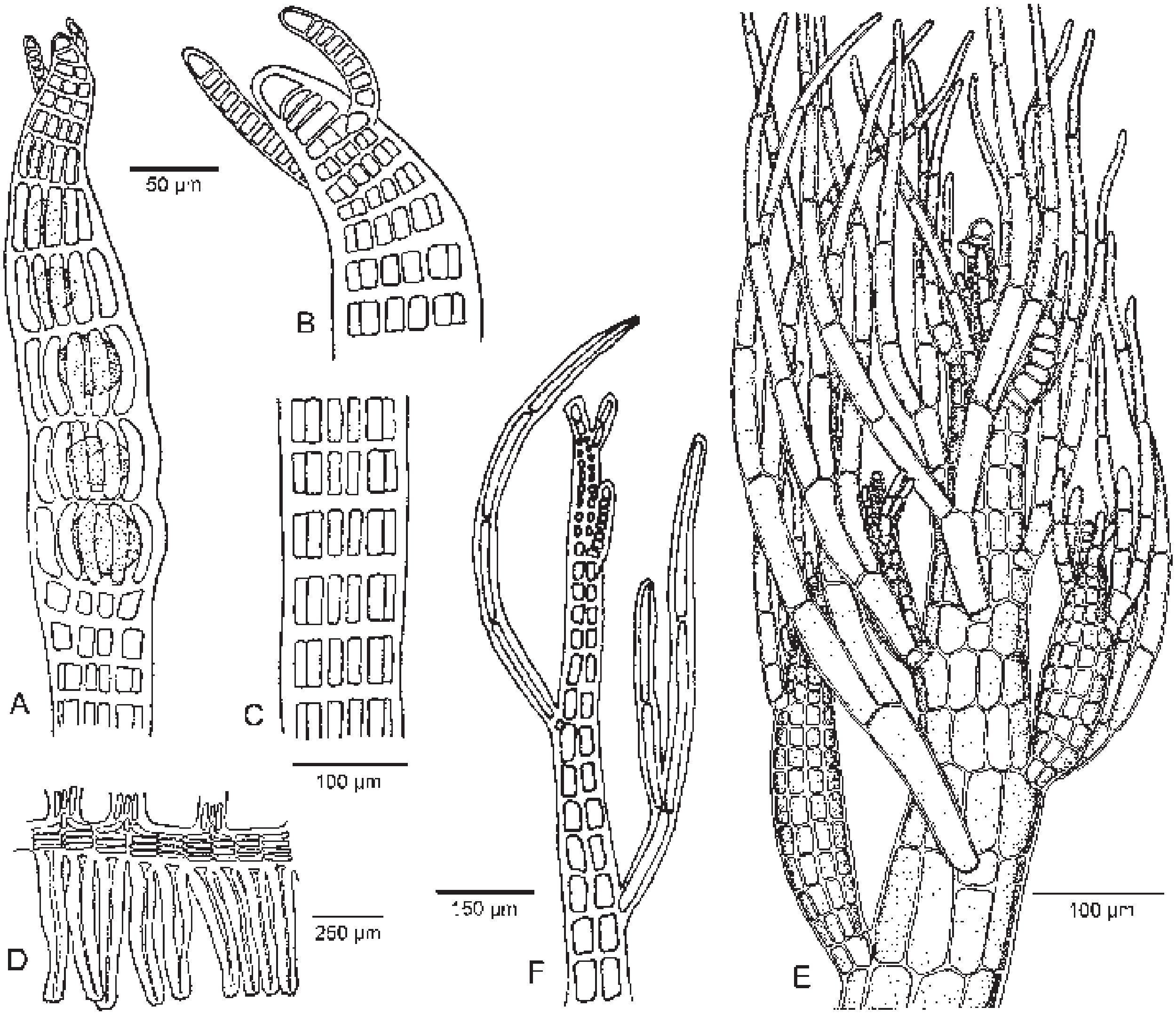


FIGURE 132. Species of *Neosiphonia* and *Polysiphonia*. A–D. *Neosiphonia mexicana*: A. Tetrasporangia in a series near apex. B. Apical region. C. Surface view of polysiphonous segments. D. Prostrate axis issuing erect axes and rhizoids (after Dawson, 1944a: pl. 48: figs. 7–10, as "*Lophosiphonia mexicana*"). E. *Neosiphonia paniculata*: Apical region with trichoblasts (after Hollenberg, 1944: fig. 7, as "*Polysiphonia paniculata*"). F. *Polysiphonia sonorensis:* Apical region (after Hollenberg and Norris, 1977: fig. 2C).

Type Locality. Isla Estanque (Pond Island), off southeast end of Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

Remarks. Problems concerning the taxonomic status of the genus *Lophosiphonia* Falkenberg (in Schmitz and Falkenberg, 1897; Falkenberg, 1901) have long been noted (e.g., Hollenberg, 1942b; Dawson, 1963a), although many recognize the genus (e.g., Norris, 1992a; Silva et al., 1996a; Abbott, 1999). Following the taxonomic criteria of Hollenberg (1968a:56), the Gulf of California *L. mexicana* E. Y. Dawson would not be a member of *Lophosiphonia* sensu stricto. Reexamination of isotype specimens of *Lophosiphonia mexicana* (*E. Y. Dawson-430*, US Alg. Coll.-6678, microscope slides 2836–2839) showed the attachment rhizoids are cut off from the basal pericentral cells of the segment, and the tetrasporangia illustrated by Dawson (1944a: pl. 48: fig. 10, a paratype from Isla Clarión) show a tendency toward spiraling in their arrangement. These characters suggest the taxon may be a *Neosiphonia,* and the combination *Neosiphonia mexicana* is tentatively proposed.

Described from the northern Gulf, *Neosiphonia mexicana* is known only from a few specimens. The longitudinal division of 6 pericentral cells in lower portions of erect branches to 12 pericentral cells in the mid to upper portions is unique among the Gulf species. Dawson (1944) observed the broad mid to upper portions of the branches tended towards being complanate and the 12 cells in the segments appeared to be paired (Figure 132C). More collections from the Gulf, particularly reproductive spermatangial and cystocarpic specimens, are needed to clarify and molecularly test its generic placement (Hollenberg and Norris, 1977).

Neosiphonia paniculata (Montagne) J. N. Norris, *comb. nov.*

FIGURES 132E, 133

Polysiphonia paniculata Montagne, 1842a:254; Kützing, 1863:15, pl. 45c–e; Howe, 1914:142; Hollenberg, 1944:480, fig. 7; Taylor, 1947:86, pl. 2: fig. 2; Dawson, 1954d:160; Dawson et al., 1960b:26; Dawson, 1961b:450; Hollenberg, 1961:362, pl. 7: fig. 1; Dawson et al., 1964:89, pl. 78: fig. a, pl. 79; Dawson, 1966a:29; Smith, 1969:725; Abbott and Hollenberg, 1976:701, fig. 652; Hollenberg and Norris, 1977:11, figs. 5a, 7; Silva, 1979:331; R. Aguilar-Rosas and Aguilar-Rosas, 1984:185, figs. 1–5; Scagel et al., 1989:234; Santelices, 1989:368, pl. ÑÑ: figs. 17, 18; Stewart, 1991:166; Ramirez and Santelices, 1991:377; R. Aguilar-Rosas and Aguilar-Rosas, 1994:524; González-González et al., 1996:256; Hoffman and Santelices, 1997:394, figs. 111.1–111.5; L. Aguilar-Rosas et al., 2000:132; 2002:235; Mateo-Cid et al., 2006:57.

Polysiphonia californica Harvey, 1853:48; Setchell and Gardner, 1903:327; Howe, 1911:508; Kylin, 1941:36, fig. 7A–F; Dawson, 1944a:332; Smith, 1944:362, pl. 93: fig. 1.

Algae densely tufted, soft, dark brownish red, 10–25 cm high (adhering to paper when dried); uncorticated; polysiphonous segments of (8–)10–12(–14) pericentral cells. Erect axes 300–430 µm in diameter, segments 2.0–2.5(–4.0) times longer than diameter; unbranched to loosely branched in lower portions, becoming densely branched above; ultimate branches mostly densely plumose, narrowed at the base; arising endogenously at close intervals from lower, densely matted, prostrate branches; attached by numerous unicellular rhizoids, usually with digitate ends. Rhizoids usually 2 or 3 per segment, cut off as separate cells from the proximal end of pericentral cells. Trichoblasts up to 800 µm long, sometimes unbranched or mostly with 1 or 2 dichotomies; 1 per segment in spiral sequence with ¼ divergence; later deciduous, leaving relatively large scar cells; branches of all orders exogenous (arising in association with trichoblasts).

Tetrasporangia 80–100 µm in diameter, more or less spiraling in the ultimate and subultimate branches. Cystocarps globular to ovoid, somewhat truncate, 350–400 µm in diameter. Spermatangial stichidia 130–250 µm long, 50–70 µm in diameter; apex without sterile cell.

Habitat. Mostly on rocks, sometimes on shells, and also epizoic on the sand dollar, *Encope grandis* L. Agassiz (1840); usually in protected bays and estuaries; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Guaymas. Eastern Pacific: southeast Alaska to northern Baja California; Peru; Chile.

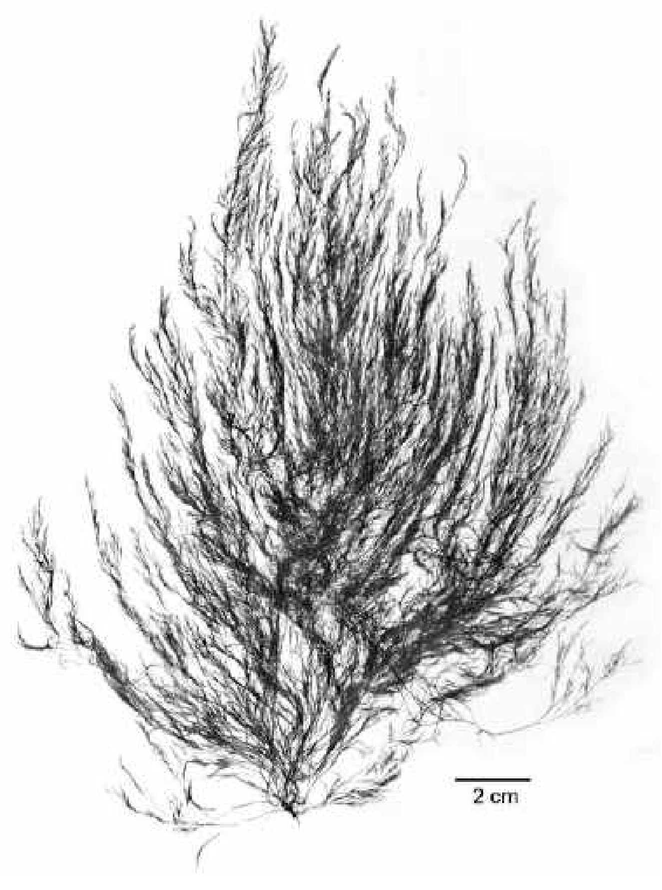


FIGURE 133. *Neosiphonia paniculata*: Habit (*JN-4552*, US Alg. Coll.-160578).

Type Locality. Intertidal, on *Ulva nematoidea*; Peru.

Remarks. The occurrence of both tetrasporangia and cystocarps on the same individual thallus of *Neosiphonia paniculata* from northwestern Baja California was reported by R. Aguilar-Rosas and Aguilar-Rosas (1984, as "*P. paniculata*"). Specimens from Laguna Agiabampo referred to "*Polysiphonia* aff. *paniculata*" by Ortega et al. (1987) may also be this species.

Polysiphonia Greville

Polysiphonia Greville, 1823: pl. 90, *nom. cons*.; M.-S. Kim et al., 2000:83; H.-G. Choi et al., 2001a:1465.

Algae are usually erect (flaccid to semirigid) or partially erect and prostrate or rarely entirely prostrate axes and mostly indeterminate branches of cylindrical, polysiphonous filaments composed of segments of an axial cell with four or more pericentral cells (up to 25 or more), the same length as the axial cells. Upper portion of the branches are usually straight, with a conspicuous apical cell and forming exogenous branches. Branches may develop endogenously adventitiously from various parts of the thallus or from scar cells on older parts of branches (cicatrigenous development). Thalli may be uncorticated throughout or have some degree of rhizoidal or pseudoparenchymatous cortication formed from the pericentral cells. Erect upper portions are developed from a creeping, usually extensive, base of prostrate axes that are attached to substratum by usually unicellular rhizoids developed from and remaining in open communication with basal pericentral cells. Secondary prostrate branches can develop from the attaching decumbent branches or determinate attaching branches. Trichoblasts are rare or lacking, and if present, they are colorless (lacking chloroplasts), usually branched once to many times, and deciduous, often soon after formation, leaving scar cells. Scar cells result from the breaking off of a deciduous trichoblast that leaves behind its embedded basal cell.

Asexual propagation is possibly by fragmentation, and asexual propagules have been noted for a few of the species (Kapraun, 1977; Womersley, 1979). Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia are tetrahedrally divided, with one per segment in a straight series usually in the upper portion of determinate branches. Gametangial thalli are usually dioecious. Carpogonial branch is four-celled, borne on polysiphonous branches. Cystocarps are surrounded by a pericarp of small cells, ostiolate and usually borne in upper portions of branches. Carposporangia are produced on short gonimoblast filaments emerging from a fusion cell. Spermatangial stichidia are elongate or cylindrical and develop from a lateral branch initial in upper portions of branches, with apices that either lack sterile cells or have one to a few sterile terminal cells.

Generitype. *Polysiphonia urceolata* (Lightfoot ex Dillwyn) Greville, 1824:309; basionym: *Conferva urceolata* Lightfoot ex Dillwyn, 1809: pl. G (now a synonym of *Polysiphonia stricta* (Dillwyn) Greville, 1824:309; basionym: *Conferva stricta* Dillwyn, 1804: pl. 40).

Remarks. Species of *Polysiphonia* can be epiphytic on other algae, sea grasses, or other aquatic vegetation, epizoic on sea turtles, or grow on rocks or other hard substratum from the intertidal to subtidal. *Polysiphonia* differs from *Neosiphonia* in having lateral branch development separated by one or more polysiphonous segments, erect determinate and indeterminate branches that develop from an extensive creeping base, attachment rhizoids that are in open communication with their pericentral cell, trichoblasts that are rare or lacking, a four-celled carpogonial branch, spermatangia that develop from a lateral branch initial, and tetrasporangia in straight series in determinate branches.

Some *Polysiphonia* species with numerous pericentral cells per segment are also seemingly close to the eastern Atlantic *Leptosiphonia* Kylin (1956), a genus separated primarily by its two tetrasporangia per segment. Comparative studies of the generitype, *L. schousboei* (Thuret) Kylin (basionym: *Polysiphonia schousboei* Thuret, in Bornet and Thuret, 1876), are needed to clarify its generic status. The relationship of the genus *Polyochetum* Chevallier (1836), considered congeneric with *Polysiphonia* (see Farr et al., 1979; Wynne and Schneider, 2010), should also be reinvestigated.

There are six taxa reported in the southern Gulf: *Polysiphonia bifurcata* Hollenberg (in Taylor, 1945), *P. decussata* Hollenberg (1942b), *P. hendryi* N. L. Gardner (1927f), *P. homoia* Setchell et N. L. Gardner (1930), and *P. pacifica* var. *gracilis* Hollenberg (1942b) from Bahía de La Paz (Huerta-Múzquiz and Mendoza-González, 1985); *P. nathanielii* Hollenberg (1958a) from Jalisco (near the entrance to the Gulf) and Colima (Sentíes-G., 1995); and, with a taxonomic query, *P. scopulorum* Harvey (1855) from Mazátlan (Mendoza-González et al., 1994).

Six taxa, including five species and three varieties of *Polysiphonia* are currently recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *POLYSIPHONIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Trichoblasts in general very rudimentary or absent; scar cells regularly 1 per segment .... ***P. hollenbergii***
1b. Trichoblasts and scar cells either lacking or, if present, not regularly 1 per segment 2
2a. Thalli delicate; mostly intertidal; mostly forming spreading mats or furry patches .... ***P. scopulorum* var. *villum***
2b. Thalli not as delicate; mostly subtidal, not forming mats or patches 3
3a. Thalli up to 4 cm high; trichoblasts numerous, arising at irregular intervals .... ***P. sonorensis***
3b. Thalli 2–4 or more than 10 cm tall; trichoblasts infrequent to rare 4
4a. Thalli 10–30 cm tall; 100–300 µm in diameter; segments mostly 4–10 times longer than diameter .... ***P. pacifica* var. *pacifica***
4b. Thalli shorter, 2–4 cm tall; 50–130 µm in diameter; segments much shorter, 1–3 times longer than diameter 5

5a. Thalli short, usually less than 2 cm tall; axes 50–110 µm in diameter, segments 1.0–2.0(–3.0) times longer than diameter . . . . *P. pacifica* var. *delicatula*
5b. Thalli taller, up to 4 cm tall; middle portions of axes 70–130 µm in diameter, segments 1–2 times longer than diameter . . . . *P. subtilissima*

Polysiphonia sect. *Oligosiphonia* J. Agardh

Polysiphonia sect. *Oligosiphonia* J. Agardh, 1863:910.

Members of this section are characterized by having four pericentral cells per polysiphonous segment.

The five species of *Polysiphonia* currently known in the northern Gulf of California are members of this taxonomic section (="*Polysiphonia* group" of H.-G. Choi et al., 2001a).

Polysiphonia hollenbergii J. N. Norris, sp. nov.

FIGURE 134

Polysiphonia sp. of Hollenberg and Norris, 1977:18 [in part], figs. 10A,B (only).

Latin Description. Algae a 3 cm alta; segmentae cellule pericentrales 4 ecorticatae, aeque 1.0–1.5 longa ac diametros; axes erectis 320 µm diametro; ramosis saepenumero subdichotomous; trichoblastae rudimenta ipsa o absentis, at segmenta irregulariter interpositis de cerca 8–10 segmenta; cellulis constans cicatriceum unum segmentum per spiralis sequence; non servati rhizoideas; tetrasporangia et cystocarpum invisus; stichidia spermatangia totum de integro primoedium trichoblast.

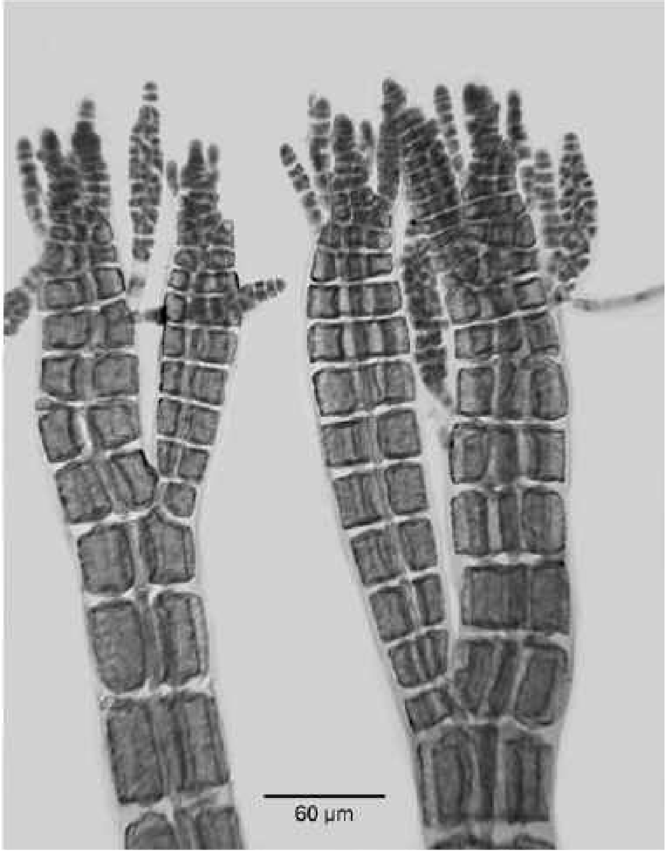


FIGURE 134. *Polysiphonia hollenbergii:* Upper portion of axes with spermatangial stichidia; trichoblasts rare to absent (holotype: *JN-2998b*, US Alg. Coll. microscope slide 5004).

Algae up to 3 cm tall; polysiphonous segments of 4 pericentral cells, 1.0–1.5 times as long as the diameter, uncorticated. Main axes up to 320 µm in diameter in lower portions; branching repeatedly subdichotomous at irregular intervals of mostly 8–10 segments. Rhizoids unicellular, in open communication with basal pericentral cells. Trichoblasts very rudimentary or absent; if present, soon deciduous leaving a scar cell.

Tetrasporangia and cystocarps not seen. Spermatangial stichidia arising from an entire trichoblast primordium.

Habitat. Epiphytic on other algae; shallow subtidal, about 7.6 m depth.

Distribution. Gulf of California: Isla la Ventana, Bahía de Los Ángeles.

Holotype. *JN-2998b*, ♂ (US Alg. Coll. microscope slide 5004). Isotype: *JN-2998b*, ♂ (US Alg. Coll. microscope slide 5003).

Type Locality. Isla la Ventana, Bahía de Los Ángeles, Baja California, Gulf of California, Mexico.

Etymology. It is my pleasure to name this species in honor of George J. Hollenberg (1897–1988, Professor, University of Redlands; Abbott, 1989) in recognition of his numerous phycological contributions, especially the detailed morphological studies of Pacific *Polysiphonia,* including those of Baja California and the Gulf of California, and studies of the California marine flora, most notably the *Marine Algae of California* (with I. A. Abbott). As a beginning student of the marine algae, I was introduced to "Uncle George" Hollenberg by "Izzie" Abbott (Professor Isabella Aiona Abbott, 1919–2010; Huisman and Norris, 2004). It was "Uncle George" who encouraged and fostered my interest in the genus.

Remarks. The development of spermatangia from a lateral branch initial (replacing a trichoblast primordium) was observed in the holotype specimen of *Polysiphonia hollenbergii* (*JN-2998b,* ♂; see Hollenberg and Norris, 1977: figs. 10A, B, as "*Polysiphonia* sp."). Although only a few attachment rhizoids were observed, they were unicellular and remain in open communication with basal pericentral cells (*JN-2998b*; US Alg. Coll. microscope slide 5003). Both of these features are characteristics of the genus *Polysiphonia*.

There is another specimen from a different northern Gulf locality that was also referred to as "*Polysiphonia* sp." (Hollenberg and Norris, 1977:16): a tetrasporophyte, epizoic on a pen shell from Bahía San Francisquito; (*JN-3265b*; US Alg. Coll. slide 5016; Hollenberg and Norris, 1977: figs. 10C, D) that has a spiral arrangement of the tetrasporangia, suggesting that this specimen is a different species. It may also be new and probably belongs to *Neosiphonia*.

Polysiphonia pacifica var. *delicatula* Hollenberg

FIGURE 135

Polysiphonia pacifica var. *delicatula* Hollenberg, 1942b:778; Smith, 1944:360; Dawson et al., 1960b:13; Hollenberg, 1961:362; Dawson, 1961b:450; Abbott and Hollenberg, 1976:690; Hollenberg and Norris, 1977:10, fig. 6b; Young and Kapraun, 1985: figs. 23–28; Huerta-Múzquiz and Mendoza-González, 1985:54; Mendoza-González and Mateo-Cid, 1985:32; Stewart, 1991:166; Mateo-Cid and Mendoza-González, 1992:23; Serviere-Zaragoza et al., 1993a:484; Mendoza-González et al., 1994:109; González-González et al., 1996:255; Mendoza-González and Mateo-Cid, 1996b:69, pl. 14: figs. 56–58; L. Aguilar-Rosas et al., 2000:132; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:469; Dreckmann et al., 2006:155; Pacheco-Ruíz et al., 2008:213.

Algae erect, usually 0.5–2.0 cm tall; uncorticated polysiphonous segments of 4 pericentral cells, (50–)60–110 µm in diameter, 1.0–2.0(–3.0) times as long as wide; attached by rhizoids, 1 per segment from pericentral cells of prostrate branches; rhizoids not cut off from the pericentral cell by a cross wall. Erect branches develop endogenously from prostrate branches; all branches indeterminate, short and mostly blunt; often with more or less forcipate apices. Trichoblasts lacking or exceedingly rare.

Tetrasporangia 50–60 µm in diameter; in straight series of upper branches. Cystocarps slightly urceolate, 200–500 µm in diameter. Spermatangial stichidia developing from entire trichoblast primordium; slender, 140–200 µm long by 30–40 µm in diameter; on very short pedicels, leaving persistent scar cells when shed.

HABITAT. Epiphytic on various algae and growing on rocks or other hard substratum; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; San Felipe to Bahía de San Lucas; Mazátlan, Sinaloa to Nayarit. Eastern Pacific: Alaska; Oregon to Baja California; Santa Catalina Island (California Channel Islands); Chiapas; Galápagos Islands.

TYPE LOCALITY. On wharf piling, low tide level; Monterey Municipal Wharf, Monterey, Monterey County, central California, USA.

REMARKS. *Polysiphonia pacifica* var. *delicatula* differs from the other varieties in being the smallest (less than 2 cm tall) and in having narrow main branches (60–100 µm in

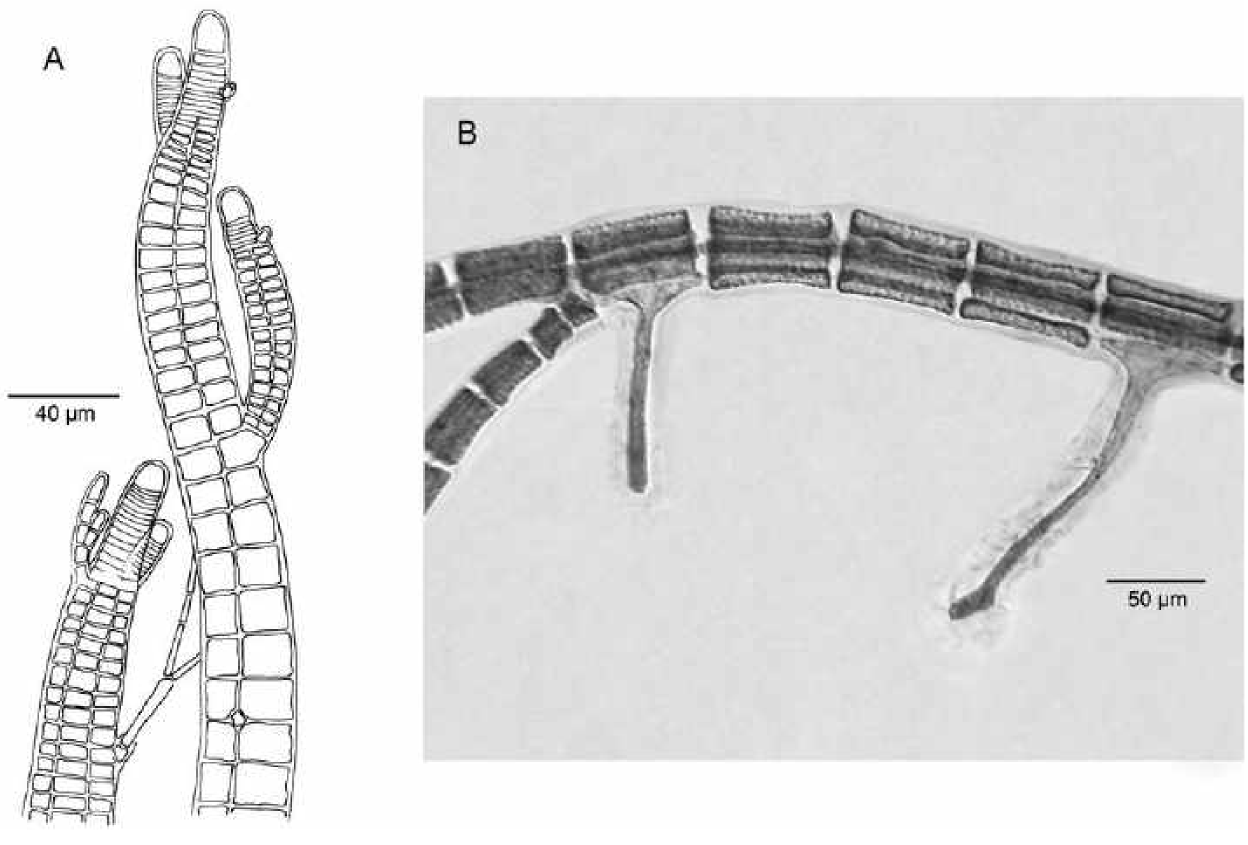


FIGURE 135. *Polysiphonia pacifica* var. *delicatula*: A. Trichoblasts rare or lacking on branch apices (after Hollenberg and Norris, 1977: fig. 6B). B. Rhizoids remaining in open connection to pericentral cell (A, B, *JN-4848a*, US Alg. Coll. microscope slide 4260).

diameter). *Polysiphonia pacifica* var. *delicatula* is not to be confused with another taxon that bears the same name, the tropical *P. delicatula* Hollenberg (1968a). The latter is a different species that was later described from Hawaii (Hollenberg, 1968a; Abbott, 1999) and has since been reported from Micronesia (Lobban and Tsuda, 2003) and in the Indian Ocean from the Seychelles (Silva et al., 1996a).

Polysiphonia pacifica Hollenberg var. *pacifica*

Polysiphonia pacifica Hollenberg, 1942b:777, figs. 2–3, 12(type specimen)–13; Smith, 1944:359, pl. 94: fig. 3; Hollenberg, 1961:361, pl. 5: fig. 5, pl. 7: figs. 2–3; Dawson, 1961b:450; Abbott and Hollenberg, 1976:689, fig. 637; Silva, 1979:331; Mendoza-González and Mateo-Cid, 1985:32; Huerta-Múzquiz and Mendoza-González, 1985:54; L. Aguilar-Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1986:421; Scagel et al., 1989:233; Mendoza-González et al., 1994:109; Anaya-Reyna and Riosmena-Rodríguez, 1996:864 (tbl. 1); González-González et al., 1996:255; M.-S. Kim and Yang, 2005:17, figs. 5–8; Pérez-Estrada et al., 2012:191.

Algae of erect axes, (5–)10–25 cm tall, and less conspicuous lower creeping axes; main axes little branched; branching more or less alternate, up to several orders; branch intervals of (2–)4–5 segments but often longer between branches; polysiphonous segments of 4 pericentral cells, uncorticated, 100–300 µm in diameter, 4–10(–20) times as long as wide (shorter in ultimate branchlets); lower prostrate portions attached by unicellular rhizoids issued from center of lower pericentral cells at irregular intervals and not cut off by cross walls. Trichoblasts and scar cells absent or exceedingly rare.

Tetrasporangia 60–70 µm in diameter in straight series within ultimate branchlets. Cystocarps slightly urceolate, 200–500(–675) µm in diameter; on an inconcpicuous to very short pedicel. Spermatangial stichidia, cylindrical, with apices of one to several sterile cells; developed from lateral branch initial.

Habitat. Usually found growing in lagoons and esteros; on rocks and shells, and epiphytic of mangroves (on pneumatophores of *Avicennia germinans* and aerial roots of *Rhizophora mangle*) and probably other algae; intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Chueca to Estero Santa Rosa, Sonora; Estero Zacatecas (Ensenada de La Paz) to Bahía La Paz; Cabo Pulmo to Punta Los Frailes; Mazátlan. Eastern Pacific: Alaska to central California; Islas Coronados; Las Playitas, Ensenada to estero Punta Banda, Baja California; El Salvador.

Type Locality. Santa Cruz, Santa Cruz County, central California.

Remarks. *Polysiphonia pacifica* var. *pacifica* (Hollenberg, 1942b) has been reported in the northern Gulf by Mendoza-González and Mateo-Cid (1986). Since I have not seen their specimens, the description is based on Hollenberg (1961). *Polysiphonia pacifica* var. *pacifica* is much larger than those of the northern Gulf *P. pacifica* var. *delicatula*,10–25 cm tall, with axes 100–200(–300) µm in diameter, and with segments much longer than wide.

Polysiphonia pacifica is considered to be a highly variable species, with six varieties, including *P. pacifica* var. *pacifica*, recognized (Hollenberg, 1942b; Abbott and Hollenberg, 1976; Gabrielson et al., 2004). M.-S. Kim and Yang (2005: fig. 13) found that although one of the varieties, the Pacific Northwest *P. pacifica* var. *disticha* Hollenberg (1942b), differed morphologically, it had identical *rbc*L sequences, clustering with *P. pacifica* var. *pacifica*. *Polysiphonia pacifica* has also been reported from El Salvador (Avilés and Canjura, 1979; Fernández-García et al., 2011) and Chile (Hoffmann and Santelices, 1997), but without noting their varietal identifications.

Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg

FIGURE 136

Polysiphonia villum J. Agardh, 1863:941.

Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg, 1968a:81, fig. 7a; Abbott and Hollenberg, 1976:692, fig. 640; Hollenberg and Norris, 1977:14, fig. 8b; Santelices and Abbott, 1978:219; Kapraun and Norris, 1982:233, fig. 111a–b; Schnetter and Bula-Meyer, 1982:175, pl. 32: figs. M,N; Stewart and Stewart, 1984:147; Huerta-Múzquiz and Mendoza-González, 1985:54; Young and Kapraun, 1985:113, figs. 35–40; Santelices and Abbott, 1987:9; Santelices, 1989:369, pl. ÑÑ: fig. 19; Stewart, 1991:167; León-Tejera et al., 1993:200; R. Aguilar-Rosas and Aguilar-Rosas, 1994:524; González-González et al., 1996:324; Mendoza-González and Mateo-Cid, 1996b:69, pl. 15: figs. 59–63; M.-S. Kim and Lee, 1996:143; Hoffman and Santelices, 1997:397, figs. 112:1–7; Mateo-Cid et al., 2000:67; Riosmena-Rodríguez et al., 2005a:34; Dreckmann et al., 2006:155; Pacheco-Ruíz et al., 2008:213; R. Aguilar-Rosas and Aguilar-Rosas, 2010:187, fig. 1; Fernández-García et al., 2011:63; Pérez-Estrada et al., 2012:191.

Lophosiphonia villum (J. Agardh) Setchell et N. L. Gardner, 1903:329; Kylin, 1941:40; Hollenberg, 1942a:535; Dawson, 1944a:332, pl. 48: figs. 1–6; Smith, 1944:364, pl. 94: fig. 1; Taylor, 1945:304; Dawson, 1954b:161; 1963b:421, pl. 169: figs. 1–3; Stewart and Stewart, 1984:147; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:243.

Algae to 5–10 mm high, composed of uncorticated polysiphonous axes with segments of 4 pericentral cells around a central axial filament cell; prostrate system well developed; erect axes sparingly branched or unbranched, arising at irregular intervals in a strictly endogenous manner from prostrate axes attached by unicellular rhizoids developed from center of the pericentral cells and not cut off by cross walls. Branch segments usually 40–60 µm in diameter and 1.0–1.5 times as long as wide. Lateral branches on erect axes, if present sparse, exogenous or endogenous, independent of trichoblasts. Trichoblasts usually infrequent or lacking; if present, with 1 or 2 dichotomies, 250–480 µm long; soon deciduous.

Tetrasporangia 50–60 µm in diameter; in straight series, somewhat distending the segments. Cystocarps ovoid, 150–190 µm in diameter. Spermatangial stichidia cylindrical, without sterile apices; arising from an entire trichoblast primordium.

Habitat. On rocks and shells and on tidal platforms; intertidal.

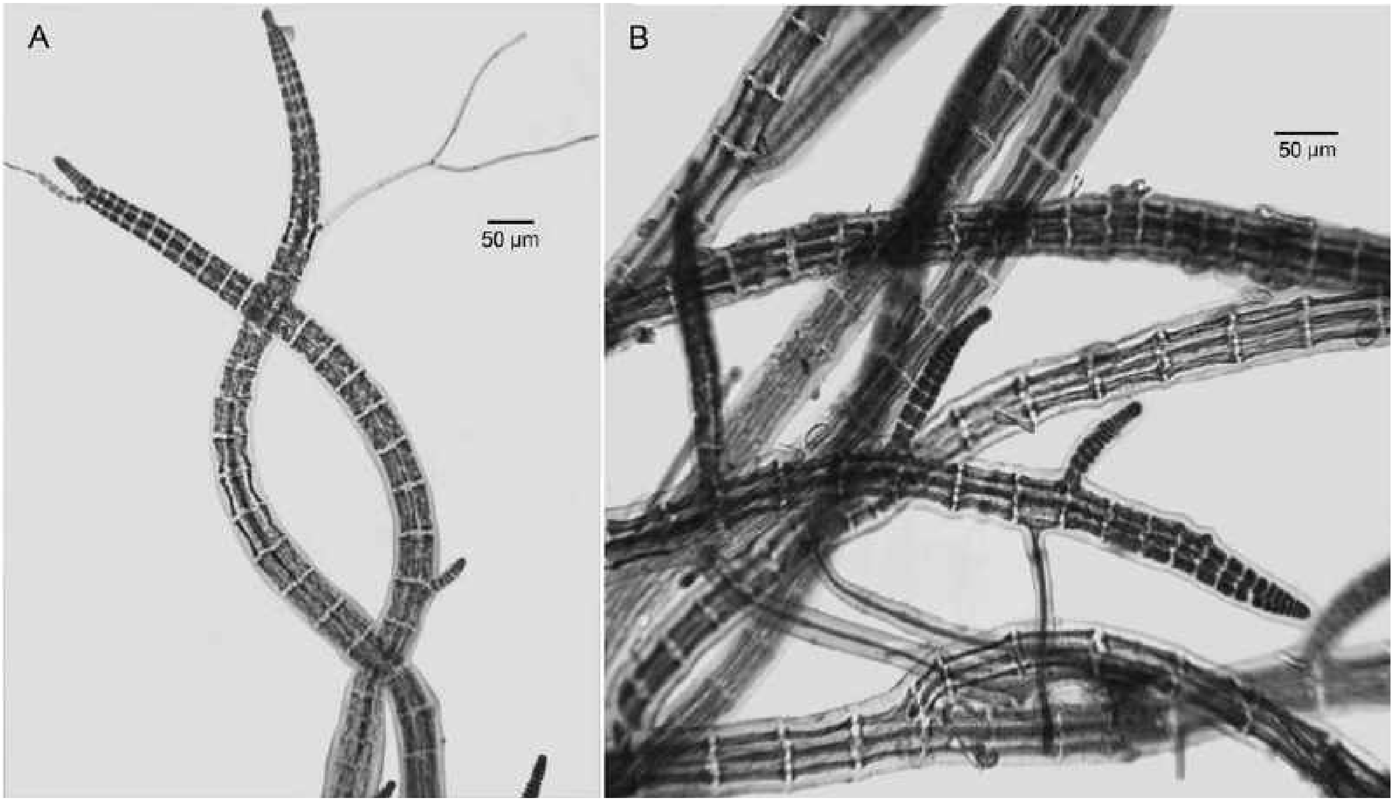


FIGURE 136. *Polysiphonia scopulorum* var. *villum*: A. Axes with a branched trichoblast (*JN-5098a*, US Alg. Coll. microscope slide 4995). B. Prostrate axes with rhizoids in open communication with pericentral cell (JN-3744, US Alg. Coll. microscope slide 5025).

Distribution. Gulf of California: Puerto Peñasco; Isla Ángel de la Guarda; Isla Partida; Isla Turner (Turners); Isla Estanque; Punta Arena to Cabo Pulmo; Nayarit. Eastern Pacific: Kodiak Island, Alaska to Oregon; central California to Baja California Sur; Santa Catalina Island (California Channel Islands); Isla Guadalupe; Chiapas to Costa Rica; Colombia; Chile; Rapa Nui (Easter Island; Isla de Pascua).

Type Locality. "*Ad littus americae tropicae*" (J. Agardh, 1863); Dawson (1944a:333) stated "probably on the central coast of [Pacific] Mexico."

Remarks. Originally described as a species of *Polysiphonia*, *P. villum* J. Agardh (1863) was later transferred to the genus *Lophosiphonia* Falkenberg (in F. Schmitz and Falkenberg, 1897), where it was recognized as *L. villum* (e.g., Dawson, 1944a, 1963b; Smith, 1944) until Hollenberg (1968a) considered it to be one of three taxonomic varieties of *Polysiphonia scopulorum*. One of these, *P. scopulorum* var. *villum,* is found in the northern Gulf (Hollenberg and Norris, 1977) and California (Abbott and Hollenberg, 1976; Young and Kapraun, 1985). *Polysiphonia scopulorum* var. *villum* primarily differs from the other varieties in having segments of the branches that are mostly longer than wide. Masuda et al. (2000) observed similarities between their Malaysian *P. scopulorum* var. *scopulorum* and *P. scopulorum* var. *villum* and suggested these two varieties were the same. Cystocarps and tetrasporangia have been reported on the same thallus of Pacific Mexico *P. scopulorum* var. *villum* from northern Baja California (R. Aguilar-Rosas and Aguilar-Rosas, 2010). Herein the northern Gulf specimens are referred to *P. scopulorum* var. *villum* until its generic and specific status is clarified by comparisons with the types and type locality materials of these taxonomic varieties.

Polysiphonia sonorensis Hollenberg

FIGURE 132F

Polysiphonia sonorensis Hollenberg, 1942b:779, figs. 5, 20; Dawson, 1944a:330; 1954d:161; Hollenberg, 1961:365, pl. 5: fig. 2, pl. 6: fig. 1; Dawson, 1961b:450; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Hollenberg and Norris, 1977:16, fig. 2c; González-González et al., 1996:257; Serviere-Zaragoza et al., 2007:11.

Algae erect, usually dense tufts of filaments; up to 5 cm high, terracotta color (not strongly adherent to herbarium paper on drying); erect main axes indistinct usually densely branched; polysiphonous segments of 4 pericentral cells, uncorticated, 70–100 µm in diameter, mostly 1.5–2.0 times as long as the diameter; above prostrate, creeping branches, 120–175 µm in diameter; attached by unicellular rhizoids developed from center of the pericentral cells and not cut off as separate cells. Erect branches usually develop endogenously or sometimes exogenously from the prostrate branches; exogenously produced branches at irregular intervals of mostly 1–20 segments, usually at an acute angle with the parent branch; branches replacing trichoblasts. Trichoblasts delicate, numerous, up to 1 mm long, with 1 or 2 dichotomies arising at irregular intervals; deciduous, leaving inconspicuous scar cells.

Reproductive material has not been found.

Habitat. On rocks; intertidal.

Distribution. Gulf of California: Guaymas to the bay (bahía) near Empalme.

Type Locality. "Afloat," southeastern shore of the bay, near Empalme, Sonora, Gulf of California, Mexico (Hollenberg, 1942b).

Remarks. As a little-known species, more collections of *Polysiphonia sonorensis*, particularly reproductive specimens, are needed to determine its taxonomic status. It has also been reported from the Golfo de Tehuantepec, Oaxaca (Huerta-Múzquiz and Tirado-Lizárraga, 1970), and Isla Socorro, Islas Revillagigedo (Huerta-Múzquiz and Garza-Barrientos, 1975; Serviere-Zaragoza et al., 2007).

Polysiphonia subtilissima Montagne

Polysiphonia subtilissima Montagne, 1840:199; Taylor, 1947:86; Dawson et al., 1964:90, pl. 80: figs. G–J; Ramírez and Santelices, 1991:379; Sheath et al., 1993:115, figs. 19–21; Sentíes-G., 1995:50, figs. 37–44; Abbott, 1999:430, fig. 128A; Mateo-Cid et al., 2006:57; Dreckmann et al., 2006:155; Bernecker, 2009:CD-Rom p. 68; Fernández-García et al., 2011:64; Lam et al., 2013:156, figs. 1–6.

Polysiphonia subtilissima var. *abbottiae* Hollenberg, 1968a:92, figs. 5F, 6A.

Algae up to 4 cm tall; polysiphonous filaments uncorticated, with 4 pericentral cells per segment; erect portions above prostrate axes; attachment rhizoids, unicellular, with lobed tips, remain in open connection with pericentral cells. Erect axes endogenous, slender, 70–130 µm in diameter in middle portions; about 50 µm in diameter in upper branches; pericentral cell segments 1–2 times longer than diameter. Lateral branches develop independent of trichoblasts at varying intervals. Trichoblasts infrequent, with 1–2 dichotomies; usually poorly developed (occasionally up to 400 µm long).

Reproductive structures not reported in the northern Gulf.

Habitat. On tidal rocks, aquatic vegetation, and mangroves in shallow esteros and bays; intertidal.

Distribution. Gulf of California: Punta Pelícano (vicinity of Puerto Peñasco). Eastern Pacific: Chiapas; El Salvador; Costa Rica; Peru. Central Pacific: Oahu, Hawaiian Islands. Western Pacific: Korea; Vietnam.

Type Locality. Cayenne, Arrondissement of Cayenne, French Guiana (Guyane).

Remarks. *Polysiphonia subtilissima* is only known in the upper Gulf of California from the report of Mateo-Cid et al. (2006). Since I have not seen their material, the description herein follows Abbott (1999) and Womersley (2003). Apparently widely distributed, *P. subtilissima* has been reported in the Mediterranean Sea, Eastern and Western Atlantic (including the Caribbean Sea), Eastern and Western Pacific, and Indian Oceans (e.g., Adams, 1991; Silva et al., 1996a; John et al., 2004; Suárez, 2005; Wynne, 2005; Mamoozadeh and Freshwater, 2012; Guiry and Guiry, 2012). Also physiologically very tolerant, *P. subtilissima* has been reported in a wide range of habitats including brackish waters in Hawaii (Abbott, 1947), freshwater in Florida (Sheath and Cole, 1990; Sheath et al., 1993), and in shallow bays and low intertidal rocks on marine shores (Womersley, 2003). Lam et al. (2013) recently confirmed that freshwater collections from Spain, Jamaica, and Florida were the same as *P. subtilissima* from marine habitats. Different taxonomic treatments that include "*P. subtilissima*" have given varying descriptions of the taxon, suggesting some may be misidentified or there may be more than one species. Mamoozadeh and Freshwater (2012) found three genetic species that had only slight morphological differences but were in general agreement with a broadly defined "*P. subtilissima.*" Thus further studies are needed to determine if there are any cryptic or overlooked species within those referred to "*P. subtilissima.*"

RHODOMELACEAE TRIBUS PTEROSIPHONIEAE

Rhodomelaceae tribus Pterosiphonieae Falkenberg, 1901:261.

The tribe is represented by two of its genera in the northern Gulf of California.

Pterosiphonia Falkenberg in F. Schmitz and Falkenberg

Pterosiphonia Falkenberg in F. Schmitz and Falkenberg, 1897:443.

Thalli are erect, bilaterally branched, terete to strongly compressed axes that arise from indeterminate prostrate, mostly terete, rhizome-like axes. Rhizoids cut-off from prostrate axes form multicellular discs that adhere to substratum. Axes are polysiphonous and uncorticated or corticated, with segments composed of an axial filament cell surrounded by 4–20 pericentral cells, and lateral indeterminate axes replacing or developing from determinate axes. Axes are distichously branched from 1 to several orders, alternately arranged, laterals emerging every 2–4 segments. The basal portion of each branch is coalesced (fused) with its parental axis for 1 to a few segments. Ultimate branchlets are determinate and may be simple or pinnately branched and generally lack vegetative trichoblasts. Cells are uninucleate.

Asexual reproduction by fragmentation has been reported. Tetrasporangia are tetrahedrally divided and 1 per segment in a straight series in the determinate laterals. Gametophytes are dioecious, procarps and spermatangial structures borne on modified trichoblasts. Cystocarps are globular to ovoid, borne on short stalks on determinate laterals. Spermatangial stichidia are in alternate distichous arrangement or spirally arranged, forming clusters at apices of determinate branchlets or on short, spur-like branchlets from the ultimate determinate branchlets, borne on suprabasal cell of a modified trichoblast.

Two species of *Pterosiphonia* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *PTEROSIPHONIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli small, up to 2.5 cm high, main axes only slightly compressed, with few branches; base of branches coalesced with bearing axis for 1.5 proximal segments; lateral branchlets cylindrical, mostly simple, sometimes with incurved ultimate branchlets . . . . *P. californica*

1b. Thalli usually larger, markedly compressed throughout; with numerous branches; base of branches coalesced with bearing axis for 2–2.5 proximal segments; lateral branchlets compound . . . . *P. dendroidea*

Pterosiphonia californica Kylin

FIGURE 137B

Pterosiphonia californica Kylin, 1941:39; Hollenberg, 1948:160; Dawson, 1961b:452.

Pterosiphonia pennata sensu Dawson, 1944a:334; 1961b:452; 1963b:427; Abbott and Hollenberg, 1976:708, fig. 660; R. Aguilar-Rosas, 1982:84; Pacheco-Ruíz and Aguilar-Rosas, 1984:74; L. Aguilar-Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1985:32; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Stewart, 1991:169; González-González et al., 1996:263; CONANP, 2002:139 [non *Pterosiphonia pennata* (C. Agardh) Sauvageau, 1897:287; basionym: *Hutchinsia pennata* C. Agardh, 1824:156].

Algae mostly 1.0–2.5 cm tall, 125–140(–200) µm in diameter; uncorticated, polysiphonous segments of 8–11(–12) pericentral cells. Erect axes percurrent, distichously and alternately branched; axes slightly compressed, arise above prostrate axes at every third segment. Branchlets cylindrical, 1.0–1.5 mm long, mostly simple, and usually slightly incurved, arising from every second segment.

Tetrasporangia in upper portion of determinate branchlets, in a series with 1 per segment. Cystocarps not seen in Gulf material. Several spermatangial stichidia, each on modified trichoblast primordium; borne distichous or adaxially, near apices of ultimate determinate branches.

Habitat. On rocks or occasionally epiphytic; intertidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas; Cabeza Ballena to Cabo San Lucas. Eastern Pacific: southern California to northern Baja California.

Type Locality. La Jolla, San Diego County, southern California, USA.

Remarks. Dawson (1944a, as *Pterosiphonia pennata*) initially considered his northern Gulf (Bahía Tepoca, *EYD-372*) specimen to be different from the southern California *Pterosiphonia californica*. But later Dawson (1963b) placed *P. californica* in synonymy with the Mediterranean *P. pennata*, stating the size differences noted by Kylin (1941) were not enough to keep them as separate species. More recently, Uwai and Masuda (1999b:248, tbl. 1) noted that the marked disjunct distribution between the two requires further consideration. Until detailed comparative morphological and genetic studies can be done on the northern Gulf *P. californica* and type localities of the California *P. californica* and the Mediterranean *P. pennata*, I herein follow their suggestion that they may be separate species.

The taxon has often been incorrectly cited as "*Pterosiphonia pennata* (Roth) Falkenberg, 1901." However there are nomenclatural problems with the basionym. Silva et al. (1996a:549) noted *Ceramium pennatum* Roth (1806) is to be treated as new species, but since that name is a later homonym of *Ceramium pennatum* (Hudson) Roth (1800; basionym: *Conferva pennata* Hudson, 1762) it is illegitimate. However, *Hutchinsia pennata* C. Agardh (1824) can be treated as a new name (ICBN, Art. 58.3) and is the correct basionym of *Pterosiphonia pennata* (C. Agardh) Sauvageau (Silva et al., 1996a). Although *Conferva pennata* Hudson also had been treated earlier as basionym of *Sphacelaria pennata*, that use was rejected by Prud'homme van Reine (1982; see also Dixon and Parkes, 1968).

Pterosiphonia dendroidea (Montagne) Falkenberg

FIGURE 137A

Polysiphonia dendroidea Montagne, 1837:353.

Pterosiphonia dendroidea (Montagne) Falkenberg, 1901:268; Howe, 1914:144; Kylin, 1941:39; Dawson, 1944a:335; Smith, 1944:366, pl. 95: fig.3; Taylor, 1945:304, pl. 96: fig. 2; Dawson et al., 1960a:76, pl. 41: figs. 3, 4; Dawson, 1961b:452; 1963b:426, pl. 157: fig. 2; Dawson et al., 1964:84, pl. 69: fig. B; Dawson, 1966a:29; Norris, 1973:16; Abbott and North, 1972:76; Abbott and Hollenberg, 1976:708, fig. 659; Pacheco-Ruíz and Aguilar-Rosas, 1984:74; Stewart and Stewart, 1984:147; Mendoza-González and Mateo-Cid, 1985:32; L. Aguilar-Rosas et al., 1985:125; Sánchez-Rodríguez et al., 1989:46; Scagel et al., 1989:248; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Aguilar-Rosas et al., 1990:126; Stewart, 1991:168; Ramírez and Santelices, 1991:380; R. Aguilar-Rosas and Aguilar-Rosas, 1994:524; Mateo-Cid and Mendoza-González, 1994b:42; González-González et al., 1996:263; Hoffman and Santelices, 1997:400, fig. 113; L. Aguilar-Rosas et al., 2000:132; Pacheco-Ruíz and Zertuche-González, 2002:469; Riosmena-Rodríguez et al., 2005b:34; Hernández-Herrera et al., 2005:148; Mateo-Cid et al., 2006:57; Pacheco-Ruíz et al., 2008:213; Castañeda-Fernández de Lara et al., 2010:200.

Algae 2–8 cm tall; of main axes 200–500 µm wide, gradually attenuating upward; uncorticated, markedly compressed, polysiphonous segments of 8–12 pericentral cells, segments of main axis typically broader than long. Erect axes percurrent, distichously and alternately branched up to 3 orders, generally at intervals of 2.0–2.5 segments; arising from prostrate axes, attached by groups of unicellular rhizoids issued from pericentral

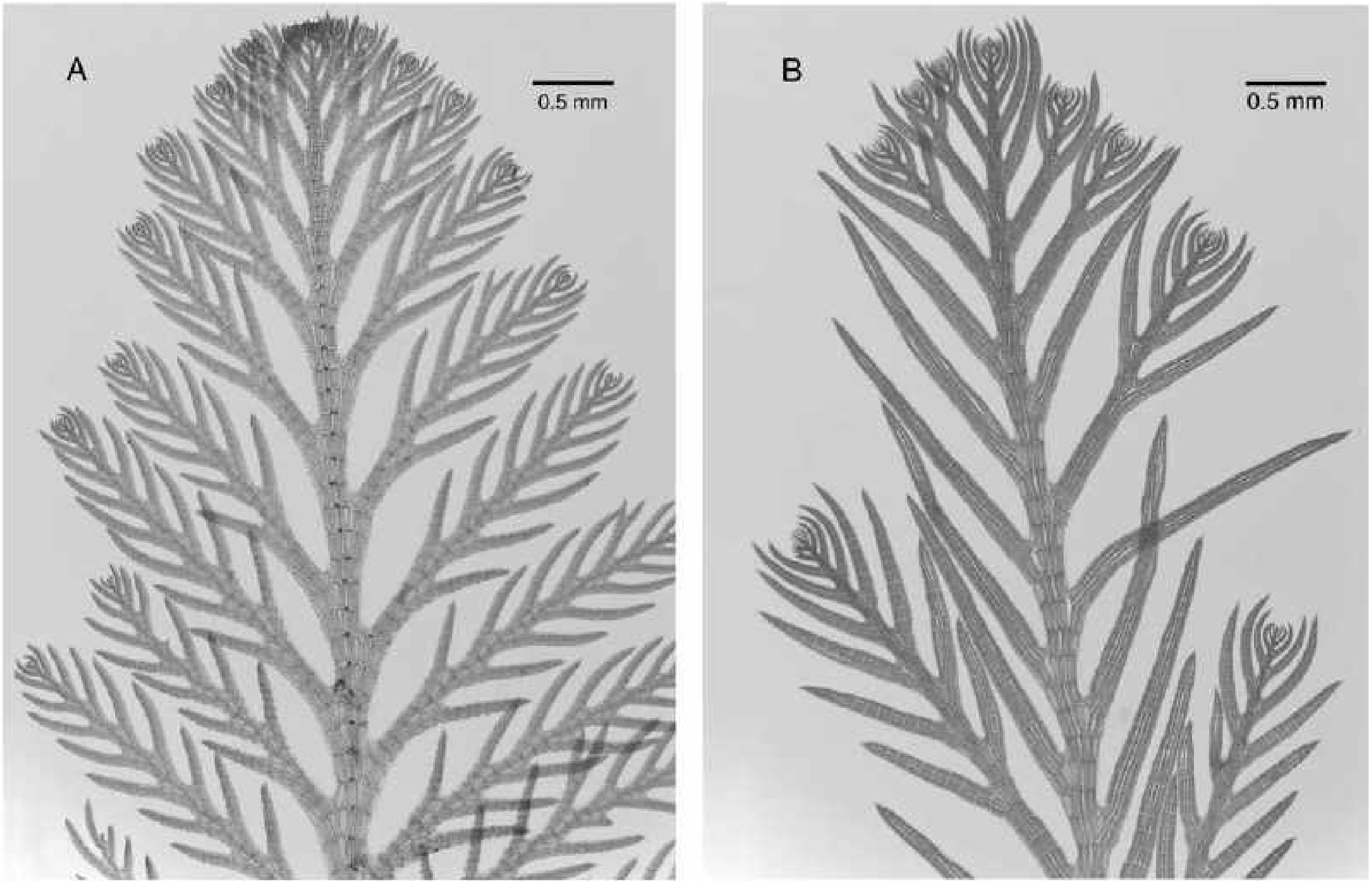


FIGURE 137. Species of *Pterosiphonia*. A. *Pterosiphonia dendroidea:* Branching pattern and apex (*JN-4742*, US Alg. Coll. microscope slide 4899). B. *Pterosiphonia californica:* Branching pattern and apex (*JN-5021*, US Alg. Coll. microscope slide 4900).

cells. Lateral branches compound, with determinate branchlets, all of nearly same length (0.5–1.3 mm long).

Tetrasporangia spherical, 60–70 µm in diameter, 1 per segment in straight series in determinate branchlets. Cystocarps not seen in Gulf of California specimens. Spermatangial stichidia on 1-celled pedicels (unbranched modified trichoblasts), up to 150 µm long, incurved, with 1 to a few sterile terminal cells; arising 1 per segment near tips of indeterminate axes.

Type Locality. Callao (city), Bahía Callao, Provincia Callao, Peru.

Habitat. Among algal turfs on rocks, on tidal platform, and in tide pools or epiphytic; intertidal.

Distribution. Gulf of California: Playa Tucson and Playa Las Conchas (Playa Estación), Puerto Peñasco to Guaymas; Puerto Refugio, Isla Ángel de la Guarda, and Isla Tiburón (Islas de la Cintura); San José del Cabo; Jalisco. Eastern Pacific: Alaska to Todos Santos, Baja California Sur; Islas Todos Santos and Isla Guadalupe, off Baja California; Islas Revillagigedo; Galápagos Islands; Peru; Chile.

Remarks. Dawson (1963b) noted most Gulf *Pterosiphonia dendroidea* were more lax and clearly percurrent, except in the last order of branching, than Pacific Coast specimens.

Pterosiphoniella E. Y. Dawson

Pterosiphoniella E. Y. Dawson, 1963b:422.

Algae of erect, compressed, uncorticated polysiphonous axes that arise from creeping, cylindrical axes attached by unicellular rhizoids cut off from ventral pericentral cells. Indeterminate axes covered with determinate short laterals, the upper portions of erect axes are initially multifariously branched (spirally arranged) and below the laterals become distichously arranged (bilateral). Lateral branches sometimes strictly determinate or may sympodially develop short determinate secondary axes that bear several secondary determinate laterals. Vegetative trichoblasts are occasional to abundant at apices. Pericentral segments are mostly of 8 cells, but a segment can appear to be of 10–16 cells where its parental axis and the proximal segments of laterals are juxtaposed.

Tetrasporangia develop 1 per segment, in a straight series within determinate lateral branchlets. Gametophytes are presumed to be dioecious, however female reproductive structures are unknown. Spermatangial branches are pedicellate, arising from an entire trichoblast primordium.

Remarks. Dawson (1963b) observed that *Pterosiphoniella* shared some characters with both the "*Polysiphonia* group" (radially organized) and the "*Pterosiphonia* group" (bilaterally arranged) sensu Kylin (1956). Comparison of *Pterosiphoniella* to related genera (i.e., *Pterosiphonia*; *Tayloriella* Kylin, 1938; *Boergeseniella* Kylin, 1956; *Pterochondria* Hollenberg, 1942a; *Kintarosiphonia* Uwai et Masuda, 1999a) was provided by Uwai and Masuda (1999a:225, 233: tbl. 1). *Pterosiphoniella* primarily differs from these genera in having vegetative trichoblasts on its apices that are initially radial (spiral) in arrangement and later secondarily develop a bilateral habit.

Described from Pacific Mexico, Dawson (1963b) also observed that North Carolina specimens of Williams (1948, as "*Pterosiphonia pennata*") may also belong to *Pterosiphoniella*, suggesting the genus may also occur in the western Atlantic. Dawson (1963b) concluded *Pterosiphoniella* was closest to *Pterosiphonia* but was distinguished by vegetative trichoblasts on the tips of its branches, and the initial multifarious (spiral) branching of its erect axes. Later, Wynne (1985d) noted that, although rare, vegetative trichoblasts had also been occasionally reported in one species of *Pterosiphonia, P. pennata* (e.g., Ardré, 1967), and suggested that character may not be enough to separate *Pterosiphoniella* from *Pterosiphonia.* Abundant vegetative trichoblasts were described on the axes of another species, *Pterosiphonia tanakae* Uwai et Masuda (1999b). Although recognized as distinct by some (e.g., Stewart and Stewart, 1984; González-González et al., 1996; Uwai and Masuda, 1999a, 1999b), these two genera were considered congeneric by Schneider and Wynne (2007). Another species mentioned by Wynne (1985d), *Pterosiphonia fibrillosa* Okamura (1912; Yoshida, 1998), was subsequently removed to establish the genus *Kintarosiphonia* as *K. fibrillosa* (Okamura) Uwai et Masuda (1999a). When female reproductive structures of *Pterosiphoniella williamsii* can be found and studied and genetic testing of type locality and Gulf specimens can be completed, its taxonomic status and phylogenetic relationships with these genera can be elucidated.

A monotypic genus, its one species occurs in the Gulf of California.

Pterosiphoniella williamsii E. Y. Dawson

FIGURE 138

Pterosiphoniella williamsii E. Y. Dawson, 1963b:423, pl. 135: figs. 3, 4, pl. 160: figs. 1, 2 (holotype); Stewart and Stewart, 1984:147; González-González et al., 1996:263.

Algae up to 2 cm tall, polysiphonous axes and branch segments of mostly 8 pericentral cells, but may appear to be 10–16 cells where basal segments of a branch are adjacent to their parental axis, with central axial cells of similar size and shape to pericentral cells; erect axes compressed, about 300 μm wide; covered with determinate short laterals; apices of main axes multifariously (radially) branched at intervals of 2–3 segments; branch initials developed spirally at tips, soon becoming irregular after first few segments by slight twisting of tip and by bilateral growth of branches, then within 15 segments becoming distinctly bilateral. Lateral branches basically determinate, usually develop a new axis sympodially and abaxially that produces 1–10 secondary short lateral branches, which in turn often develop 1–2 laterals sympodially. Determinate branchlets terete to compressed, 300–600 μm long, with subacute tips with a single terminal conical cell. Trichoblasts sparse, soon deciduous; or absent on most primary axis tips that produce regular lateral branches; abundant and densely branched on tips of secondary axes and secondary determinate lateral branches.

Tetrasporangia spherical, tetrahedrally divided, 50–60 μm in diameter; 1 per segment, in straight series in determinate laterals. Cystocarps unknown. Spermatangial branches borne on 1-celled pedicel and terminate in a 1- to 2-celled sterile tip. Mature spermatangial branches conical, up to 100 μm or more in length (after Dawson, 1963b).

Habitat. On partially sand covered rocks; low intertidal to shallow subtidal, 2–5 m depths.

Distribution. Gulf of California: Cabeza Ballena. Eastern Pacific: Isla Guadalupe; Punta Santa Rosaliita ("Punta Santa Rosalía"), Baja California to Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur.

Type Locality. On fine sand and rock bottom, dredged at 6 m depth; Isla Concha, Laguna Ojo de Liebre (Laguna de Scammon), Baja California Sur, Pacific Mexico.

Remarks. Collections from Cabeza Ballena, Baja California Sur, referred to *Pterosiphoniella williamsii* represent a new record for the Gulf of California (US Alg. Coll.: *JN-4103*, microscope slide 4915; *JN-4126,* microscope slide 4914; and *JN-4149*, microscope slide 4950). Gulf specimens tentatively identified as *P. williamsii* are only in partial agreement, and they differ in having determinate branches that remain multifariously arranged, not only in upper portions but also in lower portions of axes, and the determinate lateral branches are also multifariously branched, and trichoblasts that are few to rare at apices. Spermatangial branches of the Gulf specimens also differ in their lack of the 1–2 sterile cells that were noted by Dawson (1963b) at the tips of those of Pacific Mexico specimens. Although thus far only known in the southern Gulf, *P. williamsii* is included here since it is apparently rare, and this easily overlooked species may be found elsewhere in the Gulf. Molecular analyses of Gulf *P. williamsii* are necessary for comparison with type locality specimens to test their taxonomic status and relationship to each other and to other related genera.

Tayloriella Kylin

Tayloriella Kylin, 1938:18.

Algae form small turfs or clumps of erect and decumbent, cylindrical, uncorticated, polysiphonous axes and branches that

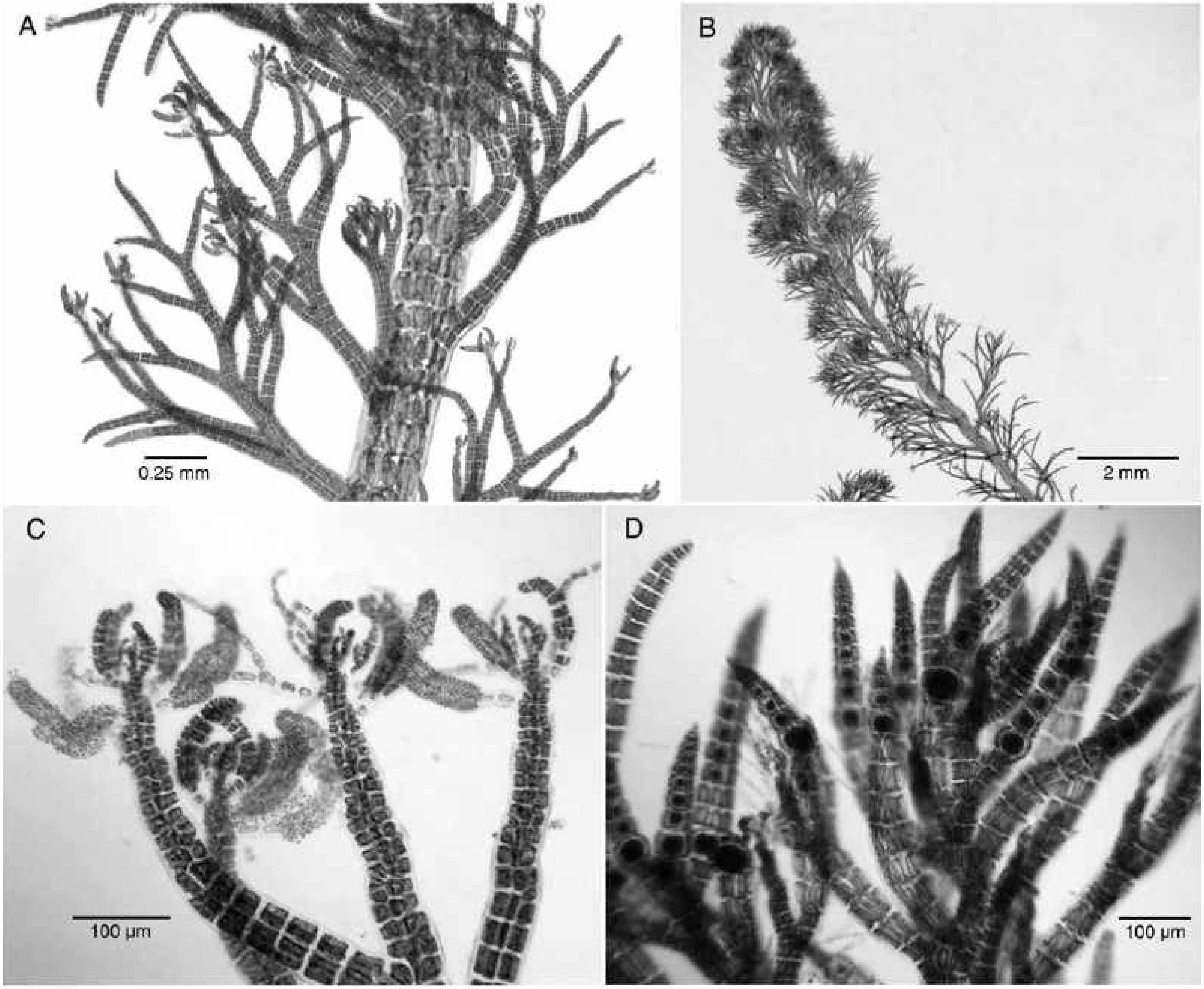


FIGURE 138. *Pterosiphoniella williamsii*: A. Portion of an indeterminate branch with determinate laterals bearing spermatangial stichidia near their apices. B. Upper portion of indeterminate branch. C. Spermatangial stichidia and trichoblasts at apices (A–C, *JN-4126*, US Alg. Coll. microscope slide 4914). D. Tetrasporangia borne in series, 1 per segment (*JN-4103*, US Alg. Coll. microscope slide 4915).

are composed of 4–16 pericentral cells depending on species (or sometimes of variable number on the same thallus). Single-celled attachment rhizoids are cut off from the proximal ends of ventral pericentrals of prostrate axes in some species, but in others they are not cut off. Rhizoids may sometimes be in groups, having developed from the pericentrals on the same segment (Wynne, 1985d). Erect axes can be branched in a zigzag or distichous arrangement. Branches are exogenously developed, with branch initials at first radially arranged, later becoming bilaterally or distichously arranged. Growth is monopodial, often with abaxial determinate laterals extending above parent axes. Branchlets are formed in regular sequence, although usually not on every segment but at intervals of 2–3(–4) segments. Indeterminate axes are irregular, produced in the position of a determinate branch. Determinate laterals in some species have monosiphonous portions at their apices. Trichoblasts are absent on the vegetative axes in many species, but although sometimes rare, they are present in at least one species (i.e., *T. dictyurus*).

Tetrasporangia are tetrahedrally divided, with one per segment, in straight, usually short, series within a tetrasporangial branchlet. Reproductive branchlets are developed in the position of a determinate lateral. Cystocarps, globose to urceolate, are borne terminal on short lateral branchlets. Spermatangial structures are conical with a sterile fork (Uwai and Masuda, 1999a), borne on trichoblasts that terminate with one (or more) sterile apical cells (after Wynne, 1985d; Abbott, 1999).

One species of *Tayloriella* has been reported in the northern Gulf of California.

Tayloriella dictyurus **(J. Agardh) Kylin**

Polysiphonia dictyurus J. Agardh, 1847:16.

Tayloriella dictyurus (J. Agardh) Kylin, 1956:505; Dawson, 1961b:421; 1963b:416, pl. 129: fig. 5, pl. 138: fig. 4; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Huerta-Múzquiz, 1978:339; Pedroche and González-González, 1981:68; Huerta-Múzquiz and Mendoza-González, 1985:52; Mendoza-González and Mateo-Cid, 1986:426; Dreckmann et al., 1990:32, pl. 2: figs. 6–7; Sentíes-G. et al., 1990:101, pl. 5; González-González et al., 1996:271; Abbott, 1999:441, fig. 132A–E.

Bryocladia dictyurus (J. Agardh) W. R. Taylor, 1945:298, pl. 98: fig. 2; Dawson, 1954e:345; Hollenberg, 1958a:63; Salcedo-Martínez et al., 1988:83; González-González et al., 1996:180.

Algae in erect tufts, 1.5–2.0 cm tall, above basal creeping axes attached to substrate by haptera; axes of uncorticated, polysiphonous segments with an axial filament cell encircled by 5–10(–12) pericentral cells. Pericentral cells more or less quadrate and short in mid to upper parts, about 50 μm long; in lower parts up to 100 μm long (about twice the diameter). Main axes simple or occasionally divided, 150–330 μm in diameter, with spirally arranged determinate laterals, simple or forked, 0.5–2.0 mm long, 80–110 μm in diameter at base. Branches exogenous or, less frequently, adventitious from the pericentral cells; final order of spirally arranged simple branchlets up to 20 segments in length; basally to 80–110 μm wide, tapered to unicellular apex. Trichoblasts apical, branched, apparently deciduous (description after Taylor, 1945; Dawson, 1963b).

Tetrasporangia in series of 6–8, one per segment, in midportions of upper determinate branchlets (after Dawson, 1963b). Gametangial reproduction not reported in northern Gulf specimens. Cystocarps in Hawaiian specimens borne on short determinate branchlets, close to the axes in apical portions of thallus. Spermatangial branches with basal pedicel, cylindrical, up to 140 μm long, about 40 μm in diameter near base, slightly tapered to blunt apices, about 26 μm in diameter; borne on modified trichoblasts, abundant near apices (gametophytes as described by Abbott, 1999).

HABITAT. Growing on rocks among turf algae; intertidal.

DISTRIBUTION. Gulf of California: Segundo Cerro Prieto (north of Kino Nuevo), Bahía Kino; Jalisco. Eastern Pacific: Guerrero to Oaxaca; El Salvador; Ecuador. Central Pacific: Hawaiian Islands.

TYPE LOCALITY. "Pochetti" (J. Agardh, 1847); "presumably in the Isthmus of Tehuantepec, Oaxaca" (Dawson, 1963b:417); probably near Pochutla, Oaxaca, Pacific Mexico (note that Pochutla is Spanish for the place of "pochotes," the Spanish name for the Mexican tree species of *Ceiba*, Malvaceae).

REMARKS. *Tayloriella dictyurus* has been recorded from Sonora in the northern Gulf of California by Mendoza-González and Mateo-Cid (1986) and in the southern Gulf from La Paz by Huerta-Múzquiz and Mendoza-González (1985). Since I have not seen their material, the description is based on Dawson (1963a).

Placophora Group

Placophora group sensu Kylin, 1956:497, 528; Womersley, 2003:359.

Members are flattened, foliose, simple or irregularly branched, with broad rounded apices; attached by rhizoids from the ventral surface. Apices formed by rows of polysiphonous filaments laterally conjoined, each with a terminal apical cell and 5 pericentral cells, 3 on the dorsal side and 2 on the ventral surface. Thalli ecorticate, mostly 2 cells thick; unicellular or multicellular attachment rhizoids cut off from ventral pericentral cells.

REMARKS. The *Placophora* group is characterized by the dorsiventrally arranged pericentral cells and contains only two genera, *Amplisiphonia* Hollenberg (1939) and *Placophora* J. Agardh (1863).

There is one genus, *Amplisiphonia*, represented in the Gulf of California marine flora.

Amplisiphonia Hollenberg

Amplisiphonia Hollenberg, 1939:380; Hollenberg and Wynne, 1970:175, figs. 1–5; Kraft and Wynne, 1992:33.

Algae prostrate, dorsiventral, flat-lobed thallus formed by numerous laterally adherent polysiphonous branches; attached to the substratum by unicellular rhizoids issued from the ventral surface. Lobed thallus uncorticated, often overlapping. Growth from apical cells at the margin of the foliose thallus, vegetative thalli without trichoblasts, each apical cell cuts off 5 pericentral cells, dorsiventrally arranged (3 dorsal, 2 ventral) with the polysiphonous branches laterally conjoined to form the flat uncorticated blade. The central axial cells of the polysiphonous branches form a pattern of fine veins that branch dichotomously within the flat thallus.

Tetrasporangia in flat marginal lobes of thallus, obliquely cruciately divided; in longitudinal series, 1 per segment. Gametophytes dioecious, reproductive structures radial in construction borne along margins of lobed thallus. Procarpial branchlets, usually 2 segments long with a single trichoblast; in short polysiphonous branchlets. Cystocarps spherical to ovoid. Spermatangial branchlets, forming a fringe along blade margins; spermatangia in conical stichidia borne on a monosiphonous stalk from a 5-celled polysiphonous filament.

REMARKS. The tribe placement of *Amplisiphonia* has been variously interpreted. In studying some dorsiventral Rhodomelaceae, Scagel (1953) considered *Amplisiphonia* and *Placophora* in the Herposiphonieae with affinities close to members of the Polysiphonieae and the Pterosiphonieae. On the basis of finding the reproductive structures in *Amplisiphonia*, Hollenberg and

Wynne (1970) placed the genus in the tribe Polysiphonieae sensu Hommersand (1963). Kraft and Wynne (1985) later concluded that *Amplisiphonia* was closer to *Pterosiphonia,* and Womersley (2003) retained it in the *Placophora* group sensu Kylin (1956), close to but different than the genera of the tribe Pterosiphonieae.

A monotypic genus, its one known species is now reported in the northern Gulf of California.

Amplisiphonia? *pacifica* Hollenberg

FIGURE 139

Amplisiphonia pacifica Hollenberg, 1939:382, figs. 1–13; Smith, 1944:372, pl. 96: figs. 7–9; Scagel, 1953:39, fig. 5a–e; Scagel, 1957:239; Dawson et al., 1960a:44, pl. 43: fig. 2; 1960b:29; Dawson, 1961b:452; 1963b:438, pl. 170: figs. 1, 2, pl. 171: figs. 5–7; Hollenberg and Wynne, 1970:175, figs. 1–5; Abbott and Hollenberg, 1976:720, fig. 670; Lindstrom and Scagel, 1980:400; Scagel et al., 1989:141; R. Aguilar-Rosas et al., 1990:120; Stewart, 1991:153; González-González et al., 1996:173.

Small, prostrate, dorsiventral blades, up to 6 mm long and to 2 mm wide; lobes often overlapping; growth from apical cells at blade margins; apical cells without trichoblasts, develop polysiphonous axes of 5 pericentral cells, dorsiventrally arranged (3 dorsal, 2 ventral); axes laterally adjoining, branched dichotomously, central axial filament cells often form pattern of delicate veins within blade. Thallus uncorticated, attached by unicellular rhizoids from ventral surface.

Reproduction not found in Gulf material. As reported elsewhere: tetrasporangia obliquely, cruciately divided, developed in marginal lobes (Abbott and Hollenberg, 1976); cystocarps subspherical, 400–550 μm by 530–700 μm; spermatangial stichidia on a single cell off polysiphonous branchlets, up to 525 μm long, fringing along blade margins (Hollenberg and Wynne, 1970).

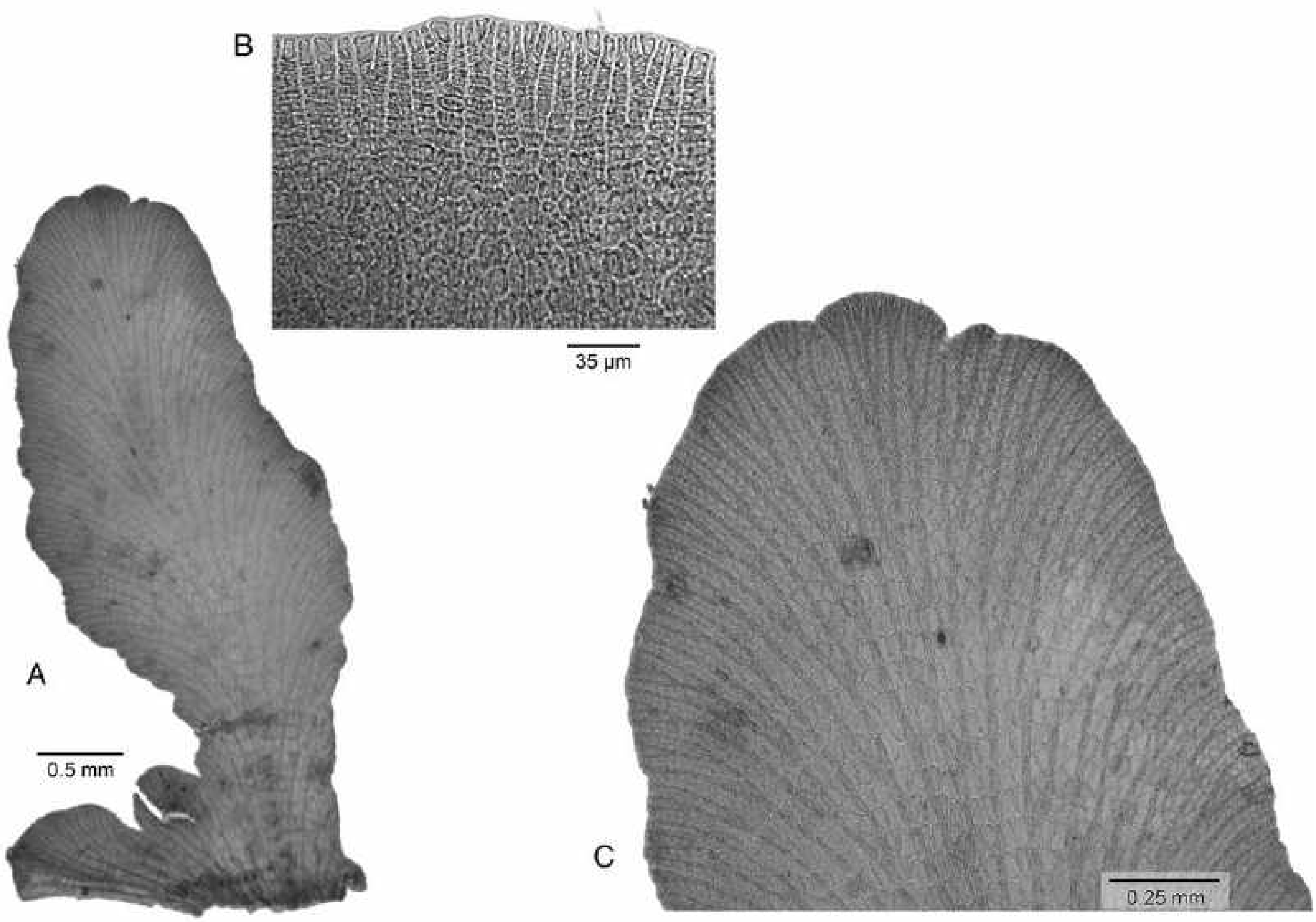


FIGURE 139. *Amplisiphonia*? *pacifica*: A. Habit of small blade. B. Margin of numerous apical cells that initiate polysiphonous axes that laterally unite behind the margin to form the flat blade. C. Dorsal surface view of blade with internal pattern of fine veins (axial filaments) (A–C, *JN-4682*, US Alg. Coll. microscope slide 4984).

Habitat. Epiphytic on *Palisada paniculata*; low intertidal to shallow subtidal, down to at least 10 m depths.

Distribution. Gulf of California: Puerto Calamajue. Eastern Pacific: Aleutian Islands, Alaska to Islotes Chester (islets about 0.8 km [0.5 mile], NW of Punta Falsa), Bahía Sebastián Vizcaíno, Baja California Sur.

Type Locality. On rocky shore, lower intertidal; Corona Del Mar, Orange County, southern California, USA.

Remarks. Apparently rare in the Gulf, a few, small, nonreproductive specimens are tentatively referred to *Amplisiphonia*? *pacifica* (*JN-4682*, US Alg. Coll. microscope slide 4984). Epiphytic on *Palisada paniculata* from Puerto Calamajue, they represent a new record of the genus in the Gulf of California.

The northern Gulf *A.*? *pacifica* differs from those of southern California in being partially prostrate with a free blade that is not as lobed, and the characteristic attaching rhizoids on the lower surface were not observed (cf. Smith, 1944: pl. 96: figs. 7, 8; Abbott and Hollenberg, 1976: fig. 670). With these differences and lacking reproductive specimens, we cannot be sure of the generic placement of the Gulf material. Superficially, the northern Gulf *Amplisiphonia*? *pacifica* is also somewhat similar to blades of *Pollexfenia? anacapensis* E. Y. Dawson et Neushul (1966: cf. fig. 7; with taxonomic query on generic placement). However, according to Womersley (2003), the genus *Pollexfenia* Harvey (1844) is restricted to southern Australia. The Gulf material referred to *A.*? *pacifica* is dorsiventral and has five pericentral cells, whereas *P.? anacapensis* is not dorsiventral and has an unusual hollow internal structure traversed by a network of veins and the strut work of four pericentral cells (two dorsal and two ventral) attached to the cortical cells. Gulf *A.*? *pacifica* is also somewhat similar to another dorsiventral genus, *Placophora* J. Agardh (1863). More Gulf *A.*? *pacifica* is needed for molecular and morphological comparisons with type locality material of California *A. pacifica* and *Pollexfenia? anacapensis* and members of *Placophora* to resolve its taxonomic status.

RHODOMELACEAE TRIBUS BRONGNIARTELLEAE

Rhodomelaceae tribus Brongniartelleae M. Parsons, 1975:691.

Thalli radially branched, polysiphonous with uncorticated or corticated segments, of 4–7 pericentral cells; some genera with adventitious filaments develop from pericentral or cortical cells; branches with usually persistent pigmented trichoblasts, spirally arranged on successive segments. Gametophtyes dioecious; procarps at base of trichoblasts, 4-celled carpogonial branch with 2 sterile cell groups; spermatangial structures borne on branch of trichoblasts. Tetrasporangia1–2 in linear rows or spirally arranged, usually with 3 cover cells (2 presporangial and in most genera 1 postsporangial), in normal polysiphonous axes.

Remarks. Dawson (1944a) suggested the genus *Veleroa* was close to *Lophocladia* F. Schmitz (1893). Later, Parsons (1975), in describing the tribe Brongniartelleae, included *Veleroa* along with some members of the *Lophothalia* group sensu Kylin (1956:510). Millar (2000) noted that the two tribes were separated by the number of sterile groups associated with procarps, and treated *Veleroa* as a member of tribe Brongniartelleae. Womersley and Parsons (2003) included it in a more broadly defined tribe Lophothalieae F. Schmitz et Falkenberg (1897). Millar (2000) and, more recently, Abbott and Ballantine (2012) in their studies of *Veleroa* supported its placement in tribe Brongniartelleae.

The tribe is represented by one genus in the northern Gulf of California.

Veleroa E. Y. Dawson

Veleroa E. Y. Dawson, 1944a:335.

Algae composed of both erect and prostrate polysiphonous axes of uncorticated to corticated segments of 4 pericentral cells. Some species are either predominately prostrate, others predominately erect. Main axes are usually much branched, up to 4(–5) orders, and bear persistent, irregularly radially arranged, monosiphonous, pigmented trichoblasts. Trichoblasts are simple or branched up to 4 times, spirally arranged, and more or less curved upward. Lateral branches develop at the base of trichoblasts. Prostrate polysiphonous axes produce holdfasts of uniseriate or multiseriate rhizoids with a terminal discoid pad.

Tetrasporangia, each with 3 cover cells, are in spiral series, 1 per segment within either slightly swollen upper portions of axes or in short indeterminate branches. Each segment of the tetrasporangial branch bears simple or rarely branched monosiphonous trichoblasts. Gametophytes, where known, are dioecious (not yet known from northern Gulf of California type locality). Procarps, where reported, have a 4-celled carpogonial branch with the carpogonium bearing a short trichogyne, developed on the suprabasal cell of trichoblasts. Cystocarps are more or less ovoid with a pericarp 2 cells thick and a prominent neck. Spermatangia are produced on intercalary cells of the trichoblasts; they may either cover the cells of the trichoblast filaments, have sterile cells that extend distally, or a sterile basal cell and no sterile distall cells (gametophyte descriptions after Womersley and Parsons, 2003; Abbott and Ballantine, 2012).

Remarks. Cystocarps and spermatangia have yet to be found in the northern Gulf generitype *Veleroa subulata*. Finding them from the Gulf type locality and the elucidation of procarpic and cystocarpic development are particularly important so they can be morphologically and molecularly compared to test their relationship with other members of the genus.

Veleroa is currently a genus of seven species, with one species known in the Gulf of California.

Veleroa subulata E. Y. Dawson

FIGURE 140

Veleroa subulata E. Y. Dawson, 1944a:335, pl. 72: fig. 2 [type specimen]; 1961b:451; 1963a:414, pl. 133; Abbott and Hollenberg, 1976:702, fig. 654; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; González-González et al., 1996:272; R. Aguilar-Rosas et al., 1997:19, fig. 2; 2000:132; Riosmena-Rodríguez et al., 2005a:34; Abbott and Ballantine, 2012:388, fig. 1A–H.

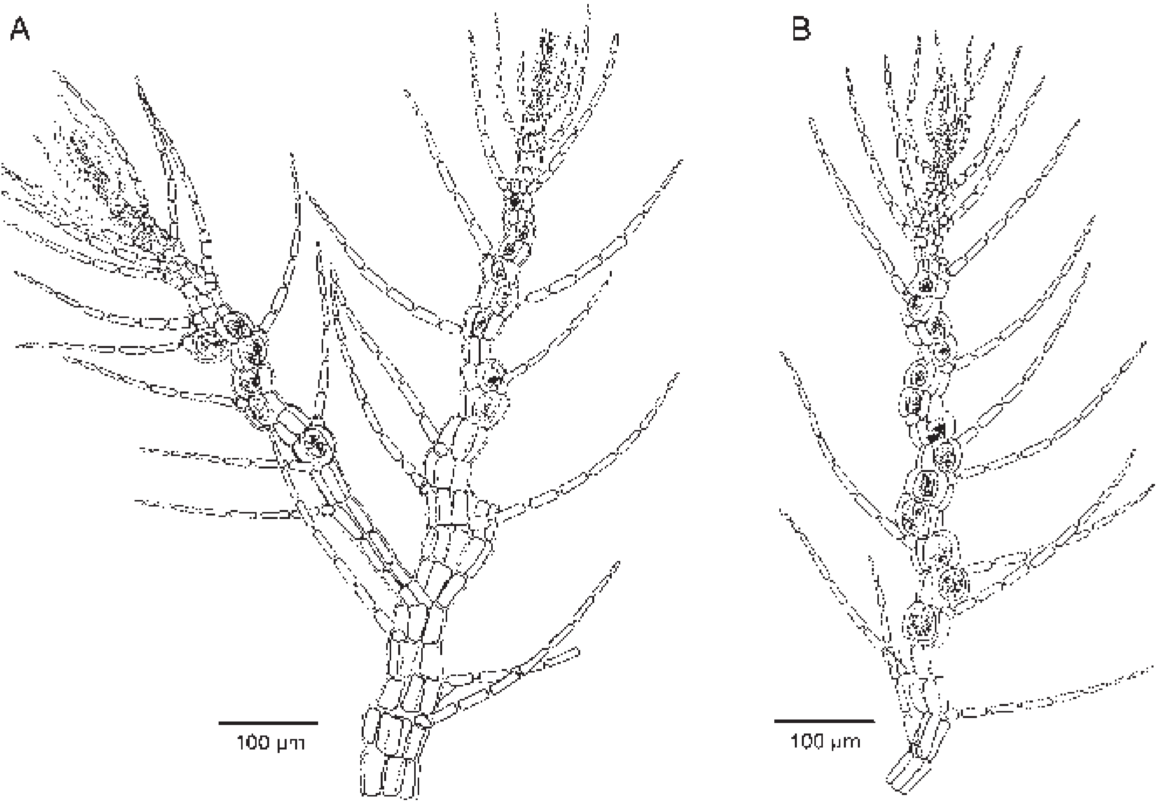


FIGURE 140. *Veleroa subulata*: Polysiphonous main axes with tetrasporangia in spiral series, one per segment, and monosiphonous laterals (drawn from holotype: *EYD-381d-40*, AHFH-63, now UC).

Algae up to 15 mm tall with erect main axes and branches consisting of 4 uncorticated pericentral cells per polysiphonous segment, mostly 50–70 µm in diameter, 100–140 µm long; arising from protrate axes, up to 100 µm in diameter, attached to substratum by multicellular rhizoids with terminal pads, 250–500 µm in diameter. Pericentral cells connected lengthwise by secondary pit connections. Erect axis, usually sparingly branched with indeterminate branches, 50–70 µm in diameter, irregularly radially arranged at intervals of up to 16 cell segments between branches. Axes and branches with exogenous, persistent, pigmented monosiphonous trichoblasts, typically one per segment. Trichoblasts arranged in a spiral sequence, usually simple or occasionally branched, mostly 400–800 µm long and 25–40 µm in diameter; slightly curved upward and often tapering to a acute terminal cell.

Tetrasporangia tetrahedrally divided, 37–50 µm in diameter, 42–60 µm in length; intercalary, 1 per segment in spiral series of 8–15(–34) within slightly swollen segments of upper portions of indeterminate main axes and branches. Gametophytes unknown in the Gulf of California, presumed to be dioecious. As described from Pacific northern Baja California and southern California: procarps on the second segment of a trichoblast (Stewart, 1989, included *Murrayellopsis*); cystocarps unknown; spermatangia develop from intercalary cells, encircling trichoblast filaments forming subcylindrical clusters up to 130 µm in length, 30–70 µm in diameter between 1–3 basal sterile cells and 6–8 sterile terminal cells (after Aguilar-Rosas et al., 1997; Abbott and Ballantine, 2012).

HABITAT. On rocks or hydroids; shallow subtidal, 3.0–15 m depths (also dredged from 22 m depth).

DISTRIBUTION. Gulf of California: El Coloradito; Bahía Tepoca; Punta Los Frailes to Cabo Pulmo.

TYPE LOCALITY. Epizoic on a small hydroid, dredged from 22 m depth; Bahía Tepoca, Sonora, Gulf of California, Mexico.

REMARKS. Once gametangial thalli of *Veleroa subulata* are found from its type locality, comparison to the other known species is needed to resolve their phylogenetic relationships. The taxonomic status of *Murrayellopsis* E. Post (1962; type locality: New Hope Rock, off Point Loma, San Diego County) is problematic, and its relationship to *Veleroa* requires further investigation.

Millar (1999) suggested another species, the Hawaiian *Micropeuce setosus* I. A. Abbott (1996), may also be *Veleroa subulata*. Stewart (1989, 1991) concluded the southern California

Murrayellopsis was congeneric with *Veleroa*, thus making *M. dawsonii* E. Post (1962) a synonym of *V. subulata*. Others however, recognize *Murrayellopsis* (Dawson, 1963a; Post, 1963, 1964; Abbott and Hollenberg, 1976; Millar, 2000) on the basis of its polysiphonous segments of 5 pericentral cells and 2 tetrasporangia per segment, differing from *Veleroa* with strictly 4 pericentral cells per segment and 1 tetrasporangia per segment. *Murrayellopsis dawsonii* is reported in the Eastern Pacific from central California to northern Baja California, Pacific Mexico (Abbott and Hollenberg, 1976), from Islas Todos Santos (off Ensenada), northern Baja California (R. Aguilar-Rosas et al., 1990; González-González et al., 1996), and from Jalisco (Hernández-Herrera et al., 2005). In the California Channel Islands, *M. dawsonii, Tiffaniella snyderae,* and *Pterosiphonia dendroidea* are the predominant components of the cultivated nests of living algae maintained by a pomacentrid fish, the garibaldi, *Hypsypops rubicundus* (Dawson, 1963a; Foster, 1972, both as "*Murrayellopsis dawsonii*"; Foster and Scheil, 1985).

SPYRIDIACEAE

Spyridiaceae J. Agardh, 1851:vii, 337 [as "Spyridieae"].

Thalli are erect, uniaxial in structure, radially branched, and differentiated into nearly completely corticated indeterminate axes and determinate branchlets that are corticated only at the nodes. Determinate branchlets develop from the primary axes and indeterminate lateral branches, and are simple or sparsely branched and monosiphonous, with a narrow band of small corticating cells at the distal end of their axial cells (i.e., nodes); the internodes remain uncorticated. Cells are multinucleate. Gland cells are absent.

Tetrasporangia are tetrahedrally divided, sessile and naked on the cortical bands of determinate branchlets. Gametophytes are dioecious. The carpogonial branch is 4-celled and borne on a periaxial cell of the fully corticated axes. Carposporophyte surrounded by pericarpic filaments from segments above and below the fertile axial cell. Spermatangia originating on the corticated nodes of determinate branchlets, later forming a confluent cylinder around several successive cells of fertile segments on lower portions of determinate branchlets.

The family contains the single genus *Spyridia,* which occurs in the northern Gulf of California.

Spyridia Harvey

Spyridia Harvey, 1833:259, 336.

Thallus erect, most species richly radially branched, giving axes a fuzzy appearance; branches distichous or irregularly arranged; indeterminate branches with unbranched or sparsely branched determinate branchlets. Axes terete, composed of large axial cells completely corticated by tiers of cells and in older portions of the thallus additionally corticated by descending rhizoid-like filaments. Axial filament cells of indeterminate branches cut off a ring of periaxial cells around the node between 2 axial cells. Each periaxial cell of the encircling ring cuts off 2 basipetal cells from its proximal (lower) end, and these basipetal cells elongate and become pit connected to the periaxial cells of the node or segment below to completely cover the axial filament cells. This repeated pattern builds a cortex of short, relatively broad nodal cells alternating with a band of twice as many longer narrower cells (basipetal cells) that lengthen as the axial filament cells grow and enlarge. Determinate branchlets simple or sparsely branched and radially arranged; spiraled or in whorls. Determinate branchlets consisting of uniseriate axes of larger translucent axial cells that are corticated by a band of smaller cells at all or nearly all (depending on species) their nodes, internodes uncorticated; with or without short apical spines or hooks, these often shed early. Cells multinucleate.

Tetrasporangia tetrahedrally divided, naked and sessile at the nodes of determinate branchlets. Tetrasporangial production begins on adaxial side, and as more tetrasporangia are issued, they appear whorled about the cortical bands. Gametophytes dioecious. Procarps are borne on the periaxial cells that corticate a indeterminate branch, carpogonial branch 4-celled. Cystocarps are borne near ends of a short, indeterminate branch (apparently restricted in growth); often bilobed and surrounded by slender pericarpic filaments developed from segments above and below the fertile axial cell. Spermatangial parent cells are produced by the nodal band of cortical cells of determinate branchlets, and the spermatangia form a continuous colorless surface layer over several segments (node and internode) in lower portions of determinate branchlets.

REMARKS. Agardh (1897) wrote that there were many opinions concerning the true affinity of *Spyridia*. Schmitz (1889) placed the genus in the Ceramiaceae, and this has been generally followed, but Phillips (1924) thought it was closer to the Wrangeliaceae and should be given an ordinal position. Since then, phylogenetic data supported *Spyridia* belonging in the family Spyridiaceae (H.-G. Choi et al., 2008). However the species are problematic and still in need of elucidation (e.g., Zuccarello et al., 2002a, 2004b). Studies by Feldmann and Feldmann-Mazoyer (1943) and West and Calumpong (1989) have shown *Spyridia* to have a triphasic life history.

One species of uncertain identity occurs in the northern Gulf of California.

Spyridia cf. *filamentosa*

FIGURE 141

Spyridia filamentosa sensu McClatchie, 1897:357; Setchell and Gardner, 1930:167; Dawson, 1962a:69, pl. 30: figs. 1–3; Abbott and Hollenberg, 1976:608, fig. 551; Huerta-Múzquiz, 1978:336; L. Aguilar-Rosas, 1982:84; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Stewart and Stewart, 1984:145; Huerta-Múzquiz and Mendoza-González, 1985:52; Ibarra-Obando and Aguilar-Rosas, 1985:95, 102; Mendoza-González and Mateo-Cid, 1986:425; Ortega et al., 1987:74; Sánchez-Rodríguez et al., 1989:44; Stewart, 1991:136; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:48; González-González et al., 1996:325, 413; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl.

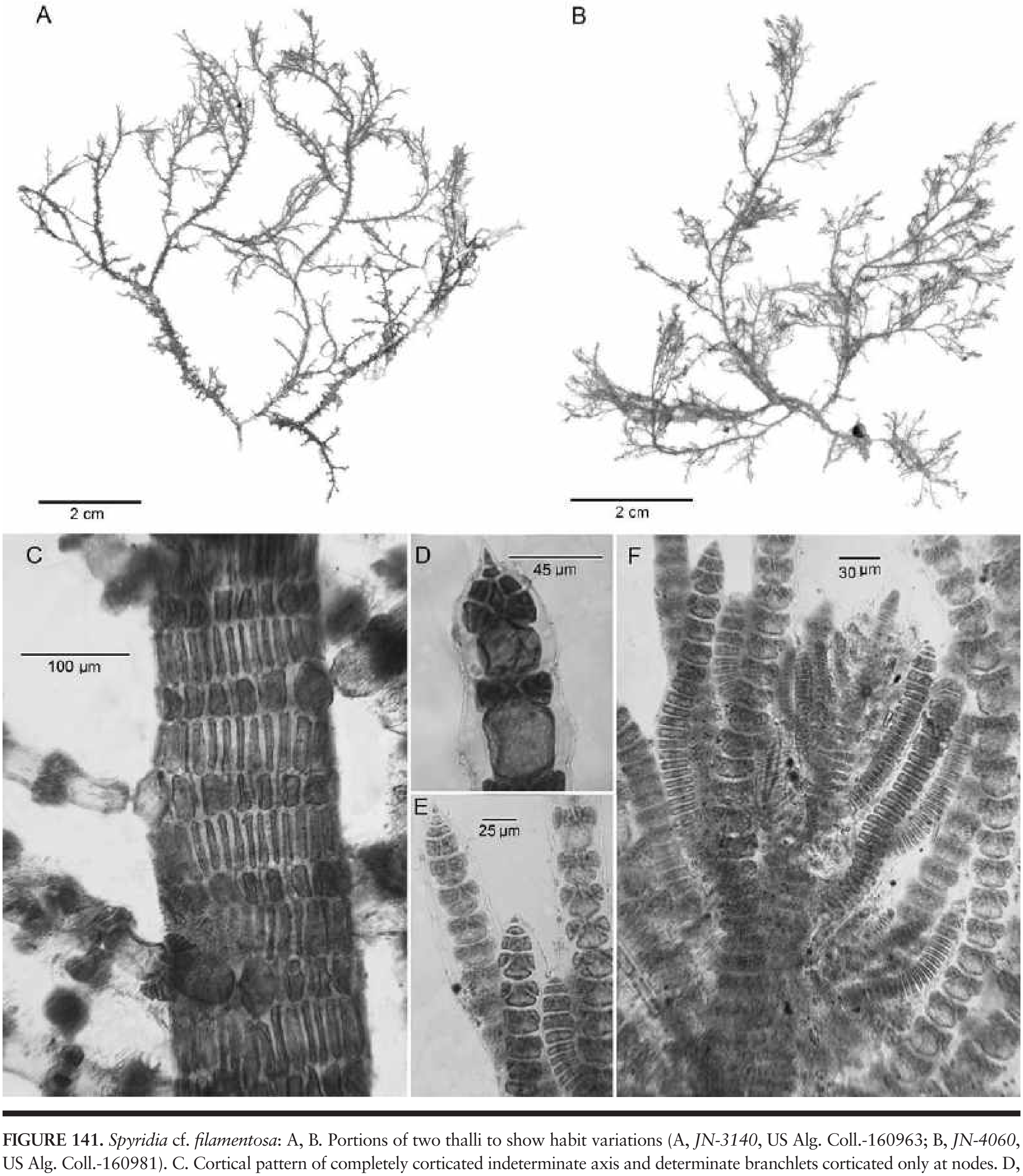


FIGURE 141. *Spyridia* cf. *filamentosa*: A, B. Portions of two thalli to show habit variations (A, *JN-3140*, US Alg. Coll.-160963; B, *JN-4060*, US Alg. Coll.-160981). C. Cortical pattern of completely corticated indeterminate axis and determinate branchlets corticated only at nodes. D, E. Apices of determinate branchlets, each with a single, terminal spine. F. Apical region of main axis with radially arranged indeterminate and determinate branches (C, D, *JN-4075*, US Alg. Coll. microscope slide 4836; E, F, *JN-4019*, US Alg. Coll. microscope slide 4834).

1; Riosmena-Rodríguez et al., 1998:26; Cruz-Ayala et al., 1998:191; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:138; Cruz-Ayala et al., 2001:191; L. Aguilar-Rosas et al., 2002:235; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:57; Serviere-Zaragoza et al., 2007:12; Pacheco-Ruíz et al., 2008:211; Piñón-Gimate et al., 2008:116; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:64; Pérez-Estrada et al., 2012:191 [non *Spyridia filamentosa* (Wulfen) Harvey, 1833:337; basionym: *Fucus filamentosus* Wulfen, 1803:64].

Algae soft and bushy, to 20 cm long, lax, pink to grayish rose in color, epiphytic, saxicolous, or free floating in entangled masses. Axes terete, with 1 to several main axes, 1–2 mm in diameter, main axes of large uniseriate cells completely corticated, except near the apices. Axial filament cells producing a ring of periaxial cells that surrounds the node between adjacent axial cells. Each periaxial cell issues (1–)2 basipetal cells from below that elongate to cover the axial cell as it grows and lengthens. In the upper portions of the axes, the cortex in surface view is composed of alternating tiers of 14–18 short, wide cells (periaxial cells) and then a tier of about twice that number of elongate thinner cells (basipetal cells); the regular cortical pattern is visible in upper portions, but in older portions below, this pattern becomes obscured by the growth of descending rhizoidal corticating cells that cover and thicken the original cortex to 2–3 cell layers deep. Indeterminate axes with numerous, slender, unbranched, irregularly spirally arranged, determinate branchlets (35–60 µm in diameter, to about 1.5 mm in length, and about 15–25 cells long). Determinate branchlets cylindrical, not tapering toward the base, composed of axial cells, cortication confined to distinct bands at their nodes (similar to some *Ceramium* species); arising from enlarged periaxial cells of the indeterminate branch cortex, typically 1 determinate branchlet per segment. Each axial cell of a determinate branchlet issues about 9 periaxial cells at its distal end that divide to form 1–3 cell tiers of small pigmented cells that constitute the corticating band. Uncorticated internode length reduced toward branchlet tip; determinate branchlets usually terminating in a single short 1- to 2-celled spine.

Tetrasporangia sessile, spherical, 45–80 µm in diameter, including large clear envelope, tetrahedrally divided; 1 to several tetrasporangia whorled about nodes of determinate branchlets, particularly on the proximal cells (but not the basal cell). Carpogonia and spermatangia not reported for Gulf material (for descriptions, see Womersley, 1998; H.-G. Choi et al., 2008).

HABITAT. Epiphytic on or entangled with other algae or aquatic vegetation, including mangroves, on rocks or tidal platforms or in coastal lagoons, or free floating in often large, entangled masses; intertidal.

DISTRIBUTION. Gulf of California: El Tornillal (Gulfo de Santa Clara) to Punta Los Frailes; Laguna Agiabampo; Bahía de Navachiste to Teacapán; Bahía de Banderas, Sinaloa to Nayarit. Eastern Pacific: La Jolla, southern California to Bahía Magdalena, Baja California Sur; Isla Guadalupe; Isla Clarión (Islas Revillagigedo); El Salvador; Nicaragua; Costa Rica; Panama.

TYPE LOCALITY. Vienna? (Maggs and Hommersand, 1993:427); Adriatic Sea (Silva et al., 1996a:136).

REMARKS. *Spyridia* cf. *filamentosa* is apparently a recent invader into the upper Gulf of California. First recorded in the drift at Punta Los Frailes, near the Gulf's southern entrance (Dawson, 1962a:69), the species had not been noted in earlier algal studies of the northern Gulf (e.g., Setchell and Gardner, 1924; Dawson, 1944a, 1962a; Norris, 1973). Collections beginning in 1972 revealed *Spyridia* at several northern Gulf locales (Norris, 1975), where, seasonally, it sometimes formed sizable floating rafts and was abundant in beach drift. Although the phycology courses from the University of Arizona (1964–1972) included collecting field trips to Puerto Peñasco in the upper Gulf, Robert Hoshaw (University of Arizona, personal communication, 1972) noted *S. filamentosa* was never observed or collected during that time, nor was it included by Dawson (1966a). During our year-round work at Puerto Peñasco (Laboratorio de Biología Marina, 1972–1975) we would seasonally observe floating rafts of *Spyridia*, sometimes entangled with other drift algae, some of which eventually would be cast ashore. These were conspicuous, particularly in summer, suggesting if the species had been there prior to 1972 it probably would have been observed.

Seasonal biomass studies in Bahía La Paz of Cruz-Ayala et al. (1998) found southern Gulf "*S. filamentosa*" to be one of the most abundant macroalga during summer (second only to *Sargassum sinicola*) and also in winter. Observations of L. Aguilar-Rosas et al. (2002) indicated "*S. filamentosa*" was one of the most common species in the upper Gulf at their study sites in Gulfo de Santa Clara, Sonora.

Molecular data and morphological and culture studies of "*S. filamentosa*" as identified from specimens throughout the world's oceans showed a complex phylogeographic pattern and distinct evolutionary lineages that led Zuccarello et al. (2002a, 2004b) to conclude that there are several cryptic species identified under the name "*S. filamentosa*." One of the "cryptic" species with disparate DNA sequences was recognized from Europe, *S. griffithsiana* (J. E. Smith) Zuccarello, Prud'homme van Reine et Stegenga (2004b; basionym: *Conferva griffithsiana* J. E. Smith, 1812). Morphologically, this species can be distinguished by determinate branchlets that strongly taper toward their base, and the proximal two (or one) segments have a small axial cell that is without a cortical ring. The determinate branchlets of northern Gulf of California *S.* cf. *filamentosa* are cylindrical, not tapering strongly toward their base, and all segments of determinate branchlets have a cortical ring at the nodes.

Zuccarello et al. (2002a, 2004b) found two sister clades in the Pacific *S. filamentosa* lineage, one of which was an anomalous group that although morphologically similar, may be a separate species. Molecular and morphological analyses of "*S. filamentosa*" in Hawaii revealed five clades that grouped in two lineages (Conklin and Sherwood, 2012: fig. 1). A southern Gulf of California "*S. filamentosa*" from Mulege, Baja California Sur, was included in their Lineage I. Comparative testing needs to be conducted on northern Gulf "*S.* cf. *filamentosa*" to determine if they can be identified with one of these lineages or if they are possibly different. Until these studies are completed, the northern Gulf specimens are tentatively referred to "*S.* cf. *filamentosa*."

WRANGELIACEAE

Wrangeliaceae J. Agardh, 1851:x, 701 [as "Wrangelieae"].

Thalli usually erect or with erect and prostrate axes, uniseriate filaments. Axial cells with none to 6 determinate branches or whorl branches. Gland cells usually absent.

Meiosporangia tetrahedrally divided or with polysporangia, sessile or stalked on cells of the whorl branches or determinate branches. Gametophytes usually dioecious. Procarps subapical, carpogonial branches 4-celled. The supporting cell is a subapical cell of a short fertile axis with 2 or 3 periaxial cells. Procarps formed from a periaxial cell of a fertile axial cell with or without 1 sterile cell group on the supporting cell. A multicellular fusion cell is present in the carposporophyte of most tribes. Carposporophytes naked or involucrate or, in one genus(*Lejolisia*), surrounded by a "pericarp-like" structure. Spermatangia are sessile or pedicellate in clusters of cap or subspherical to elongate "head-like" structures, terminal on short lateral branches, or in whorls from the distal end of axial cells or from basal cell of a trichoblast.

The Wrangeliaceae is represented by five genera in the northern Gulf of California.

KEY TO THE GENERA OF THE WRANGELIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. In upper portions of thallus nearly every axial cell with a lateral branch; main axes alternately branched . . . . **_Pleonosporium_**
1b. In upper portions not every axial cell with a lateral branch; branching not as above 2
2a. Thallus cells uninucleate; carposporophyte surrounded by a loose "pericarp-like" structure of 1 layer of cells within a common gelatinous sheath . . . . **_Lejolisia_**
2b. Thallus cells multinucleate; cystocarp naked or may be surrounded by involucres but not a "pericarp-like" structure . . . 3
3a. Carposporophyte naked, lacks surrounding involucres . . . . **_Tiffaniella_**
3b. Carposporophyte surrounded by involucres 4
4a. Tetrasporangia borne singly on a pedicel without involucres, solitary or in whorls; spermatangia clustered in a single "head," each borne on 1-celled pedicel or on basal cell of a trichoblast, several "heads" borne in a whorl . . . . **_Anotrichium_**
4b. Tetrasporangia borne 2 or more to a fascicle, usually with involucres; spermatangia on branched fascicles that are borne between axial cells or cap-like on terminal cell . . . . **_Griffithsia_**

WRANGELIACEAE TRIBUS GRIFFITHSIEAE

Wrangeliaceae tribus Griffithsieae F. Schmitz, 1889:449.

The tribe Griffithsieae is represented by two genera in the northern Gulf of California.

Anotrichium Nägeli

Anotrichium Nägeli, 1862:397.

Algae are uniseriate filaments that may be erect or with prostrate and erect portions, attached by elongate unicellular rhizoids issued from cells in basal or prostrate regions. Branching may be subdi(tri)chotomous, subsecund, to irregular. Most species are ecorticate, or some species corticated basally by descending rhizoids. Axial cells are cylindrical, usually elongate, and multinucleate. Whorls of di- to polychotomous unpigmented trichoblasts are produced from the distal ends of cells near the apices. The slender trichoblasts are typically shed early or may not always develop, although trichoblasts are frequently found persisting on reproductive plants.

Tetrasporangia are borne in upper portions of the thallus and are divided tetrahedrally, without involucral filaments. Each tetrasporangia is single and terminal or subterminal "adaxial" on a pedicel, pedicels borne solitary or in whorls of 2 or more from the distal ends of axial cells; or tetrasporangia borne adaxial from the basal cell of a trichoblast. Gametophytes dioecious. Cystocarps terminating branchlets, the hypogenous cell bearing a whorl of postfertilization involucral branches, usually single cells that elongate around the gonimoblasts. Spermatangia clustered, forming spherical to oblong "heads," each head on a clavate pedicel, which is solitary or in whorls from the distal end of axial cells; or borne adaxial from the basal cell of a trichoblast in the whorl. Spermatangial heads not involucrate (after Baldock, 1976.)

Four species of *Anotrichium* are reported to occur in the northern Gulf of California.

KEY TO THE SPECIES OF *ANOTRICHIUM* AND *GRIFFITHSIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli often decumbent; branching subsecund to irregular, most branching adventitious; adventitious branches issued from proximal end of axial cells . . . . **_Anotrichium secundum_**
1b. Thalli more or less erect; dichotomously to subdichotomously branched 2
2a. Ultimate cells 5.0–30 μm in diameter; tetrasporangia without involucres 3
2b. Ultimate cells larger, mostly 70–125 μm in diameter; tetrasporangia with or without involucres 4

3a. Filaments with apical cells 14–20 μm in diameter; mid to upper cells 170–250 μm in diameter, 600–1200 μm (or more) long; lower cells up to 2000 μm long, 300–500 μm in diameter with thick cell walls (up to 28 μm) . . . . ***Anotrichium furcellatum***

3b. Filaments with larger apical cells, 15–30 μm in diameter; mid to upper cells narrower in diameter, about 125 μm, up to 970 μm long; lower cells up to 1350 μm long by 300 μm in diameter . . . . ***Anotrichium multiramosum***

4a. Thalli 3–5 cm tall, 300–500 μm in diameter in middle to lower portions; tetrasporangia borne 2 or more to a fascicle, usually with involucres, borne on richly branched fascicles between the upper axial cells or as a cap terminating lateral branches . . . . ***Griffithsia pacifica***

4b. Thalli shorter, 1–2 cm high, and narrower; 150–280 μm diameter in middle portions; tetrasporangia borne singly on 1(–2)-celled pedicels, without involucres . . . . ***Anotrichium anthericephalum***

Anotrichium anthericephalum (E. Y. Dawson) Baldock

Griffithsia anthericephala E. Y. Dawson, 1950b:155, figs. 20, 21; 1961b:444; 1962a:70, pl. 28; Stewart and Stewart, 1984:146; González-González et al., 1996:219.

Anotrichium anthericephalum (E. Y. Dawson) Baldock, 1976:560.

Thalli to 2 cm high, uniseriate, composed of dichotomously branched filaments, occasionally trichotomous in uppermost portion. Middle portions of thallus with axial cells 150–280 μm in diameter, 4–6 diameters long, increasing in diameter toward the distal end of a cell, appearing somewhat clavate. Apical cells oblong, blunt; subapical cells without whorls of trichoblasts.

Tetrasporangia up to 75 μm in diameter, naked, borne on 1-celled pedicels, 2 to several tetrasporangial branches whorled about distal end of upper axial cells. Cystocarps borne on 1-celled lateral branches, with a prominent involucre of incurved 1-celled filaments. Spermatangia forming dense, ovoid cluster, borne on 1-celled pedicels at the distal end of upper axial cells.

Habitat. Epiphytic on various algae; intertidal to shallow subtidal, down to 20 m depths.

Distribution. Gulf of California: Puerto Peñasco to El Desemboque. Eastern Pacific: Isla Guadalupe (off Baja California); Punta Eugenia ("San Eugenio"), Baja California Sur.

Type Locality. Intertidal; north side of reef, on southwest tip of Isla Guadalupe, Baja California, Pacific Mexico.

Anotrichium furcellatum (J. Agardh) Baldock

FIGURE 142

Griffithsia furcellata J. Agardh, 1842:75; L'Hardy Halos, 1968a:523; Abbott and Hollenberg, 1976:621, fig. 563; Stewart and Stewart, 1984:146; R. Aguilar-Rosas et al., 1985:84; Ibarra-Obando and Aguilar-Rosas, 1985:96; Sánchez-Rodríguez et al., 1989:45; Stewart, 1991:132; González-González et al., 1996:219; Pacheco-Ruíz and Zertuche-González, 2002:468; Riosmena-Rodríguez et al., 2005a:33.

Anotrichium furcellatum (J. Agardh) Baldock, 1976:560; Maggs and Hommersand, 1993:181, fig. 59A–C; Pacheco-Ruíz et al., 2008:211.

Neomonospora furcellata (J. Agardh) Feldmann-Mazoyer et Meslin, 1939:193, figs. 1, 2.

Filamentous tufts, up to 6 cm tall, rose pink in color, and subdichotomously branched in 1 plane, occasionally in upper portions irregularly branched; upper portions much branched, corymbose; attached to substratum by numerous, entangled rhizoids. Axial cells cylindrical to slightly clavate, in middle to upper portions exceedingly elongate, mostly 600–1200 μm long, 170–250 μm in diameter; in lower portions, up to 2000 μm long, 300–500 μm in diameter, with cell walls 20–28 μm thick. One or more rhizoidal filaments, developed from axial cells, may wrap around or fuse to adjoining filaments. Ultimate cells tapered toward apex, 14–20 μm in diameter, with blunt apices. Trichoblasts absent (at least in sterile and tetrasporangial thalli).

Tetrasporangia pyriform to spherical, without involucre, 45–60 μm in diameter, with thick outer wall (about 8 μm thick); borne singly on short, 1-celled pedicels at branch forks near distal ends of cell. Sexual reproduction for Gulf specimens: procarpic thalli with numerous trichoblasts; procarp with 1 carpogonial branch and 1 sterile cell on fertile pericentral. Spermatangia forming dense oval "heads," borne on 1-celled pedicels.

Habitat. Usually epiphytic on other algae, in sheltered bays, lagoons, and calm subtidal habitats; dredged to approximately 40 m depths.

Distribution. Gulf of California: Puerto Peñasco to Punta Gorda; San José del Cabo. Eastern Pacific: Newport Bay to San Diego, southern California; Isla Guadalupe; Bahía Todos Santos and Estero Punta Banda to Bahía San Quintín, Baja California; Bahía de Ballenas to Bahía Magdalena, Baja California Sur.

Type Locality. Near Amalfi, Sorrentine Peninsula, province of Naples, Tyrrhenian Sea, Italy.

Remarks. Gulf of California specimens that are referred to *Anotrichium furcellatum* are similar to those of Gulf *A. multiramosum*. The two are separated in the Gulf primarily on cell sizes of the filaments and the corymbose nature of the upper thallus of *A. furcellatum*. Additional material needs to be critically studied and the molecular and morphological data used to evaluate the taxonomic status of these species as known in the Gulf of California.

Anotrichium multiramosum (Setchell et N. L. Gardner) Baldock

Neomonospora multiramosa Setchell et N. L. Gardner, 1937:87, pl. 4: fig. 10a–c; González-González et al., 1996:245.

Anotrichium multiramosum (Setchell et N. L. Gardner) Baldock, 1976:560.

Griffithsia multiramosa (Setchell et N. L. Gardner) W. R. Taylor, 1939:14; Dawson, 1944a:315; 1945b:58; 1951:54; 1961b:444; 1962a:71, pl. 32; Stewart and Stewart, 1984:146; González-González et al., 1996:220; Pacheco-Ruíz et al., 2008:211.

Griffithsia multiramosa var. *balboensis* Hollenberg, 1945:447, fig. 1; Dawson, 1961b:444.

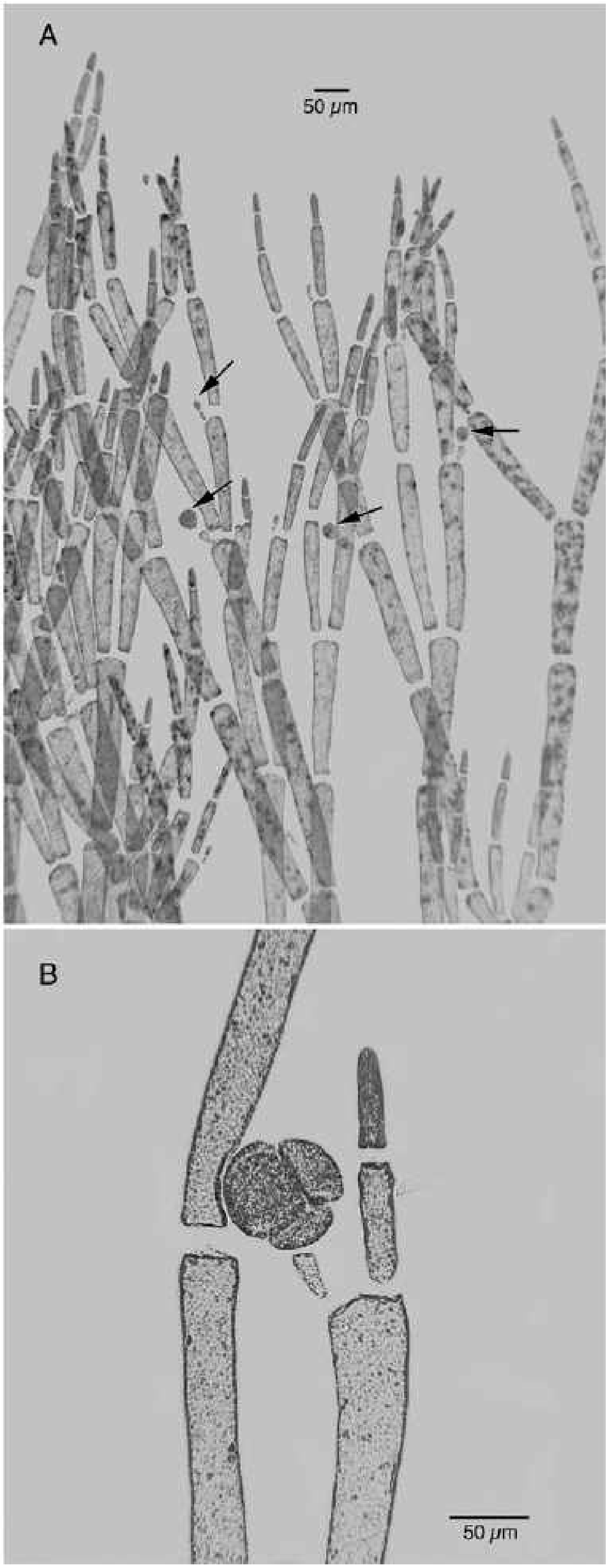


FIGURE 142. *Anotrichium furcellatum*: A. Upper portion of thallus showing subdichotomous branching, elongate axial cells, and tetrasporangia (arrows) usually borne solitary at nodes. B. Tetrasporangium borne on single-celled pedicel (A, B, *JN-4487*, US Alg. Coll. microscope slide 4969).

Griffithsia multiramosa var. *minor* W. R. Taylor, 1939:14, pl. 2; Dawson, 1961b:444; González-González et al., 1996:220.

Anotrichium multiramosum var. *minor* (W. R. Taylor) Baldock, 1976:560.

Algae in tufts, mostly 2–4 cm tall; filaments usually pseudodichotomously to alternately branched (occasionally slightly irregular in upper portions), ultimate branching dichotomous. Filament cells in lower portion of thallus, thick walled, up to 1,350 μm long, up to 300 μm in diameter, branched at wide angles; in middle to upper portions cells slender, up to 970 μm long, mostly subcylindrical, about 125 μm in diameter; ultimate branchlet cells 100–200 μm long, 15–30 μm in diameter, with tapered apical cells with acute to rounded tips. Trichoblasts absent.

Tetrasporangia spherical, 50–75 μm in diameter; borne single on a 1-celled pedicel at branch nodes in upper and middle portions of thallus; without involucre cells. Carpogonial and spermatangial thalli not known.

HABITAT. On rocks; intertidal to subtidal, down to 12 m depths (also dredged from 20–50 depths).

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Ensenada San Francisco; Punta Gorda (Gulfo de Santa Clara) to San José del Cabo. Eastern Pacific: Bahía San Quintín to Punta María (Baja California); Isla Guadalupe; Isla Cedros; Laguna de Ojo de Liebre (Scammon's Lagoon) to Bahía Magdalena (Baja California Sur).

TYPE LOCALITY. San José del Cabo, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Anotrichium multiramosum* is morphologically similar to *A. furcellatum*. Although it has been suggested the two are conspecific (L'Hardy-Halos, 1968a; Abbott and Hollenberg, 1976), they are kept separate in this treatment. The relationship of *A. multiramosum*, a species described from the southernmost Gulf of California, to Gulf material referred to *A. furcellatum* and to the Mediterranean *A. furcellatum* (type locality: Amalfi, Italy) remains to be genetically tested and elucidated.

Anotrichium secundum (Harvey ex J. Agardh) G. Furnari

FIGURE 143

Griffithsia secunda Harvey ex J. Agardh, 1851:85.

Anotrichium secundum (Harvey ex J. Agardh) G. Furnari in Cormaci, Furnari et Pizzuto, 1994:635; Abbott, 1999:245, fig. 68A–C.

Anotrichium tenue var. *secundatum* (Harvey ex J. Agardh) Stegenga, 1985a:154, *nom. invalid.*

Anotrichium tenue var. *secundatum* (Harvey ex J. Agardh) Stegenga ex H.-S. Kim et I. K. Lee, 1991:19.

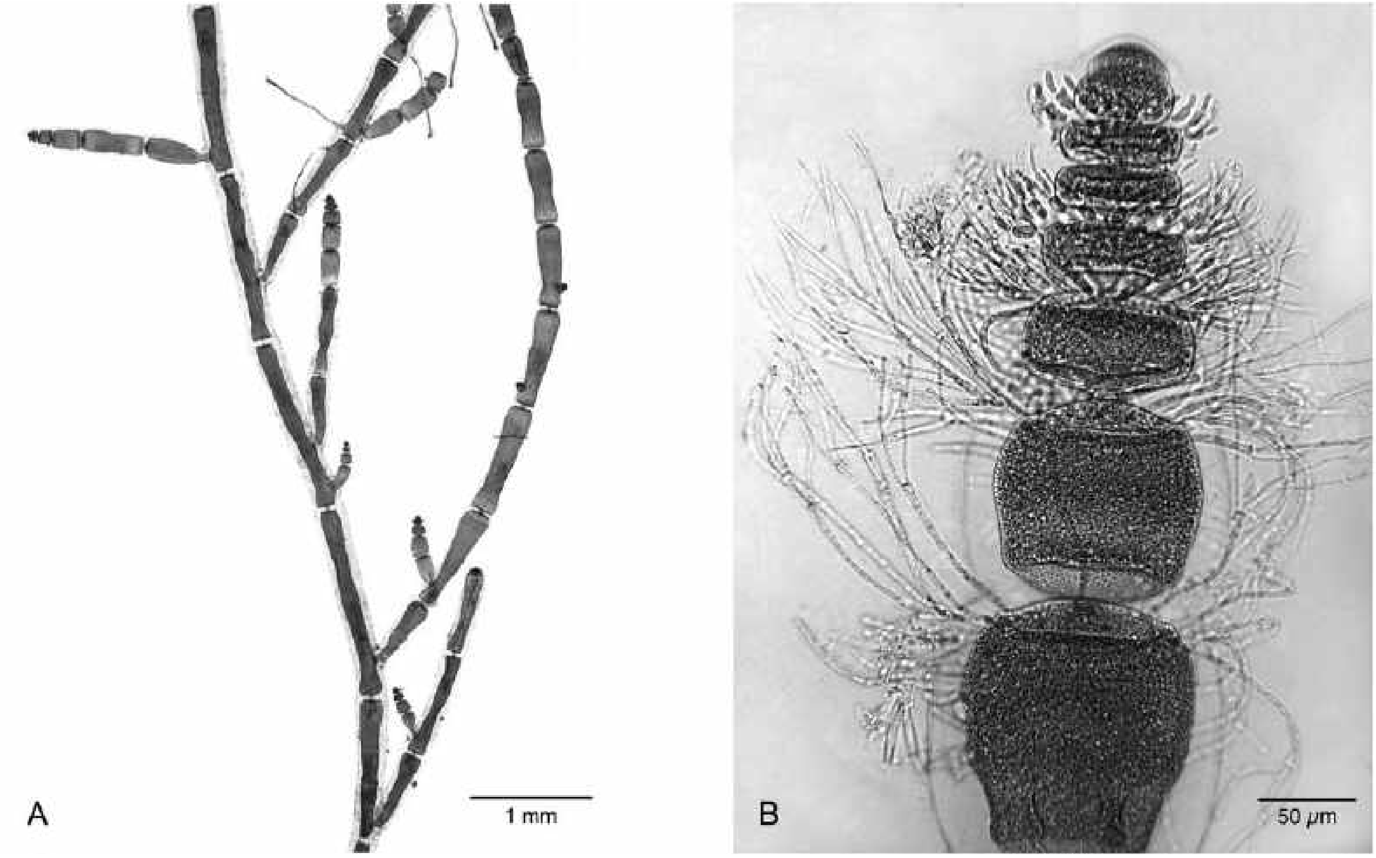


FIGURE 143. *Anotrichium secundum*: A. Portion of thallus showing subsecund, adventitious branching from proximal ends of axial cells (*JN-5187*, US Alg. Coll. microscope slide 4952). B. Subapical cells bearing polychotomously branched trichoblasts that are later shed (*JN-4032*, US Alg. Coll. microscope slide 4961).

Callithamnion thyrsigerum Thwaites ex Harvey, 1855:559.

Griffithsia thyrsigerum (Thwaites ex Harvey) Grunow, 1874:30.

Anotrichium tenue var. *thyrsigerum* (Thwaites ex Harvey) H.-S. Kim et I. K. Lee in I. K. Lee, 1992:159 [*Anotrichium tenue* var. *thyrsigerum* (Thwaites ex Harvey) H.-S. Kim et I. K. Lee, 1991:19, *comb. invalid*.].

Griffithsia tenuis sensu Dawson, 1944a:315; 1959a:32; 1961b:444; 1962a:73, pl. 31: figs. 5–7; 1966a:28; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Chávez-Barrear, 1972b:269; Baldock, 1976:556, figs. 59–64, 90; González-González et al., 1996:316 [in part]; CONANP, 2002:138; Pacheco-Ruíz and Zertuche-González, 2002:468 [non *Griffithsia tenuis* C. Agardh, 1828:131, which is now *Anotrichium tenue* (C. Agardh) Nägeli, 1862:399].

Anotrichium tenue sensu Mateo-Cid et al., 1993:48; Mendoza-González et al., 1994:108;Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:211 [non *Anotrichium tenue* (C. Agardh) Nägeli, 1862:399, 415; see Cormaci et al., 1994:635].

Thalli forming loose mat of filaments, up to 5 cm high in the Gulf, decumbent with erect axes, branching subsecund to irregular, much of the branching adventitious; adventitious branches developing from proximal ends of axial filament cells; rarely, when subdichotomous, branches developing from a subapical cell after it cuts off an apical lobe. Axial cells cylindrical, elongate, in basal portions up to 300 μm in diameter and up to 1200 μm long, decreasing in dimensions in upper portions. Apical cells 35–70 μm in diameter, 30–45 μm long, and several subapical cells below short subcylindrical, the cell just below the apical cell the shortest (10–35 μm long), subapical cells each often producing a whorl of protrusions at their distal end that elongate and develop into slender, unpigmented trichoblasts. Trichoblasts to about 150 μm long, and di- to polychotomously branched to 2 orders. The dense whorls of apical trichoblasts (8–16 in a ring) are often soon shed. Thallus attached by elongate unicellular rhizoids issued from prostrate axes, rhizoids sometimes terminate in elaborate digitate discs.

Tetrasporangia spherical, tetrahedrally divided, 60–80 μm in diameter; single, somewhat subterminal and adaxial on 1-celled pedicel, in a whorl of 8–10(–12) on the distal end of axial cells near thallus apices. Carposporangia and spermatangia not observed in Gulf material.

HABITAT. On rocks, in crevices, and in tide pools or epiphytic on other algae; intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Puerto Escondido; Punta Arena to Cabo Pulmo; Mazatlán. Eastern Pacific: Isla Guadalupe (off Baja California); Isla Socorro and Isla Clarión (Islas Revillagigedo); Guerrero to Oaxaca. Central Pacific: Hawaiian Islands. Western Pacific: Korea.

Type Locality. "Ad oras Capenses" (J. Agardh, 1851:85); Muizenberg, False Bay, Cape Province, South Africa (Silva et al., 1996a:376).

Remarks. Cormaci et al. (1994) helped clarify a confused taxonomy and nomenclature, involving misidentifications and misapplication of names of some taxa of *Anotrichium*. On the basis of recent interpretations, the northern Gulf material is identified as *Anotrichium secundum*. Changes in taxonomy and nomenclature for *Anotrichium* necessitate reexamination of Pacific Mexico specimens previously referred to *Griffithsia tenuis* or *A. tenue* (e.g., Chávez-Barrear, 1972b; Huerta-Múzquiz and Mendoza-González, 1985; León-Tejera and González-González, 1993).

Sexual thalli of *Anotrichium secundum* are not known from the Gulf of California. Descriptions of gametangial thalli from the Hawaiian Islands can be found in Abbott (1999).

Griffithsia C. Agardh

Griffithsia C. Agardh, 1817:xxviii.

Thalli of erect, uniseriate filaments, subdichotomously or rarely subtrichotomously to unilaterally branched to several orders. Cells often relatively large, from cylindrical to oblong or globose, and multinucleate, with discoid plastids. Some species are constricted at the nodes or moniliform, except at the very base. Filaments ecorticate or in some species loosely rhizoidally corticated below, attached by rhizoids from the basal cells. Gland cells are absent.

Tetrasporangia are borne, with or without 1-celled involucres (some species with peripheral tetrasporangial fascicles that have large flat, ear-like or "curved-lobed" involucres), in groups of 2 or more per fascicle. Tetrasporangial fascicles are usually numerous and whorled in between the axial cells in apical regions or on the tops of special lateral branches. (One species, *G. chilensis* Montagne in Kützing (1849), is reported with polysporangia; see Hoffmann and Santelices, 1997:344). Gametophytes dioecious or occasionally monoecious. Carpogonial branch is of 3 small discoid cells; the basal cell bearing, abaxially, involucral branches each composed of 2(–3) cells, a small lower ovoid cell and an upper elongate, incurving cell that forms a cup-like involucre. Spermatangia are in small, densely branched spermatangial fascicles, which are whorled between axial cells or clustered in a cap terminal on a special lateral branch (after Baldock, 1976).

One species of *Griffithsia* is recognized in the northern Gulf of California (included in the key under the related genus *Anotrichium*).

Griffithsia pacifica Kylin

FIGURE 144

Griffithsia pacifica Kylin, 1925:58, figs. 38a–d, 39a–g; Smith, 1944:324, pl. 83: fig.2; Taylor, 1945:268 [with a query]; Dawson et al., 1960a:64, pl. 36: fig. 3; Dawson, 1961b:444; 1962a:72, pl. 29: fig. 2, pl. 30: fig. 6,

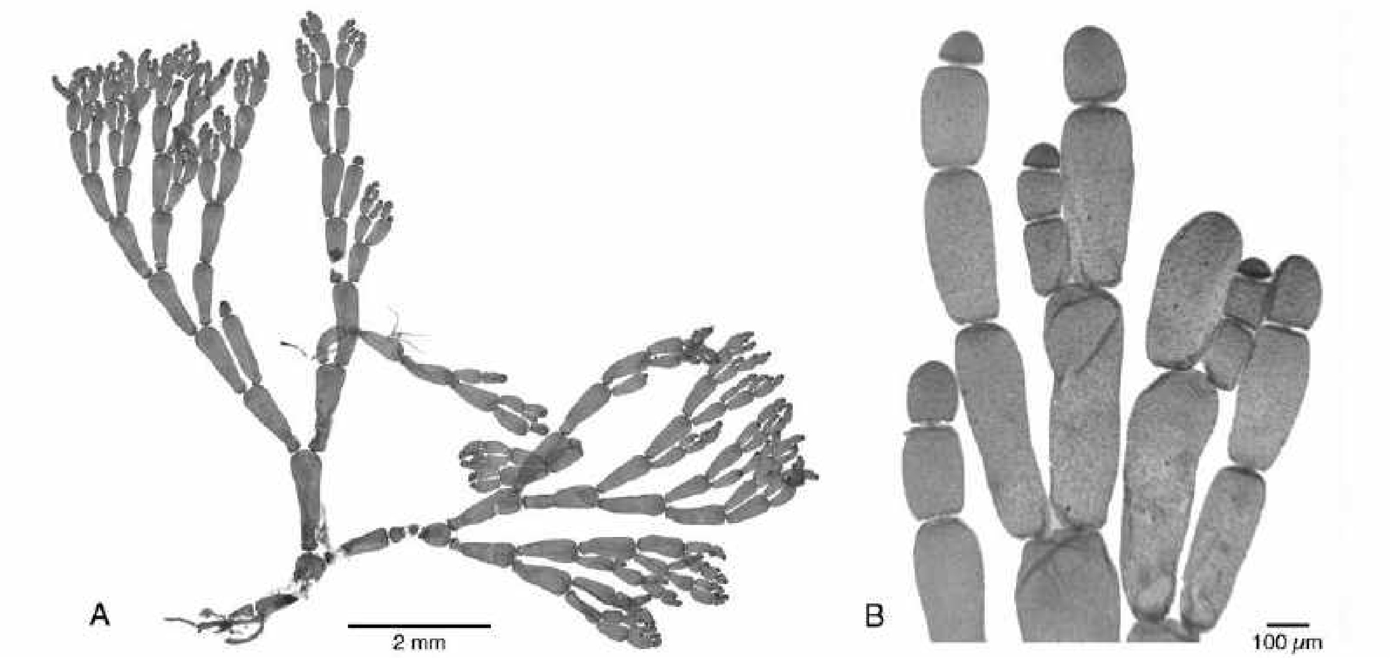


FIGURE 144. *Griffithsia pacifica*: A. Habit showing subdichotomous branching (*JN-5159*, US Alg. Coll. microscope slide 4980). B. Apical cells hemispherical to dome-like, trichoblasts absent (*JN-5148*, US Alg. Coll. microscope slide 4955).

pl. 31: figs. 1–4; 1966a:28; Abbott and North, 1972:76; Abbott and Hollenberg, 1976:621, fig. 564; Mendoza-González and Mateo-Cid, 1985:30; Mendoza-González and Mateo-Cid, 1986:425 [with a query]; Sánchez-Rodríguez et al., 1989:45; Scagel et al., 1989:189; Stout and Dreckmann, 1993:15; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:220; L. Aguilar-Rosas et al., 2000:131; Mateo-Cid et al., 2006:53; Serviere-Zaragoza et al., 2007:10.

Algae 1–2(–5) cm high; axes 300–500 μm in diameter in basal through middle portions, becoming narrower, (50–)75–150 μm in diameter toward apices; regularly subdichotomously (sometimes subtrichotomously) branched (occasionally less regular in upper portions). Cells mostly cylindrical, with thick cell walls; (3–)5–7 times as long as broad in lower portions of the thallus; becoming a little inflated at their distal ends, especially in upper portions; apical (terminal) cells often hemispherical or elongated hemisphere.

Tetrasporangial fascicles, usually numerous; each fascicle with 2 to more tetrahedrally divided tetrasporangia; borne in dense whorls in between upper axial cells or cap-like on the top of short, lateral branches; the inner fascicles with less elaborate involucre, peripheral fascicles with larger, lobed, and curvy, somewhat "ear-shaped," involucres. Gametophytes dioecious. Female thalli not known in the northern Gulf. Procarps lateral. Carposporophyte with gonimoblasts terminating short laterals; surrounded by 2-celled involucral branches, with a small, lower cell and an elongate, incurved upper cell that form the cup-like involucre. Spermatangia without involucres; on branched fascicles whorled around the distal ends of axial cells.

HABITAT. On rocks, in crevices or tide pools, or epiphytic on larger algae; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; San Felipe to Santa Teresa; Sinaloa to Jalisco. Eastern Pacific: southern Alaska to Todos Santos, Baja California Sur; Isla Clarión (Islas Revillagigedo); Colima to Michoacán; Oaxaca.

TYPE LOCALITY. Dredged off Turn Island, east of Friday Harbor, San Juan Island, San Juan County, Washington, USA.

WRANGELIACEAE TRIBUS SPERMOTHAMNIEAE

Wrangeliaceae tribus Spermothamnieae F. Schmitz, 1889:449.

Ceramiaceae tribus Spermothamnieae F. Schmitz, in Schmitz and Hauptfleisch, 1897b:485; Gordon, 1972:112; Womersley, 1998:208.

Algae are composed of erect, sparingly to moderately branched, uncorticated filaments that arise from prostrate filaments attached to substratum or other algae by haptera. Cells are multinucleate.

Life histories, where known, are of isomorphic tetrasporophytes and monoecious or dioecious gametophytes. Tetrasporangia are sessile or pedicellate on the erect filaments. Procarps are developed on a subapical cell of a fertile axis, within a gelatinous sheath with associated sterile cells, which remain undivided after fertilization in most, or may divide to form erect filaments in small groups or a loose pericarp-like layer of filaments. Spermatangia are produced in compact clusters.

Two genera of the tribe Spermothamnieae are known to occur in the northern Gulf of California.

KEY TO THE GENERA OF THE SPERMOTHAMNIEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Carposporophyte with inner involucral filaments that form a pericarp-like layer of associated filaments within a gelatinous sheath, with an ostiole . . . . *Lejolisia*

1b. Carposporophyte without inner or outer involucral filaments . . . . *Tiffaniella*

Lejolisia Bornet

Lejolisia Bornet, 1859:91.

Algae are small, composed of erect monosiphonous, uncorticated, simple or irregularly branched filaments that arise from spreading prostrate filaments attached by unicellular rhizoidal haptera that terminate in digitate or irregular expanded discs. Cells are multinucleate.

Tetrasporangia tetrahedrally divided and borne terminally on pedicels or borne laterally off erect filaments. Gametophytes are dioecious. Carpogonial branch is 4-celled and borne on a supporting cell of 3 pericentral cells. Auxiliary cell is cut off from the supporting cell and develops a carposporophyte with a stellate fusion cell that divides to develop a terminal gonimoblast initials that in turn produces chains of gonimoblast cells and terminal carposporangia. The carposporophyte is surrounded by erect inner involucre filaments forming a loose pericarp-like structure of 1 layer of cells issued from sterile cells associated with the procarp, all enclosed in a gelatinous sheath. Spermatangia develop in short, subspherical to elongate spermatangial heads that are terminal on short laterals.

Two species of *Lejolisia*, one of which is endemic, are known in the northern Gulf of California.

KEY TO THE SPECIES OF *LEJOLISIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Erect filaments about 18 μm in diameter; tetrasporangia oval, 42 μm long, 28 μm in diameter, on short, lateral branchlets . . . . *L. colombiana*

1b. Erect filaments 25–30 μm in diameter; tetrasporangia subspherical, 65 μm long, 50 μm in diameter, sessile on branches . . . . *L. hoshawii*

***Lejolisia colombiana* W. R. Taylor**

Lejolisia colombiana W. R. Taylor, 1945:265, pl. 4: figs. 3–10; Dawson, 1962a:43, pl. 17: figs. 1–5; 1962b:186, fig. 41; González-González et al., 1996:235; Mateo-Cid et al., 2000:66; Mateo-Cid et al., 2006:57; Littler and Littler, 2010:[4 figs.]; Fernández-García et al., 2011:63.

Algae forming small tufts, 3–5 mm tall, of erect and prostrate, uniseriate filaments; cells of erect filaments about 18 µm in diameter, lower cells about 100 µm long, upper cells 70 µm long; filaments simple (unbranched) or sparingly branched, alternate or rarely unilateral; terminating with long cells with an obtuse apex; erect filaments arising on dorsal side of cells of basal stoloniferous filaments, stoloniferous filaments to 24 µm in diameter.

Tetrasporangia oval, tetrahedrally divided, 42 µm long, 28 µm in diameter; borne terminal on a short, 1- to 2-celled, upcurved, lateral branch of erect branches. Cystocarps turbinate, 138–150 µm long, 110–175 µm in diameter, surrounded by a pericarp-like cellular layer (see Dawson, 1962a: pl. 17: fig. 5); borne terminal on erect branches or on lateral branchlet of a few cells. Spermatangia in cylindrical-oval clusters, (80–)100–115 µm long, 35 µm in diameter (description after Taylor, 1945; Dawson, 1962a).

HABITAT. On rocks and probably tidal platform; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Cabeza Ballena to Cabo Pulmo. Eastern Pacific: Isla Gorgona, Colombia.

TYPE LOCALITY. Isla Gorgona (Parque Nacional Natural Isla Gorgona), Departamento de Valle del Cauca, Pacific Colombia.

REMARKS. Known in the southern Gulf of California (Dawson, 1962a), *Lejolisia colombiana* was more recently reported in the upper Gulf by Mateo-Cid et al. (2006).

***Lejolisia hoshawii* E. Y. Dawson**

FIGURE 145

Lejolisia hoshawii E. Y. Dawson, 1966b:64, fig. 6J,K; González-González et al., 1996:236; CONANP, 2002:138; Mateo-Cid et al., 2006:52.

Lejolisia sp. nov. sensu Dawson, 1966a:26; Mateo-Cid et al., 2006:52.

Thalli epiphytic, about 7 mm tall, composed of uniseriate, prostrate, and erect filaments. Creeping prostrate filaments attached by short, unicellular rhizoids terminating in expanded digitate discs. Axial cells of filaments 30–50 µm in diameter and 85–150 µm in length. Erect filaments sparsely branched except in fertile plants, with blunt tips; issued from prostrate filaments, up to 5–7 mm long.

Tetrasporangia tetrahedrally divided, 65 µm long by 50 µm wide (including thick hyaline envelope). Tetrasporangia sessile on diminutive protuberance of the bearing cell of erect filaments, solitary or a few multifariously positioned on successive cells. Sexual reproduction unknown.

HABITAT. Epiphytic on larger algae; shallow subtidal.

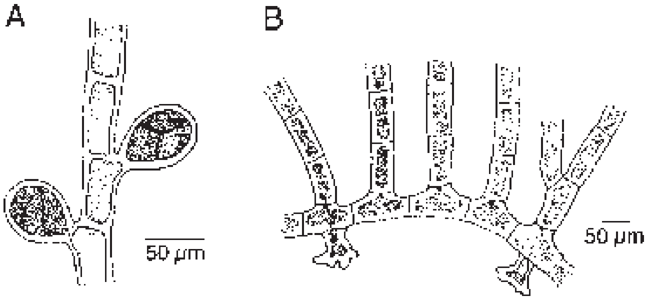


FIGURE 145. *Lejolisia hoshawii* (holotype): A. Tetrasporangia borne on erect filaments. B. Portion of creeping filament to show attachment structures and erect axes (A, B, after Dawson, 1966b: figs. 6J, K).

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena.

TYPE LOCALITY. On *Sargassum* in drift, Playa Hermosa, Puerto Peñasco, Sonora, Gulf of California, Mexico.

***Tiffaniella* Doty et Meñez**

Tiffaniella Doty et Meñez, 1960:135.

Algae are small tufts, composed of erect and prostrate, uniseriate, uncorticated filaments. The erect filaments are slender and unbranched or irregularly, unilaterally or subdichotomously branched axes that arise from the prostrate, spreading filaments that attach by rhizoids on their ventral side. Attachment rhizoids are frequent and simple (unbranched); in some species they are modified by swelling (becoming saccate) or with extensive digitate ends. Cells are multinucleate.

Sporangia are in lateral clusters or solitary and terminal on short stalks. They are tetrahedrally divided to form tetrasporangia (4 spores) or polyhedrally divided, forming polysporangia, each containing from 8 to 64 spores. Gametophytes are monoecious or dioecious; procarps subapical on laterals of erect axes. Carpogonial branches are 4-celled and borne on 1 (supporting cell) of 3 pericentral cells, with the other 2 producing auxiliary cells. Carposporophyte is developed by 2 auxiliary cells fusing to fertile axis cell, forming the characteristic T-shaped fusion cell, involving the hypogenous cell. Involucral filaments are absent, leaving the carposporophyte naked. Spermatangia form elongate heads that are sessile or pedicellate on short laterals from erect filaments.

REMARKS. Mostly epiphytic or endophytic, species of *Tiffaniella* are widespread in distribution. The "*Spermothamnion* sp." of Ortega et al. (1987) from Laguna Agiabampo should be reexamined and may possibly be a *Tiffaniella*.

There are three species of *Tiffaniella* known in the northern Gulf of California.

KEY TO THE SPECIES OF *TIFFANIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Erect filaments subdichotomously branched, rhizoids unicellular, often with markedly modified inflated rhizoids, swollen in middle and terminating in irregular saccate swelling or swollen cylinders ending in digitate disc, rhizoids 300–500 µm long . . . . *T. saccorhiza*

1b. Erect filaments sparsely, unilaterally or irregularly branched, rhizoids not swollen but may terminate in digitate attachment discs 2

2a. Erect filaments to 5 mm tall; sparingly branched; slender, 35–75 µm in diameter, attenuated upward, becoming thinner in diameter, (12–)18–25 µm near apices; sporophytes with tetrasporangia, 50–70 µm in diameter . . . . *T. phycophilum*

2b. Erect filaments taller (>5 mm); more branched; filaments thicker, 50–110 µm in diameter, all orders of branches nearly same diameter throughout; sporophytes with polysporangia (75–120 µm in diameter) . . . . *T. snyderae*

Tiffaniella phycophilum (W. R. Taylor) E. M. Gordon

Spermothamnion phycophilum W. R. Taylor, 1945:263, pl. 3:figs. 17–21, pl 4: figs. 1, 2; Dawson, 1961b:444; González-González et al., 1996:271.

Tiffaniella phycophilum (W. R. Taylor) E. M. Gordon, 1972:125; Abbott and Hollenberg, 1976:623, fig. 565; Stewart and Stewart, 1984:146; Sánchez-Rodríguez et al., 1989:45; González-González et al., 1996:272; CONANP, 2002:138.

Spermothamnion snyderae var. *attenuata* E. Y. Dawson, 1962a:45.

Algae forming short, spreading turfs, 3–5 mm high; of erect, unbranched or sparingly, alternately branched filaments arising from creeping, prostrate filaments attached on the ventral side by unicellular rhizoids. Axial cells 70–225 µm long (mostly 2–3 times longer than diameter), 35–75 µm in diameter; near apices, axial cells smaller, 25–40 µm in diameter, with obtusely rounded, blunt apices. Prostrate filaments mostly 30–60 µm in diameter. Rhizoids rarely long but can be up to 400 µm.

Tetrasporangia tetrahedrally divided, subspherical, 50–70 µm in diameter; solitary at first, on upcurved stalks that rebranch from below and successively develop clusters of tetrasporangia; borne unilateral in a series or occasionally opposite on erect filaments. Gametophytes dioecious. Carposporangia in cluster without involucres. Spermatangia heads sessile, unilateral in a series on erect filaments.

HABITAT. Epiphytic on other algae; low intertidal to shallow subtidal, down to 6 m depths.

DISTRIBUTION. Gulf of California: Bahía de Loreto. Eastern Pacific: Santa Catalina Island (California Channel Islands); Isla Guadalupe (off Baja California) to Bahía Magdalena (Baja California Sur); Galápagos Islands.

TYPE LOCALITY. Black Beach, Isla Santa María (Isla Floreana; Charles Island), Galápagos Islands, Ecuador.

Tiffaniella saccorhiza (Setchell et N. L. Gardner) Doty et Meñez

FIGURE 146A,B

Pleonosporium saccorhiza Setchell et N. L. Gardner, 1930:169, pl. 10: fig. 39.

Tiffaniella saccorhiza (Setchell et N. L. Gardner) Doty et Meñez, 1960:138, figs. 1–4; Dawson, 1961b:444; 1962a:44, pl. 16: fig. 2; 1966a: front cover illustration, 28; Stewart and Stewart, 1984:146; Mateo-Cid and Mendoza-González, 1992:22; Mateo-Cid et al., 1993:48; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid and Mendoza-González, 1994b:41; González-González et al., 1996:272; Abbott, 1999:315, fig. 88C–E; Mateo-Cid et al., 2006:53.

Spermothamnion saccorhiza (Setchell et N. L. Gardner) Feldmann-Mazoyer, 1942:16; Dawson, 1954e:343; González-González et al., 1996:271.

Erect axes, unbranched or subdichotomous to irregularly branched (up to 2–3 orders); axial cells slender, 26–30 µm in diameter, 200–360 µm long; arising from creeping prostrate axes of shorter cells; attached to the host by rhizoids that are often distinctive. Rhizoids, pigmented and unicellular, of various morphologies: expanded (swollen) in middle up to 65 µm in diameter and 300–500 µm long, with either irregular saccate ends or blunt unmodified ends; or thin to inflated cylinders with unmodified, digitate or discoid ends.

Polysporangia borne on short upcurved lateral branches, single or several in small group, oblong, about 75–85 µm, surrounded by thick cell wall. Cystocarps small and lack involucres. Spermatangia in obovate heads, solitary, heads terminal or lateral.

HABITAT. Epiphytic on *Codium* and other algae; mid intertidal to shallow subtidal, down to 9 m depth.

DISTRIBUTION. Gulf of California: Playa Arenosa (Sandy or Norse Beach), Puerto Peñasco to Bahía de Los Ángeles; Bahía Concepción. Eastern Pacific: Isla Guadalupe; Bahía Sebastián Vizcaíno to Todos Santos, Baja California Sur; Nayarit. Central Pacific: Hawaiian Islands.

TYPE LOCALITY. Epiphytic on *Codium* sp.; Isla Guadalupe, Baja California, Pacific Mexico.

REMARKS. In the field, *Tiffaniella saccorhiza* can often been seen as pink-reddish fuzz growing on species of *Codium*. It is the generitype of *Tiffaniella*.

Tiffaniella snyderae (Farlow) I. A. Abbott

FIGURE 146C,D

Spermothamnion snyderae Farlow, 1899:74 [as "*snyderiae*"]; Drew, 1937:463, figs. 1, 2, pl. 21; Smith, 1944:322, pl. 82: figs. 3–5; Dawson, 1945d:67; 1949c:220; 1950b:155, figs. 24, 25; 1951:53; Dawson et al., 1960a:80, pl. 36: figs. 1, 2; Dawson, 1961b:444; 1962a:45, pl. 16: figs. 3–5; 1966a:27; Norris and West, 1966:177; González-González et al., 1996:271.

Tiffaniella snyderae (Farlow) I. A. Abbott, 1971:352, figs. 1f, 2a,b; Abbott and Hollenberg, 1976:624, fig. 566; Devinny, 1978:360; Silva, 1979:328; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Scagel et al.,

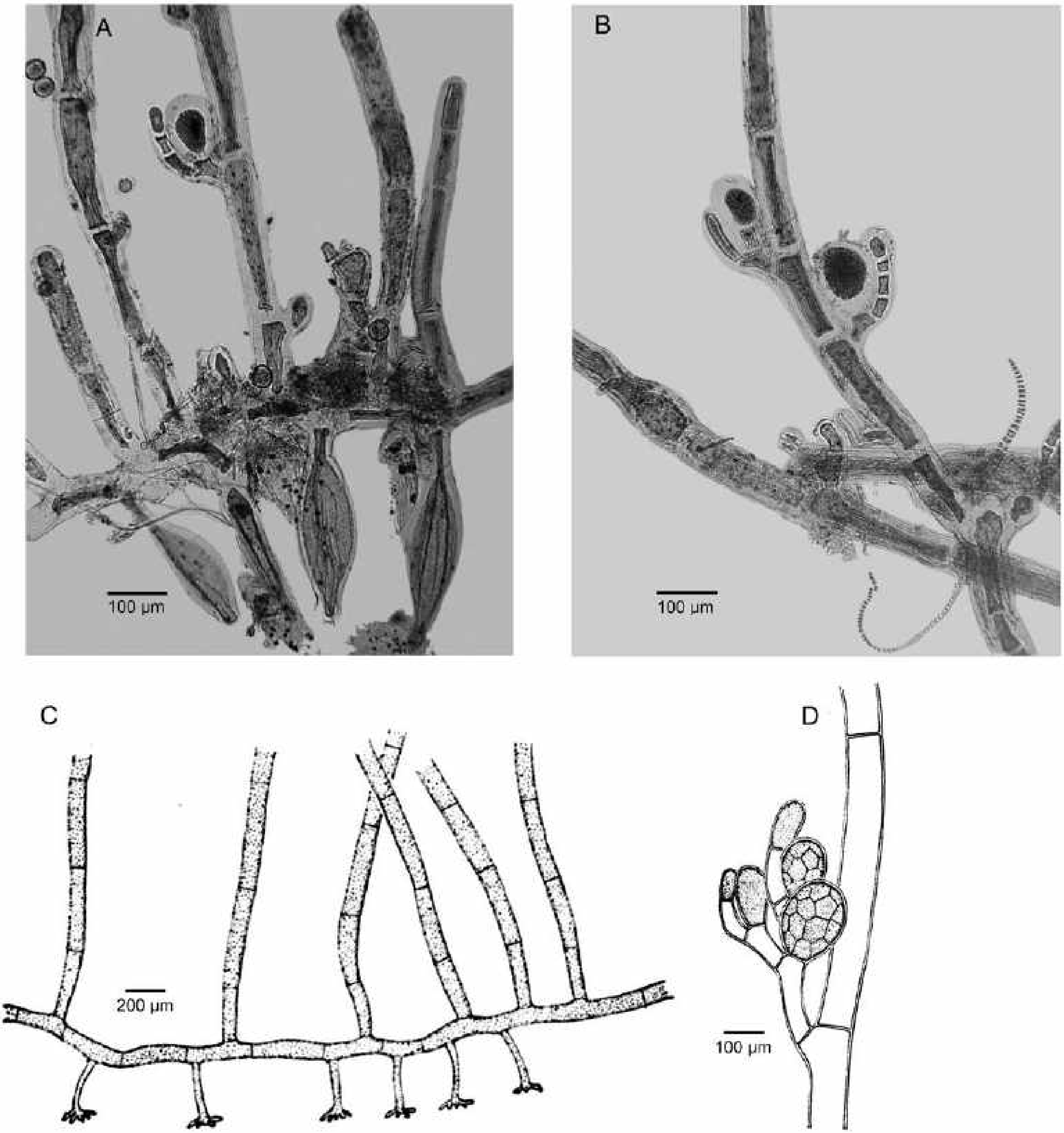


FIGURE 146. Species of *Tiffaniella*. A, B. *Tiffaniella saccorhiza*: A. Erect filaments arising from creeping portion attached by distinctive inflated rhizoids. B. Polysporangia on lateral branches off erect filaments (A, B, *EYD-46-1330*, US Alg. Coll. microscope slide 917). C, D. *Tiffaniella snyderae*: C. Erect filaments arising from creeping portion showing rhizoids. D. A group of developing polysporangia (C, D, after Dawson, 1962a: pl. 16: figs. 4, 3).

1989:262; Stewart, 1991:137; Ramírez and Santelices, 1991:332; R. Aguilar-Rosas and Aguilar-Rosas, 1994:523; Hoffmann and Santelices, 1997:349, pl. 96: figs. 1–4; González-González et al., 1996:272.

Algae of uniseriate, uncorticated filaments, forming erect tufts or sometimes mats, mostly 1–3 mm high; differentiated into creeping prostrate axes and erect branches; attached below by unicellular rhizoids that terminate in expanded digitate discs. Axes and branches of nearly uniform diameter, slightly thinner in upper portions of thallus; erect branches more or less uniform in height. Axial cells cylindrical, 40–70(–110) µm in diameter and (100–)350–1000 µm long. Erect axes predominately unilaterally branched, sometimes irregularly; usually branched 1–3 orders; apical cells blunt.

Polysporangia broadly ellipsoidal, 95–130 µm long, 75–120 µm in diameter, borne terminally on short, simple or compound branchlets, usually in lateral clusters (occasionally single) off erect axes; with (8–)12–16(–32) polyspores. Gametophytes dioecious. Carposporophyte reported as an ovate, loose cluster of carpospores, about 350 µm in diameter; without an involucre. Spermatangia forming cylindrical, compact heads, about 150 µm long, 50 µm in diameter; sessile on short, simple or compound, incurved branchlets in lateral clusters off erect axes.

Habitat. On rocks and in tide pools, epizoic on sponge or epiphytic on other larger algae; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Puerto Libertad; Isla San Jorge; Ensenada de San Francisco (vicinity of Guaymas). Eastern Pacific: Aleutian Islands, Alaska to Isla Santa Margarita (barrier island of Bahía Magdalena), Baja California Sur; Chile.

Type Locality. Syntype localities: Santa Cruz, Santa Barbara, and San Diego, California, listed by Farlow (1899:75). Lectotype locality: Santa Cruz, Santa Cruz County, California, USA (Smith, 1944:323).

Remarks. Dawson (1962a, as *Spermothamnion snyderae*) suggested that in the northern Gulf *Tiffaniella snyderae* was a winter annual. Our collections seem to support Dawson, as we found *T. snyderae* only during the winter months from November to March (1972–1976). Our specimens were all nonreproductive; the descriptions of reproductive structures are after Dawson (1962a).

Wrangeliaceae tribus Spongoclonieae

Wrangeliaceae tribus Spongoclonieae F. Schmitz, 1889:450.

The tribe Spongoclonieae is represented by one genus in the northern Gulf of California.

Pleonosporium Nägeli

Pleonosporium Nägeli, 1862:326, 339.

Algae are erect, uniseriate branched filaments, and usually epiphytic; attached to substrate by rhizoids, at times terminating in digitate discs. Main axes are alternately branched and spirally, radially, or distichously arranged. Axes are completely uncorticated or partly corticated by descending rhizoids. Laterals, one per segment (axial cell), are simple or unilaterally, pinnately, alternately, or irregularly branched, 1–4(–5) orders. Gland cells are absent. Cells are multinucleate.

Asexual reproduction is by polysporangia or tetrasporangia. Polysporangia are sessile or pedicellate and borne adaxial and secund or alternately in abaxial and adaxial sequence along lateral branchlets. Tetrasporangia are tetrahedrally divided, sessile or pedicellate, and borne on branchlet cells. Gametophytes are dioecious. Procarps are subapical on differentiated fertile axes. Cystocarps of one or more round masses of carposporangia are naked or surrounded by one to several involucral branches. Spermatangia, forming oblong to cylindrical heads, are on special short branchlets that are borne unilaterally (adaxially) or alternately (in a sequence, adaxial to abaxial) or terminal on branchlets.

Remarks. There is one species reported in the southern Gulf: *Pleonosporium squarrulosum* (Harvey) I. A. Abbott (1972; basionym: *Callithamnion squarrulosum* Harvey, 1853; synonym: *Pleonosporium dasyoides* (J. Agardh) De Toni, 1903; see Dawson, 1962a) from Bahía de Loreto (CONANP, 2002).

Four species of *Pleonosporium* occur in the northern Gulf of California.

KEY TO THE SPECIES OF *PLEONOSPORIUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli with alternately radial branching . . . . *P. globuliferum*
1b. Thalli with alternately distichous branching 2
2a. Determinate branchlets alternately branched, polysporangia and spermatangia arranged alternately on adaxial and abaxial sides; polysporangia divided into about 16 spores . . . . *P. vancouverianum*
2b. Determinate branchlets usually simple; polysporangia divided into about 32 spores 3
3a. Lower portions abundant with more or less loosely entangled descending rhizoids; polysporangia spherical, sessile and alternate, grouped on short, irregular, specialized, densely branched polysporangial branchlet system . . . . . *P. rhizoideum*
3b. Lower portions not noticeably clothed with rhizoids; polysporangia ovoid, seriate, sessile and adaxial on determinate lateral branchlets . . . . *P. mexicanum*

Pleonosporium globuliferum Levring

FIGURE 147

Pleonosporium globuliferum Levring, 1941:647, fig. 19; Dawson, 1957c:21; 1960a:50; 1961b:443; 1962a:41, pl. 15: fig. 2–6; Navas, 1966:112, pl. 8: fig. 4A–C; Stewart and Stewart, 1984:145; Sánchez-Rodríguez et al., 1989:45; Ramírez and Santelices, 1991:329; González-González et al., 1996:250; Mateo-Cid et al., 2000:66; Bernecker, 2009:CD-Rom p. 65; Fernández-García et al., 2011:62.

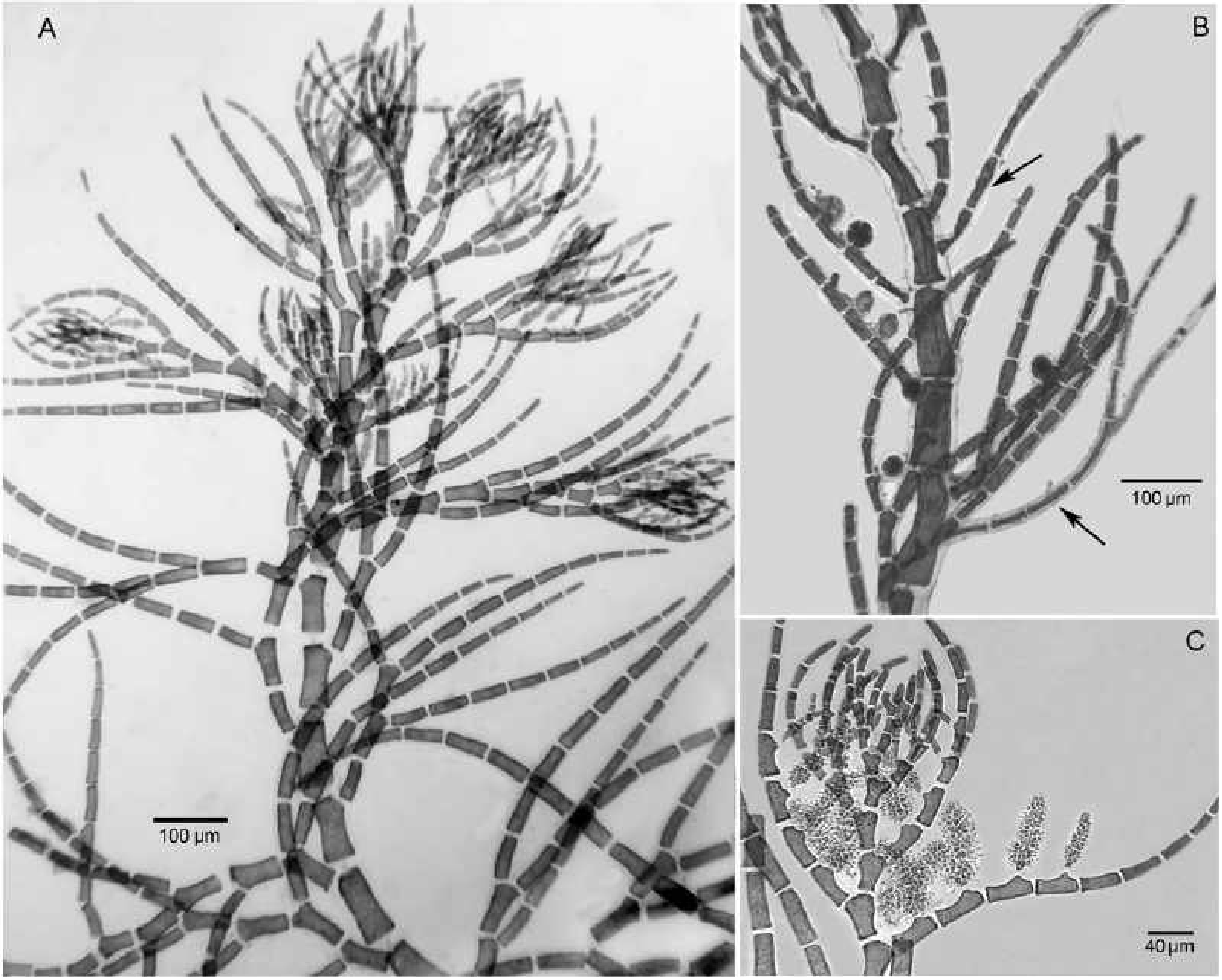


FIGURE 147. *Pleonosporium globuliferum*: A. Habit showing multifarious branching. B. Adaxial polysporangia; note the rhizoids (arrows) from some of the axial cells (*JN-7175*, US Alg. Coll. microscope slide 4673). C. Upper portion of axis showing serial, adaxial arrangement of cylindrical spermatangial heads (A, C, *JN-4147*, US Alg. Coll. microscope slide 4682).

Thalli of several uncorticated erect axes, up to 1.5 cm tall, alternately and multifariously radially, spirally branched; attached by multicellular rhizoids, often terminating in digitate attachment discs. Axial cells up to 200–400 µm long and to 100 µm in diameter basally (2–4 times longer than wide). Branchlets alternately divided, upcurved, about 30 µm in diameter at their base, with cells 2–3 times as long as wide (60–90 µm long). Tips of ultimate branchlet cells blunt, up to 14 µm diameter.

Polysporangia 28–45(–70) µm in diameter, subspherical, sessile, and scattered (infrequently in a short series) along lateral branches, 1 to a cell. Spermatangial heads oblong, to 75 µm long and to 30 µm in diameter, sessile and adaxial on the ultimate branchlets, 1 per cell, usually on the proximal cells of branchlets, in upper portions of the thallus.

Habitat. Epiphytic on *Codium* and *Sargassum* or entangled with other algae; intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco; Cabo Pulmo to San José del Cabo. Eastern Pacific: Isla Guadalupe (off Baja California); Oaxaca; El Salvador; Costa Rica; Chile.

Type Locality. Sta. 13, "Ausserhalb Sanchez, Masafuera" (Levring, 1941:604, 647); Quebrada Sánchez, Isla Alejandro Selkirk (Más Afuera), Islas Juan Fernandez, Valparaiso Region, Chile.

Pleonosporium mexicanum **E. Y. Dawson**

FIGURE 148

Pleonosporium mexicanum E. Y. Dawson, 1962a:41, pl. 16, fig 1; 1966a:26; 1966b:65; Stewart and Stewart, 1984:145; Dreckmann et al., 1990:32, pl. 6: fig. 2; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:250; CONANP, 2002:138; Pacheco-Ruíz et al., 2008:211; Fernández-García et al., 2011:62.

Thalli erect, to 2 cm tall, composed of several uncorticated axes. Distichous and alternately branched; richly branched in upper parts, but not from every cell in lower parts. Axial cells of primary axes 110–225 µm in diameter basally, and cells longest in middle portions (2–4 times the diameter long), reduced in both dimensions above. Attached by long, little-divided multicellular rhizoids. Most determinate branchlets unbranched, from 15–30 cells long, somewhat incurved and corymbose. Cells of branchlets 40–60 µm in diameter at their base and about 1.5 times as long, ultimate cells blunt tipped and about 25 µm in diameter.

Polysporangia ovoid, 70–90 µm in diameter when hyaline envelope is included. Polysporangia borne sessile and adaxial on determinate branchlets, in a series, 1 per cell toward distal end of cell. Polysporangia divided into about 32 spores. Sexual reproduction not seen.

HABITAT. Epiphytic or saxicolous; low intertidal to subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Bocochibampo (near Guaymas); Cabo San Lucas; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Isla Guadalupe; El Salvador; Costa Rica.

TYPE LOCALITY. Lowermost intertidal on small reef, 3 km north of Belmar Hotel; Playa de Olas Atlas, vicinity of Mazatlán, Sinaloa, Gulf of California, Mexico.

REMARKS. Although some *Pleonosporium mexicanum* can be somewhat vegetatively similar to members of the *Callithamnion rupicola-uncinatum* complex, members of the latter complex do not have polysporangia.

Pleonosporium rhizoideum **E. Y. Dawson**

Pleonosporium rhizoideum E. Y. Dawson, 1962a:42, pl. 14: figs. 1–3, pl. 17: fig. 7; Mendoza-González et al., 1994:108; González-González et al., 1996:250, fig. 36; Mateo-Cid et al., 2006:57.

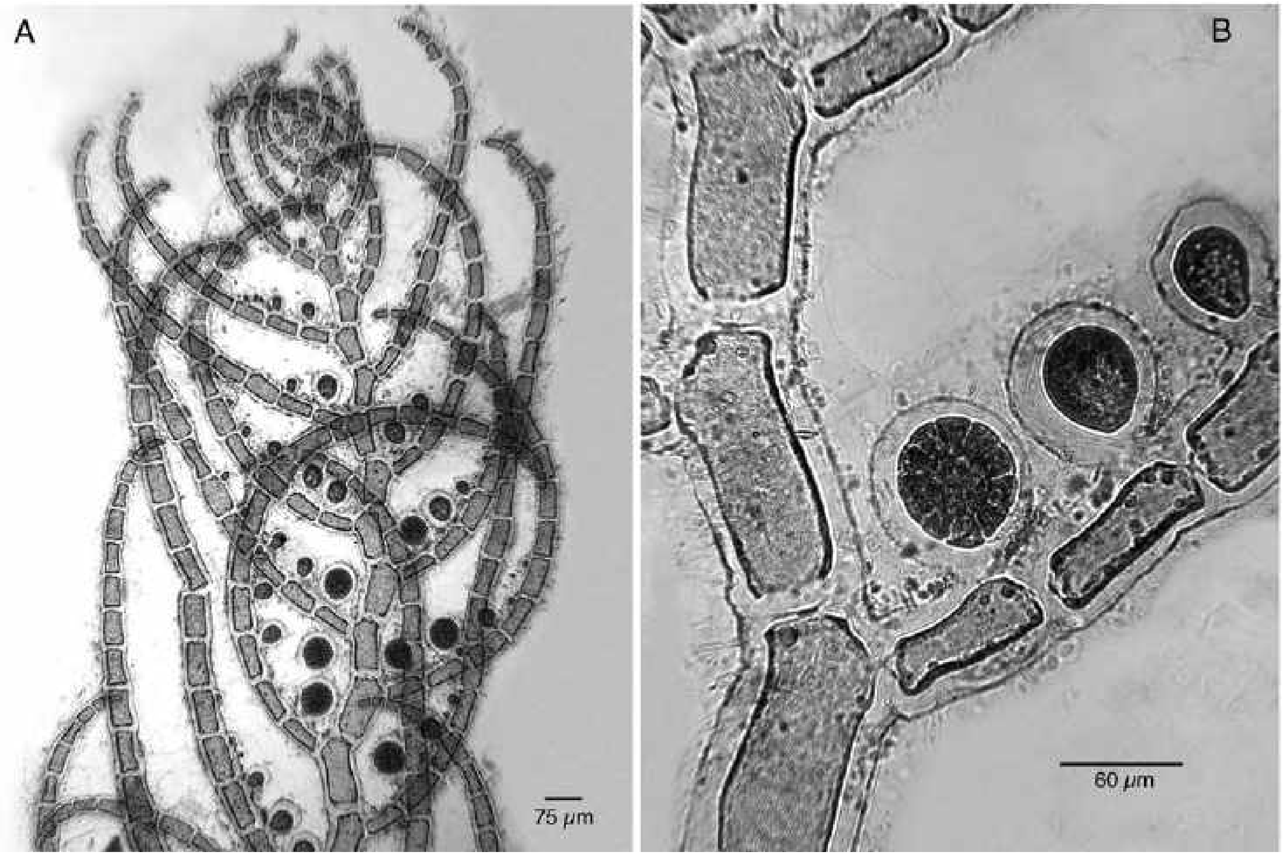


FIGURE 148. *Pleonosporium mexicanum*: A. Upper portion of axis showing distichous alternately arranged determinate branchlets bearing sessile polysporangia adaxially, in a series. B. Branchlet with developing and mature polysporangia (A, B, holotype, *EYD-3610*, US Alg. Coll. microscope slide 398).

Thalli erect tufts, up to 2.5 cm tall; composed of uncorticated axes, 125–170 µm in diameter basally, (125–)180–340 µm long (about [1–]1.5–2.0 times as long as diameter); more or less loosely clothed in lower potions by entangled rhizoids (see Dawson, 1962a: pl. 17: fig. 7); more or less distichously branched. Branches mostly simple, 60–70 µm in diameter, long and initially incurved, later becoming recurved or irregularly curved, little attenuated; terminating in blunt apices (sometimes prolonged to form a rhizoid). Basal felt-like attachment composed of numerous, descending rhizoids.

Polysporangia spherical, divided into about 32 spores; about 60 µm in diameter; sessile and alternate, borne in groups on specialized, short, irregular branches in densely branched portions of thallus. Cystocarps subspherical, about 90 µm in diameter, with several low irregular lobes; borne in densely branched fertile portions (similar to those of sporangial thalli). Spermatangia not known (description after Dawson, 1962a).

DISTRIBUTION. Gulf of California: Puerto Peñasco; Mazátlan. Eastern Pacific: Oaxaca.

TYPE LOCALITY. Salina Cruz, Oaxaca, Pacific Mexico.

REMARKS. *Pleonosporium rhizoideum* was reported in the upper Gulf of California by Mateo-Cid et al. (2006); since I have not seen their specimens, the description is based on Dawson (1962a).

Pleonosporium vancouverianum (J. Agardh) J. Agardh

FIGURE 149

Callithamnion vancouverianum J. Agardh, 1876:30.

Pleonosporium vancouverianum (J. Agardh) J. Agardh, 1892:37; Kylin, 1925:57, fig. 37A–C; Smith, 1944:321, pl. 82: figs. 1, 2; Dawson, 1961b:444; Dawson and Neushul, 1966:182; Hollenberg and Abbott, 1966:101; Abbott and Hollenberg, 1976:620, fig. 562; Devinny, 1978:359; Stewart and Stewart, 1984:145; Scagel et al., 1989:228; R. Aguilar-Rosas et al., 1990:126; González-González et al., 1996:250.

Pleonosporium abysicola N. L. Gardner, 1927d:380, pl. 81: fig. 1, pl. 82; Dawson, 1961b:443; 1962a:39, pl. 13: fig. 3; Dawson and Neushul, 1966:182; Huerta-Múzquiz, 1978:339; Mateo-Cid and Mendoza-González, 1992:21; González-González et al., 1996:249.

Thalli uniseriate filaments, of several erect axes, up to 1.0(–1.8) cm tall, distichous and repeatedly regularly alternately branched to 4(–5) orders; branching from almost every cell, each order progressively smaller than proceeding one. Axes uncorticated, percurrent, axial cells of primary axes cylindrical, basally 150–240 µm diameter and to 340–680 µm long, smaller above and cuboid. Proximal cell of laterals slightly shorter than adjoining cells. Algae attached by a few wide filament-like rhizoids at axes base and by long, thin (to 20 µm in diameter), unbranched, uniseriate, multicellular rhizoids issued singly, from the middle of some lower axial cells. Ultimate branchlets of 2–6 cells, ultimate cells blunt tipped, about 10 µm in diameter.

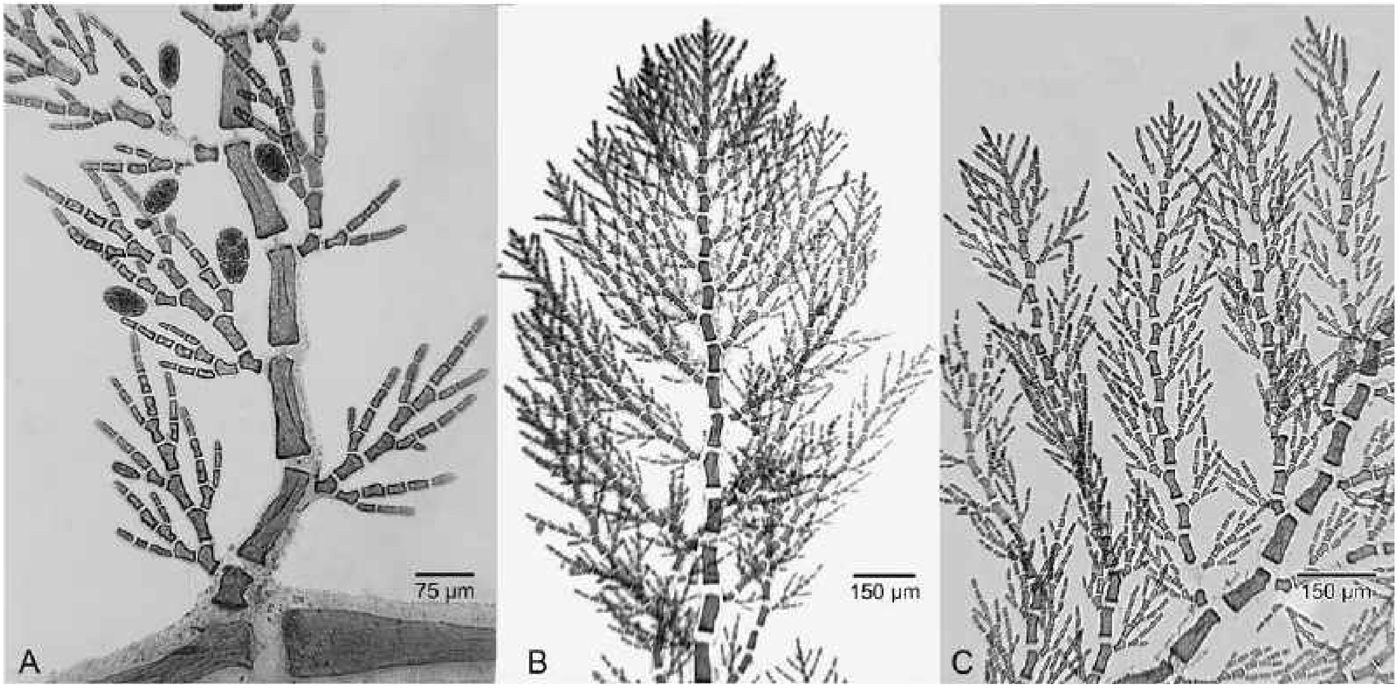


FIGURE 149. *Pleonosporium vancouverianum*: A. Alternate adaxial-abaxial arrangement of polysporangia along branchlet. B. Upper portion of axis showing alternate, distichous branching pattern (*JN-4745*, US Alg. Coll. microscope slide 4690). C. Alternately distichously branched to several orders, cells diminishing in width and length at each order (A, C, *JN-4745*, US Alg. Coll. microscope slide 4689).

Mature polysporangia ovate to oblong-ellipsoidal, to 75 µm long and to 45 µm wide, divided into about 16 spores; sessile, borne alternately in position of ultimate branchlets. Sexual plants not found in Gulf of California material. Elsewhere reported: carposporophytes involucrate; spermatangia in short, ovoid heads, sessile or pedicellate, borne alternately in position of ultimate branchlets.

HABITAT. Epiphytic or entangled with larger algae; shallow subtidal, down to 20 m depths.

DISTRIBUTION. Gulf of California: Isla Coronado (Isla Smith) and Islas de Los Gemelos (Islas los Hermanitos), both off Bahía de Los Ángeles; Nayarit. Eastern Pacific: Vancouver Island, British Columbia, to Santa Cruz Island (California Channel Islands); Islas Todos Santos and Isla Guadalupe, off Baja California; Isla Magdalena (west side of Bahía Magdalena), Baja California Sur.

TYPE LOCALITY. Vancouver Island, British Columbia, Canada.

REMARKS. Apparently rare in occurrence, the collection of subtidal specimens of *Pleonosporium vancouverianum* at Isla Coronado (*JN-4419*, US Alg. Coll. microscope slide 4687) and Islas de Los Gemelos, Bahía de Los Ángeles (*JN-4745*, US Alg. Coll. microscope slide 4689–4691) represent new distribution records for the Gulf of California.

GELIDIALES*

Gelidiales Kylin, 1923:132; Hommersand and Fredericq, 1998:254 [revised description].

Members of this order are erect individuals or few to many in tufts or clumps or form cushions or turfs or spreading mats; they are composed of cylindrical to compressed branching axes and branches, developing from prostrate axes. Most are freely branched in one plane, but some branch in various directions. The uprights develop from prostrate axes, which are generally subcylindrical to slightly compressed and less pigmented than the erect parts. The lower prostrate axes are often entangled and attach the alga to the substratum at various intervals by either (1) thick-walled rhizoidal filaments developed from the surface cortical layer (Gelidiellaceae), (2) brush-like holdfasts of independent (not coalescing) thick-walled unicellular rhizoidal filaments developed from the inner cortical cells and pigmented multicellular uniseriate filaments from the surface cells (Gelidiaceae), or (3) peg-like holdfasts of coalescing (into a thick sheath) thick-walled, unicellular rhizoidal filaments from the inner cortical cells and pigmented multicellular uniseriate filaments (Pterocladiaceae).

All of the species are uniaxial, with a usually distinct apical cell. In transection the single axial filament is often obscured by longitudinal filaments, which develop around it from the inner cortex. The medulla is composed of large longitudinal cells that are sparsely to densely entwined with internal rhizoidal filaments (rhizines, or hyphae) and a cortex of successively smaller cells toward the surface.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangial thalli have tetrasporangia embedded beneath the surface of branchlets. Carpogonial branches are one- to three-celled and deeply embedded in the cortex. Carpogonia are intercalary, developed within branchlets. Gonimoblasts are produced either from the fertilized carpogonia, which in turn fuses with the hypogynous cells, or from the long nutritive filaments, which develop from the fusion cells following fertilization. Auxiliary cells are absent in this order. Cystocarps are bilocular and protrude with ostioles on both sides of the blade, with a conspicuous bulge on only one surface of a branch. Spermatangia are developed in superficial sori below branch and branchlet apices.

REMARKS. In the field some of the smaller Gelidiales in the Gulf of California could be confused with Gulf *Wurdemannia miniata* (Sprengel) J. Feldmann et G. Hamel and some very small specimens of Gulf *Ceratodictyon tenuis* (Setchell et N. L. Gardner) J. N. Norris (herein). In the families of Gelidiales, species are uniaxial (apical usually evident), semirigid to cartilaginous (mostly over 250 µm in diameter); tetrasporangia are cruciately, tetrahedrally, or irregularly divided, and elongated, internal rhizoidal filaments (rhizines, hyphae) are present among the medullary cells (and sometimes cortical cells) of Gelidiaceae and Pterocladiaceae but are absent in the Gelidiellaceae. In contrast, both *Ceratodictyon* (Lomentariaceae) and *Wurdemannia* (Solieriaceae) are multiaxial, rigid, wiry (mostly less than 250 µm in diameter), and internal rhizoidal filaments are absent; and the tetrasporangia are zonately divided in *Wurdemannia* and cruciately divided in *Ceratodictyon*.

It has long been considered difficult to distinguish the genera of many Gelidiales (especially in absence of cystocarpic material) and, in many cases, the species. Their taxonomy has been complicated by a high degree of morphological plasticity, and the unreliability of using the branching pattern as a character makes it difficult to recognize discrete taxa and understand species limits. Several recent studies have supported the usefulness of anatomical characters in separating the families; for example, the internal rhizoidal filaments (also referred to as "rhizines" or "hyphae") among the medullary cells and/or in the cortex are present in members of the Gelidiaceae and Pterocladiaceae but absent in the Gelidiellaceae. Perrone (1994), Shimada et al. (1999), and Perrone et al. (2006) described different kinds of attachment structures that also helped to separate the families: brush-like haptera in the Gelidiaceae and peg-like haptera in the Pterocladiaceae. More recently, Santelices (2007) tested these attachment characters and found support for the Perrone et al. (2006) hypothesis that the kind of attachment is unique to each family.

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* Contributed by James N. Norris and Joan G. Stewart. J. G. Stewart: Scripps Institution of Oceanography, University of California, San Diego, La Jolla, California, USA.

KEY TO THE FAMILIES OF GELIDIALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Anatomically, species completely lack internal rhizoidal filaments (hyphae, rhizines); thalli adhere to or penetrate substratum by single-celled rhizoids originating from outer cortical cells . . . . **Gelidiellaceae**

1b. Anatomically, internal rhizoidal filaments among medullary cells and/or cortical cells (sometimes not apparent or lacking in small thalli); prostrate axes of thalli attached to substratum by haptera-like structures of two kinds of filaments: (1) unicellular, colorless rhizoidal filaments produced from inner cortical cells that protrude between surface cells and (2) multicellular, pigmented uniseriate filaments that develop from the outer (surface) cortical cells 2

2a. Brush-like haptera; of internal rhizoidal filaments growing independently (remain free; not coalescing) between surface cells and pigmented, multicellular filaments developed from surface cells that form basal cortication . . . . . **Gelidiaceae**

2b. Peg-like attachment haptera; of internal rhizoidal filaments growing between surface cells and coalescing in a thick sheath and pigmented multicellular filaments from surface cells that form a basal cortication . . . . **Pterocladiaceae**

GELIDIACEAE

Gelidiaceae Kützing, 1843:390, 405 [as "Gelidieae"]; Perrone et al., 2006:31 [emended description].

Algae are composed of erect, terete, compressed or flattened, slender to narrow axes that are sparsely to densely and pinnately to irregularly branched (rarely unbranched). Uprights develop from a prostrate system of often entangled, irregularly branched, terete to compressed axes, opposite the small brush-like haptera of rhizoidal filaments and pigmented filaments that group together but remain single (do not coalesce) and adhere to or penetrate the substratum. The brush-like haptera are composed of two kinds of noncoalescing filaments: thick-walled, refractive, colorless rhizoidal filaments originating internally from inner cortical cells that grow independently and protrude between the surface cells and pigmented, multicellular, uniseriate filaments developed externally from the surface cells.

Growth is uniaxial. Internally, there are few to many thick-walled, refractive unicellular internal rhizoidal filaments (rhizines or hyphae), originating from the inner cortical cells and growing basipetally, obliquely or transversally through the thallus.

Life histories, where known, are generally triphasic (more rarely biphasic), with isomorphic tetrasporophytes and gametophytes. Tetrasporangia are cruciately or tetrahedrally divided and in sori in branchlet tips or scattered in ultimate branchlets. Tetraspores usually have an ordered arrangement in parallel rows in young sori, whereas mature tetrasporangia are either irregularly arranged or in parallel rows. Gametophytes are mostly dioecious or sometimes monoecious. Cystocarps are bilocular, within and raised or protruding above the surface of ultimate branchlets or either terminal or below on the branches. Spermatangia develop in sori, forming superficial colorless patches on upper branches and ultimate branchlets.

There are currently nine genera recognized in the Gelidiaceae; one of these, *Gelidium,* is found in the Gulf of California.

Gelidium J. V. Lamouroux

Gelidium J. V. Lamouroux, 1813:128.
Acropeltis Montagne, 1837:355.

Algae are erect, semirigid and cartilaginous, terete, subterete, or compressed, upright axes that arise from unbranched to branched prostrate axes. Thallus morphology is varied, and species may be turf mats with extensive prostrate axes, in tufts, or discrete clumps composed of one to several branched axes. The uprights are narrow and distichously, plumosely, or irregularly branched, often with branches regularly arranged and bilaterally symmetrical. Color is variable between and within species, ranging from yellowish green, red, or dark purple to nearly black; color is partly related to the degree of solar and tidal exposure in an individual's habitat. They are attached to or penetrate the substratum by characteristic short, brush-like haptera along the prostrate axes. These are composed of independent (not coalescing), colorless rhizoidal filaments that develop from the inner cortical cells and grow outward between the surface cortical cells and, together with pigmented, multicellular, uniseriate filaments produced from the outer (surface) cortical cells, form short, brush-like attachments.

Growth is uniaxial, and a single apical cell is usually evident. The medulla is usually compressed, composed of rounded, colorless cells; in transection it is up to 30 μm in diameter. Elongated internal rhizoidal filaments (rhizines or hyphae) are interspersed among the medullary cells and/or cortical cells. The cortex is of several rows of small, compacted pigmented cells, 2–15 μm in diameter, becoming smaller outward; in surface view cortical cells may be regularly or irregularly arranged.

Life histories are triphasic. Fertile branches can be simple or pinnately compound, often with a sterile margin around the reproductive structures. Tetrasporangia are developed in sori, covering the somewhat expanded or broadly rounded tips of lateral branches, and the main axes' branch tips. Tetrasporangia are tetrahedrally divided and embedded in the cortex. Carpogonial filament is unicellular and, after fertilization, fuses with adjacent cells. Carposporangia develop on both sides of fertile branch. Mature cystocarps are bilocular, with two ostioles, and protrude equally on both surfaces of the branch near apices. Spermatangia are in sori on branch surfaces.

REMARKS. Large and small thalli of *Gelidium* are occasional to abundant in the intertidal habitats throughout the Gulf of California and are less common in the shallow subtidal. Some species are commercially important and utilized by industry as agar sources (Friedlander, 2007; Arvizu-Higuera et al., 2007). In Mexico companies such as Industrias Gel-Mex of Baja California have harvested species of *Gelidium*. Sulfated polysaccharides of Brazilian *Gelidium crinale* exhibited anticoagulant activity (Pereira et al., 2005). The chemical properties of the species in northern Gulf of California have not yet been investigated.

There are two species reported in the southern Gulf: *Gelidium coronadense* E. Y. Dawson (1953a) is listed without comment from Bahía de Loreto (CONANP, 2002), and *G. microdentatum* E. Y. Dawson (1960a), described from San Blas, Nayarit (near the southern entrance to the Gulf of California), is a small, flat species with dentate margins occurring from Nayarit to Jalisco (Serviere-Zaragoza et al., 1993b; González-González et al., 1996).

Eight species of *Gelidium* are recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *GELIDIUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. One to several thalli in clumps; equal to or taller than 2 cm in height (some 5–15 cm tall) 2
1b. Thalli smaller, shorter, usually less than or sometimes up to 2 cm tall; in tufts, cushion-like or forming often extensive mats or smaller patches; sometimes within or entangled in algal turfs 4
2a. Erect, wiry thalli, 1.0–2.0(–3.5) cm tall; sparsely branched, axes and branches similar; terete (occasionally only slightly compressed), very slender, 125–225 μm in diameter . . . . ***G. crinale***
2b. Erect thalli mostly (3–)5–15 cm tall; branches terete to flattened, much broader, over 600 μm in diameter (up to 3 mm in width) 3
3a. Thalli 6–9 cm tall; axes subcylindrical, much branched irregularly, alternately to pinnately (2–4 orders); branches flattened, slender, 0.6–0.8(–1.5) mm in diameter, narrower in width at each order outward; ultimate branchlets most slender, of varying lengths, usually densely congested . . . . ***G. decompositum***
3b. Thalli 5–12 cm tall; flat throughout, mostly 1.5–3.0 mm wide; branching distichously, mostly opposite, regular, pinnate; ultimate branchlets of uniform size, 1–2 mm long, up to 0.5 mm wide (not markedly congested) . . . . ***G. johnstonii***
4a. Axes either terete to slightly compressed throughout or only partially in lower portions with upper portions flattened; mostly less than 600 μm wide (range, 200–700 μm wide); variably branched 5
4b. Axes of compressed to flat branches; broader, mostly over 600 μm wide (range, 600–900 μm wide) 6
5a. Thalli terete to only slightly compressed throughout; narrower, 150–250 μm in diameter, and thicker, 150 μm or more thick; subdichotomously to irregularly branched; tetrasporangial branchlets with acute apices . . . . ***G. refugiensis***
5b. Thalli terete to compressed basally and markedly flat upper axes and branches; sparsely to more or less densely, pinnately to irregularly branched 7
6a. Thalli of slightly compressed to flattened branches, 200–650 μm wide, mostly less than 100 μm thick; simple or sparingly branched or sometimes branched pinnately; flat branches usually extended into long, slender, subcylindrical, flagellate extensions . . . . ***G. mcnabbianum***
6b. Thalli compressed to flattened, broader, 600–900(–1200) wide, and thicker, greater than 150 (up to 350) μm thick; irregularly pinnately branched; branches without apical extensions . . . . ***G. microphysa***
7a. Branches 200–700 μm wide, mostly 100–120 μm thick; pinnately to irregularly branched; tetrasporangial sori without a thick sterile margin, on tetrasporangial branchlets with broad rounded apices . . . . ***G. pusillum***
7b. Branches up to 1 mm wide; tetrasporangial sori with a thick sterile margin, on tetrasporangial branchlets with an indented apical margin . . . . ***G. sclerophyllum***

Gelidium crinale (Hare ex Turner) Gaillon

FIGURE 150F,G

Fucus crinalis Hare ex Turner, 1819:4, pl. 198: figs. a–c, e–g (see Remarks below).

Gelidium crinale (Hare ex Turner) Gaillon, 1828:362; Okamura, 1915:195, pl. 14: figs. 1–10; Dawson, 1944a:259; Taylor, 1945:155; Dawson, 1953a:64, pl. 4: fig. 5; 1961b:408; 1966a:16; Dixon and Irvine, 1977a:140; Santelices, 1977:67, fig. 2A–C; Stewart and Stewart, 1984:142; Santelices and Stewart, 1985:22, fig. 11; Santelices, 1988:96, fig. 5; Rodríguez-Vargas and Santelices, 1988:117, tbls. 1, 2, fig. 5; Ramírez and Santelices, 1991:189; Rodríguez-Vargas et al., 1993:446; Serviere-Zaragoza et al., 1993a:483; Serviere-Zaragoza et al., 1993b:48; H.-B. Lee, 1994:70, figs. 5–8; H.-B. Lee and Kim, 1995:164, fig. 5; Abbott, 1999:192, fig. 49A; L. Aguilar-Rosas et al., 2000:130; 2002:234; Xia et al., 2002:187, figs. 7, 8, 78; Perrone et al., 2006:24, fig. 14; Mateo-Cid et al., 2006:55; Santelices, 2007:294, tbl. 1.

Gelidiella mexicana sensu Dawson, 1944a:262 [in part; only Guaymas specimens; non *Gelidiella mexicana* E. Y. Dawson, 1944a:262, which is now *Gelidiella hancockii* E. Y. Dawson, 1944a:261—see also Dawson, 1953a:64].

Algae erect, wiry tufts, 1.0–3.0(–3.5) cm tall; axes unbranched or sparsely irregularly branched, up to 2 orders; axes and branches thin, terete to only slightly compressed, 125–225 μm in diameter; arising from entangled, more or less terete, prostrate branches, attached by brush-like haptera directly to substratum or sometimes partially penetrating substratum. Transection with inner medulla of 1–2 or small group of rows of thick-walled cells; outer medulla of cells 6–15 μm in diameter; rhizoidal filaments

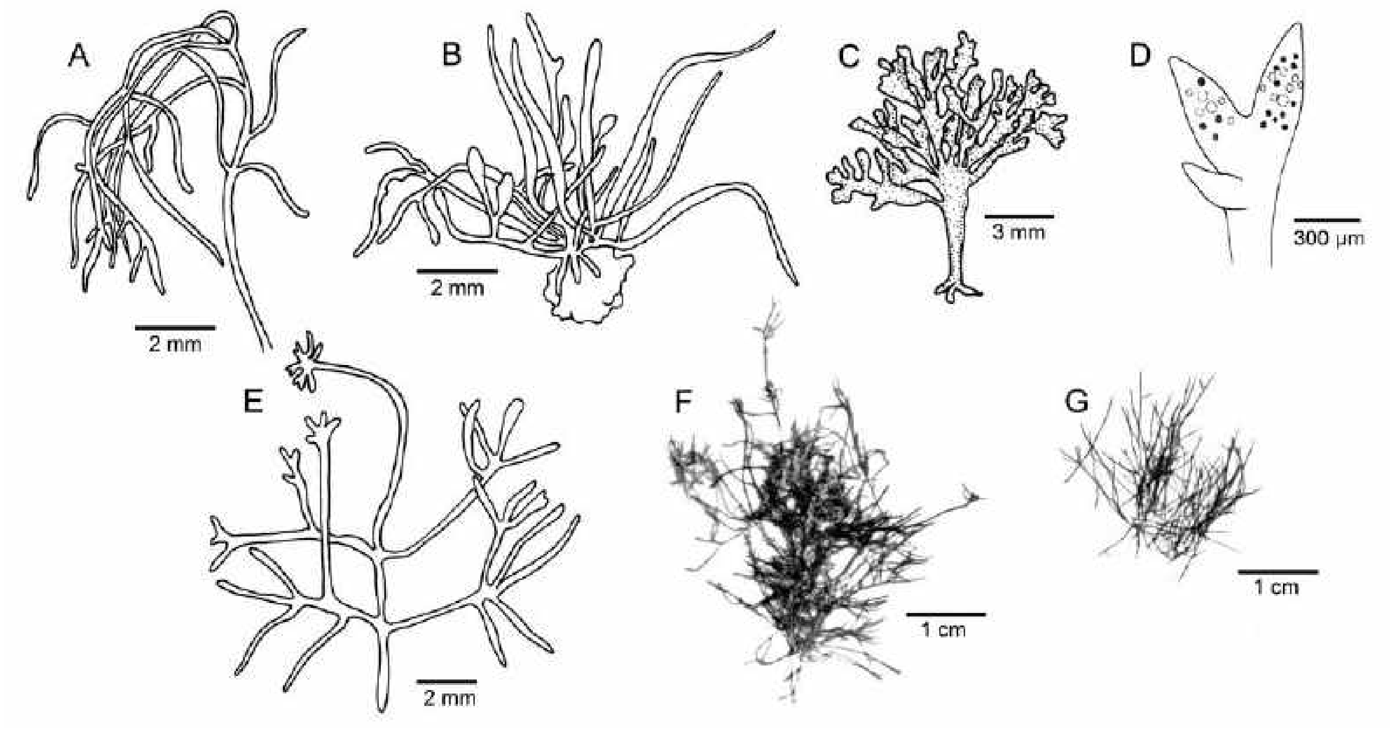

FIGURE 150. Species of *Gelidium*. A, B. *Gelidium mcnabbianum*: Habits of specimens from the type collection (after Dawson, 1957c: figs. 4c, d). C. *Gelidium microphysa*: Habit of the type specimen (after Setchell and Gardner, 1930: pl. 9: fig. 31). D, E. *Gelidium refugiensis*: D. Tip of sporangial branch showing openings through cortex. E. Portion of type showing habit (D, E, after Dawson, 1944a: pl. 43, figs. 4, 5). F, G. *Gelidium crinale*: Habits of two Gulf specimens (F, *JN-3310,* US Alg. Coll.-159270; G. *JN-3483,* US Alg. Coll.-159274).

among cells of medulla and subcortical regions. Cortex of 3–5 layers of small cells, mostly 4–6 µm long, 6–8 µm in diameter.

Tetrasporangia in upper portions of simple, pinnate or digitate-shaped, terminal branchlets; tetrasporangia spherical, about 30 µm in diameter. Cystocarpic and spermatangial thalli not known in the northern Gulf. Cystocarps as reported elsewhere: ovoid, 500–600 µm in diameter, 500 µm thick (Santelices and Stewart, 1985).

Habitat. On exposed rocks and tidal platforms or sometimes in sand-covered substratum; intertidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to El Coloradito; Bahía San Luis Gonzága; Isla Turner (Islas de la Cintura); Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Isla Guadalupe; Bahía Magdalena, Baja California Sur; Colima to Oaxaca; Galápagos Islands; Chile. Central Pacific: Hawaiian Islands. Western Pacific: China; Korea; Japan; Vietnam.

Type Locality. Ilfracombe, Devonshire, England, UK (Lipkin and Silva, 2002).

Remarks. Although *Gelidium crinale* has been widely reported in distribution (Guiry and Guiry, 2008–2010), its species limits are not fully understood. In the northern Gulf *G. crinale* is wiry, with slender, terete axes, and unbranched to sparsely, irregularly branched. The other small turf species of *Gelidium* in the Gulf are usually shorter: *G. refugiensis*, although similarly terete to slightly compressed, is subdichotomously branched with slightly wider branches, and *G. pusillum* and *G. sclerophyllum* have flattened upper axes and branches and are pinnately to irregularly branched. Specimens of Gulf of California *G. crinale* need to be molecularly compared with *G. crinale* from other regions (Freshwater et al., 2002), particularly those of the type locality.

"*Fucus crinalis* Hare ex Turner" in volume 4 of Turner is usually cited as 1819, but the exact publication date is uncertain. Turner's volumes were published in fascicles "possibly" from 1811 to 1819 (Price, 1984:442), but the "details are lacking" (Stafleu and Cowan, 1986:346). More recently, Lipkin and Silva (2002:9) gave the date for *F. crinalis* as "1815," but this has been queried by Guiry and Guiry (2010). Herein Turner (1819) is used for volume 4 until the exact date of publication can be resolved.

Gelidium decompositum Setchell et N. L. Gardner

FIGURE 151

Gelidium decompositum Setchell et N. L. Gardner, 1924:743, pl. 71; Dawson, 1944a:260; 1953a:67; Norris, 1973:9; González-González et al., 1996:205, 392; CONANP, 2002:139.

Pterocladia capillacea sensu Stewart and Norris, 1981:279 [in part; only northern Gulf of California specimens], fig. 5 [non *Pterocladia capil-*

FIGURE 151. *Gelidium decompositum*: Habit, some portions of thalli are dense and congested (*JN-4611*, US Alg. Coll.-159296).

lacea (S. G. Gmelin) Bornet in Bornet et Thuret, 1876:57, which is now *Pterocladiella capillacea* (S. G. Gmelin) Santelices et Hommersand, 1997:118].

Algae bushy, up to 9 cm tall; of 1 to a few erect, narrow, flattened main axes, (600–)750–800(–1500) μm wide and 160–370 μm thick; attached to substratum by loose, creeping prostrate basal branches, sometime more or less penetrating substratum such as crustose corallines. Axes irregularly divided some distance above base into several primary branches, further irregularly dividing upward 2–3 times to form branches in a more or less alternately pinnate arrangement. Each different order of branches of variable lengths, nearly perpendicular to branch of origin, becoming successively more slender and remaining flattened; subultimate and ultimate branchlets often densely matted to each other. Transection showing rhizoidal filaments scattered through medulla of main axes but not observed in terminal or subterminal branchlets.

Reproduction not known.

Habitat. On rocks and tidal platforms and in crevices and tide pools, sometimes growing on crustose coralline algae; mid intertidal to shallow subtidal, down to 4 m depths.

Distribution. Gulf of California: Puerto Calamajué to Bahía San Francisquito; Isla Partida and Isla Rasa (Isla Raza; southwestern Islas de la Cintura); Bahía de Loreto.

Type Locality. Bahía San Francisquito, Baja California, Gulf of California, Mexico.

Remarks. *Gelidium decompositum* is apparently restricted to a rather narrow distribution on the central Baja California coast of the northwestern Gulf of California and two of the Islas de la Cintura (Midriff Islands). Dawson (1953a, 1959a) commented that *Gelidium decompositum* was almost the same as *Pterocladia pyramidale* (N. L. Gardner) E. Y. Dawson (1945e), and later, he suggested that *G. decompositum* might belong in *Pterocladia* (Dawson, 1961b). Reexamination of northern Gulf specimens suggests that there may be two taxa, and for now *Gelidium decompositum* sensu Setchell and Gardner (1924) is tentatively recognized as being separate from northern Gulf *Pterocladiella capillacea.*

However, this needs further study, as Dawson (1959a) noted the tropical-subtropical eastern Pacific specimens identified as "*Pterocladia pyramidale*" from Rocas Alijos, Isla Clarión (Islas Revillagigedo), and the Galápagos Islands may also belong in *G. decompositum*. The generic placement and taxonomic status of *Gelidium decompositum* needs to be confirmed by the finding of cystocarpic specimens and comparative molecular and phylogenetic analyses to elucidate its relationship to *Pterocladia pyramidale* and *Pterocladiella capillacea*.

Gelidium johnstonii Setchell et N. L. Gardner

FIGURE 152

Gelidium johnstonii Setchell et N. L. Gardner, 1924:742, pl. 46: fig. A, pls. 72, 73 [type specimen]; Dawson, 1944a:260; 1953a:73; 1959a:20; 1961b:408; 1966a:16; Norris, 1973:9; Huerta-Múzquiz, 1978:336, 337; Littler and Littler, 1981:151; Stewart and Norris, 1981:274, tbl. 1, 277; Mendoza-González and Mateo-Cid, 1985:28; Santelices and Stewart, 1985:26, fig. 25; Mendoza-González and Mateo-Cid, 1986:422; Mateo-Cid et al., 1993:47; Serviere-Zaragoza et al., 1993b:48; González-González et al., 1996:206; Mateo-Cid et al., 2000:64; L. Aguilar-Rosas et al., 2000:130; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz and Zertuche-González, 2002:467; R. Aguilar-Rosas et al., 2005:32; Mateo-Cid et al., 2006:55.

Algae of several, erect, narrow, distinctly flattened axes, up to 12 cm high, 1.0–1.5 mm wide (more narrow near bases and apices), repeatedly pinnately branched in 1 plane; ultimate branchlets more or less uniform in length; arising from a holdfast of branched stolons. Rhizoidal filaments interlaced in medulla and sometimes in subcortex; usually abundant, but sometimes varying in abundance in young and mature parts of thalli.

Tetrasporangia in sori of various sizes and shapes on ultimate branchlets. Cystocarps, often inconspicuous, borne distally on branch apices. Spermatangia unknown.

Habitat. On rocks, usually in semiprotected, shaded areas and in crevices and tide pools; low intertidal to shallow subtidal, down to 6 m depths.

Distribution. Gulf of California: Puerto Peñasco to Bahía Agua Verde; Puerto Refugio, Isla Ángel de la Guarda; Caleta Partida (in shallow channel between Isla Partida and Isla Espíritu Santo) to Cabo Pulmo. Eastern Pacific: Punta Santa Rosaliita ("Punta Santa Rosalía"), Baja California to Bahía Magdalena, Baja California Sur.

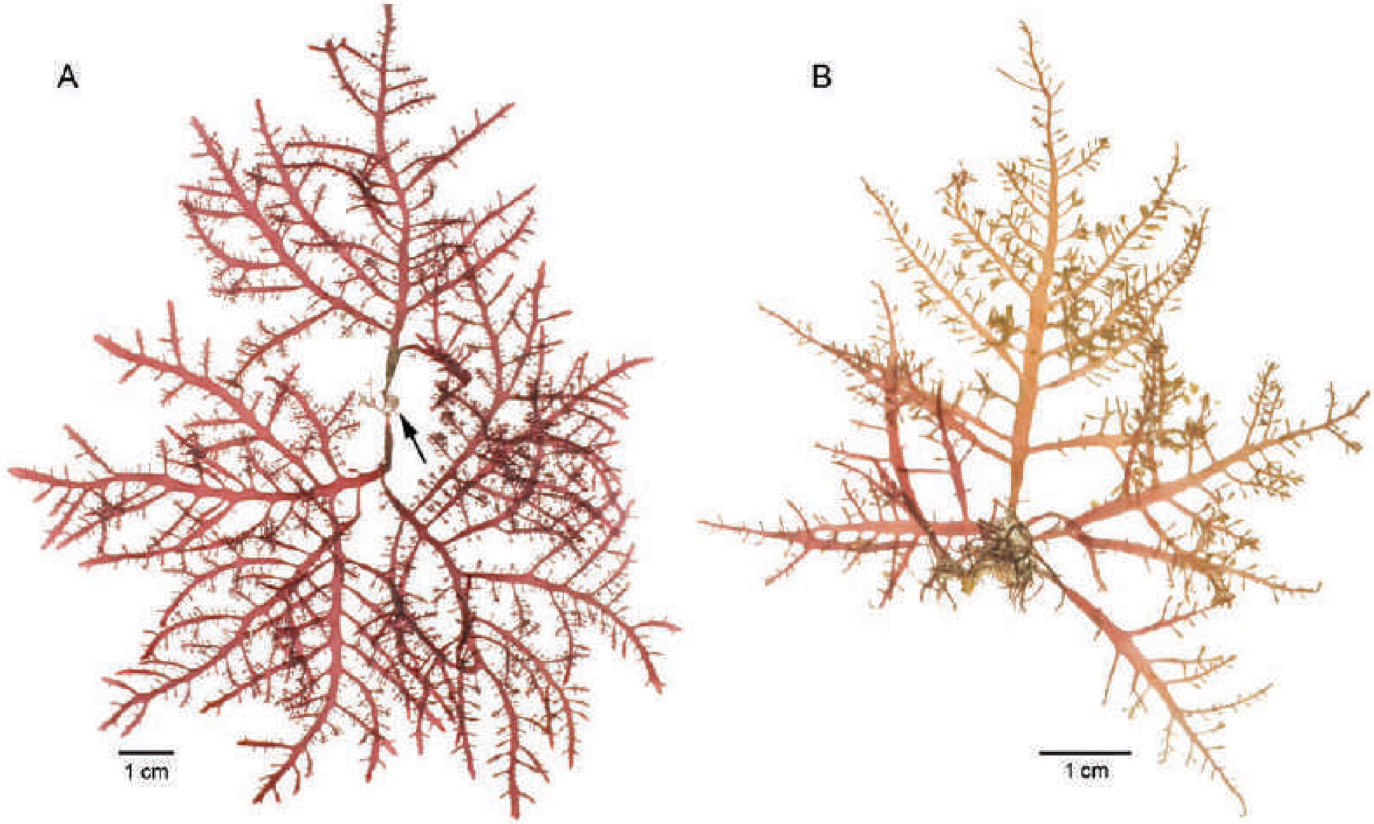

FIGURE 152. *Gelidium johnstonii*: A. Habit of female gametophyte with holdfast (arrow) (*JN-5539*, US Alg. Coll.-159337). B. Habit of tetrasporophyte (*JN-3796*, US Alg. Coll.-159339).

Type Locality. Bahía San Francisquito, Baja California, Gulf of California, Mexico.

Remarks. *Gelidium johnstonii* can be distinguished from other species of Gelidiaceae in the northern Gulf by its larger size, notably flattened axes, more regular pinnate habit, and ultimate branchlets of similar length.

Western Pacific records of *G. johnstonii* need to be verified. For example, Yoshida (1998) referred "*G. johnstonii*" as identified in Japan by Segi (1955) to *G. elegans* Kützing (1868), and H.-B. Lee and Kim (1995) considered "*G. johnstonii*" as reported in Korea (Sohn and Kang, 1978) to be a variant of *G. amansii* (J. V. Lamouroux) J. V. Lamouroux (1813). Reports of "*G. johnstonii*" from Guangdong Province, Hong Kong, and Taiwan (Tseng et al., 1980; Zhang and Xia, 1988) were later recognized to be *G. tsengii* K.-C. Fan (1961) by Xia et al. (2002).

Gelidium mcnabbianum (E. Y. Dawson) Santelices

FIGURES 150A,B, 153A,B

Pterocladia mcnabbiana E. Y. Dawson, 1957c:14, fig. 4C,D; 1961c:409, pl. 2: figs. 5–6; 1966a:16; 1966b:59; Stewart and Norris, 1981:274, tbl. 1; Ramírez and Santelices, 1991:195; González-González et al., 1996:262; Mateo-Cid et al., 2006:51; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:64.

Gelidium mcnabbianum (E. Y. Dawson) Santelices, 1998:245; Santelices, 1999:74; López et al. 2004:11.

Algae of several erect or decumbent, terete to partly flattened, branched axes, up to 2 cm tall, up to 650 µm wide; axes simple or sparingly branched, sometimes branched pinnately; arising from prostrate subcylindrical, much branched attachment stolons, up to 100 µm in diameter. Upper portions of some branches sometimes becoming narrower, elongated, and attenuated (flagellate), sometimes as long subcylindrical extensions (Figure 153A). Internally, rhizoidal filaments scattered through medulla, varying in abundance.

Tetrasporangia in sori on flat, elliptical branches. Cystocarps bilocular, ostiolate, and embedded on branch apices. Spermatangial thalli unknown.

Habitat. in algal mats on rocks, and shells; intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco. Eastern Pacific: Guerrero; El Salvador; Costa Rica; northern Peru.

Type Locality. Small mats on hull of shipwreck; Bahía Golfito, SW of Golfo Dulce, Pacific Costa Rica.

Remarks. Santelices (1998), in studying the type material of *Pterocladia mcnabbiana,* found the internal structure to

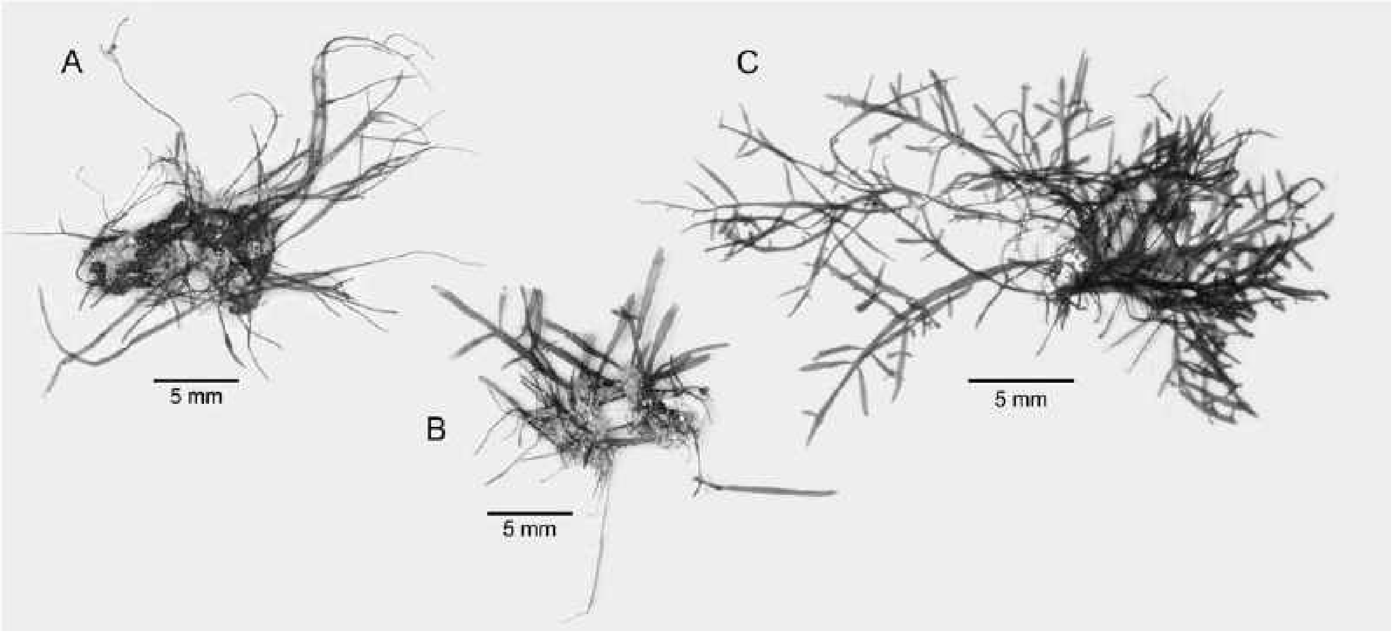

FIGURE 153. Species of *Gelidium*. A, B. *Gelidium mcnabbianum*: Habits (*EYD-27340*, US Alg. Coll.-40743). C. *Gelidium pusillum*: Habit (*JN-3482*, US Alg. Coll.-159272).

be that of the *Gelidium*. Earlier, Dawson (1957c) contrasted the type specimen of *Pterocladia mcnabbiana* with other small species of *Gelidium* and *Pterocladia* and noted it to differ in having a mixture of both terete and flattened erect branches and prominent flagellate terminal extensions on some of the branches. Gulf of California *Geldium mcnabbianum* and the other small species of the *Gelidium–Pterocladia* complex are in need of critical study, after fertile material has been found for each and compared to type locality *G. mcnabbianum*.

Gelidium microphysa Setchell et N. L. Gardner

FIGURE 150C

Gelidium microphysa Setchell et N. L. Gardner, 1930:151, pl. 9: fig. 31; Dawson, 1944a:260; 1953a:61; 1961b:409; 1966a:16; González-González et al., 1996:206; Mateo-Cid et al., 2006:50.

Algae erect, forming short, spreading mats, 0.6–1.5 cm tall; axes irregularly pinnately or flabellately branched, compressed to flattened throughout; short branches, 600–900(–1200) µm wide; branch apices usually rounded, with an apical cell within a slight to notable notch; uprights arising from creeping, prostrate axes attached below by short, peg-like holdfasts. Transection, a broad medulla, abundant internal rhizoidal filaments more or less evenly distributed in medulla and subcortex; cortex of small spherical cells, outer cortical cells very small, 3–5 µm in diameter.

Tetrasporophytes unknown. Cystocarps 350–550 µm in diameter; usually 1, sometimes 2, on branchlets of compound, generally narrower, fertile branches. Spermatangia unknown.

HABITAT. On rocks and tidal platforms or along upper edges of tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco; Isla Patos (off N end of Isla Tiburón); Isla Turner (off SE end of Isla Tiburón); Isla Partida; Bahía de Los Ángeles. Eastern Pacific: Isla Guadalupe; Isla Cedros (both off Baja California).

TYPE LOCALITY. Growing on rocks; Bahía Sur (South Bay), Isla Guadalupe, off Baja California, Pacific Mexico.

REMARKS. *Gelidium microphysa* is a not well known in the northern Gulf. The only cystocarp specimen is from Isla Partida. More collections, particularly from the Pacific Mexico type locality, Isla Guadalupe, are needed for morphological and molecular comparisons with the northern Gulf specimens referred to *G. microphysa*. Dawson (1953a) also noted several tubercular nodules on Isla Partida *G. microphysa* that might be parasitic red algae, but none were reproductive and their identity remains undetermined.

Gelidium pusillum (Stackhouse) Le Jolis

FIGURES 153C, 154

Fucus pusillus Stackhouse, 1795:16, pl. 6.

Gelidium pusillum (Stackhouse) Le Jolis, 1863b:139; Okamura, 1909:11, pl. 54: figs. 10–14; 1934b:38, pl. 17: figs. 1, 2, pl. 31: figs. 1, 2; Dawson, 1944a:258, pl. 42: figs. 1–6; Taylor, 1945:152; Dawson, 1953a:62; 1959a:20; 1961c:408, pl. 10: figs. 1–2, 5; 1966a:16; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Norris, 1973:9; Chávez-Barrear, 1972b:268; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Stewart, 1976:347, fig. 290; Huerta-Múzquiz, 1978:338; Stewart and Norris, 1981:274, tbl. 1, 275; Littler and Littler, 1981:148, 150–151; Littler and Arnold, 1982:309; Schnetter and Bula-Meyer, 1982:116, pl. 13: figs. A–E, H, I, pl. 14: figs. A–D; Pacheco-Ruíz and Aguilar-Rosas, 1984:71,

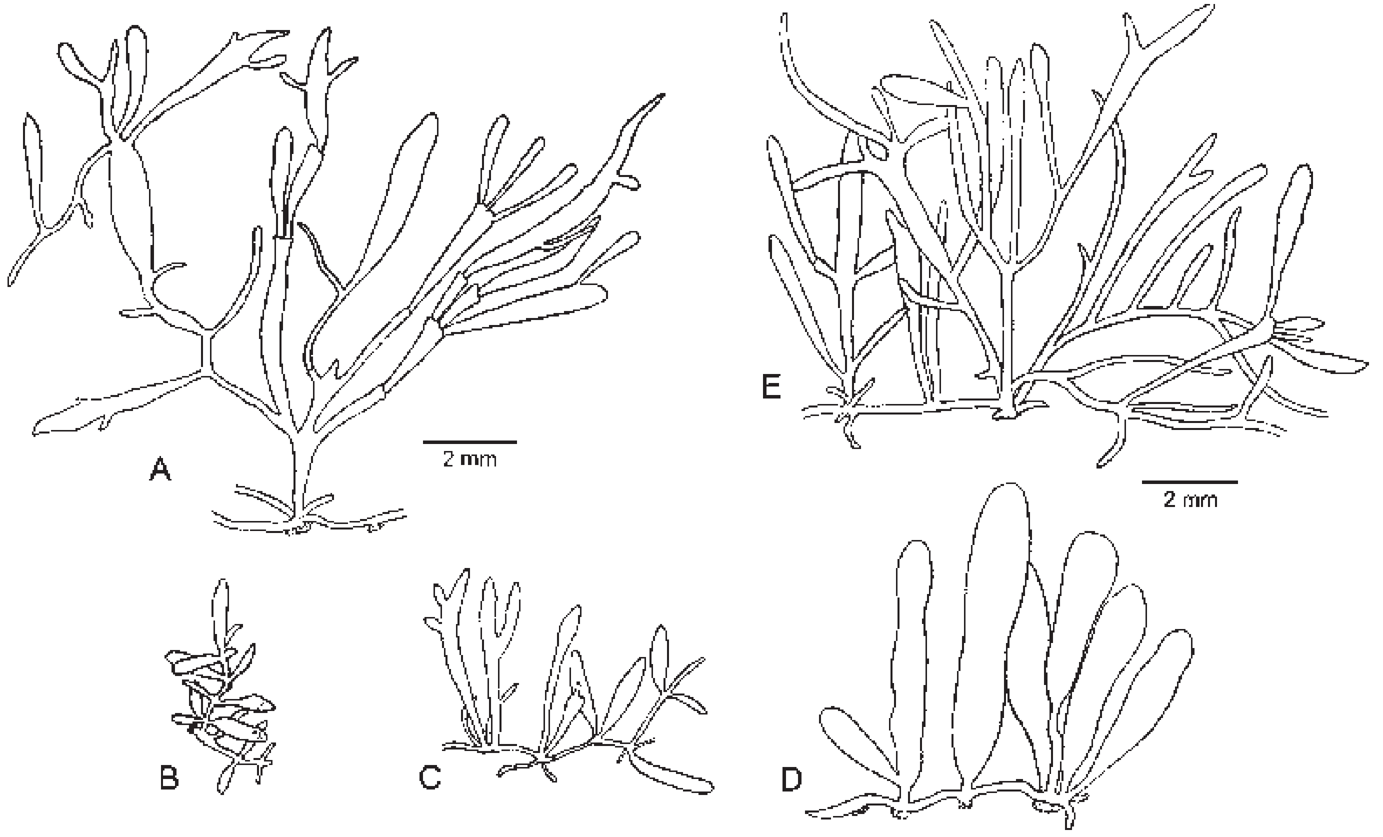

FIGURE 154. Morphological variation in habits of *Gelidium pusillum* throughout its range: A, C. Habits (from Pacific Costa Rica). B. Depauperate form. D. Broad blade form (B, D, from Isla Clarión, Islas Revillagigedo; after Dawson, 1953a). E. Habit (from the Gulf of California) (A–E, after Dawson, 1944a: pl. 42: figs. 1–5).

76; Stewart and Stewart, 1984:142; Santelices and Stewart, 1985:22, fig. 9; Huerta-Múzquiz and Mendoza-González, 1985:48; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:422; Santelices, 1988:102, fig. 9; Dreckmann et al., 1990:27, pl. 4: fig. 5; Ramírez and Santelices, 1991:192; Stewart, 1991:70; Mateo-Cid and Mendoza-González, 1992:19; Mendoza-González and Mateo-Cid, 1992:16; Rodríguez-Vargas et al., 1993:447; León-Tejera et al., 1993:200; Serviere-Zaragoza et al., 1993a:483; Serviere-Zaragoza et al., 1993b:48; Mateo-Cid et al., 1993:47; Mateo-Cid and Mendoza-González, 1994b:38; R. Aguilar-Rosas and Aguilar-Rosas, 1994:520; Mendoza-González et al., 1994:105; Womersley and Guiry, 1994:133, figs. 35E, 39E–K; González-González et al., 1996:312; Athanasiadis, 1996b:85; Abbott, 1999:194: fig. 50A; Yoshida, 1998:637; León-Tejera and González-González, 2000:327; Mateo-Cid et al., 2000:64; CONANP, 2002:139; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:50, 55; Perrone et al., 2006:24, 28, figs. 4, 38; Serviere-Zaragoza et al., 2007:10; Santelices, 2007:294, tbl. 1; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:62.

Gelidium crinale var. *crinale* sensu Dawson, 1944a:259; 1953a:64 [non *Gelidium crinale* (Hare ex Turner) Gaillon, 1828:362].

Algae clumps or spreading turfs, 0.3–1.0(–2.0) cm tall; arising from peg-like or disc-like structures (brush-like haptera). Axes and branches compressed to flattened; main axes (0.5–)1.0–1.5(–2.0) mm wide, 100–300 μm thick; axes may be terete below but flattened above. Branching generally distichous, along margins and mostly irregular; branches flat, lanceolate to spatulate, usually with blunt apices. Rhizoidal filaments few to abundant, scattered or congested. Medullary cells up to 10 μm in diameter; rhizoidal filaments abundant in inner medulla. Cortex of 2–3 layers of small cortical cells, mostly 4–6 μm in diameter.

Reproductive structures on ovoid to rounded branchlets. Tetrasporangial sori generally oval, central on apical portions of branchlets, bordered by sterile margin; tetraspores ovoid, 25–35 μm in diameter. Bilocular cystocarps round to ovoid, mostly 600 μm in diameter, 500 μm thick. Spermatangia not seen in Gulf specimens.

Habitat. Often common on rocks and mollusk shells; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Cabo Pulmo; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: San Clemente Island (California Channel

Islands) to Playa Los Cerritos (vicinity of Todos Santos), Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Colima to Oaxaca; El Salvador; Costa Rica; Panama; Colombia to Chile; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: China; Taiwan; Japan; Korea; Vietnam.

TYPE LOCALITY. Sidmouth, Devon, England, United Kingdom (Dixon and Irvine, 1977a).

Gelidium refugiensis (E. Y. Dawson) Santelices

FIGURE 150D,E

Gelidiella? refugiensis E. Y. Dawson, 1944a:262 [with a generic query], pl. 43: figs. 4–6; 1953a:84; 1961b:410; Stewart and Norris, 1981:274, tbl. 1; González-González et al., 1996:204; Santelices, 2007:295, tbls. 2, 3.

Gelidium refugiensis (E. Y. Dawson) Santelices, 2007:298, figs. 11–13.

Algae of small, subcylindrical to compressed erect axes, up to 1.5 cm tall, 150–250(–300) μm in diameter, loosely, subdichotomously to irregularly branched, mostly in 1 plane; apices rounded or sometimes acute; basal portion not completely known, probably attached by small, brush-like haptera. Medulla of 3–4 rows of medullary cells; internal rhizoidal filaments more frequent in medulla than in cortex and in lower portions of erect axes than in upper portions. Cortex of 3–4 layers of small, pigmented cortical cells.

Reproduction by large undivided spores (monospores), 20–40(–50) μm in diameter; borne in terminal branchlets; monospores leave openings in cortex after being discharged. Cystocarpic and spermatangial thalli unknown.

HABITAT. Unknown; type and only specimens collected to date are from drift.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Bahía San Carlos.

TYPE LOCALITY. In beach drift on north shore; Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

REMARKS. This taxon was originally placed in *Gelidiella* by Dawson (1944a) with a generic query. Its generic status remained uncertain until it was clarified by Santelices (2007) and recognized as *Gelidium refugiensis*.

Gelidium sclerophyllum W. R. Taylor

Gelidium sclerophyllum W. R. Taylor, 1945:156, pl. 5: fig. 13, pl. 33: fig. 2; Dawson, 1953a:63; 1957c:14; 1961b:409; 1961c:409, pl. 10: fig.7; 1962c:229; Dreckmann et al., 1990:27; Mateo-Cid et al., 1993:47; Rodríguez-Vargas et al., 1993:447; Serviere-Zaragoza et al., 1993b:48; González-González et al., 1996:208; Mateo-Cid et al., 2000:64; Tejada, 2003:11; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:62.

Algae of small, more or less dense tufts, up to 2.0 cm tall; of numerous erect, flattened fronds arising from creeping, prostrate branched axes attached to substratum by peg-like haptera. Erect axes terete to compressed at base; ligulate above, up to 1 mm wide; branching sparse to irregularly pinnate, with 1 to several lateral branchlets. Branchlets constricted at base; apices of fertile branchlets usually deeply indented. Medulla dense with thick-walled cells, surrounded by closely packed rhizoidal cells, which become scattered in the subcortex.

Tetrasporangial sori depressed in central region of lateral and terminal branchlets, with thicker sterile margins. Cystocarps 400–500 μm in diameter; borne near ends of lateral and terminal branchlets. Spermatangia not known.

HABITAT. Growing on crustose corallines, barnacles, and attached mollusks; intertidal.

DISTRIBUTION. Gulf of California: Isla Pelícanos, Bahía Kino; Bahía Concepción to Cabeza Ballena; Mazatlan, Sinaloa to Jalisco. Eastern Pacific: Isla Clarión (Islas Revillagigedo); Baja California Sur; Colima to Oaxaca; El Salvador; Nicaragua; Costa Rica; Ecuador.

TYPE LOCALITY. Dredged from 5.4 m depth; near northeast side of Ensenada de San Francisco, Provincia de Esmeraldas, northern Ecuador.

REMARKS. The small, flat *Gelidium sclerophyllum* is distinguished by its branchlets constricted at their base, dense medulla of thick-walled cells and tetrasporangial sori with thicker, sterile margins, on tetrasporangial branchlets with indented tips.

Uncertain Record:
Gelidium coulteri Harvey

Gelidium coulteri Harvey, 1853:117; Smith, 1944:196, pl. 44: fig. 5; Dawson, 1953a:70; Stewart, 1976:344, fig. 287; Rodríguez-Vargas and Santelices, 1988:115, tbls. 1, 2, figs. 3, 5; Stewart, 1991:69; Serviere-Zaragoza et al., 1993b:48; González-González et al., 1996:205.

REMARKS. Recorded from Segundo Cerro Prieto, Bahía Kino, by Mendoza-González and Mateo-Cid (1986); further collections will be helpful to verify its presence in the northern Gulf of California.

GELIDIELLACEAE

Gelidiellaceae K.-C. Fan, 1961:317; Norris, 1992b:159; Perrone et al., 2006:31 [emended description].

Algae are composed of erect and prostrate axes. Uprights are terete to flattened and sparsely, irregularly or pinnately branched. In some the main stolon represents the main axis. Growth is uniaxial, with the apical cell dividing distichously or decussately. Internally, the thallus anatomy is completely without the thick-walled, refractive, unicellular rhizoidal filaments (rhizines or hyphae) that are characteristic of the Gelidiaceae and Pterocladiaceae. The creeping, prostrate axes are attached to the substratum only by single-celled, thick-walled, refractive rhizoidal filaments produced from the surface cells of the prostrate axes that remain in open connection with their parent cortical cells.

Life histories are not fully understood. Tetrasporangial and spermatangial thalli are isomorphic, but cystocarpic thalli remain unknown. Tetrasporangia are tetrahedrally or decussately divided and are arranged irregularly in transverse parallel rows or in chevron-like rows, within tetrasporangial sori in conical or compressed apical regions of main axes and lateral branches.

Female reproductive system is unknown. Spermatangia develop in raised spermatangial sori or form colorless patches in upper portions of the main axes and/or lateral branchlets.

Remarks. Currently there are two genera in the Gelidiellaceae. One of these, *Parviphycus* Santelices (2004) is known from Isla San Benedicto (Islas Revillagigedo) with the report of *P. adnata* (E. Y. Dawson) Santelices, 2004; Serviere-Zaragoza et al., 2007; basionym: *Gelidiella adnata* E. Y. Dawson, 1954b; Dawson, 1954a; Schnetter and Bula-Meyer, 1982; Santelices, 2002).

In the northern Gulf of California the Gelidiellaceae is represented by *Gelidiella*.

Gelidiella J. Feldmann et G. Hamel

Gelidiella J. Feldmann et G. Hamel, 1934:529, *nom. nov*.

Echinocaulon Kützing, 1843:405 [non *Echinocaulon* (Meisner) Spach, 1841:521; basionym: *Polygonum* sect. *Echinocaulon* Meisner, 1832:58].

Algae composed of a few to several entangled, terete to slightly compressed, erect to decumbent branched axes, mostly up to 5 cm tall, with creeping, prostrate axes. Uprights are sparsely to abundantly, irregular branched and arise from very similar prostrate axes that attach to the substratum by single-cell rhizoids. Branches sometimes gradually tapered toward the apices and may be with sparse, filiform, distichously arranged, opposite or subopposite laterals. A single apical cell is evident at the branch apices. The cortex and medulla are similar in most respects to the other gelidiaceous algae, but differ in the notable lack of internal rhizoidal filaments (hyphae, rhizines), which are not found in any part of the thallus. In surface view the outer cortical cells may or may not be arranged in longitudinal rows. In transection the outer cortical cells are generally anticlinally elongated, gradually increasing in size inward. Medulla is composed of larger, colorless cells.

Tetrasporangial sori are in upper portion of lateral branchlets, usually swollen conical shape. Tetrasporangia are irregularly or regularly arranged in the sori, oblong, and tetrahedrally or irregularly cruciately divided. Those in lower portion of the sori are usually in a more advanced stage of development than those near the apex. Carposporophytes are unknown in the genus. Spermatangial sori are slightly elevated, 75–150 μm in diameter, with a raised, thick cuticle. Spermatia, 7–10 μm by 5–7 μm, are cut off by transverse divisions of spermatangial parent cells in rows of up to 5 (spermatangia description after Santelices and Flores, 2004; based on *G. acerosa* from Haiti).

Gelidiella is represented by two species in the Gulf of California.

KEY TO THE SPECIES OF *GELIDIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli up to 5.0 cm tall; branches cylindrical to compressed, up to 1.0 mm in diameter . . . . *G. acerosa*
1b. Thalli shorter, mostly 1.0–1.5 cm tall; branches cylindrical throughout, much narrower, 100–120 μm in diameter . . . . *G. hancockii*

Gelidiella acerosa (Forsskål) Feldmann et G. Hamel

Fucus acerosus Forsskål, 1775:190.

Gelidiella acerosa (Forsskål) Feldmann et G. Hamel, 1934:533; Dawson, 1944a:261; 1953a:82; 1961b:410; Huerta-Múzquiz and Garza-Barrientos, 1975:8, 11; Santelices, 1977:63, fig. 1A–C; Huerta-Múzquiz and Mendoza-González, 1985:48; Santelices and Stewart, 1985:21, fig. 6; Lewis and Norris, 1987:17; Santelices, 1988:93, figs. 1; Mateo-Cid and Mendoza-González, 1991:20; Ramírez and Santelices, 1991:188; Norris, 1992b:154, figs. 4, 5; Melo, 1992:173, figs. 1–8; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:312, 391; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Santelices, 1997:77, figs. 1–14; Abbott, 1999:202, figs. 53A–C; Mateo-Cid et al., 2000:64; Cruz-Ayala et al., 2001:191; Santelices and Flores, 2004:109, figs. 1–11; Serviere-Zaragoza et al., 2007:10; Lin and Freshwater, 2008:172, figs. 13–19; Fernández-García et al., 2011:61.

Echinocaulon acerosum (Forsskål) Børgesen, 1932b:5, pl. 1; fig. 3 [type illustration of *Fucus acerosus* Forsskål, 1775].

Algae in tufts or clumps of usually entangled, narrow, cylindrical to slightly compressed, determinate erect or semierect to arching axes, up to 5 cm tall, mostly (550–)600–800 μm in diameter, with 1–2 orders of pinnate branchlets; uprights arising from creeping, prostrate, indeterminate stoloniferous axes, 500–600 μm in diameter. Growth from a single apical cell. Medulla of large longitudinally elongated colorless cells, about 25–35 μm in diameter; grading into rounded, inner cortical cells. Outer cortex of 3–4 layers of small, ovoid to slightly elongated, pigmented cells, up to 7–8 μm long, (4–)5–7 μm in diameter. Rhizoidal filaments (rhizines) absent.

Tetrasporangia tetrahedrally or sometimes more or less cruciately divided, 40–50 μm long, 20–30 μm in diameter; developed from inner cortical cells; in 1–3 sori, each about 1 mm long and to 500 μm wide near distal end of lateral, comparatively swollen, branchlets. Gametangial thalli not known in Gulf of California.

Habitat. On rocks or crustose corallines and in tide pools, sometimes in or around sand and pebbles; intertidal to about 1 m depths.

Distribution. Gulf of California: El Coloradito to Santa Teresa; Bahía Gabriel, Isla Espíritu Santo, and Bahía de La Paz to Cabeza Ballena; Nayarit to Jalisco. Eastern Pacific: Isla Guadalupe; Baja California; Colima to Guerreo; Isla Socorro and Isla Clarión (Islas Revillagigedo); Central America; Chile. Central Pacific: Hawaiian Islands; Guam. Western Pacific: China; Taiwan; Japan; Vietnam.

Type Locality. “Ad Mochhae littoral” (Forsskål, 1775:190); Al Mukha, Red Sea, Yemen.

Remarks. *Gelidiella acerosa* has generally been accepted as being a geographically widespread species throughout tropical to warm temperate seas. In China *G.acerosa* is an economically important seaweed that is harvested in Hainan Province, notably on Hainan Island and the Xisha (Paracel) Islands (Tseng, 1983).

Santelices and Flores (2004), finding differences between specimens of "*G. acerosa*" from the Caribbean and Pacific, suggested they may be two separate taxa. In another study, molecular sequences of specimens identified as "*G. acerosa*" from the Caribbean, southeastern Australia, and the Indo-Pacific were found to be separate species from each other, and one from Taiwan was described as a new, *Gelidiella fanii* S.-M. Lin (in Lin and Freshwater, 2008). Future morphological and molecular comparisons will elucidate the taxonomic status of Gulf of California specimens referred to *G. acerosa* and their relationship to those of other geographical areas, particularly those of the type locality in the Red Sea, Yemen.

Gelidiella hancockii E. Y. Dawson

FIGURE 155A

Gelidiella hancockii E. Y. Dawson, 1944a:261, pl. 43: figs. 1, 2; 1953a:83, pl. 12: figs. 6–7; 1959a:20; 1960a:37; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Stewart and Norris, 1981:274, tbl. 1; Huerta-Múzquiz and Mendoza-González, 1985:48; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:422; Ortega et al., 1987:71, pl. 2: figs. 9–12; León-Tejera et al., 1993:200; González-González et al., 1996:203; Silva et al., 1996b:232; L. Aguilar-Rosas et al., 2000:130; Santelices, 2007:298, tbls. 2, 3; Bernecker, 2009:CD-Rom p. 60; Fernández-García et al., 2011:61.

Gelidiella mexicana E. Y. Dawson, 1944a:262 [in part; excluding Guaymas specimens], pl. 43: fig. 3; Santelices, 2007:295, tbl. 2.

Algae of densely entangled tufts, up to 2 cm high; erect axes cylindrical throughout, 120–200 μm in diameter, irregularly branched; arising from prostrate, mostly unbranched axes (only occasionally secondarily branched) attached by unicellular rhizoids to substratum; apices acute, not attenuated. Internally of compacted colorless medullary cells and pigmented cortical cells of similar diameter; lacking internal rhizoidal filaments.

Tetrasporangia borne in short branchlets or on branch apices. Cystocarpic and spermatangial thalli unknown.

HABITAT. On rocks, sometimes entangled among other turf algae; intertidal.

DISTRIBUTION. Gulf of California: El Coloradito to Bahía San Luis Gonzága; Puerto Refugio, Isla Ángel de la Guarda, Isla Tiburón, and Isla Estanque (Isla Pond) (Islas de la Cintura); Bahía Kino; Laguna Agiabampo; La Paz; Nayarit. Eastern Pacific: Isla Margarita, Bahía Magdalena, Baja California Sur; Rocas Alijos; Golfo de Tehuantepec, Oaxaca; Costa Rica; Panama.

TYPE LOCALITY. On mid intertidal rocks; rocky point, about 4.8 km (3 miles) north of Bahía Kino, Sonora, Gulf of California, Mexico.

REMARKS. *Gelidiella hancockii* and another small species, *G. mexicana,* were both described by Dawson (1944a) from the northern Gulf. *Gelidiella mexicana* (type locality: Isla Estanque, off the southeast end of Isla Ángela de la Guarda) was later considered to be conspecific with *G. hancockii* (Dawson, 1953a). Santelices (2007) studied the types of each species and found them to lack internal rhizoids and to be attached by externally produced, single-celled rhizoids, characters that supported their placement in *Gelidiella*.

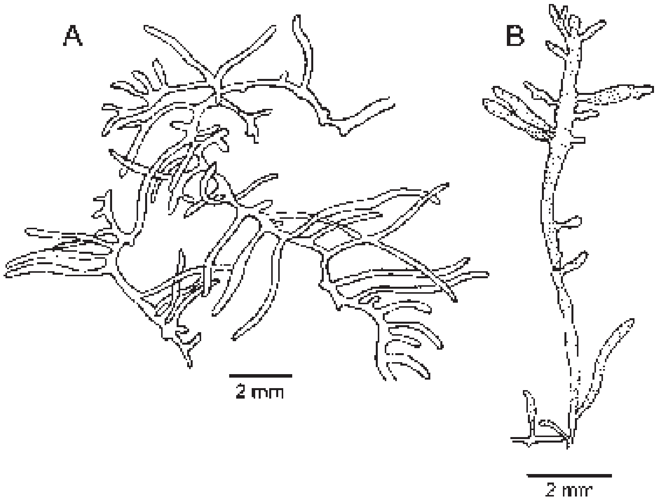

FIGURE 155. Species of *Gelidiella* and *Pterocladiella*. A. *Gelidiella hancockii*: Habit (after Dawson, 1944a: pl. 43: fig. 1). B. *Pterocladiella caloglossoides*: A small, suberect branch from the type collection (after Dawson, 1953a: pl. 6: fig. 2, as *Pterocladia parva*).

PTEROCLADIACEAE

Pterocladiaceae Felicini et Perrone in Perrone, Felicini, et Bottalico, 2006:31.

Algae consisting of narrow, compressed to flattened, erect uprights that are sparsely to pinnately branched and always develop opposite the attachment haptera of the lower prostrate, terete to compressed stolon-like axes. The prostrate system is composed of irregularly branched, prostrate axes that bear complex, peg-like haptera that either adhere directly to the substratum or penetrate it, producing a circular hole. These attachment structures consist of two kinds of filaments: thick-walled, refractive, unicellular, colorless rhizoidal filaments that originate from inner cortical cells and grow through the thallus, protruding between the surface cells and coalescing in a thick sheath, and pigmented, multicellular, uniseriate filaments that develop from the surface cells and form a basal cortication around the hapteron base. Growth is uniaxial. Internally, thick-walled, refractive, unicellular rhizoidal filaments (rhizines or hyphae) develop from the inner cortical cells and grow basipetally through the thallus; these vary in abundance and distribution within the medulla and cortex and may be numerous or sometimes not present.

Life histories, where known, are triphasic, of isomorphic tetrasporophytes and gametophytes. Tetrasporangia are in apical sori, arranged irregularly or in rows meeting at an angle (chevron-like). Gametangial thalli may be dioecious or monoecious. Cystocarps are unilocular, usually with 1 ostiole, and protrude on either or both sides of reproductive branches. Spermatangia are in sori on the branch surfaces.

Two genera of Pterocladiaceae are known in the northern Gulf of California.

KEY TO THE GENERA OF PTEROCLADIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Unilocular cystocarps with 1 ostiole; placental tissue only on floor of cystocarp cavity . . . . ***Pterocladia***
1b. Unilocular cystocarps usually with 1 ostiole (rarely with 2); placental tissue surrounding central axis . . . . . ***Pterocladiella***

Pterocladia J. Agardh

Pterocladia J. Agardh, 1852a:482.

Algae are tufts or clumps or may occur in mats of algal turf, 2.0–40 cm tall, and composed of one to several cartilaginous, terete or compressed, erect narrow axes that are mostly irregularly branched. The upright axes are cylindrical at their base and become subcylindrical to compressed above and arise from cylindrical or compressed, branched or unbranched, creeping, prostrate axes that attach to the substratum by numerous short peg-like haptera. In surface view the cortical cells may or may not be arranged in longitudinal series. In transection, the cortex is often of several rows of pigmented cells, mostly 2.0–15 µm in diameter, the smaller usually toward the outside. Medullary cells are generally rounded, up to 30 µm in diameter, colorless, compacted or loosely appressed. Rhizoidal filaments (also called rhizines or hyphae) among the medullary and/or cortical tissue are elongated, thick-walled, colorless cells, up to 5 µm in diameter, and often vary in number and position within a given species.

The tetraspores in the sori occupy the entire, somewhat expanded or broadly rounded tips of lateral branches or main axes. Sporophylls can be single or pinnately compound. Tetrasporangia are cruciately divided, up to 35 µm in diameter, and are generally arranged without order in the sori, although a few species may exhibit tetrasporangia borne in regular V-shaped rows. The mature cystocarps are unilocular, protruding on only one of the surfaces of the branches, usually with one or more openings on only one surface of the frond. Carposporangia are usually formed in short chains. Spermatangial sori are sometimes apparent as relatively unpigmented areas on the apices of branchlets.

REMARKS. *Pterocladia* species can often be similar to species of *Gelidium* and *Pterocladiella,* both in morphology and anatomy (see discussion of *Gelidium*). The axes of *Pterocladia* are generally flattened in both erect and prostrate parts, rather than being partly terete or compressed, and thalli are often not as rigid as most *Gelidium* specimens. Rhizoidal filaments in some species of *Pterocladia* tend to be more central in the medulla, but this in itself does not separate species of the genera.

The position of the reproductive structures is also the same in these genera. Tetrasporangia are borne in sori on ultimate branches. The unilocular cystocarps are the only positive diagnostic character for *Pterocladia* species. These bulge prominently on one side of the upper branches. Spermatangia are superficial in sori near branch apices. The only positive way to separate *Pterocladia, Pterocladiella,* and *Gelidium* is by examining the attachment structures of carpogonial thalli. The cystocarps are unilocular, protruding and opening on only one side of the branch in *Pterocladia*, and bilocular, protruding and opening on both sides of the branch in *Gelidium*.

There are two species of *Pterocladia* in the Gulf of California.

KEY TO THE SPECIES OF *PTEROCLADIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli mostly up to 2 cm tall, branching sparse; flat axes 150–300 µm wide, and thin, 100–200 µm thick . . . . ***P. media***
1b. Thalli up to 6 cm tall, branching widely irregular; flat axes broader, 900–1100 µm wide, and usually thicker, 180–230 µm thick . . . . ***P. sonorense***

Pterocladia media E. Y. Dawson

Pterocladia media E. Y. Dawson, 1958:68, pl. 21: figs. 3, 4, pl. 24: fig. 11; 1961b:410; Stewart, 1974b:105, fig. 1; 1976:351, fig. 294; Stewart and Norris, 1981:277; Pacheco-Ruíz and Aguilar-Rosas, 1984:76; Ramírez and Santelices, 1991:195; Stewart, 1991:73; 1992:184, fig. 5; Mendoza-González and Mateo-Cid, 1992:16; Rodríguez-Vargas et al., 1993:448; Serviere-Zaragoza et al., 1993a:483; Serviere-Zaragoza et al., 1993b:45; González-González et al., 1996:262, 407.

Gelidium crinale f. *luxurians* F. S. Collins in Collins, Holden and Setchell, 1903: Exsiccate No. 1138; Collins, 1906a:111.

Gelidium crinale var. *luxurians* (F. S. Collins) N. L. Gardner, 1927b:277, pl. 46: fig. 1, pl. 47: fig. 3; Dawson, 1953a:65, pl. 4: figs. 4, 5; 1961b:408; Dawson et al., 1964:39, pl. 31: fig. C; Dawson, 1966a:16; 1966b:59; González-González et al., 1996:205; Mateo-Cid et al., 2006:50.

Algae forming tufts, mostly up to 2(–5) cm tall, of sparsely, irregularly branched (more or less distichous) axes; branching in upper portions sometimes may be secund or alternate or more or less pinnate; axes and branches compressed, narrow, 150–300 µm wide, and thin, 100–200 µm thick; above a basal system of prostrate branches, attached by short, peg-like rhizoids to substratum. Medulla of irregularly shaped cells; rhizoidal filaments scarce or in some few to numerous, mostly to entirely in central inner medulla, and either lacking or occasionally occurring in outer medulla. Outer cortex of rows of small pigmented cortical cells; inner cortex of rows of cells similar in size or up to 2 times larger than outer cortical cells.

Tetrasporangia within sori on upper branchlets (arranged in rows in young sori and apices). Cystocarps unilocular, usually with a single ostiole; protruding on one surface of upper branches.

HABITAT. On rocks, exposed or sometimes partially buried in sand, in crevices, and on edges of tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Playa Arenosa (Norse Beach), Puerto Peñasco; Nayarit to Jalisco. Eastern Pacific: Oregon; San Francisco, California, to northern Baja California; Peru.

TYPE LOCALITY. "Rocky beach just north of Wind and Sea ('Windansea' surfing beach), La Jolla" (Stewart, 1991:73), San Diego County, southern California, USA.

REMARKS. In the northern Gulf, *Pterocladia media* can be similar in size and habit to some *Gelidium pusillum.* Thalli of *P. media* are soft and lax, with more slender axes and irregular branching; in contrast, those of *G. pusillum* are cartilaginous and stiff, slightly wider, with branching that tends to be more or less pinnate. Santelices (1999) has noted that *Pterocladia media* may actually belong to *Pterocladiella,* and its generic placement needs to be tested.

Pterocladia sonorense (E. Y. Dawson) J. S. Stewart et J. N. Norris, *comb nov.*

FIGURE 156

Gelidium? *sonorense* E. Y. Dawson, 1953a:75 [with taxonomic query of genus], pl. 5: fig. 5, pl. 21: fig. 2 [type specimen]; 1961b:409; Stewart and Norris, 1981:274, tbl. 1; González-González et al., 1996:208, 393.

Prionitis delicatula sensu Dawson, 1966a:20 [in part]; 1966b:59 [non *Prionitis delicatula* (W. R. Taylor) E. Y. Dawson, 1961a:424].

Pterocladia capillacea sensu Stewart and Norris, 1981:279 [in part; Puerto Peñasco specimens only, figs. 2, 3; non *Pterocladia capillacea* (S. G. Gmelin) Bornet in Bornet et Thuret, 1876:57, which is now *Pterocladiella capillacea* (S. G. Gmelin) Santelices et Hommersand, 1997:118].

Algae forming loose clumps, up to 8 cm tall; composed of few to several semierect or spreading narrow, ligulate, stipitate, flat fronds, 900–1100(–1500) µm wide, 180–230 µm thick, that develop above a few short, stoloniferous basal branches attached to hard substratum by several small discs or pegs. Primary axes openly irregularly to pinnately branched at often wide, irregular intervals; branching up to 3 orders; branches very variable in length, thus showing no regular branching pattern; branches almost always about same width, tapering toward their base, with blunt apices. Transection of axes and branches sowing abundance of rhizoidal filaments throughout medulla and subcortex.

Tetrasporangia in narrow, elongated sori bordered by sterile margins, on middle portions of ultimate and subultimate branches. Cystocarpic and spermatangial thalli not known.

HABITAT. On rocks, tidal platforms, and edges of tide pools; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas.

TYPE LOCALITY. Puerto San Carlos, west side of Ensenada de San Francisco (northeast of Guaymas), Sonora, Gulf of California, Mexico.

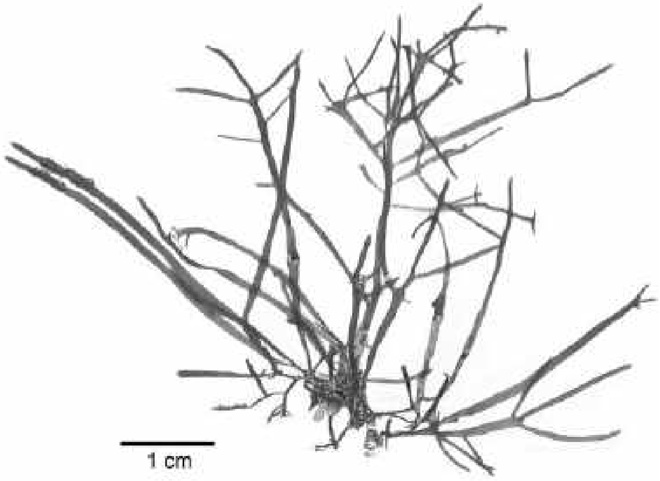

FIGURE 156. *Pterocladia sonorense*: Habit (*EYD-27304*, US Alg. Coll.-40860).

REMARKS. *Pterocladia sonorense* differs from other Gulf of California Gelidiales in having branches of each order that are nearly uniform in width but have irregular and variable lengths, an abundance of rhizoidal filaments (rhizines) in the medulla and subcortex, and narrow, elongated tetrasporangial sori. We tentatively place this species in *Pterocladia* but recognize that it may be a *Pterocladiella*. Once cystocarps are found and elucidated, its taxonomic status and generic placement and relationship to *Pterocladiella capillacea* need to be tested by molecular analyses.

Pterocladiella Santelices et Hommersand

Pterocladiella Santelices et Hommersand, 1997:117.

Algae are usually in clumps of erect, compressed to flattened axes that are sparsely to more regularly branched, usually in one plane. The branching is regularly to irregular pinnate. Branched axes arise from compressed prostrate axes that are attached to the substratum by peg-like haptera. The single apical cell is prominent in some of the species but not always distinct in others. The medulla is densely packed with moderately sized medullary cells that outward become smaller in diameter and grade into cortex. Cortex is of 2–3 layers of small, pigmented cortical cells. Rhizoidal filaments (rhizines) are variable in abundance but usually more numerous in the medulla than in the inner cortex.

Tetrasporangial sori are variable in size but generally elongated on the upper branches and ultimate branchlets; tetrasporangia about 25 µm in diameter. Gametangial thalli not seen in Gulf material. Cystocarps elsewhere reported: 500–600(–1200) µm in diameter, usually with single ostiole, occasionally with 2 ostioles; borne single or sometimes more than 1, near base of ultimate branchlets and upper branches. Spermatangia in elongated sori; on either sides of ultimate branchlets or upper branches.

There are two species in the northern Gulf of California.

KEY TO THE SPECIES OF *PTEROCLADIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli mostly less than 1 cm tall; main axes slender, 45–570(–750) μm wide, and thin, usually 60–120 μm thick . . . . *P. caloglossoides*

1b. Thalli mostly greater than 2 cm high; main axes mostly 1.2–2.0 mm wide, and thicker, 160–370 μm thick . . . . *P. capillacea*

Pterocladiella caloglossoides (M. Howe) Santelices

FIGURE 155B

Gelidium caloglossoides M. Howe, 1914:96, pl. 34: fig. 7, pl. 35: figs. 1–12; Hollenberg, 1942a:534; Smith, 1944: pl. 44: figs. 3, 4.

Pterocladiella caloglossoides (M. Howe) Santelices, 1998:244; Santelices, 1999:72; Abbott, 1999:198, fig. 52A,B; Xia and Wang, 1999:81, figs. 1–8; L. Aguilar-Rosas et al., 2000:130; Shimada and Masuda, 2002:170, figs. 7–10; Pacheco-Ruíz and Zertuche-González, 2002:467; López et al., 2004:12; Mateo-Cid et al., 2006:50.

Pterocladia caloglossoides (M. Howe) E. Y. Dawson, 1953a:76, pl. 6: fig. 1; Dawson et al., 1960b:15; Dawson, 1961b:410; Acleto O., 1973:31; Stewart, 1976:349, fig. 292; Santelices, 1977:78; Santelices and Abbott, 1978:218; Stewart and Norris, 1981:274, tbl. 1, 281; Stewart and Stewart, 1984:143; L. Aguilar-Rosas et al., 1985:125; Renfew et al., 1989:3308, figs. 34–41; Ramírez and Santelices, 1991:194; Mateo-Cid and Mendoza-González, 1992:19; Stewart, 1992:183, fig. 4; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:16; Rodríguez-Vargas et al., 1993:448; Serviere-Zaragoza et al., 1993a:484; León-Tejera et al., 1993:200; González-González et al., 1996:261.

Pterocladia parva E. Y. Dawson, 1953a:77, pl. 6: fig. 2 [type]; 1961b:410; Stewart and Norris, 1981:274, tbl. 1; Mendoza-González and Mateo-Cid, 1985:32; González-González et al., 1996:262.

Algae mostly less than 1.0 cm (occasionally up to 2.0 cm) high; of few to several, erect to repent, very slender, flattened axes, mostly 45–570 μm wide and 60–120 μm thick (intertidal specimens can be up to 750 μm wide; subtidal specimens predominantly 60–200 μm); axes variably branched, from simple to sparsely, more or less pinnately to irregularly branched; above prostrate flattened axes (similar in sizes to erect axes), attached at frequent intervals to substratum by disc-like or peg-like structures developed on lower surfaces, axes sometimes also attaching to each other; decumbent repent branches also secondarily attached to substratum.

Tetrasporangia often (but not always) in diagonally opposed V-shaped rows in apical sori. Gametangial thalli not reported in the northern Gulf. Unilocular cystocarps and spermatangial sori distal on branches on southern California subtidal thalli (Stewart and Norris, 1981); spermatangia in clusters of 2–4 below rounded apices (Renfew et al., 1989).

Habitat. On rocks and in tide pools; low intertidal to shallow subtidal, 3–12 m depths (also dredged from 28 m depths).

Distribution. Gulf of California: Puerto Peñasco to Bahía de Los Ángeles; Sinaloa to Jalisco. Eastern Pacific: Alaska to Playa Los Cerritos (vicinity of Todos Santos, Baja California Sur; Isla Guadalupe; Colima to Guerrero; Peru to northern Chile. Central Pacific: Hawaiian Islands. Western Pacific: Vietnam.

Type Locality. Isla de San Lorenzo, off the port of Callao (west of Lima), Peru.

Pterocladiella capillacea (S. G. Gmelin) Santelices et Hommersand

FIGURE 157

Fucus capillaceus S. G. Gmelin, 1768:146, pl. 15: fig. 1 [lectotype illustration]; Womersley and Guiry, 1994:139 [epitype].

Pterocladiella capillacea (S. G. Gmelin) Santelices et Hommersand, 1997:118, figs. 1a, 2b, 3b, 4, 5; Santelices, 1999:73; Abbott, 1999:199, fig. 52C–F; Scrosati and Serviere-Zaragoza, 2000:1061; Scrosati, 2002:96, fig. 1; CONANP, 2002:139; Shimada and Masuda, 2002:172, figs. 11–18; Mateo-Cid et al., 2006:50; Santelices, 2007:294, tbl. 1.

Gelidium corneum var. *capillaceum* (S. G. Gmelin) Greville, 1830:143.

Gelidium capillaceum (S. G. Gmelin) Meneghini in Frauenfeld, 1854:334; Kützing, 1868:18, pl. 53a–d.

Pterocladia capillacea (S. G. Gmelin) Bornet in Bornet et Thuret, 1876:57, pl. 20: figs. 1–7; Stewart, 1968:76; 1976:350, fig. 293; Stewart and Norris, 1981:274, tbl. 1, 279 [in part; excluding *Gelidium sonorense* and *G. decompositum*]; L. Aguilar-Rosas, 1981:93; Pacheco-Ruíz and Aguilar-Rosas, 1984:76; Stewart and Stewart, 1984:143; Huerta-Múzquiz and Mendoza-González, 1985:48; Mendoza-González and Mateo-Cid, 1985:32; Santelices and Stewart, 1985:25, fig. 1; Mendoza-González and Mateo-Cid, 1986:422; Santelices and Abbott, 1987:12; Sánchez-Rodríguez et al., 1989:42; Mateo-Cid and Mendoza-González, 1991:20; Ramírez and Santelices, 1991:194; Stewart, 1992:183, figs. 1–3, 7; Mateo-Cid and Mendoza-González, 1994b:39; González-González et al., 1996:325, fig. 38; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Silva et al., 1996b:232; CONANP, 2002:139; Pacheco-Ruíz and Zertuche-González, 2002:467; Serviere-Zaragoza et al., 2007:11.

Gelidium pyramidale N. L. Gardner, 1927b:273, pl. 36, pl. 37: fig. 1, pl. 45, pl. 46: fig. 2.

Pterocladia pyramidale (N. L. Gardner) E. Y. Dawson, 1945e:93; 1953a:79; 1957a:7; 1959a:20; Dawson et al., 1960b:76, pl. 18: fig. 3, pl. 19: fig. 1; Dawson, 1961b:410; Stewart, 1968:76–81; Acleto O., 1973:32; Brusca and Thomson, 1975: 37; Stewart and Stewart, 1984:143 ; González-González et al., 1996:262.

Pterocladia mexicana W. R. Taylor, 1945:159, pl. 35; González-González et al., 1996:262.

Pterocladia complanata Loomis, 1949:4, pl. 6: figs. 1, 2, pl. 7: figs. 1–4, pl. 10 [type specimen]; Dawson, 1953a:78; 1961b:410; Silva, 1978:260; Mendoza-González and Mateo-Cid, 1985:32; Mendoza-González and Mateo-Cid, 1986:422; González-González et al., 1996:262.

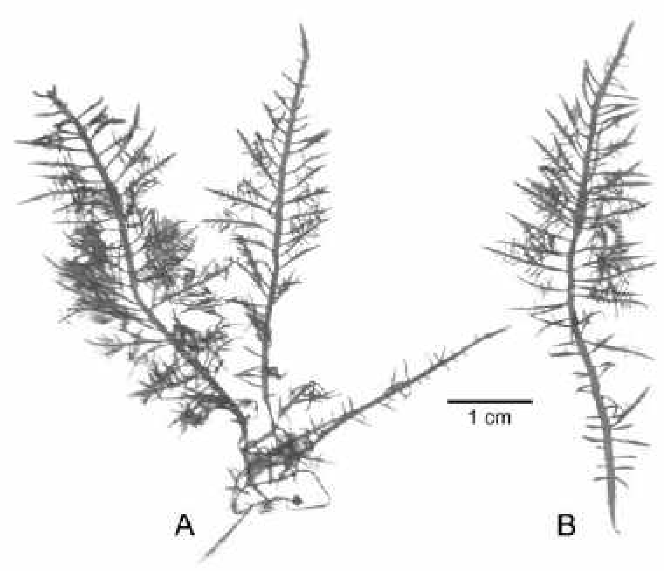

FIGURE 157. *Pterocladiella capillacea*: A, B. Habits (*JN-4611b*, US Alg. Coll.-159295).

Algae forming loose tufts or clumps; of several erect, flattened axes, 4–9 cm high, (0.6–)1.2–2.0 mm wide, (100–)160–370 µm thick; arising from a creeping rhizoidal base, attached by peg-like haptera; branching 2–5 orders, more or less to regularly pinnate, first order branches at up to 5-mm intervals and up to 4.5 cm in length, and second order branches at intervals of 0.1–1.5 mm, narrower, 0.2–1.0 mm wide. Medulla densely packed; medullary cells, (12–)20–30 µm in diameter; becoming smaller outward, grading into cortex of 2–3 layers of small, pigmented cortical cells; outermost cells slightly elongated, about 5.0–7.0 µm tall. Rhizoidal filaments (rhizines) varying from several to being numerous in medulla (generally more concentrated in middle of medulla).

Tetrasporangial sori, variable in size, generally elongated from middle to distal ends of upper branches and ultimate branchlets; tetrasporangia 40–48 µm long and 16–28 µm in diameter. Gametangial thalli not seen in Gulf material. Cystocarps elsewhere reported: 500–600(–1200) µm in diameter, usually with single ostiole; developed near apices of ultimate branchlets and upper branches. Spermatangia in elongated sori; on either sides of ultimate branchlets or upper branches; spermatangial parent cells, 8–10 µm long and 1.5–2.0 µm in diameter (after Shimada and Masuda, 2002).

Habitat. On rocks and in tide pools; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía de Los Ángeles; Isla Coronado (Isla Smith). Eastern Pacific: Santa Barbara, southern California to Punta Lobos (vicinity of Todos Santos), Baja California Sur; Isla Guadalupe; Isla Cedros; Islas San Benitos; Rocas Alijos; Isla Clarión (Islas Revillagigedo); Galápagos Islands; Ecuador; Peru; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: Japan; China; Taiwan.

Type Locality. Mediterranean Sea (Gmelin, 1768). Lectotype: illustration of Gmelin (1768: pl. 15: fig. 1); epitype specimen selected by Womersley and Guiry (1994:139).

Remarks. *Pterocladiella capillacea*, the type species for the genus, has been widely reported in tropical to warm-temperate seas (Womersley and Guiry, 1994; Santelices, 1999). An economically important species, *P. capillacea* provides a high-quality agar and has been commercially harvested in southern California and Baja California (Stewart, 1991). *Pterocladiella capillacea* had generally been considered to be a broadly defined species that included a wide range of morphological variation (Stewart, 1968). More recently in an *rbc*L analysis, the Japanese "*P. capillacea*-complex" was found to contain three species that were molecularly and morphologically distinct (Shimada et al. 2000; Shimada and Masuda, 2002).

Pterocladiella capillacea is probably in the northern Gulf, but its presence awaits the finding of cystocarpic specimens and molecular confirmation in comparisons with type locality Mediterranean and Western Pacific materials. Morphologies that are similar to "*Gelidium decompositum*" sensu Dawson (1957a, 1959a) could probably be included here (Dawson, 1961b) but not specimens of *G. decompositum* Setchell et N. L. Gardner (1924) sensu stricto. Although the Gulf of California species *G. decompositum* and *Pterocladia sonorense* were tentatively treated as forms of *Pterocladiella capillacea* by Stewart and Norris (1981, as "*Pterocladia capillacea*"), limits of these species are not fully understood, and for now, they are treated as separate species from each other and from *P. capillacea* until their taxonomic status can be genetically tested and their phylogenetic relationships can be elucidated.

Some specimens of the northern Gulf *P. capillacea* are similar in habit to the southern California *P. pyramidale* (N. L. Gardner) E. Y. Dawson (1945e; type locality: La Jolla, California), which is generally accepted as being conspecific, but it too should be genetically compared with the Mediterranean (type locality) *Pterocladiella capillacea*.

GIGARTINALES

Gigartinales F. Schmitz in Engler, 1892:18

Members of the Gigartinales exhibit a wide range of diverse morphologies. The erect species can be cylindrical to compressed or flattened and blade-like. Most of these are repeatedly branched; others are blade-like and entire, divided, or lobed. There are also a few crustose species, and some that are minute parasites. Thalli are uniaxial or multiaxial in structure and internally may be filamentous or pseudoparenchymatous.

Tetrasporangia may be cruciately or zonately divided. The Gigartinales differs from the Cryptonemiales Kylin by the formation of the auxiliary cells from converted vegetative cells. In the Cryptonemiales the auxiliary cells differentiate before fertilization, but in the Gigartinales they are intercalary cells of a cortical filament or subsidiary and do not arise in specialized branches. The carpogonial branch is oriented inward or outward, and postfertilization gonimoblast development may be inward or outward. The zygote is the result of direct fusion or transfer via connecting filaments or cells. Carposporophytes usually have a fusion cell and extensive sterile tissue; however, in some members the carposporophyte is almost entirely composed of carposporangia.

REMARKS. Clarification of the vegetative and reproductive developmental morphology, particularly the ontogeny of reproductive structures, is needed before the taxonomy is well understood for many members of this group.

The Gigartinales are represented by nine of its families in the northern Gulf of California.

KEY TO THE FAMILIES OF GIGARTINALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Auxiliary cells terminal or intercalary in specialized branches that develop laterally from inner cortical or outer medullary cells 2
1b. Auxiliary cells transformed from ordinary vegetative cells or from vegetative cells of specialized reproductive short filaments 4
2a. Nonprocarpic; carpogonial branch single, carpogonium terminal on 5- to 10-celled branch; auxiliary cell 1–4 cells from end of 5- to 12-celled auxiliary cell branch; fertilized carpogonium connecting with a subterminal cell of carpogonial branch, producing connecting filaments that fuse with auxiliary cells prior to development of carposporophytes. Gulf members uniaxial in structure; soft and mucilaginous; tetrasporangia zonately divided . . . . **Dumontiaceae**
2b. Procarpic or nonprocarpic; carpogonial branch single to several per supporting cell; carpogonial branch and auxiliary cell branch systems both with large rounded to lobed subsidiary cells; thalli multiaxial in structure; texture slippery but not mucilaginous; tetrasporangia cruciately divided 3
3a. Medulla with elongate, sometimes dendroid refractive cells; connecting filaments contact both auxiliary cells and special accessory filaments, and both issue gonimoblasts that develop carposporangia . . . . **Crossocarpaceae**
3b. Medulla with stellate refractive cells; connecting filaments contact only auxiliary cells, and only the auxiliary cells issue gonimoblasts that develop carposporangia . . . . **Kallymeniaceae**
4a. Thallus multiaxial (gametophytes and tetrasporophytes isomorphic or a few heteromorphic, with erect gametophytes and a crustose tetrasporophyte); tetrasporangia zonately or cruciately divided 5
4b. Thalli of Gulf of California members uniaxial; tetrasporangia zonately divided 8
5a. Thalli procarpic; tetrasporangia cruciately divided 6
5b. Thalli nonprocarpic; tetrasporangia zonately divided 7
6a. Medulla pseudoparenchymatous throughout; tetrasporangia in catenate rows, developed within nemathecia on surface produced from outer cortical cells . . . . **Phyllophoraceae**
6b. Medulla a meshwork of elongated filaments; tetrasporangia formed in inner cortical or medullary sori . . . . **Gigartinaceae**
7a. Carpogonial branches develop directed outward toward surface, with comparatively straight trichogynes . . . . **Dicranemataceae**
7b. Carpogonial branches develop directed inward toward inner cortical layer/outer medulla, with reflexed trichogynes . . . . **Solieriaceae**
8a. Gulf members with slightly compressed to flattened branches; axial filament cells distinct throughout in transection, medulla usually pseudoparenchymatous; cystocarps conspicuous, sessile on branches, usually nonostiolate . . . . . **Cystocloniaceae**
8b. Thalli of Gulf members wiry; axial filament cells not always distinct in transection; medulla of lax, often widely separated filaments; cystocarps internal, usually ostiolate . . . . **Caulacanthaceae**

CAULACANTHACEAE

Caulacanthaceae Kützing, 1843:389.

Algae in this family are erect, often bushy, with terete, usually entangled, axes that branch laterally or divaricately. Growth is uniaxial with a single apical cell evident at branch tips. There are two periaxial cells per axial cell, and in some species the central axial filament can also be seen. In other species this axis is obscured by the medulla of rounded cells, with branched filaments that grade into smaller cells of the cortex. The subcortex is composed of large cells, and the outer cortex is composed of small cells.

Tetrasporangia are zonately divided and scattered in the slightly thickened cortex of the branches. Cystocarps are internal, developing around the central axis. The gonimoblast develops outward from the large fusion cell of the female reproductive apparatus. Carposporangia are borne terminally on short gonimoblast filaments.

One genus of the Caulacanthaceae is known in the northern Gulf of California.

Caulacanthus Kützing

Caulacanthus Kützing, 1843:395.

Algae are erect, with terete axes, sparsely to moderately branched, that arise from prostrate branches attached to the substrate by small discs. Internally, there is a single, usually conspicuous, axial filament with two periaxial cells and a pseudoparenchymatous medulla that at first is loosely arranged but later becomes densely arranged toward the surface, with filaments alternately branched from the axial filament. The outer cortex is compact, thick, and cartilaginous, with thick-walled outer cortical cells.

Tetrasporangia are zonately divided, scattered over branches. Gametophytes are monoecious. Carpogonial branches are three-celled. After fertilization the carpogonium develops a single, short connecting filament. The gonimoblast develops around the central axial filament of the lateral branchlets, with a central fusion cell with numerous rows of cells radiating outward; the outer two to three layers produce carposporangia. Each carposporangium is single and terminal. Cystocarps are embedded and swollen, often protruding in upper portions of axes and branches, with an ostiole. Spermatangia are in sori near the branch apices.

REMARKS. The number and distinctiveness of some species of *Caulacanthus* are uncertain, although recent genetic analyses suggest there may be cryptic or overlooked species that require further study.

One species is known in the northern Gulf of California.

***Caulacanthus okamurae* Yamada**

Caulacanthus okamurae Yamada, 1933:278, as *C. okamurai*; Okamura, 1936:621, fig. 294; Tseng, 1983:112, pl. 59: fig. 1; H.-G.Choi and Nam, 2001:315, figs. 4–17; H.-G. Choi et al., 2001b:353.

Caulacanthus ustulatus sensu Dawson, 1961a:224, pl. 26: fig. 3; 1961b:429; 1966a:23; Searles, 1968:46 (in part, excluding *C. okamurae*); González-González et al., 1996:184; Yoshida, 1998:657, fig. 3-42B,C; Abbott, 1999:104, fig. 20D–F; Xia and Zhang, 1999:10, fig. 6; Y.-P. Lee, 2008:332, figs. A–C; Bernecker, 2009:CD-Rom p. 62; Fernández-García et al., 2011:60 [non *Caulacanthus ustulatus* (Mertens ex Turner) Kützing, 1843:395; 1868:3, pl. 8: figs. a–c; basionym: *Fucus acicularis* Wulfen var. β *ustulatus* Mertens ex Turner, 1809:143, figs. 126a–f].

Caulacanthus indicus sensu Dawson, 1957c:17, as *Caulacanthus* sp. aff. *C. indicus*; 1961b:429 [non *Caulacanthus indicus* Weber-van Bosse, 1921:222, fig. 67].

Endocladia complanata sensu Okamura, 1908:121, pl. 27: figs. 12–20, pl. 28: figs. 13–17 [non *Endocladia complanata* Harvey, 1860:333 (see Yamada, 1933:278); Dawson, 1959b:24; Searles, 1968:47].

Hypnea esperi sensu Dawson, 1944a:292 [in part; non *Hypnea esperi* Bory de Saint-Vincent, 1828:157, *nom. illeg.*; see Silva et al., 1987, 1996a].

Thalli forming small clumps or mats, 1(–3) cm high and to 6 cm wide, of loosely entangled, terete, erect and prostrate irregularly branched axes, 150–200 μm in diameter; attached to substrate and secondarily to other branches by numerous small discs; ultimate branchlets subulate. Medulla a large, thick-walled, central filament; surrounded by a cortex of inner and outer cortical cells

Tetrasporangia zonate, in swollen parts of ultimate branchlets. Cystocarpic and spermatangial thalli not known in the Gulf of California.

HABITAT. On rocks; mid intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía Tecopa; Isla Turner (of SE end of Isla Tiburón); Punta San Pedro (near Guaymas); Bahía Agua Verde. Eastern Pacific: Los Angeles County to San Diego Bay (southern California); Santa Catalina Island and Anacapa Island (California Channel Islands); Isla Cedros (Baja California) to Isla Santa Margarita, off Bahía Magdalena (Baja California Sur); Costa Rica. Central Pacific: Hawaiian Islands. Western Pacific: China; Taiwan; Korea; Japan.

TYPE LOCALITY. Probably Hokkaidô, Japan; although not specifically designated, distribution was given as "Hokkaidô to Formosa" (Yamada, 1933:278).

REMARKS. *Caulacanthus okamurae* forms inconspicuous small tufts or mats in the northern Gulf. It is also often unevenly distributed in the intertidal zone and may be easily overlooked. *Caulacanthus okamurae* Yamada (1933) is considered by some to be a unique western Pacific species (e.g., Tseng, 1983; H.-G. Choi and Nam, 2001; H.-G. Choi et al., 2001b). Earlier, Searles (1968) had concluded *C. okamurae* was probably not distinct on a morphological basis from *C. ustulatus* (generitype; lectotype locality: Cádiz, Iberian Peninsula, SW Spain). Since then the two have generally been considered conspecific (e.g., Rueness, 1997; Yoshida, 1998).

Rueness and Rueness (2000, as *C. ustulatus*) found that *Caulacanthus* from Brittany, France, was in a lineage genetically identical with those of China and Japan, and they concluded that it was introduced from the Pacific, possibly along with oysters from Japan. However, their "Pacific group" was separate from the "southern Europe group" (Gibraltar and Portugal), and, noting some minor morphological differences between them, they raised the question of whether the groups were conspecific or not. *Caulacanthus* was recently discovered in intertidal communities of southern California (Murray et al., 2007), and it was found by Whiteside et al. (2007, as *C. ustulatus*) to be genetically close to the Asian *C. okamurae*. Zuccarello et al. (2002b) found three distinct lineages of *Caulacanthus*—a Pacific lineage (China, Korea, United States, Philippines, and Australia), an Atlantic lineage (Spain and Portugal), and another cryptic lineage—but suggested they be referred to as one cosmopolitan species, *C. ustulatus*. *Caulacanthus ustulatus* has been reported in the eastern Pacific from British Columbia to Washington (Norris and Wynne, 1969; Gabrielson and Scagel, 1989). Norris and Wynne (1969) noted little morphological difference between their northeastern Pacific specimens and Dawson's (1961a, 1966a) from the northern Gulf of California. At this point the morphological distinctiveness of these species remains problematic.

Although more work is needed, on the basis of the genetic evidence, *C. ustulatus* and *C. okamurae* are for now treated as two species. Those of the northern Gulf referred to *C. okamurae* will need to be genetically tested and further compared with eastern Pacific, Asian, and European materials, including type locality specimens, to elucidate their phylogenetic relationships and taxonomic status.

CYSTOCLONIACEAE

Cystocloniaceae Kützing, 1843:390, 404; Saunders et al., 2004:46, 58, figs. 4, 5.

Hypneaceae J. Agardh, 1851:viii, 430.

Algae are commonly cushion-like, bushy, or tufted in growth form and composed of cylindrical, compressed to flattened branches. In some species the branches have numerous short, spine-like lateral branchlets. Growth is uniaxial, and the single apical cell is usually evident. The medulla consists of a single axial filament surrounded by large pseudoparenchymatous cells. The cortex is of small cells.

Tetrasporangia are zonately divided and borne in sori, which partly or completely surround short, lateral branchlets. In the female reproductive apparatus, the supporting cell of the three-celled carpogonial branch bears an auxiliary cell. Cystocarps have the gonimoblast associated with nutritive filaments from the surrounding pericarp, and an ostiole is present in some and absent in others.

REMARKS. As currently understood, the Cystocloniaceae includes 14 genera, two of which are known in Pacific Mexico (Dawson, 1961a), the free-living *Hypnea* J. V. Lamouroux and the parasitic *Hypneocolax* Børgesen (1920).

There is one genus of the Cystocloniaceae found in the Gulf of California.

Hypnea J. V. Lamouroux

Hypnea J. V. Lamouroux, 1813:131.

Algae are erect, tufted, or repent, cylindrical to subcylindrical or compressed, with a main axis and branches, which are attached by a discoid holdfast and lower network of entangled branches with secondary discoid holdfasts. The main axis is often obscured by irregular and often repeated branching of determinate and indeterminate branches (appearing similar to the main axis). Branches are usually slender and may be straight or sometimes have spinose branchlets or curled or hooked branchlets. Uniaxial in structure, the medulla surrounding the axial filament cell is composed of large cells with or without lenticular thickenings. In some there are smaller periaxial cells and inner medullary cells around the axial cell. The cortex consists of successively smaller cells toward the surface.

Tetrasporangia are zonately divided and aggregated within short, often swollen, branchlets or proliferations. Cystocarps are globose to hemispherical, surrounded by a pericarp lacking an ostiole, and borne on branches or short branchlets. Spermatangia are in sori, often whitish, on the surface of portions of ultimate branchlets.

REMARKS. The genus *Hypnea*, with over 60 species, is widespread in subtropical to tropical seas. Several are edible species, e.g., *H. cervicornis* is eaten in China (Xia and Wang, 1997) and in parts of the Pacific and Asia (Payri et al., 2000, as "*H. spinella*"), although it is not commonly eaten in Hawaii (Fortner, 1978). Some species of *Hypnea* are of commercial potential and are harvested or cultivated for their phycocolloid products, which are used as thickening or emulsifying agents, such as kappa carrageenans (Mshigeni, 1976c; Santos and Doty, 1979) and hypnean or a gelan (Hoppe, 1969; Masuda et al., 1997).

The genus is in need of detailed studies of the type specimens and type locality material, as species limits are often poorly understood and many of the species apparently have overlapping morphologies or have been misidentified or confused with other taxa. The vegetative and reproductive morphologies and phenotypic variation of each taxon need elucidation, and DNA studies will be helpful to clarify their phylogenetic relationships and taxonomic status.

Tetrasporangial branchlets, usually considered to be of determinate growth (e.g., Dawson et al., 1964), were found to be of indeterminate growth in cultured Hawaiian *H. cervicornis* (Mshigeni, 1976e). These reproductive branchlets continued vegetative growth even after spore shedding, and if they became detached, they produced a holdfast on contact with substratum, became attached, and developed new branches. This phenomenon can occur in natural populations and would be an important method of vegetative propagation.

Dawson (1961a) referred one species from Mazatlán in the southern Gulf, with doubt, to the Indian Ocean *Hypnea spicifera* (Suhr) Harvey in J. Agardh (1847; basionym: *Gracilaria spicifera* Suhr, 1834).

Six species of *Hypnea* are found in the northern Gulf of California.

KEY TO THE SPECIES OF *HYPNEA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus compressed to flattened, at least in part 2
1b. Thalli essentially terete throughout 3
2a. Low-growing mats or clumps; branches mostly compressed to flattened, 0.5–2.0 mm wide, often attached to each other; surface layer of cortex of uniformly small (8–10 µm) cells . . . . ***H. pannosa***
2b. Entangled around other algae; branches compressed, 600–750 µm wide; surface layer of cortex composed of cells with great range in size . . . . ***H. volubilis***
3b. Thalli erect, comparatively delicate; of freely branched, loose and lax, terete branches 4
3b. Thalli low growing to partially erect; forming mats or clumps; of entangled; comparatively coarse, branches, with or without spine-like laterals 5
4a. Thallus without a distinct main axis; branches more or less uniform diameter throughout; mostly 250–600(–1000) µm in diameter; branching more or less irregularly divaricately dichotomous . . . . ***H. cervicornis***
4b. Thallus with a definite main axis; branching monopodial; axes up to 2000 µm in diameter; branches reduced in diameter upward . . . . ***H. valentiae***

5a. Thallus bushy or in clumps, of relatively coarse axes, 1.5–2.5 mm in diameter, with suberect (repent) entangled tapering branches; apical cell not evident . . . . *H. johnstonii*

5b. Thallus forming a clump of slender branches, up to 600 μm in diameter, semicartilaginous; irregularly, densely branched; with spine-like laterals; apical cell evident . . . . *H. spinella*

Hypnea cervicornis J. Agardh

FIGURE 158

Hypnea cervicornis J. Agardh, 1852a:451; Taylor, 1945:228; Dawson, 1961a:234, pl. 34: figs. 3, 4, pl. 35: fig. 3; 1966a:24; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Norris, 1973:12; Huerta-Múzquiz and Garza-Barrientos, 1975:9, 11; Mshigeni, 1976a:217; 1976b:223, figs. 1–12; 1976c:227, figs. 1–4; 1976d:309, fig. 5; 1976f:341, figs. 1, 4; 1978a:868, figs. 1, 2; Huerta-Múzquiz, 1978:336; Stewart and Stewart, 1984:144; Mendoza-González and Mateo-Cid, 1985:30; Ibarra-Obando and Aguilar-Rosas, 1985:96; Sánchez-Rodríguez et al., 1989:43; León-Tejera et al., 1993:200; Mendoza-González et al., 1994:107; González-González et al., 1996:318, 412; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Xia and Wang, 1997:196: figs. 6–10; Riosmena-Rodríguez et al., 1998:27; Abbott, 1999:113, fig. 24A; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; Bernecker, 2009:CD-Rom p. 62.

Hypnea esperi sensu Kützing, 1868:9, pl. 26: figs. a–c [non *Hypnea esperi* Bory de Saint-Vincent, 1828:157, *nom. illeg.*; see Silva et al., 1996a:298].

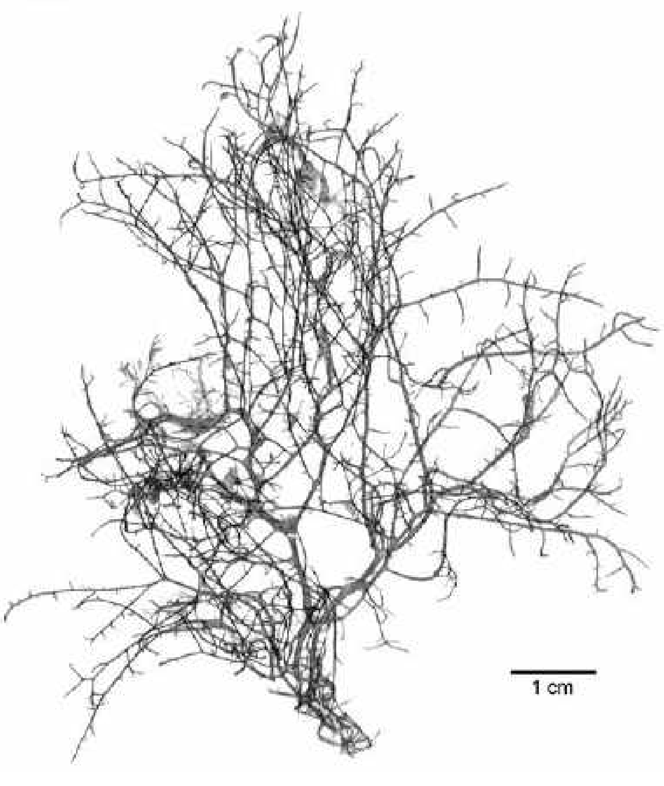

FIGURE 158. *Hypnea cervicornis:* Habit (*EYD-27213*, US Alg. Coll.-40586).

Algae, semierect, epiphytic, clumped or mat-like on substratum or forming loosely entangled soft masses; 1.5–3.0(–6.0) cm high; without definite main axes, of narrow, terete branches of more or less uniform diameter throughout (not narrowing or tapering upward), but ranging from (110–)250 to 600(–1000) μm in diameter. Attached by discoid holdfasts developed from basal rhizoids (Mshigeni, 1976b). Indistinct primary axes, irregularly divaricate-dichotomously branched, with few to many straight or curved, antler-like branchlets with acute apices.

Tetrasporangia in swollen sori, encircling short branchlets below tips. Sexual reproduction not known in Gulf of California material. As reported in Hawaii (Mshigeni, 1976f): cystocarps globose, up to 1000 μm in diameter; on axes and branchlets; spermatangia in slightly swollen sori, on branchlets below apices.

HABITAT. Epiphytic on various algae or entangled on gorgonians or growing loosely on rocks or shells; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de San Lucas; Mazatlán. Eastern Pacific: Isla Guadalupe (off Baja California) to Isla Magdalena and Bahía Magdalena, Baja California Sur; Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Guerrero to Oaxaca; El Salvador; Costa Rica; Panama. Central Pacific: Hawaiian Islands. Western Pacific: China; Japan; Korea.

TYPE LOCALITY. Not specifically designated; “oceano atlantico calidiori, ad oras Brasiliae, ad insulas Indiae occidentialis et littus mexicanum; in oceano indico ad insulam Mauritii” (Agardh, 1852a:452); localities given are in the warm Atlantic from Brazil, the West Indies, and Mexico, and in the Indian Ocean from Mauritius.

REMARKS. *Hypnea cervicornis* as currently interpreted is widespread in tropical seas (Mshigeni, 1978b). There has been much confusion on the taxonomic separation of *H. cervicornis* from *H. spinella* (e.g., Lawson and John, 1987; Guiry and Guiry, 2008–2010). On the basis of sometimes overlapping morphologies, some considered these two species to be one, as *H. spinella,* e.g., Haroun and Prud’homme van Reine (1993) from Macaronesia and Yamagishi and Masuda (1997) from Japan. Others have questioned if *H. cervicornis* should be conspecific with *H. spinella* (e.g., Cribb, 1983; Xia and Wang, 1997; Xia and Zhang, 1999). Since these two are morphologically relatively distinct in the Gulf of California, they are herein treated as being separate, following Guiry and Guiry (2008–2010). The elucidation of *H. cervicornis* and *H. spinella* on the basis of morphological and molecular studies of the type and type locality material is needed. Future studies comparing the molecular findings of type locality specimens have to be done on Gulf of California material referred to *H. cervicornis* and *H. spinella* to clarify their taxonomic status.

Hypnea johnstonii Setchell et N. L. Gardner

Hypnea johnstonii Setchell et N. L. Gardner, 1924:758, pl. 23: figs. 19–21, pl. 57; Dawson, 1944a:292; Taylor, 1945:227; Dawson, 1958:71; 1959a:25; 1961a:236; 1961b:428; 1966a:24; Norris, 1973:12; Abbott and Hollenberg, 1976:489, fig. 433; Huerta-Múzquiz, 1978:337; Littler and Littler, 1981:149, fig. 2; Mendoza-González and Mateo-Cid, 1985:30; Sánchez-Rodríguez et al., 1989:43; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid and Mendoza-González, 1994b:40; González-González et al., 1996:226; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:27; Mateo-Cid et al., 2000:65; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; Riosmena-Rodríguez et al., 2005a:33; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:209; Pérez-Estrada et al., 2012:191.

Algae of rigid, branched axes, 7–10(–15) cm long; forming dense, low-growing clumps, spreading to 20 cm or more, or sometimes becoming suberect above basal caespitose portion; attached by discoid holdfasts from lowermost branches. Main axes terete to only slightly compressed, coarse, 1.5–2.5 mm in diameter, branching near decumbent base into long, rigid, tapering, branches mostly with numerous short branchlets along sides; branches reduced in length upward; apices rounded, single apical cell not evident.

Tetrasporangia zonately divided; throughout very short, simple to compound, branchlets. Sexual reproduction unknown.

Habitat. On rocks, pebbles, and shells; mid to low intertidal, occasional in shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía Agua Verde; Isla San Pedro Nolasco; Punta Arena to Cabo Pulmo-Los Frailes; Mazatlan, Sinaloa to Jalisco. Eastern Pacific: Newport Harbor (southern California); Isla Cedros and Islas San Benitos (off Baja California); Punta Santa Rosaliita (Punta Santa Rosalía; Punta Santa Rosalillita), Baja California to Punta Lobos (vicinity of Todos Santos), Baja California Sur; Isla San Benedicto (Islas Revillagigedo).

Type Locality. On intertidal rocks; Isla Estanque (Pond Island), off southeastern end of Isla Ángel de la Guarda, Gulf of California, Mexico.

Remarks. *Hypnea johnstonii* is apparently an annual species in the northern Gulf, particularly abundant in the spring and maturing in the summer. It can be recognized in the field by its caespitose (low–growing, clump-like) habit, distinctive coarse branches, and the dark blackish red color, which often has an iridescent bluish sheen (becoming blackish upon drying). Millar (1990) has reported *H. johnstonii* from the southwestern Pacific from New South Wales, Australia.

Hypnea pannosa J. Agardh

Hypnea pannosa J. Agardh, 1847:14; Kützing, 1868:9, pl. 27: figs. i, k; Setchell and Gardner, 1924:758; Okamura, 1907:47, pl. X: figs. 18–20; Tanaka, 1941:247, fig. 20; Dawson, 1944a:291; Taylor, 1945:227, pl. 71: fig. 2; Dawson, 1961a:236, pl. 35: figs. 4, 5; 1961b:428; 1966a:24; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Norris, 1973:12; Mshigeni, 1978a:874, figs. 8, 11, 12; Huerta-Múzquiz, 1978:339; Pedroche and González-González, 1981:66; Schnetter and Bula-Meyer, 1982:137, pl. 21: fig. E; Tseng, 1983:100, pl. 53: fig.1; Mendoza-González and Mateo-Cid, 1985:30; Mendoza-González and Mateo-Cid, 1986:424; Salcedo-Martínez et al., 1988:83; Sánchez-Rodríguez et al., 1989:43; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:484; León-Tejera et al., 1993:200; Mateo-Cid and Mendoza-González, 1994b:40; Mendoza-González et al., 1994:107; González-González et al., 1996:318; Yamagishi and Masuda, 1997:145, figs. 22–25; Chiang, 1997:173, fig. 14; Xia and Wang, 1997:203, figs. 33–38; Yoshida, 1998:742, fig. 3-62E,F; Abbott, 1999:117, fig. 25A; Xia and Zhang, 1999:87, fig. 52; Mateo-Cid et al., 2000:65; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; López et al., 2004:11; Hernández-Herrera et al., 2005:148; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:209; Bernecker, 2009:CD-Rom p. 62; Fernández-García et al., 2011:62.

Hypnea nidulans sensu Dawson, 1944a:291; 1959a:25; Pacheco-Ruíz et al., 2008:209 [non *Hypnea nidulans* Setchell, 1924:161].

Algae forming densely entangled irregularly shaped mats or clumps, up to 6 cm thick; of subcartilaginous and brittle (often easily breaking); subterete to compressed (sometimes flattened) branches, 0.5–2.0 mm in diameter; branches often adhering to each other; ultimate branchlets short, with acute apices; attached by a primary discoid holdfast and by secondary discoid holdfasts from entangled caespitose lower branches. Branching in more than 1 plane; irregularly alternate and close together, occasionally appearing pinnate; lateral proliferations usually absent or rare. In transection, central axial cell surrounded by large medullary cells; cells becoming smaller to outer cortex of small cells; lenticular thickenings absent.

Tetrasporangia zonate, mostly 30–60 µm long, 12–26 µm in diameter; developing initially on one side in the lower, middle, or upper portions, later extending around swollen ultimate branchlets, 0.7–3.0 mm long, 400–650 µm in diameter (after Yamagishi and Masuda, 1997). Sexual reproduction not found in Gulf of California material.

Habitat. On rocks or various substrate, tidal platform and in tide pools; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena; Isla Estanque (Isla Pond) to Isla Turner, off SE end of Isla Tiburón (Islas de la Cintura); Isla San Pedro Nolasco; Mazatlán, Sinaloa to Jalisco; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: Bahía Tortugas (inside southeast Bahía San Bartolomé) to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla San Benedicto and Isla Socorro (Islas Revillagigedo); Colima to Oaxaca; El Salvador; Costa Rica; Panama; Colombia. Central Pacific: Hawaiian Islands. Western Pacific: Japan; Taiwan; China.

Type Locality. San Agustín (St. Augustin), Oaxaca, Pacific Mexico.

Remarks. *Hypnea pannosa* can be distinguished from other clumping or mat-forming Gulf species by its axes and branches of uniform width (not tapering or becoming narrower upward) and tetrasporangia that are usually on one side of a branchlet (not surrounding it).

The relationship of *Hypnea pannosa* to another species, *H. nidulans* Setchell (1924), requires investigation. Tanaka (1941) and Dawson (1944a) recognized *Hypnea pannosa* and *H. nidulans* as distinct, but later, Dawson (1961a) considered them to be conspecific (see also Chiang, 1997; Yamagishi and Masuda, 1997; Lewmanomont, 1997; South, 2004). However, the Pacific Mexico *H. pannosa* and the South Pacific *H. nidulans,* described from Tutuila Island (American Samoa), are probably different species (see also Tanaka and Phạm-Hoàng, 1962; Silva et al., 1996a; Lobban and Tsuda, 2003).

Hypnea spinella (C. Agardh) Kützing

Sphaerococcus spinellus C. Agardh, 1822:323.

Hypnea spinella (C. Agardh) Kützing, 1847:23; Taylor, 1945:228; Dawson, 1961a:238, pl. 34: fig. 2; 1961b:428; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Huerta-Múzquiz, 1978:338; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:424; Salcedo-Martínez et al., 1988:83; Dreckmann et al., 1990:30; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:484; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:47; Stout and Dreckmann, 1993:10; Mateo-Cid and Mendoza-González, 1994b:40; Mendoza-González et al., 1994:107; González-González et al., 1996:319; Silva et al., 1996a:307; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:131; León-Tejera and González-González, 2000:327 [as *H.* aff. *spinella*]; L. Aguilar-Rosas et al., 2002:234; López et al., 2004:12; Hernández-Herrera et al., 2005:148; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:10; Bernecker, 2009[in part]:CD-Rom p. 62; Castañeda-Fernández de Lara et al., 2010:199; Fernández-García et al., 2011:62.

Gigartina spinella (C. Agardh) Greville, 1830: lviii.

Algae usually very entangled, forming low-growing tufts or mats; of somewhat cartilaginous, irregularly and often densely branched terete axes, 400–600 μm in diameter; branching multifarious; branches often with short, spine-like ultimate branchlets with acute apices; branches often attached to each other and to substratum by discoid attachments. Medulla with lenticular thickenings.

Tetrasporangia developed terminally on short branchlets. Cystocarpic and spermatangial not observed in Gulf.

Habitat. On rocks or sometimes epiphytic on or entangled with other algae; high to low intertidal.

Distribution. Gulf of California: Piedras del Burro (Gulfo de Santa Clara) to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Bahía Sebastián Vizcaino, Baja California to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Clarión and Isla Socorro (Islas Revillagigedo); Colima to Oaxaca; El Salvador; Costa Rica.

Type Locality. "Indiae occidentalis" (C. Agardh, 1822); in coral; West Indies, Caribbean Sea (Dawson, 1961a).

Remarks. There has been much debate as to whether *Hypnea spinella* should be a distinct species (e.g., Lawson and John, 1987; Chiang, 1997; Xia and Wang, 1997; Yoshida, 1998) or whether it is conspecific with *H. cervicornis* J. Agardh (e.g., Haroun and Prud'homme van Reine, 1993; Xia and Zhang, 1999). "*Hypnea spinella*" as reported from Japan (see Yamagishi and Masuda, 1997:151, figs. 30–32) and the Hawaiian Islands (Mshigeni, 1978a; Abbott, 1999) appears to be a different species. Yamagishi and Masuda (2000) concluded that Japanese specimens previously referred to "*H. spinella*" were also different from *H. cervicornis*. Thus, all specimens identified as *H. spinella* or *H. cervicornis* are in need of molecular and phylogenetic analyses.

Gulf of California specimens herein referred to *Hypnea spinella* follow the interpretation of the species by Dawson (1961a). C. Agardh (1822) described the thalli of *Sphaerococcus spinellus* as being 1.3–2.5 cm long and cartilaginous and rigid, characters observed in Gulf specimens. An isotype studied by Cormaci et al. (1993) was of similar length and 550 μm in diameter, also in agreement with the northern Gulf specimens. Dawson (1961a) observed that *Hypnea spinella* appears to be restricted in distribution to tropical coasts of Pacific Mexico. "*Hypnea spinella*" has also been reported in lagoons along the coast of Sinaloa (Piñón-Gimate et al., 2008).

Hypnea valentiae (Turner) Montagne

Fucus valentiae Turner, 1809:18, pl. 78: figs. a–f.

Hypnea valentiae (Turner) Montagne, 1841:161; Dawson, 1961a:238, pl. 37; 1961b:428; 1966a:24; Norris, 1973:12; Abbott and Hollenberg, 1976:489, fig. 434; Mshigeni and Lorri, 1977:381, figs. 1–6; Mshigeni, 1978a:878, fig. 15; Huerta-Múzquiz, 1978:338; Schnetter and Bula-Meyer, 1982:138, pl. 22: fig. A; Stewart and Stewart, 1984:144; Pacheco-Ruíz and Aguilar-Rosas, 1984:77; Norris, 1985d:213; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:424; Sánchez-Rodríguez et al., 1989:43; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:47; Mendoza-González et al., 1994:107; Womersley, 1994, figs. 154F, 156A–C; González-González et al., 1996:227; Riosmena-Rodríguez et al., 1998:27; Abbott, 1999:119, fig. 25F; L. Aguilar-Rosas et al., 2000:131; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; Piñón-Gimate et al., 2008:116; Pacheco-Ruíz et al., 2008:209; Bernecker and Wehrtmann, 2009:226; Castañeda-Fernández de Lara et al., 2010:200; Fernández-García et al., 2011:62; Pérez-Estrada et al., 2012:191.

Hypnea musciformis var. *valentiae* (Turner) Harvey, 1834:153.

Hypnea nidifica sensu Dawson, 1944a:290 [in part]; 1959a:25 [non *Hypnea nidifica* J. Agardh, 1852:451].

Hypnea esperi sensu Dawson, 1944a:292 [in part]; González-González et al., 1996:226 [non *Hypnea esperi* Bory de Saint-Vincent, 1828:157, *nom. illeg.*; see Silva et al., 1996a:298].

Thalli of erect, loosely and laxly branched cylindrical axes, to 20 cm tall, 0.5–1.5(–2) mm in diameter, gradually reduced in diameter upward to acuminate apices; entangled or attached by a small discoid holdfast and/or with many secondary discoid holdfasts along lower parts of branched axes. Main axes usually lax and irregularly branched, at intervals of 2–8 mm; ultimate branchlets, indeterminate, straight to curved or more or less hook-like; axes and branches beset with few to numerous simple to compound spinose determinate branchlets, 0.5–2.0(–5.0) mm long.

Tetrasporangia encircling lower or occasionally middle portion of short, swollen tetrasporangial branchlets. Cystocarps globose or dome shaped, 450–650 µm in diameter, scattered over branches. Spermatangia in moderately swollen sori at or near the bases of spermatangial branchlets.

Habitat. Growing on rocks or epiphytic or entangled on other algae or invertebrates, particularly gorgonians; also reported in coastal lagoons; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena; Bahía de Navachiste to Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Santa Barbara, southern California to Bahía Magdalena, Baja California Sur; Colima to Guerrero; Costa Rica; Colombia; Ecuador; Peru. Central Pacific: Hawaiian Islands.

Type Locality. Red Sea.

Remarks. One of the most common species of *Hypnea* in the Gulf, *H. valentiae* is reportedly widespread in subtropical and tropical seas.

The taxonomic status of the Gulf of California *H. valentiae* needs further study. For example, the southern California *H. californica* Kylin (1941; type locality: La Jolla) was considered a synonym of *H. valentiae* (Dawson, 1961a; Abbott and Hollenberg, 1976), but others have recognized it as distinct species (e.g., Stout and Dreckmann, 1993). Other eastern Pacific species, such as the southern California *H. valentiae* var. *gardneri* Hollenberg (1972) [note: Hollenberg (1972:45, figs. 1–2) also suggested the "*Hypneocolax*" reported from Bahía Magdalena (Dawson, 1961a: 234, pl. 26: fig. 1) were actually reproductive branchlets of *H. valentiae* var. *gardneri*]. This taxon and those placed in synonymy with the Red Sea *H. valentiae* (Dawson, 1961a), including *H. californica* Kylin (1941) and the Isla Guadalupe (Baja California) *H. evermannii* Setchell et N. L. Gardner (1930), also need to be reexamined and their taxonomic status tested. The southern Gulf of California *Hypnea marchantae* Setchell et N. L. Gardner (1924), also reported in southeastern Pacific from Isla Gorgona, Colombia, and Ecuador (Taylor, 1945), was also considered conspecific with *H. valentiae* by Dawson (1944a). However, on the basis of their illustrations (Setchell and Gardner, 1924:759, pl. 23: figs. 22, 23, pl. 42a, pl. 56), *H. marchantae* appears to be a different species and also needs molecular testing and taxonomic elucidation.

Yamagishi and Masuda (1997) reported a *Hypnea charoides-valentiae* complex of species in Japan that are in need of further clarification. They later concluded on the basis of molecular systematics that the Japanese complex included two species, *H. charoides* Kützing (1849) and *H. flexicaulis* Yamagishi et Masuda (2000), and presumably does not include *H. valentiae*.

Hypnea volubilis Searles

Hypnea volubilis Searles in Schneider et Searles, 1976:53, figs. 3–7, 9–10; Schneider and Searles, 1991:309, figs. 362–363.

Algae spreading 5–6 cm; of compressed axes branching from the margins; branches spaced irregularly, more or less subdichotomous; branches compressed, 600–750 µm wide, about 300–375 µm thick (approximately half as thick as wide); ultimate branchlets from less than l to 6 mm long, 160–330 µm broad; attached by pads of elongate filaments derived from cortical cells. Central axial cells up to 300(–440) µm long, connected to medullary cells by numerous pit connections; no clear distinction between medullary and cortical cells; surface cells isodiametric, 6.0–48 µm in diameter.

Tetrasporangia zonate, 25–42 µm long, 17–24 µm in diameter; borne in slightly elevated sori mostly surrounding branches and branchlets. Gametophytes unknown.

Habitat. Entangled with other algae and on tidal platforms; lowermost intertidal to very shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco.

Type Locality. At 23–24 m depths; offshore reef (33°30.5′N; 77°24.9′W), R/V *Eastwood*, Sta. No. 17665 (4 Aug 1971), North Carolina, USA.

Remarks. *Hypnea volubilis* has a very disjunct distribution and was described and reported from very different habitats. In the upper Gulf of California, *H. volubilis* occurs in the lowermost intertidal, whereas the type from North Carolina was described from a deepwater offshore reef. It has been reported in the western Atlantic from North Carolina, South Carolina, and Florida (Schneider and Searles, 1991; Dawes and Matheson, 2008), Puerto Rico (Ballantine and Aponte, 1997), and Brazil (Villaca et al., 2010). Once Gulf *H. volubilis* is re-collected, it should be critically compared with the subtidal western Atlantic *H. volubilis*.

DICRANEMATACEAE

Dicranemataceae Kylin, 1932:65 [as *Dicranemaceae*]; Kraft, 1977:223; Silva, 1980:82; Kraft and Womersley, 1994:321; Liao et al., 1994:833.

Algae are terete, dichotomously branched, and multiaxial in structure. The medulla is wide and composed of thin-walled, compacted filaments. Surrounding the medulla is the inner cortical layer of large isodiametric cells and an outer cortex of small cells.

Tetrasporophytes produce zonately divided tetrasporangia. Gametophytes are monoecious. The carpogonial branches are 2- or 3-celled, develop in an outward direction, and lack sterile cells. After fertilization, the diploidized auxiliary cells form a small fusion cell that issues multiple gonimoblast initials, and as they continue to develop, the gonimoblasts form a web of densely compacted small cells that bear the carposporangia. The mature cystocarps swelling the fertile branches. Spermatangia are clustered in sunken pits in the outer cortex at the thallus surface.

Remarks. The Dicranemataceae currently includes five genera. The family is represented by one species in the northern Gulf, whose generic status is problematic (Kraft, 1977).

Dicranema Sonder

Dicranema Sonder, 1845:56.

Algae are terete, wiry, and repeatedly dichotomously branched, with branch internodes that become shorter upward, and ultimate branches usually dense. The medulla is a dense bundle of compacted filaments. The cortex is two layered, with an inner layer of large cells and an outer layer of smaller cells.

Tetrasporangia are zonately divided, developed within prominent nemathecia scattered over the upper axes. Carpogonial branches are two-celled, aggregated around fertile branch apices. Carposporophytes are inwardly oriented, and carposporangia are single and terminal on a large mass of compacted cells developed from the outer layer of the carposporophyte. Spermatangia are in clusters of separate, sunken pits, clustered in the outer cortex.

Remarks. Carposporophyte development in *Dicranema,* illustrated by Kraft (1981), is a complex procedure that appears to progress in a series of discrete stages that involves much interaction of gametophyte and sporophyte tissue (Kraft, 1977). Kraft (1981) regards this unique carposporophyte development as arguably the most elaborate and specialized in all the red algae.

One species of *Dicranema* has been described from the northern Gulf of California.

Dicranema rosaliae Setchell et N. L. Gardner

FIGURE 159

Dicranema rosaliae Setchell et N. L. Gardner, 1924:745, pl. 22: fig. 6; Dawson, 1944a:299; Kylin, 1956:307; Dawson, 1957b:115, figs. 22a, 23a; 1961a:241, pl. 38: fig. 1; 1961b:430; 1962b:218, fig. 134; 1966a:23; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Kraft, 1977:233; Huerta-Múzquiz, 1978:340; González-González et al., 1996:199; CONANP, 2002:139; Pacheco-Ruíz et al., 2008:209; Fernández-García et al., 2011:61.

Algae erect clumps, of slender, terete branches, (125–)250–450 µm in diameter; more or less dichotomously or irregularly branched, almost divaricate near subacute apices; arising directly from a small discoid or spreading holdfast. Medulla a small, central group of compact, rounded, thin-walled, elongated cells surrounded by 2 layers of larger round cells, up to 25 µm in diameter. Inner cortex of small angular cells up to 14 µm in diameter; outer cortex a single outer layer of squarish or ellipsoidal cells.

Tetrasporangia and cystocarps unknown for the species. Spermatangia in short rows; continuous, covering surface of branches.

Habitat. On rocks and tidal platform, sometimes in calm, sandy or muddy habitats; mid to low intertidal; also dredged from 4–13 m depths (Dawson, 1961a).

Distribution. Gulf of California: Puerto Peñasco to Topolobampo, Sinaloa; Isla Espíritu Santo. Eastern Pacific: Guerrero to Oaxaca; Costa Rica.

Type Locality. Santa Rosalía, Baja California Sur, Gulf of California, Mexico (Dawson, 1961a). Note that the locale was incorrectly stated by Setchell and Gardner (1924:745) as "cast ashore, Santa Rosalía, across the bay from Guaymas." Santa Rosalía (east coast of Baja California Sur) is actually across the Gulf of California west from Guaymas (coast of Sonora). Today, the Santa Rosalía Ferry offers transport between Guaymas and Santa Rosalía.

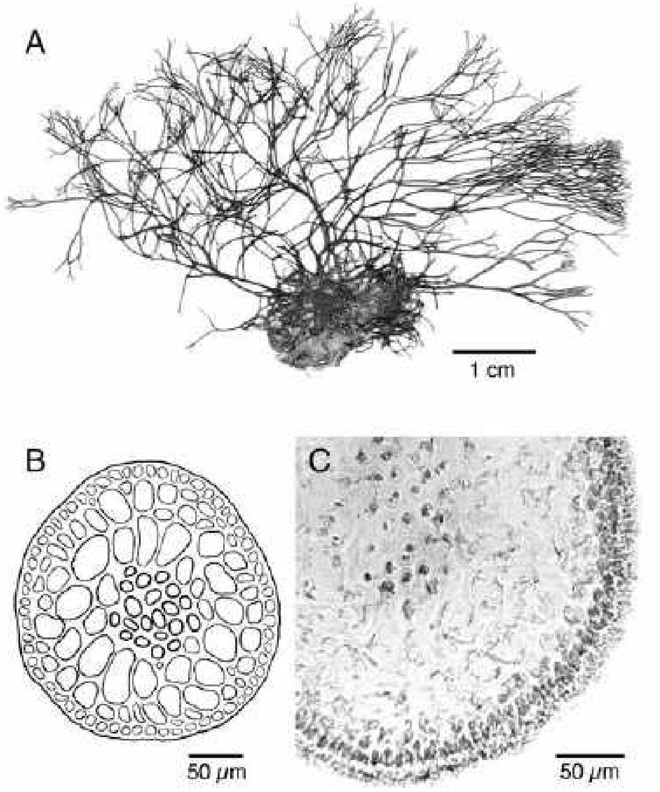

FIGURE 159. *Dicranema rosaliae*: A. Habit (*EYD-10897*, US Alg. Coll.-7137). B. Transection (after Setchell and Gardner, 1924: pl. 22: fig. 6). C. Transection showing superficial spermatangia covering branch surface (*JN-3263*, US Alg. Coll. microscope slide 4534).

Remarks. Although most species of *Dicranema* are obligate epiphytes on the woody stalks of the sea grass *Amphibolis* C. Agardh (1823), the Gulf of California *D. rosaliae* apparently occurs only on rocks. Sporangia or cystocarps of Gulf of California *Dicranema rosaliae* have yet to be found, and its taxonomic status remains uncertain. Kraft (1977:233, 235) observed similarities in the vegetative transections of Gulf *D. rosaliae* to those of other species of *Dicranema* but also noted its irregular branching pattern and anatomical structure (seen in longitudinal sections) were more like those of a *Gelidiopsis* or *Wurdemannia* Harvey (1853).

Examination of collections tentatively referred to *D. rosaliae* from Puerto Peñasco in the upper Gulf revealed superficial spermatangia on branches (*JN-3263*, US Alg. Coll. microscope slide 4534), suggesting it is probably dioecious. Thus, it differs from *Dicranema,* which are monoecious and have spermatangia in clusters of sunken pits at thallus surface (Kraft and Womersley, 1994). This further supports Kraft's (1977) suggestion that it is probably not a *Dicranema*. More northern Gulf of California collections, particularly the finding of sporophytes and female specimens, and molecular DNA testing are needed to elucidate the generic status of Gulf *D. rosaliae*.

Once thought to be a Gulf endemic (Dawson, 1944a), *D. rosaliae* has since been reported in Costa Rica (Dawson, 1961a) and Enewetak Atoll (Eniwetok), Marshall Islands (Dawson, 1957b). Records of *D. rosaliae* from Micronesia (Lobban and Tsuda, 2003) were later not accepted (Lobban and N'Yeurt, 2006), and those from Queensland, Australia, are doubtful (Lewis, 1984).

DUMONTIACEAE

Dumontiaceae Bory de Saint-Vincent, 1828:197.

Algae are cylindrical to complanate or blade-like. Some members are soft and lubricous, others are gelatinous, and some are firm. Percurrent main axes are radially to irregularly branched. Growth in most is uniaxial, but some are multiaxial. Cortical filaments are developed from whorled laterals and branch several times from elongate basal cells; outwardly, the cells become smaller and oval to spherical. Cortical filament cells lack secondary pit connections.

Tetrasporophytes may be heteromorphic, producing zonately divided tetrasporangia (e.g., *Dudresnaya*), or isomorphic, developing cruciately divided tetrasporangia (e.g., *Gibsmithia* Doty, 1963). Nonprocarpic, carpogonial branches of 6–12(–18) cells in length, usually with short sterile filaments on lower cells of carpogonial branch; carpogonium terminal. Auxiliary cells intercalary in separate branch systems. After fertilization, the carpogonium fuses with 1 or more lower cells of branch, transferring diploid nuclei to them from zygote nucleus, and issues connecting filaments (tubular connection) that contact successive auxiliary cells usually some distance from the carpogonial branch; repeatedly forming gonimoblasts that develop at the junction or from cells cut off from auxiliary cells; most gonimoblast cells become carposporangia. Spermatangia in clusters on terminal cells.

REMARKS. Some members of the family are known to produce antiviral agents, including some that could be used for treatment of herpes and other retroviruses (Ehresmann et al., 1977; Hatch et al., 1979; Neushul, 1990).

The Dumontiaceae is represented in the northern Gulf of California by one genus.

Dudresnaya P. Crouan et H. Crouan

Dudresnaya P. Crouan et H. Crouan, 1835:98.

Algae are erect, soft, mucilaginous, terete to compressed, and usually irregularly and repeatedly branched, with the branches narrowing in diameter with each branch order. Thalli are uniaxial in structure; the axial filaments may be visible in apical regions but is generally obscured below by additional filaments. Each axial cell of an axial filament has lateral whorls of (2–)4(–6) periaxial cells, each of which produces several filaments that branch for several orders (forming medulla). Descending rhizoidal filaments are commonly develop from the medullary cells, all embedded in a gelatinous matrix. Outermost cortical filaments are pigmented. Cells have a single nucleus and ultrastructurally possess pit plugs without cap layers.

Life cycles, where known, are triphasic, with isomorphic gametophytes and either an isomorphic or heteromorphic tetrasporophyte. Isomorphic tetrasporophytes have zonate tetraspores that are basally attached on the cells of the outer medulla or inner cortical filaments. Heteromorphic tetrasporophytes are crustose, with cruciately divided tetrasporangia (sometimes irregular cruciate divisions). Gametophytes are monoecious or dioecious. Carpogonial branches are of (5–)10–12(–19) cells. The auxiliary cell branch is often long, of 5–20(–43) cells. The auxiliary cell is intercalary and differentiated, usually smaller than adjacent cells. After presumed fertilization, the carpogonium divides, contacting and fusing with 1–3 other carpogonial cells. Connecting filaments, produced following fusion, contact auxiliary cells on separate branch systems. Gonimoblast initials (2–3) are developed at the auxiliary cell of the connecting filaments. Cystocarps are immersed within the thallus, with nearly all cells developing into small carposporangia. Spermatangia are in clusters; borne either terminal on outer cortical cells or in whorls around short, lateral cortical branchlets.

REMARKS. *Dudresnaya* is usually placed in the Dumontiaceae (Guiry and Guiry, 2011). Phylogenetic studies of Tai et al. (2001) and Saunders et al. (2004) found it was closer to the Kallymeniaceae. More recently on the basis of molecular analysis, D'Archino and Sutherland (2013) included the genus in the Dumontiaceae and noted that a multigene phylogeny among members of these families would help further elucidate their relationships and familial status.

One species of *Dudresnaya* is reported in the northern Gulf of California.

Dudresnaya colombiana W. R. Taylor

FIGURE 160

Dudresnaya colombiana W. R. Taylor, 1945:162; Dawson, 1961b:411; Norris and Bucher, 1976:8, figs. 7a–c, 8a,b; Mower and Widdowson, 1969:76, fig. 3a–c; Abbott and Hollenberg, 1976:355, fig. 295; Eiseman and Norris, 1981:187; Schnetter and Bula-Meyer, 1982:121, 191, pl. 15: fig. F; Bula-Meyer, 1995:35; González-González et al., 1996:199; L. Aguilar-Rosas et al., 2000:130; Pacheco-Ruíz et al., 2008:207; Fernández-García et al., 2011:61.

Algae soft and gelatinous, translucent pink to rose, up to 7(–14) cm high. Axes 3–5(–10) mm broad, terete to slightly compressed, variously branched above a short stipe. Irregularly branched to 2–4 orders, with many delicate ultimate branches. Branches narrowing with successive orders; ultimate branchlets shortest, usually with acute apices. Internally, the axial filament cells bearing lateral whorl of periaxial cells, each of these issues several branched filaments, the outermost layers form the cortex. Axial filament cells 7–16(–20) μm in diameter, whereas broader older axes often with wider axial filament cells (45–70 μm in diameter). Slender descending rhizoidal filaments (2 μm in diameter) develop from medullary cells. The assimilatory branchlets branch dichotomously and gradually taper distally. Cortical cells cylindrical, becoming shorter and ovoid toward the thallus surface, with ultimate cells 5–8 μm long and to 4 μm in diameter.

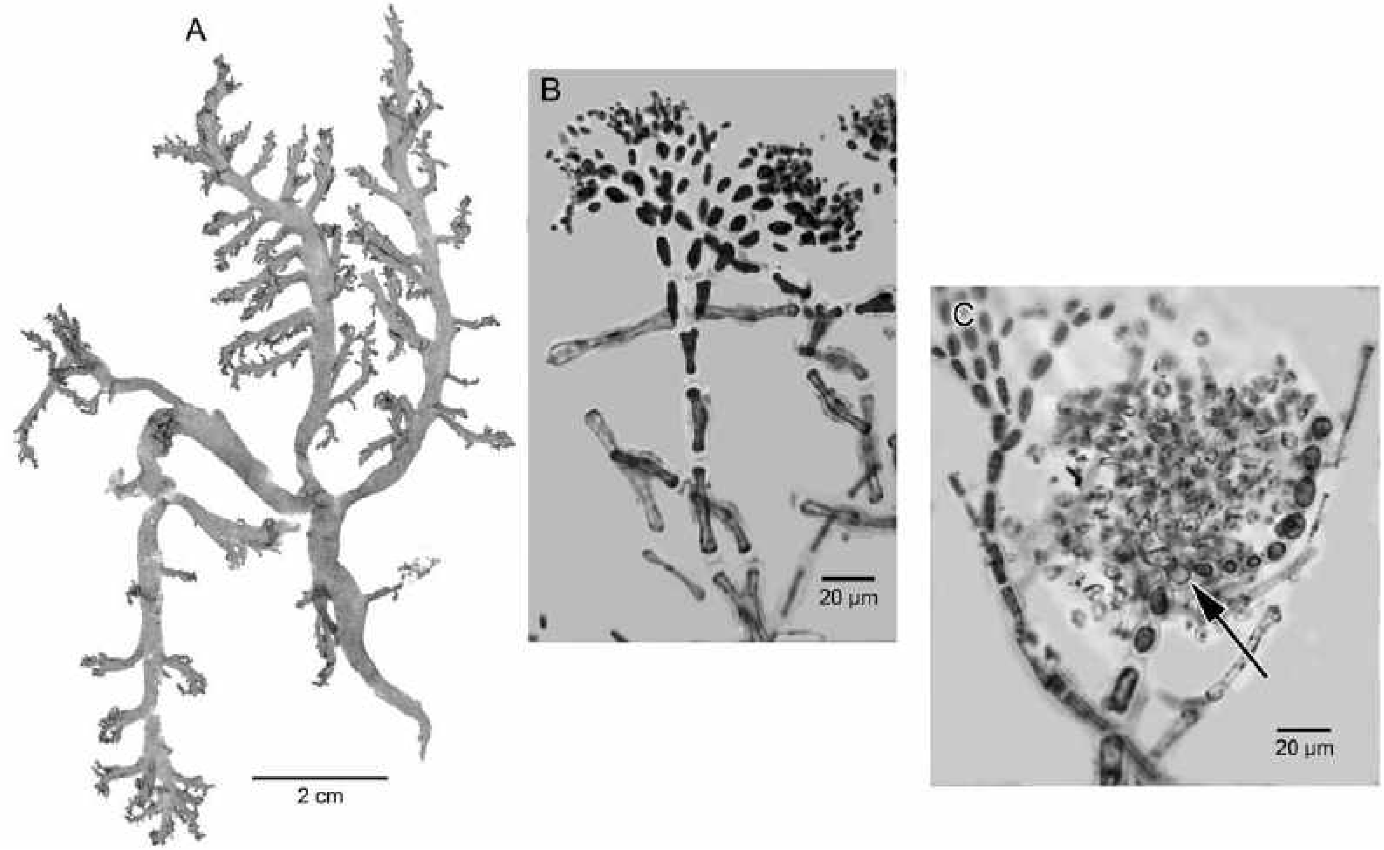

FIGURE 160. *Dudresnaya colombiana*: A. Habit (*JN-5480*, US Alg. Coll.-8760). B. Spermatangia at tips of cortical filaments (*JN-5680*, US Alg. Coll. microscope slide-3767). C. Mature carposporophyte on auxiliary cell (arrow) filament (*JN-5480*, US Alg. Coll. microscope slide_3769).

Tetrasporophytes not known in Gulf of California. Gametophytes dioecious. Auxiliary cell branch is a single series of 8–17 round cells. Cystocarps subspherical, 120–180 µm in diameter; borne on an auxiliary cell, usually the third cell from the base of the auxiliary cell filament. Spermatangia clustered terminally on the outer cells of cortical filaments.

Habitat. On rocks; low intertidal to subtidal, 15–22 m depths.

Distribution. Gulf of California: Santa Teresa (Baja California); Isla Mejía and Isla Estanque (Islas de la Cintura). Eastern Pacific: Santa Catalina Island (California Channel Islands); Colombia.

Type Locality. Intertidal; Isla Gorgona (Parque Nacional Natural Isla Gorgona), Departamento de Valle del Cauca, Pacific Colombia.

Remarks. Apparently rare in the northern Gulf, *Dudresnaya colombiana* was collected in the subtidal from two of the Midriff Islands in spring (April) (Norris and Bucher, 1976) and, more recently, in the upper Gulf from the northeast coast of Baja California (L. Aguilar-Rosas et al., 2000) in intertidal shallow water during autumn and winter.

Gigartinaceae*

Gigartinaceae Bory de Saint-Vincent, 1828:149.

The Gigartinaceae contains algae that have erect, simple or branched, cylindrical, compressed or blade-like thalli. Many are firm and fleshy and bear soft spines (spinous outgrowths) or proliferations marginally or on surfaces; others may be smooth. Growth is multiaxial. Internally, the medulla is a network of interwoven, branched, filiform filaments, and the cortex consists of anticlinally branched rows of progressively smaller cells toward the outer pigmented surface layer. Cortical filament cells have secondary pit connections.

Tetrasporangia are cruciately divided and form short rows or globose masses internally or are in round to elliptical sori. The tetrasporangia are scattered over the thallus surface or associated with spinose projections or papillae. Cystocarps are embedded within the thallus and either project from its surface on one side or

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* Contributed by James N. Norris and Suzanne Fredericq. S. Fredericq: Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504, USA.

are associated with spinose outgrowths. The female reproductive apparatus is a procarp, consisting of a three-celled carpogonial filament with its supporting cell lacking sterile filaments. The carpogonium fuses with the supporting cell of the carpogonial branch after fertilization, and the supporting cells thus becomes the auxiliary cell. The gonimoblast filaments develop toward the interior of the thallus, with nearly all cells developing into carposporangia. Spermatangia are in shallow sori or on the surface of the thallus.

There are two genera of the Gigartinaceae in the northern Gulf of California.

KEY TO THE GENERA OF GIGARTINACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Cystocarps globose, prominent above the thallus surface or in spinose laterals along margins . . . . . . ***Chondracanthus***

1b. Cystocarps embedded within inner cortex connected to medulla filaments and protruding above both thallus surface . . . . ***Mazzaella***

Chondracanthus Kützing

Chondracanthus Kützing, 1843:399.

Algae are erect, with one or more cylindrical, compressed, or foliose fronds, which arise from a discoid or peg-like holdfast. Fronds are entire, dichotomously or pinnately branched, or irregularly divided. The surface generally has papillae or spinose outgrowths, but in some it may be smooth. The medulla is composed of colorless interwoven, anastomosing filaments. The cortex consists of anticlinally branched rows of small cells.

Tetrasporangia are in globose to irregularly shaped sori organized in the inner cortex. Tetrasporangia are cruciately divided, transformed exclusively from cells in primary filaments within the cortex, and released through pores in the outer wall. Cystocarps are globose, with an ostiolate pericarp, and protrude from the frond surface or may be borne laterally along the upper axes and branch margins. Functional auxiliary cells form a few inwardly directed protrusions that bear gonimoblast initials, surrounded by a conspicuous persisting envelope composed of secondary filaments. Gonimoblast filaments penetrate between cells of the envelope, linking to them by secondary pit connections with the formation of heterokaryotic cells. Carposporangial chains are derived entirely from the gonimoblast filaments, often separated by large sterile cells that are not organized into a network. Spermatangia are in irregularly shaped sori on the frond surface. They form short, dense rows terminating on the cortical cells.

There are five species known in the northern Gulf of California.

KEY TO THE SPECIES OF *CHONDRACANTHUS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli entangled, forming clumps or irregularly shaped mats; branches slender to narrow, terete or compressed, with smooth surfaces 2

1b. Thalli mostly free (not tightly clumped), semierect to erect; of compressed to flattened, narrow to wide branches; surfaces smooth or with spinose proliferations 3

2a. Branches terete, wire-like, 0.5–0.75 mm in diameter; in irregular mats . . . . **C. acicularis**

2b. Branches compressed to flattened, 1.0–2.0 mm wide, repent, recurved, densely overlapping; in low growing clumps . . . . **"C. intermedius"**

3a. Branches narrow, 0.5–1.0 mm in diameter; upper portions freely branched; with spinose branchlets . . . . . . **C. tepidus**

3b. Branches over 2.0 mm wide, up to 12 mm 4

4a. Axes and branches narrow, mostly 2–4 mm wide, with smooth surfaces; occasionally with short subterete laterals . . . . **C. zertuchei**

4b. Axes and branches mostly over 4 mm wide; 4–12 mm in width 5

5a. Axes and branches usually less than 6 mm wide; surfaces beset with very short, branched spines throughout . . . . **C. squarrulosus (in part)**

5b. Main axes and branches wider, over 6 mm, up to 12 mm in width; surfaces smooth or partially to entirely covered with spinose outgrowths 6

6a. Blade surface smooth to partly covered; surface usually with spinose outgrowths in between smooth (lacking spines), distinct, narrow intramarginal zones . . . . **C. squarrulosus (in part, formerly "*C. johnstonii*")**

6b. Blade surface with spinose outgrowths usually covering entire surface . . . . **C. squarrulosus (in part, formerly "*C. macdougalii*")**

Chondracanthus acicularis **(Roth) Fredericq**

FIGURE 161

Ceramium aciculare Roth, 1806:114, *nom. nov.* (see Silva et al., 1996a: 290).

Chondracanthus acicularis (Roth) Fredericq in Hommersand et al., 1993:117 [as "*C. acicularis* (Wulfen) Fredericq"]; Silva et al., 1996a:290; Abbott, 1999:131, fig. 31A–D; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:209.

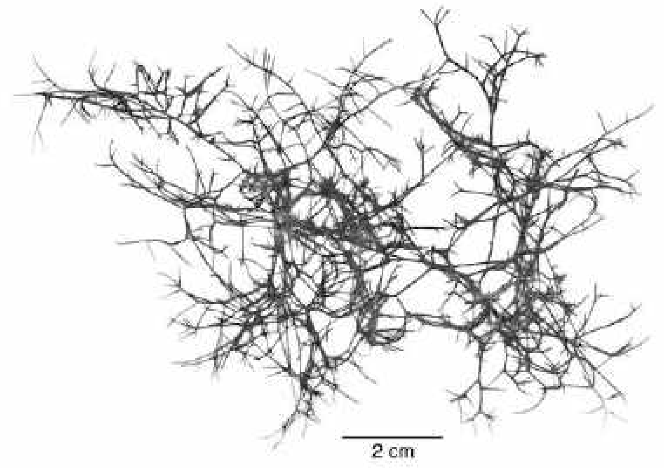

FIGURE 161. *Chondracanthus acicularis*: Habit (*EYD-27263*, US Alg. Coll.-40576).

Gigartina acicularis (Roth) J. V. Lamouroux, 1813:44; Dawson, 1966a:24; 1966b:64, fig. 4B; González-González et al., 1996:313.

Fucus acicularis Wulfen, 1803:63, *nom. illeg.* [non *Fucus acicularis* Esper, 1800:172, pl. XCI: figs. 1–2].

Algae entangled, forming irregularly shaped, low-lying clumps (occasionally solitary), up to 10 cm tall; of cartilaginous, slender, terete (sometimes slightly compressed), irregularly branched axes, 500–750 μm (to 1.0 mm) in diameter; reddish green to purplish green; repent axes below attached by small holdfasts. Branches slightly attenuated near branch origin and upward toward apex.

Tetrasporangia in irregularly shaped sori. Cystocarpic and spermatangial not seen in Gulf of California specimens.

Habitat. Occasional, on rocks; mid to low intertidal.

Distribution. Gulf of California: Punta Pelícano, Playa Arenosa, and Playa Las Conches (Playa Estación; vicinity of Puerto Peñasco) to Puerto Lobos; Bahía de Los Ángeles. Central Pacific: Hawaiian Islands.

Type Locality. "In variis submarinis corporibus" (Wulfen, 1803:63). Lectotype locality: Adriatic Sea (Dixon and Irvine, 1977b:237).

Remarks. *Chondracanthus acicularis* was first reported in the upper Gulf of California by Dawson (1966a, 1966b, as "*Gigartina acicularis*"). The Gulf material is tentatively referred to this species and should be critically compared with the European type locality *C. acicularis*.

Chondracanthus intermedius (Suringar) Hommersand

Gigartina intermedia Suringar, 1868:259; Suringar, 1870:30, pl. 17B; Okamura, 1908:172, pl. 35: figs. 1–5; Dawson, 1961a:268 [in part; description only, not pl. 54: fig. 2]; Mikami, 1965:205, fig. 14; Mendoza-González and Mateo-Cid 1985:28; Mendoza-González et al., 1994:107; Fernández-García et al., 2011:62.

Chondracanthus intermedius (Suringar) Hommersand in Hommersand et al., 1993:115; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:209; Hughey and Hommersand, 2008:152 [in part; description only].

Algae forming low-growing clumps, 2–3 cm high, spreading over substratum, purplish red to black with a bluish iridescence; of densely overlapping, compressed to flattened, branched cartilaginous axes; firmly attached where branches contact substratum. Axes arising from repent axes, 1–2 mm wide; irregularly branched; branches 8–12 mm long, mostly 0.5–1.5 mm (sometimes to 2 mm or more) in diameter, often adhering to each other by secondary attachments, often with short spinose laterals; upward branches becoming sublanceolate, recurved, with acute apices.

Tetrasporangia not seen in Gulf material. Cystocarps subglobose, about 1 mm in diameter; sessile, on margins of axes and branches. Spermatangia not seen.

Habitat. On rocks and tidal platform; low intertidal.

Distribution. Gulf of California: Santa Teresa to Puertecitos (L. Aguilar-Rosas et al., 2000); Playa Los Algodones, northwest of San Carlos (Hughey and Hommersand, 2008); Cabo Pulmo (Mateo-Cid et al., 2000); Mazatlán (Mendoza-González et al., 1994). Eastern Pacific: El Salvador; Islas Juan Fernández, Isla San Ambrosio, and Isla San Félix, Chile (Ramírez et al., 1994; Silva and Chacana, 2005). Western Pacific: China (Tseng, 1983; Xia and Zhang, 1999); Japan (Yoshida, 1998); Vietnam (Tsutsui et al., 2005).

Type Locality. Sea of Japan (East Sea), west coast of Japan.

Remarks. Some northern Gulf of California specimens are tentatively referred to "*Chondracanthus intermedius*." Dawson (1961a:268, as "*G. intermedia*") based his identification of the Gulf of California specimens on the interpretation of "Japanese *Gigartina intermedia*" by Okamura (1908:172, pl. 35: figs. 1–5), but his collections may have included more than one species. Later, Abbott (1998, 1999) concluded that the Japanese *G. intermedia* Suringar (1870:29) was a taxonomic synonym of *Chondracanthus tenellus* (Harvey) Hommersand (in Hommersand et al., 1993; basionym: *Gigartina tenella* Harvey, 1860; Dawson, 1959b:22) and that Okamura's (1908) material identified as "*G. intermedia*" represented a different species, which she described as *Chondracanthus okamurae* I. A. Abbott (1998).

On the basis of morphological and molecular studies, the phylogenetic analyses of Hughey and Hommersand (2008: figs. 1, 2) showed their specimens of Japanese *C. intermedius* and northern Gulf of California material were close to each other, but both were different from *C. tenellus*. They concluded *C. intermedius* (Suringar) Hommersand is a western Pacific species and that their Gulf of California specimens from Playa Los Algodones (Sonora) should be tentatively referred to as *C. intermedius*. Therefore, the taxonomic status of the Gulf of California "*C. intermedius*" needs to be tested and compared with type materials of *Gigartina intermedia* Surignar (1868, 1870) and *C. okamurae* I. A. Abbott (="*G. intermedia*" sensu Okamura, 1908, 1936). This will help elucidate the taxonomic status of Sonoran Gulf coast "*C. intermedius*" and clarify the status of *C. okamurae* from Japan.

There appears to be more than one species among the Gulf specimens of "*C. intermedius*" as interpreted by Dawson (1961a). There are two morphologies, which can be separated by habit, color, and size. The Gulf of California *C. intermedius* (sensu Hughey and Hommersand, 2008) is characterized by a low pulvinate habit of dense, overlapping, cartilaginous, compressed to flattened axes and branches, 1–2 mm in diameter, and purplish red to blackish in color. The second Gulf morphology differs in being semierect (not in dense clumps), taller, up to 4 cm, with wider, flattened axes, 2–4 mm in width, and greenish red to brownish red in color (cf. Dawson, 1961a: pl. 54: fig. 2). The latter is proposed to be a new species, Gulf *C. zertuchei* (described herein).

Chondracanthus squarrulosus **(Setchell et N. L. Gardner) Hughey, P. C. Silva et Hommersand**

FIGURE 162

Grateloupia? squarrulosa Setchell et N. L. Gardner, 1924:780 [with a generic query], pls. 81, 82 [type specimen]; Dawson, 1944a:281; 1954c:258; 1961b:422; 1966a:25; Littler and Littler, 1981:153; Stewart, 1982:84; González-González et al., 1996:219; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:51.

Chondracanthus squarrulosus (Setchell et N. L. Gardner) Hughey, P. C. Silva et Hommersand, 2001:1105; Pacheco-Ruíz et al., 2005a:629, figs. 2–10; Hughey and Hommersand, 2008:141, figs. 28 [type], 29–31; Pacheco-Ruíz et al., 2008:209; Pacheco-Ruíz et al., 2011:127.

Gigartina chauvinii sensu Setchell and Gardner, 1924:744. pl. 46: fig. b, pl. 70 [non *Gigartina chauvinii* (Bory de Saint-Vincent) J. Agardh, 1842:104; basionym: *Sphaerococcus chauvinii* Bory de Saint-Vincent, 1828:165, which is now *Chondracanthus chauvinii* (Bory de Saint-Vincent) Kützing, 1843:399].

Gigartina johnstonii E. Y. Dawson, 1944a:302; 1950d:339, fig. 3; 1961a:269, pl. 57; 1961b:432; 1966a:24; West and Guiry, 1982:205, figs. 1–24; McCandless et al., 1983:177, 180; Norris, 1985d:212, fig. 16.5; González-González et al., 1996:210.

Chondracanthus johnstonii (E. Y. Dawson) Guiry in Hommersand et al., 1993:115; L. Aguilar-Rosas et al., 2000:131; Mateo-Cid et al., 2006:56; Pacheco-Ruíz et al., 2008:209.

Gigartina macdougalii E. Y. Dawson, 1944a:303, pl. 64: fig. 2; 1950d:338, fig. 4; 1961a:271, pl. 58: fig. 2; 1961b:433; Norris, 1973:14; Huerta-Múzquiz, 1978:337; González-González et al., 1996:210; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:209.

Chondracanthus macdougalii (E. Y. Dawson) Guiry in Hommersand et al., 1993:115; L. Aguilar-Rosas et al., 2000:131.

Gigartina papillata sensu Norris, 1973:14; Pacheco-Ruíz et al., 2008:209 [non *Gigartina papillata* (C. Agardh) J. Agardh, 1846: pl. 19, basionym: *Sphaerococcus papillatus* C. Agardh, 1821: pl. 19, which is now *Mastocarpus papillatus* (C. Agardh) Kützing, 1843:298].

Gigartina pectinata E. Y. Dawson, 1944a:302, pl. 64: fig.1 (holotype); 1950a:339, fig. 6; 1961a:273, pl. 61: fig. 1; 1961b:433; Norris, 1973:14; Huerta-Múzquiz, 1978:337; Norris, 1985d:212; Barilotti and Zertuche-González, 1990:35; Pacheco-Ruíz et al., 1992:263; González-González et al., 1996:211.

Chondracanthus pectinatus (E. Y. Dawson) L. Aguilar-Rosas et R. Aguilar-Rosas, 1997:155, figs. 1–7; Pacheco-Ruíz and Zertuche-González, 1999:159; L. Aguilar-Rosas et al., 2000:131; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467.

Grateloupia johnstonii Setchell et N. L. Gardner, 1924:782, pl. 84; Dawson, 1944a:281; 1954c:259 [with a generic query]; 1961b:422; González-González et al., 1996:218.

Algae greenish red, reddish brown to dark purple-red, cartilaginous, up to 40 cm tall, of branched ligulate blades, (3–)5–15(–20) mm wide; sparsely to repeatedly pinnately to irregularly branched to (2–)4–6(–8) orders; attached initially by discoid holdfast, later by development of entangled, branched stoloniferous growths; also attached by secondary accessory discs from elongated outgrowths on underside of blade surfaces and branch apices. Secondary attachment discs may also grow new thalli. Axes' and branches' surfaces may be smooth, or with surfaces and margins partially smooth to entirely covered by short spinose outgrowths or simple to divided proliferations, 5.0–270 mm long (blades sometimes with a limited intramarginal zone without spinose outgrowths). Medulla of filiform filaments, variable in size and shape, sometimes vacuolated, (4–)10–30 μm in diameter. Cortex of 4–6 layers; inner cortical cells inflated 20–30 μm in diameter with prominent interstices; outward giving rise to rows of 4–5 small outer cortical cells.

Tetrasporangia aggregated in small sori and embedded near the bases of marginal and surface spinulose outgrowths or proliferations. Cystocarps globose, 300–500 μm in diameter, borne on or partly associated with spinulose outgrowths, scattered over marginal and surface outgrowths. Spermatangia in small sori, scattered over blade surface and spines.

HABITAT. On rocks, shells, or other hard substratum, in crevices, and in tide pools; sometimes entangled with other algae or sometimes unattached and freely floating; mid to low intertidal, occasionally in shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Bahía Bocochibampo (vicinity of Guaymas); Isla Ángel de la Guarda to Isla San Esteban (Islas de la Cintura); San Felipe to Puertecitos; Isla Coronado and La Sílica, Bahía de Los Ángeles to Bahía San Francisquito (Baja California); Bahía de Loreto.

TYPE LOCALITY. Isla Coronado (Isla Smith), north of Bahía de Los Ángeles, Baja California, Gulf of California, Mexico.

REMARKS. Dawson (1961a:273) noted specimens of "*Gigartina pectinata*" showed "puzzling intergrades toward those of *G. johnstonii.*" More recently, on the basis of genetic evidence from the analysis of type material, Hughey et al. (2001) and Hughey and Hommersand (2008) showed that five Gulf of California species, *Gigartina johnstonii, Gigartina pectinata*, *Gigartina macdougalii*, *Grateloupia? johnstonii*, and *Grateloupia? squarrulosa,* were all one species, i.e., *Chondracanthus squarrulosus*.

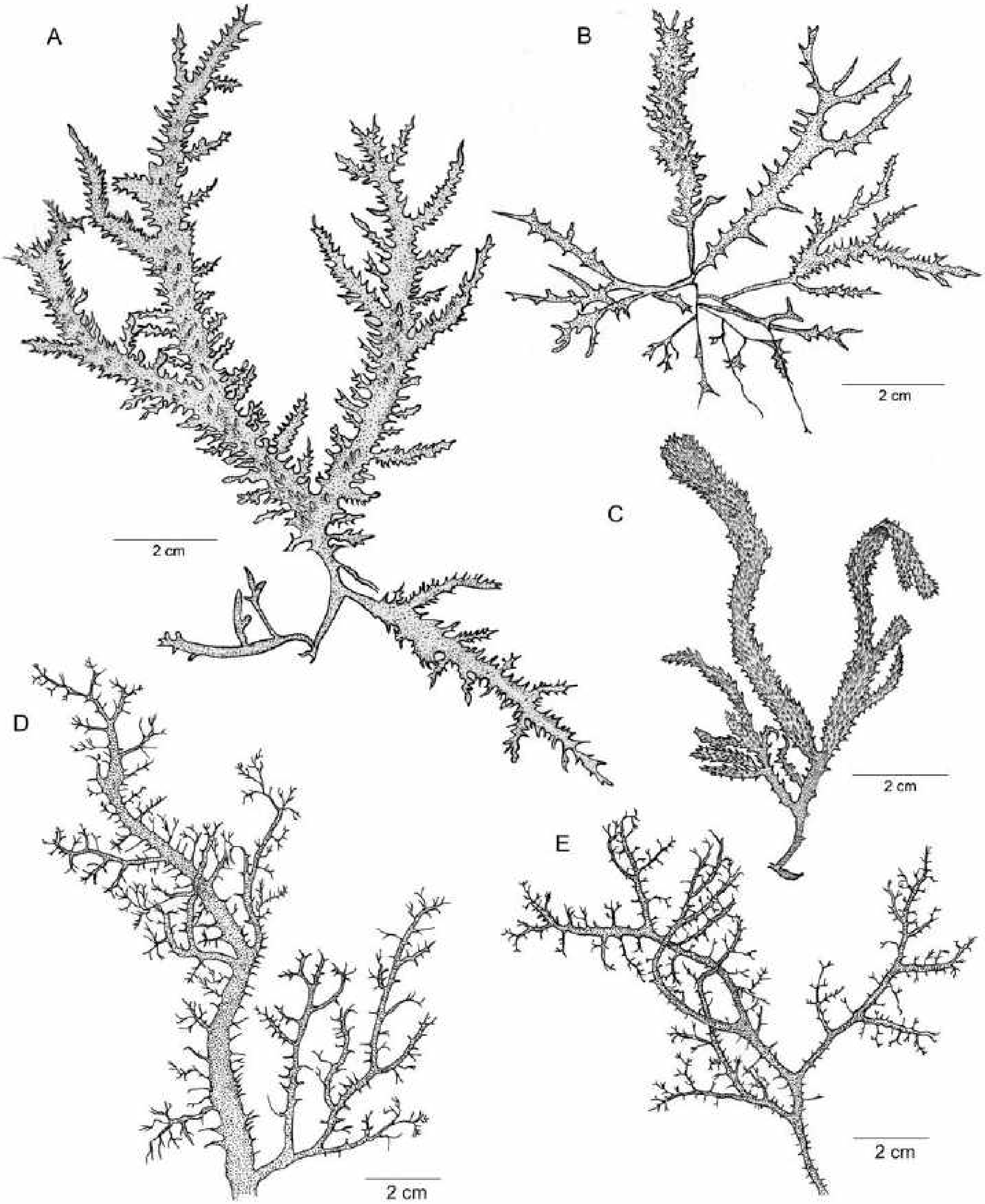

FIGURE 162. *Chondracanthus squarrulosus*: Several thalli showing morphological variability. A. Habit (*JN-3690*, US Alg. Coll.-159405). B. Habit (*JN-3690*, US Alg. Coll.-159404). C. Habit (previously "*Gigartina macdougali*") (*JN-3298*, US Alg. Coll.-159444). D, E. Portions of two thalli (previously "*G. pectinata*") (D, *JN-3026,* US Alg. Coll.-159487; E, *JN-2982*, US Alg. Coll.-159463).

Chondracanthus squarrulosus is currently recognized as a phenotypically highly variable species, exhibiting a wide range of size, shape, color, degree of branching, and surface characteristics that were once considered of taxonomic value. In fact, the taxa that are now synonyms were separated primarily on the basis of these characters. For example, surfaces on blades of some specimens are entirely lacking outgrowths on tetrasporangial blades, others may be partially smooth and partly covered or entirely covered, and some have surfaces partly lacking spinose outgrowths only within a distinct intramarginal zone. The growth and biomass of *C. squarrulosus* is greatest in spring (Pacheco-Ruíz and Zertuche-González, 1999, as "*C. pectinatus*").

Chondracanthus tepidus (Hollenberg) Guiry

FIGURE 163

Gigartina tepida Hollenberg, 1945:449, fig. 5; Dawson, 1950d:339; 1959a:26; 1961a:275, pl. 58: fig. 1; 1961b:433; 1966a:25; Abbott and North, 1972:75; Norris, 1973:14; Abbott and Hollenberg, 1976:527, fig. 472; Huerta-Múzquiz, 1978:336; Mendoza-González and Mateo-Cid, 1985:28; Mendoza-González and Mateo-Cid, 1986:424; Sánchez-Rodríguez et al., 1989:44; Stewart, 1991:112; González-González et al., 1996:211.

Chondracanthus tepidus (Hollenberg) Guiry in Hommersand et al., 1993:115; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:467; Hughey and Hommersand, 2008:145, fig. 37 [holotype]; Pacheco-Ruíz et al., 2008:209.

Gigartina teedii sensu Dawson, 1944a:301 [non *Gigartina teedii* (Mertens ex Roth) J. V. Lamouroux, 1813:137; =*Chondracanthus teedei* (Metens ex Roth) Kützing, 1843:399].

Algae usually in clumps of irregularly, distichously branched thalli, with or without a distinct main axis, usually more or less pinnately to irregularly branched, up to 5 cm tall; attached below by accessory discs on bladelet apices. Branches subcylindrical to flattened, 0.5–2.0 mm wide, with several distichous ultimate branchlets, 1.0–5.0 mm in length, surfaces usually smooth; with acute apices.

Tetrasporangia in small superficial sori, mostly marginal on branches and upper branchlets. Cystocarps globose, about 500 µm in diameter, mostly on branch margins. Spermatangia in small sori, on branchlets.

Habitat. On rocks and shells in sandy areas of tidal flats, in sheltered, shallow waters of bays and estuaries, and occasionally in semiexposed habitats on rocks, tidal platforms, and in tide pools; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas; El Coloradito to Islas de Los Gemelos (Bahía de Los Ángeles); Sinaloa. Eastern Pacific: northern Washington to San Diego, southern California (Hughey and Hommersand, 2008); San Quintín, Baja California to Bahía Tortugas (inside southeast Bahía San Bartolomé), Baja California Sur (Mendoza-González and Mateo-Cid, 1985).

Type Locality. Balboa, upper Newport Bay, Orange County, southern California, USA.

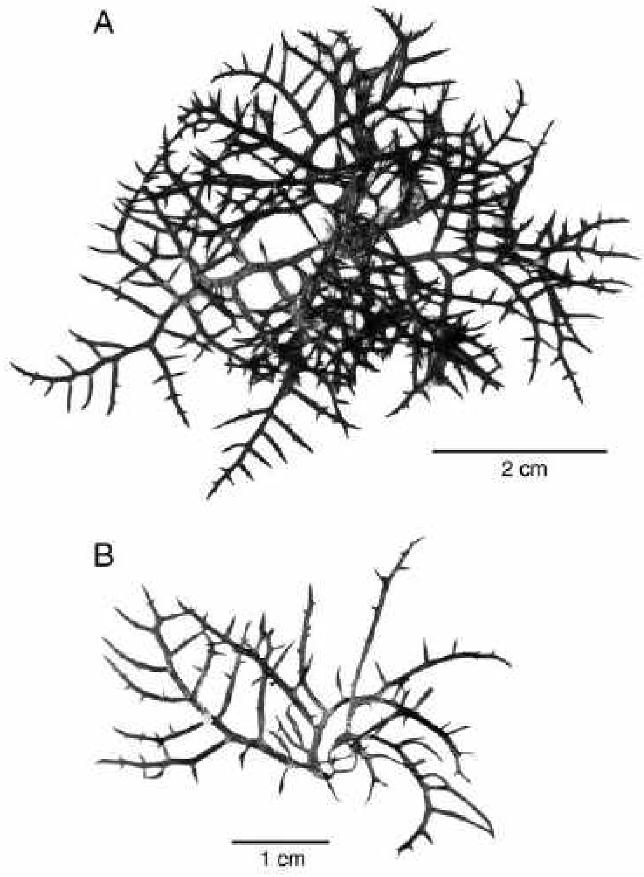

FIGURE 163. *Chondracanthus tepidus*: A. Habit of clump. B. Branch separated from clump showing branching patterns (A, B, *JN-5451*, US Alg. Coll.-159488).

Remarks. The northern Gulf of California *Chondracanthus tepidus* is an intertidal species reported from semiexposed habitats and shallow waters of protected bays and estuaries (note the deep subtidal records, reportedly dredged from 60–80 m depths off Bahía San Luis Gonzága [Dawson, 1961a:276]; the depths need to be verified by collection of attached growing specimens).

Hughey and Hommersand (2008:145) did not include records of *C. tepidus* from the Gulf of California or Pacific Baja California in their distribution list. Thus, Gulf specimens in general morphological agreement are tentatively referred to as *C. tepidus* until the taxonomic status of Gulf specimens can be tested by molecular comparisons.

Chondracanthus zertuchei J. N. Norris et Fredericq, *sp. nov.*

FIGURE 164

Gigartina intermedia sensu Dawson, 1959a:26; 1961a:268 [in part; only Gulf of California specimen on pl. 54: fig. 2]; 1966a:24; 1966b:64; González-González et al., 1996:210 [non *Gigartina intermedia* Suringar, 1868:259; Suringar, 1870:30, pl. 17B, which now is

Chondracanthus intermedius (Suringar) Hommersand in Hommersand et al., 1993:115].

Chondracanthus intermedius sensu Hughey and Hommersand, 2008:153, fig. 67 [in part; only the Gulf of California material of Dawson, 1961a; non *Chondracanthus intermedius* (Suringar) Hommersand in Hommersand et al., 1993:115].

LATIN DESCRIPTION. Thalli formantes caespites humiles axium ramosorum, usque ad 4.0 cm alti, atroviridi-sanguinei usque ad atropurpurei, semicartilaginosi; thallus infimus ramorum repentium compressorum, pro parte maxima 5–12 mm longa, 1.0–1.5 mm latus affixus per haptera discoidea ubi rami inferni contigui substratum. Rami superni formati repentibus infimis ramis; compressi, recurvati, semi-erecti vel repentes, 2–4 cm long., (1.0–)2.0–3.0(–4.0) mm lat.; irregulariter ramosi, 2–4 ordinum; plerumque aliquot sublanceolatis, curtis lateralibus ramulis (restrictis ad margines), acutis apicibus; ultimi ramuli subteretes, usque ad 1.0 cm long, fere 0.5 mm diametro.

Tetrasporangia ignota. Cystocarpia globulosa, cornata, usque ad 1 mm diametro, nata secus laminae margines. Spermatangia non visa.

Algae forming low-growing tufts of branched axes, up to 4.0 cm tall; dark greenish red to purplish red, semicartilaginous; lowermost thallus of repent, compressed branches, mostly 5–12 mm long,1.0–1.5 mm wide; attached by discoid holdfasts where lower branches contact substratum. Upper branches developed from repent lowermost branches; compressed, recurving, semierect or repent, 2–4 cm long, (1.0–)2.0–3.0(–4.0) mm wide; irregularly branched, 2–4 orders; usually with few sublanceolate, short lateral branchlets (restricted to margins), with acute apices; ultimate branchlets, subterete, up to 1.0 cm long, about 0.5 mm in diameter.

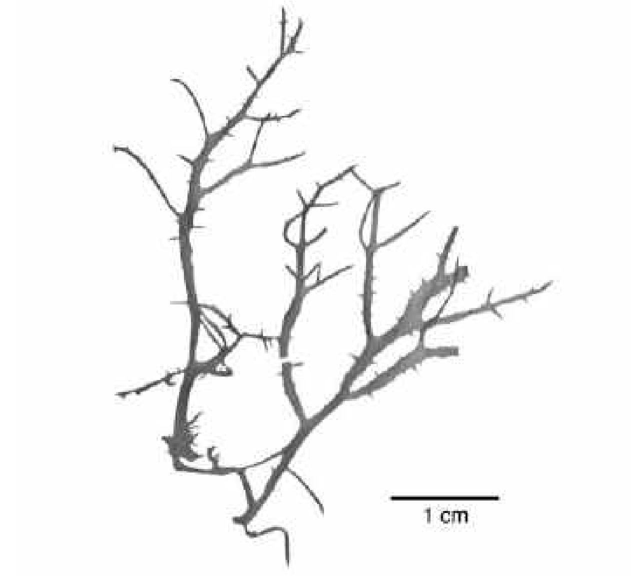

FIGURE 164. *Chondracanthus zertuchei:* Holotype (*JN-3227*, US Alg. Coll.-159436).

Tetrasporangia unknown. Cystocarps globular, cornate, up to 1 mm in diameter, borne along blade margins. Spermatangia not seen.

HABITAT. On rocks and tidal platforms; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía San Francisquito; Isla Las Ánimas (Isla San Lorenzo del Norte), southwestern Islas de la Cintura.

TYPE SPECIMEN. 24 May 1972, Coll. J. N. Norris, *JN-3227* (holotype: US Alg. Coll.-159436).

TYPE LOCALITY. Bahía San Francisquito, Baja California, Gulf of California, Mexico.

ETYMOLOGY. *Chondracanthus zertuchei* is named for José Antonio Zertuche-González (Professor, Facultad de Ciencias Marinas, Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Ensenada) in recognition of his contributions to our knowledge on the biology, uses, and cultivation of the economic species of marine algae, particularly those of the Gulf of California and Pacific Baja California.

REMARKS. The Gulf material referred to "*Chondracanthus intermedius*" sensu Dawson (1961a) included more than one species. Herein one is recognized as a new species, *C. zertuchei*. This new species also includes the Gulf specimen of Dawson (1961a: pl. 54: fig. 2, as "*Gigartina intermedia*"). *Chondracanthus zertuchei* differs from *C. intermedius,* which forms clumps of entangled, repent, flattened narrow axes that are 1–2 mm wide and 0.5–1.0 mm wide branches that have short spinose laterals (Hommersand et al., 1993; Hughey and Hommersand, 2008), and from *C. okamurae* I. A. Abbott (1998), which has subcylindrical repent axes that are 170–320 µm in diameter (see Remarks under *C. intermedius*).

Uncertain Record:
***Chondracanthus canaliculatus* (Harvey) Guiry**

Gigartina canaliculata Harvey, 1841:409.

Chondracanthus canaliculatus (Harvey) Guiry in Hommersand, Guiry, Fredericq and Leister, 1993:115.

REMARKS. Recorded with a taxonomic query from Segundo Cerro Prieto, Bahía Kino, Sonora, by Mendoza-González and Mateo-Cid (1986, as "*Gigartina canaliculata*?"), it is a doubtful record, and the specimens should be reexamined.

Mazzaella G. De Toni

Mazzaella G. De Toni, 1936b:[4].

Algae are erect, with one or more compressed to flattened blades. Blades may be simple, irregularly divided, or dichotomously branched and arise directly from a small stipe above the basal holdfast. The medulla is composed of colorless, interwoven longitudinal filiform filaments. The cortex consists of anticlinally branched rows of progressively smaller cells toward the surface.

Tetrasporangia are cruciately divided and situated in circular to elliptical sori in the inner cortex or outer medulla within the blade; they are borne in branched chains transformed from cells in primary cortical filaments or secondary lateral filaments cut off from cortical or medullary cells and linked to other cells by secondary pit connections. Cystocarps are globose, with or without an ostiole, embedded deeply in the blade, and scattered over thallus surface, or borne in spinose projections. Functional auxiliary cells form numerous lateral and inwardly directed protrusions bearing gonimoblast initials that are not surrounded by an envelope. The gonimoblast filaments are compact and short celled and displace the filiform primary and secondary medullary filaments, often linking them via terminal tubular cells. Inner gonimoblast cells expand, becoming broad. Carposporangia are borne in chains. Spermatangia are in sori, on the blade surface.

There are three species that were described from the northern Gulf of California.

KEY TO THE SPECIES OF *MAZZAELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades 10–20 cm tall, broadly expanded, 5–8(–12) cm wide, usually more or less dichotomously divided, with acute tips . . . . *M. hancockii*
1b. Thalli palmately divided or strap-like; shorter, mostly 4–6 cm tall; much narrower, less than 1.0 cm wide 2
2a. Fronds palmate, usually less than 4 cm tall, 5–9 mm wide; dichotomously divided 2–4 times; ultimate apices acute or blunt . . . . *M. digitata*
2b. Fronds strap-like, up to 6 cm tall; much narrower, 1.5–2.5 mm in width; irregularly branched, sometimes more or less subdichotomously; segments with acute apices . . . . *M. diffusa*

Mazzaella diffusa (E. Y. Dawson) J. N. Norris et Fredericq, *comb. nov.*

FIGURE 165

Rhodoglossum diffusum E. Y. Dawson, 1961a:257, pl. 49: fig. 3; 1961b:434; González-González et al., 1996:265; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:209.

Gigartina diffusa (E. Y. Dawson) D.-H. Kim, 1976:44.

Algae of a few erect, narrow, strap-like axes, up to 6 cm high and 1.5–2.5 mm wide, irregularly, diffusely branched; above a common discoid holdfast. Flattened axes irregularly subdichotomously branched at 3–17 mm intervals, often broadening upward, and tapering to branch origin; older fronds sometimes with few pinnate branchlets; ultimate branches with acute to rounded apices. Upper portions, 170–250 μm thick. Medulla dense, of slender filiform filaments. Cortex of inner cortical cells, decreasing in size to outer cortical layer of small, pigmented cells in anticlinal rows; outermost layer of elongated cells.

Tetrasporangia not seen. Cystocarps ellipsoidal, 600–900 μm in diameter; embedded in medulla and bulging equally on both blade surfaces; scattered throughout middle to upper portions of blades. Spermatangia not seen.

HABITAT. On rocks, low intertidal to subtidal, down to 17 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Isla La Ventana, offshore of Bahía de Los Ángeles.

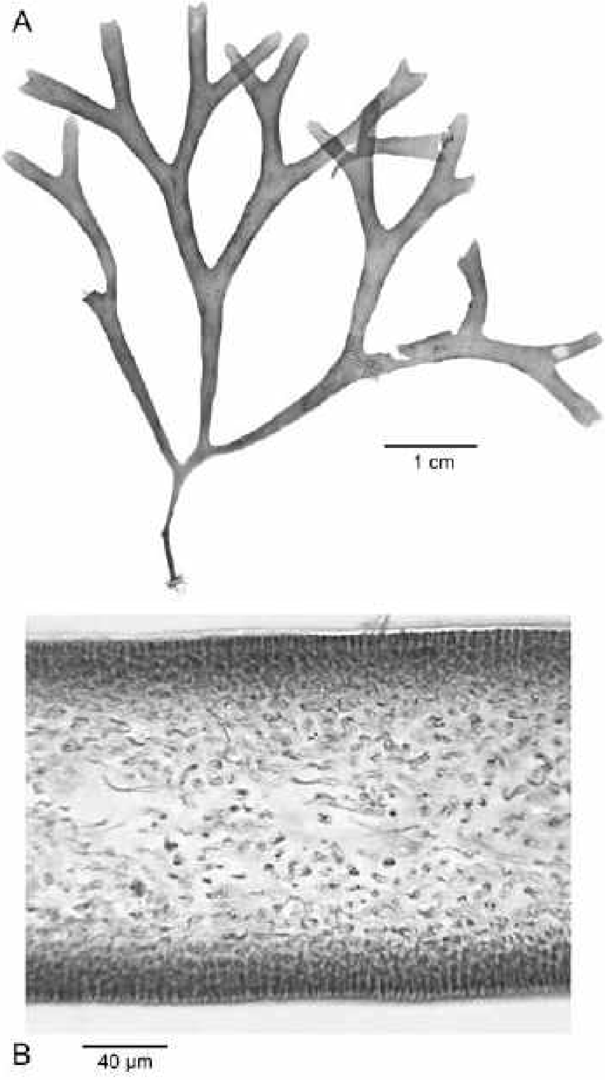

FIGURE 165. (Right) *Mazzaella diffusa*: A. Habit (*JN-2999*, US Alg. Coll.-160802). B. Transection of thallus (*JN-2999*, US Alg. Coll. microscope slide 5340).

Type Locality. Intertidal rocky shore; Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

Remarks. Endemic to the northern Gulf of California, *Mazzaella diffusa* was previously known only from one island of Islas de la Cintura and is now reported off the central Gulf coast of Baja California from Isla La Ventana (*JN-2999*, US Alg. Coll.). Although these subtidal specimens are in general agreement with *M. diffusa*, they differ in having mostly rounded to blunt apices and lack marginal laterals (Figure 165A) compared to the intertidal type of Dawson (1961a: pl. 47: fig. 3).

Dawson (1961a:258, as "*Rhodoglossum diffusum*") suggested *M. diffusa* may have been remotely derived from the *M. affinis* complex. An eastern Pacific species, the Monterey, California, *M. affinis* (Harvey) Fredericq (in Hommersand et al., 1993; basionym: *Chondrus affinis* Harvey, 1841:408) is known from Alaska to Baja California (Abbott and Hollenberg, 1976; Scagel et al., 1989; Stewart, 1991) and Chile (Ramírez, 1982; Ramírez and Santelices, 1991). Further collections of Gulf of California *M. diffusa* are needed to test Dawson's hypothesis of its origin and possible phylogenetic relationship to *M. affinis*.

Mazzaella digitata (E. Y. Dawson) J. N. Norris et Fredericq, *comb. nov.*

FIGURE 166

Rhodoglossum digitatum E. Y. Dawson, 1961a:258, pl. 45: fig. 3; 1961b:434; González-González et al., 1996:265; Pacheco-Ruíz et al., 2008:209.

Gigartina digitata (E. Y. Dawson) D.-H. Kim, 1976:44, 92.

Algae of a few, erect, flattened, palmately divided blades, up to 3.5 cm high, arising from a short, terete stipe, 1–3 mm long; attached below by a small common discoid holdfast. Blades 2–4 times dichotomously to subdichotomously divided; widening upward above stipe region, 6–16 mm long and 5–9 mm wide; ultimate divisions divaricate, short, terminally blunt or acute.

Tetrasporangial sori irregularly shaped masses, 400–1000 µm in diameter; scattered in upper portions of blades; tetrasporangia embedded in medulla and inner cortex. Cystocarps elliptical, 0.9–2.0 mm in diameter, embedded in medulla and inner cortex; scattered over and bulging from both sides of blades. Spermatangia unknown.

Habitat. On rocks, low intertidal.

Distribution. Gulf of California: Isla Partida and Isla Rasa (Isla Raza), southwestern Islas de La Cintura.

Type Locality. On rocky shore in lower intertidal; Isla Partida (Islas de la Cintura), east of Bahía de Las Ánimas, Gulf of California, Mexico.

Remarks. *Mazzaella digitata* is a northern Gulf of California endemic, apparently with a very restricted range, currently only known from two islands of Islas de la Cintura (Dawson, 1961a, as *Rhodoglossum digitatum*).

Mazzaella hancockii (E. Y. Dawson) Fredericq

FIGURE 167

Rhodoglossum hancockii E. Y. Dawson, 1944a:304, pl. 71: fig. 1 [type specimen]; 1949a:236; 1959a:26; 1961a:259, pl. 61: fig. 2; 1961b:434; Dawson et al., 1964:70, pl. 65; D.-H. Kim, 1976:15–16; Norris and Bucher, 1976:17, fig. 13; Huerta-Múzquiz, 1978:338; González-González et al., 1996:265.

Mazzaella hancockii (E. Y. Dawson) Fredericq in Hommersand et al., 1993:110.

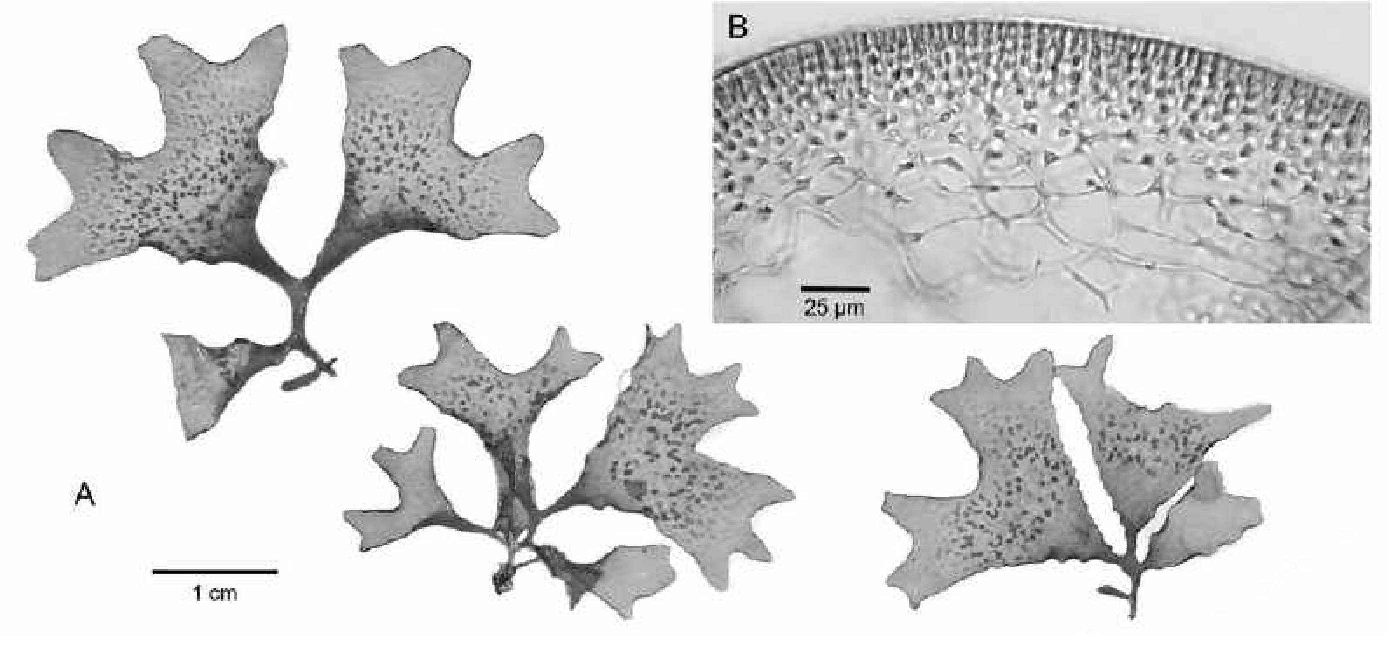

FIGURE 166. *Mazzaella digitata*: A. Habit of several fronds (paratypes) (*EYD-1045*, US Alg. Coll.-12964). B. Transection of paratype (*EYD-46-983*, US Alg. Coll. microscope slide 893).

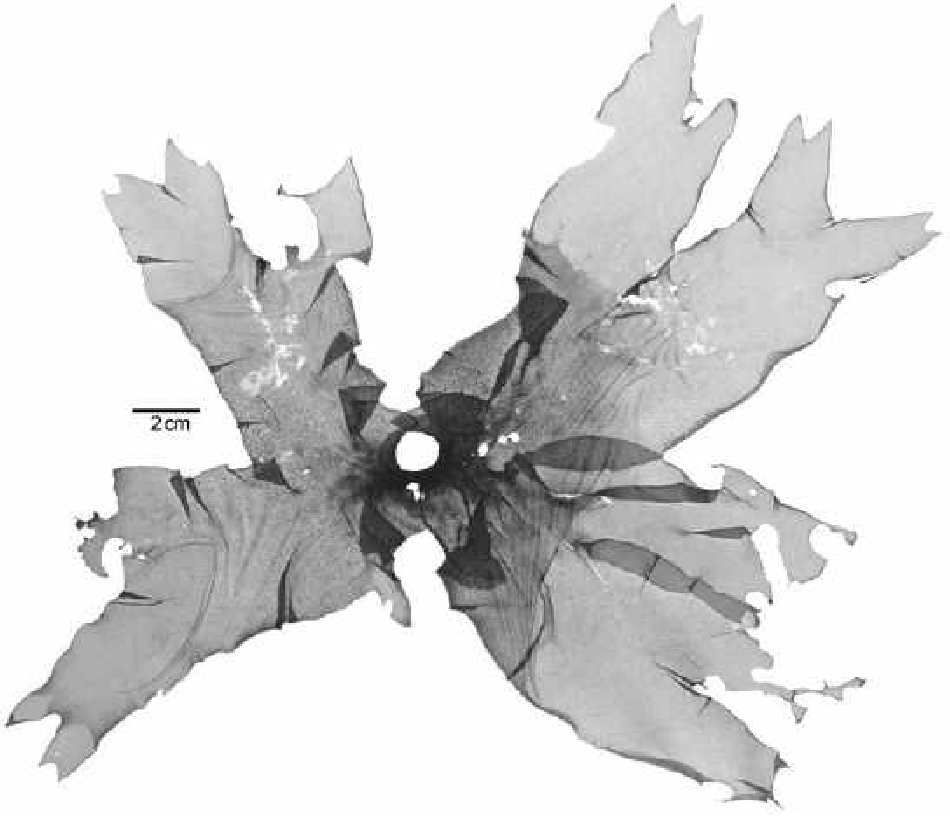

FIGURE 167. *Mazzaella hancockii*: Habit (*JN-5563*, US Alg. Coll.-160803).

Gigartina hancockii (E. Y. Dawson) D.-H. Kim, 1976:15–16, 44, 92, figs. 46–52, 61, 62, 128.

Algae of 1 to several erect, broadly expanding foliose blades, up to 20 cm high, 5–8(–12) cm wide; above a short terete stipe, 1.0–1.5 mm long, 1 mm in diameter, attached below by a discoid holdfast. Blades with subdichotomous divisions in upper portions; narrowing upward to an acute tip; margins entire, smooth; thin in cross section, only 200–300 µm thick. Medulla of filiform filaments. Cortex of 3–5 layers of small cells, 5–7 µm in diameter, with conspicuous intercellular connections; outer layer cells usually elongated anticlinally.

Tetrasporangia in sori, 500–700 µm in diameter, scattered throughout blades (but absent near blade tips), developed in the inner cortex and outer medulla, embedded within thallus. Carpogonial branches 3-celled; supporting cell serves as generative auxiliary cell. Cystocarps 500–900 µm in diameter, completely embedded internally, scattered throughout blade but absent near apices. Spermatangia not seen.

HABITAT. On rocks; low intertidal to 10 m depths.

DISTRIBUTION. Gulf of California: Isla Patos (off north end of Isla Tiburón) to Isla San Pedro Nolasco; Isla San Esteban. Eastern Pacific: Peru.

TYPE LOCALITY. On rocks, low intertidal; Isla San Esteban (Islas de la Cintura), Gulf of California, Mexico.

REMARKS. *Mazzaella hancockii* may be an endemic species in the Gulf of California. The South American record from Peru (Dawson et al., 1964; Ramírez and Santelices, 1991) should be reexamined to verify its identification.

Uncertain Record:

***Mazzaella affinis* (Harvey) Fredericq**

Chondrus affinis Harvey, 1841:408.

Mazzaella affinis (Harvey) Fredericq in Hommersand, Guiry, Fredericq, and Leister, 1993:110.

Rhodoglossum affine (Harvey) Kylin, 1928:49.

REMARKS. *Mazzaella affinis* has been recorded from Roca Rojo, Bahía Kino, by Mendoza-González and Mateo-Cid (1986, as "*Rhodoglossum affine*"). Its presence in the northern Gulf needs to be verified.

Uncertain Record:

***Mazzaella leptorhynchos* (J. Agardh) Leister**

Gigartina leptorhynchos J. Agardh, 1885:28.

Mazzaella leptorhynchos (J. Agardh) Leister in Hommersand, Guiry, Fredericq, and Leister, 1993:110.

REMARKS. Recorded with uncertainty as to its identification by Mendoza-González and Mateo-Cid (1986, as "*Gigartina leptorhynchos*?") from Roca Rojo, Bahía Kino. Their northern Gulf specimens should be reexamined to identify the species.

KALLYMENIACEAE

Kallymeniaceae (J. Agardh) Kylin, 1928:56.

Algae are erect, strongly compressed, ligulate to foliose, and usually branched, divided, lacerate, or lobed from a few to several times, but may occasionally be simple. Blades are slippery in texture and may be entire, or some species are perforated. Thallus construction is multiaxial, with a thin cortex of anticlinal filaments, two to four cells long. Medulla is generally wide, pseudoparenchymatous in some members, with large, loosely arranged ovoid cells surrounded by slender filaments, whereas others have a filamentous medulla of mostly periclinal filaments, often intermixed with large refractive stellate cells.

Life histories involve isomorphic gametophytes and sporophytes. Tetrasporangia are cruciately divided, embedded in the cortex, and scattered over blade surfaces. Gametophytes are most often dioecious, but one genus can be monoecious (i.e., *Euthroa* J. Agardh, 1847). The carpogonial branch is three-celled, and species may be monocarpogonial or polycarpogonial. Species are procarpic or nonprocarpic. In procarpic species, the carpogonial branch and its subsidiary cells develop on a large supporting cell that also functions as the auxiliary cell. In nonprocarpic species the carpogonial branch is similar to this, but the auxiliary cell is the supporting cell of a distant branch system. Auxiliary cell branches also bear several one- to two-celled chains of ovoid to lobed subsidiary cells that may function as nutritive cells for the developing carposporophyte. After fertilization, the carpogonial fusion cell produces connecting filaments for transfer of the diploid nucleus to auxiliary cells in nonprocarpic genera. Cystocarps are globose and may be large and are often surrounded by a thin filamentous involucre. Spermatangia develop in patches, cut off from outer cortical cells.

REMARKS. Two genera of the Kallymeniaceae are found in the northern Gulf of California.

KEY TO THE GENERA OF KALLYMENIACEAE AND CROSSOCARPACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Blade medulla of large pseudoparenchymatous-like cells surrounded by branching, slender filaments of short, pigmented cells; cortex mostly of 2–3 cell layers . . . . ***Pugetia***

1b. Blade medulla filamentous; of interwoven, mostly periclinal filaments, intermixed with some, usually conspicuous, refractive cells; cortex mostly of 3–4 cell layers 2

2a. Medulla with elongate, branched, spiniferous, refractive cells (not stellate) . . . . ***Kallymeniopsis***

2b. Medulla with stellate refractive cells . . . . ***Kallymenia***

Kallymenia J. Agardh

Kallymenia J. Agardh, 1842:98

Algae are simple to lobed foliose blades, with a firm but slippery texture, sometimes spinose. Blades may be intact or perforated by holes of various shapes and sizes. The medulla is composed of loosely interwoven filaments, most of which are periclinally directed. Interspersed among these medullary filaments are large stellate (arachnoid) or giant cells with long extensions. These stellate cells contain highly refractive contents and stain deeply. The cortex is composed of (2–)3–4 small, pigmented cells, in more or less anticlinal rows, decreasing in size to the thallus surface.

Tetrasporophyte and gametophytes are isomorphic. Tetrasporangia are cruciately divided and scattered in the cortex over the blade. Carpogonial branches are three-celled, either monocarpogonial or polycarpogonial, and borne on a supporting cell bearing subsidiary cells. Auxiliary cells are ovoid, surrounded by three to eight subspherical to ovoid subsidiary cells, and borne on separate filaments distant from the carpogonial branches. After presumed fertilization, the carpogonial fusion cell develops and initiates connecting filaments that grow to auxiliary cells. When the connecting filaments contact auxiliary cells, the diploid nucleus is transferred, and gonimoblast tissue develops, and carposporangia are produced. Cystocarps are globose, often large, and surrounded by loose filaments. Spermatangia are in irregular superficial patches.

REMARKS. Currently there are four species known in the Gulf of California. One of which, *Kallymenia norrisii* Hollenberg et I. A. Abbott (1965), was recently reported in the southern Gulf from off Isla San José and Isla Santo Espíritu (Hernández-Kantún et al., 2010).

There are three species of *Kallymenia*, all endemic, known in the northern Gulf of California.

KEY TO THE SPECIES OF *KALLYMENIA* (KALLYMENIACEAE) AND *KALLYMENIOPSIS* (CROSSOCARPACEAE) IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades of various shapes, mostly more or less round or oval to irregular; distinctively and thoroughly perforated with numerous holes 2–4(–10 cm) in diameter; not lacerated . . . . ***Kallymenia pertusa***

1b. Blades usually entire, cuneate to broadly lobed, or lacerated; without perforations (or if present, only with very few holes) 2

2a. Blades lacerated to within 3 cm of holdfast; 200–270 µm thick; cracking upon drying . . . . ***Kallymenia bleckii***

2b. Blade segments broadly lanceolate to lobed or deeply lacerated; not cracking upon drying 3

3a. Blade wider than tall; segments narrow, deeply, palmately lacerate down to within 1 cm of holdfast; 250–300 µm thick; medulla with stellate refractive cells . . . . *Kallymenia baldwinii*

3b. Blades broadly lanceolate or broad with cuneate divisions (not lacerated); generally thinner, 100–250 µm thick; medulla with elongate, branched, spiniferous refractive cells (not stellate) . . . . *Kallymeniopsis oblongifructa*

Kallymenia baldwinii E. Y. Dawson

FIGURE 168A

Kallymenia baldwinii E. Y. Dawson, 1966b:62, fig. 3A; Abbott, 1968:196; González-González et al., 1996:230.

Blades erect, dull rose in color; solitary; broader than tall, up to 14 cm tall and 24 cm wide; blade deeply, palmately lacerated (to within 1 cm of holdfast) into narrow segments, mostly 3–20 mm wide; without a stipe, attached by small discoid holdfast. Lowermost portion of blade, with faint, palmate, vein-like thickenings, about 1 cm long, extending into lacerate segments. Blades 250–300 µm thick. Medulla of slender filaments, outwardly joining large stellate cells, 40–50 µm in diameter. Inner cortex of rotund cells, about 20 µm in diameter; outer cortex of branched anticlinal filaments of 2–3 cells; outermost cortical cells about 5 µm in diameter.

Tetrasporangia not known. Cystocarps about 500 µm in diameter, bulging on either side of blade surface; scattered in upper portions of blade, 6–7 cm from base. Spermatangia not known.

Habitat. On rocks; subtidal, down to 20 m depths.

Distribution. Gulf of California: Islas Santa Inez (Bahía Concepción).

Type Locality. Off Islas Santa Inez (Bahía Concepción), Baja California Sur, Gulf of California, Mexico.

Remarks. Although currently known only from the type, more subtidal collecting should find *Kallymenia baldwinii* elsewhere in the Gulf.

Kallymenia bleckii E. Y. Dawson

FIGURE 168B

Kallymenia bleckii E. Y. Dawson, 1966b:59, fig. 3B; Abbott, 1968:196; González-González et al., 1996:230.

Blades erect, brownish rose to dark rose (becoming brittle and cracking on drying); apparently solitary; up to 24 (or more) cm tall and 28 (or more) cm wide; blade irregularly lacerated (to within 3 cm of base) into broad lobed segments; with only a few perforations, 2–5 mm in diameter; without a stipe, attached by small holdfast. Lowermost portion of blade with faint, divided "veins" in 3–4 cm radius around base (not seen beyond this area). Blades 200–270 µm thick in outer portions; inner medulla of slender filaments, outwardly joining 1–2 irregular layers of stellate cells, 15–25(–40) µm in diameter; cortex of anticlinal rows of 2–3 small pigmented cells; outer cortical cells, 4–8 µm in diameter.

Tetrasporangia not known. Cystocarps about 600 µm in diameter, conspicuously bulging on either side of blade; scattered in upper half of blade. Spermatangia not known.

Habitat. On rocks; subtidal, down to 15 m depths.

Distribution. Gulf of California: Isla San Pedro Nolasco (off Guaymas); Punta Púlpito (east of the southern end of Bahía Concepción on coast of Baja California Sur).

Type Locality. Punta Púlpito (El Púlpito), Baja California Sur, Gulf of California, Mexico.

Kallymenia pertusa Setchell et N. L. Gardner

FIGURE 169

Kallymenia pertusa Setchell et N. L. Gardner, 1924:746, pl. 49: fig. b; Dawson, 1944a:287; 1954c:303; 1961b:425 [with generic query]; Norris and Norris, 1973:71, figs. 1–5; Norris and Bucher, 1976:11, fig. 9; González-González et al., 1996:231; Riosmena-Rodriguez et al., 1998:28; Pacheco-Ruíz et al., 2008:208; Hernández-Kantún et al., 2010:2.

Blades of various shapes, rose red, mostly round or oval to irregular in outline, up to 50 cm long and 30 cm wide, 300–370 µm thick, with numerous conspicuous perforations; margins slightly undulate; attached at 1 or more points by small, swollen holdfasts on blade margins. Perforations initially small and round, becoming larger and irregular in shape as they merge together, (3.0–)5.0–40(–100) mm in diameter. Medulla of loosely interwoven filaments, and abundant large branched, highly refractive stellate cells. Cortex of anticlinal rows of 2–4 small, elongated pigmented cells.

Tetrasporangia cruciately divided, 24–30 µm long and 16–22 µm in diameter; embedded in the cortex and scattered over thallus surface. Carpogonial branches polycarpogonial, with up to 7 carpogonial branches on 1 supporting cell. Auxiliary cell system with several 1- to 2-celled subsidiary branches. Cystocarps 0.5–1.0 mm in diameter, surrounded by a thin involucre of narrow filaments, lacking an ostiole, and immersed and scattered over blade. Spermatangia 2.5–5.0 µm, with 1 or 2 developed from each outer cortical cell, forming superficial patches.

Habitat. On rocks, large shells, or rhodoliths or epiphytic or entangled with other algae; subtidal, from 6 to 27 m depths.

Distribution. Gulf of California: Isla Mejía (northwest side of Puerto Refugio, Isla Ángel de la Guarda); Canal de Ballenas (between west coast of Isla Ángel de la Guarda and east coast of Baja California); Punta La Gringa (Bahía de Los Ángeles); Isla San Esteban; Isla San Pedro Mártir; Isla San José.

Type Locality. Isla San Pedro Mártir (about 35 km south of Punto de Monumento on southern end of Isla Tiburón), southeastern Islas de la Cintura, Gulf of California, Mexico.

Remarks. On the basis of the finding of cystocarpic material, Norris and Norris (1973) clarified the taxonomic position of *Kallymenia pertusa*. Subtidal collections from the R/V *Dolphin* cruise have shown *K. pertusa* not to be as rare as previously thought (Norris and Bucher, 1976). Though occasional in distribution, *K. pertusa* can be abundant where found and was particularly common at 20–27 m depths, off Isla Mejía and off Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda. Diving observations suggest that *K. pertusa* develops subtidally at these depths, attached to rocks and large pieces of shells. It has also

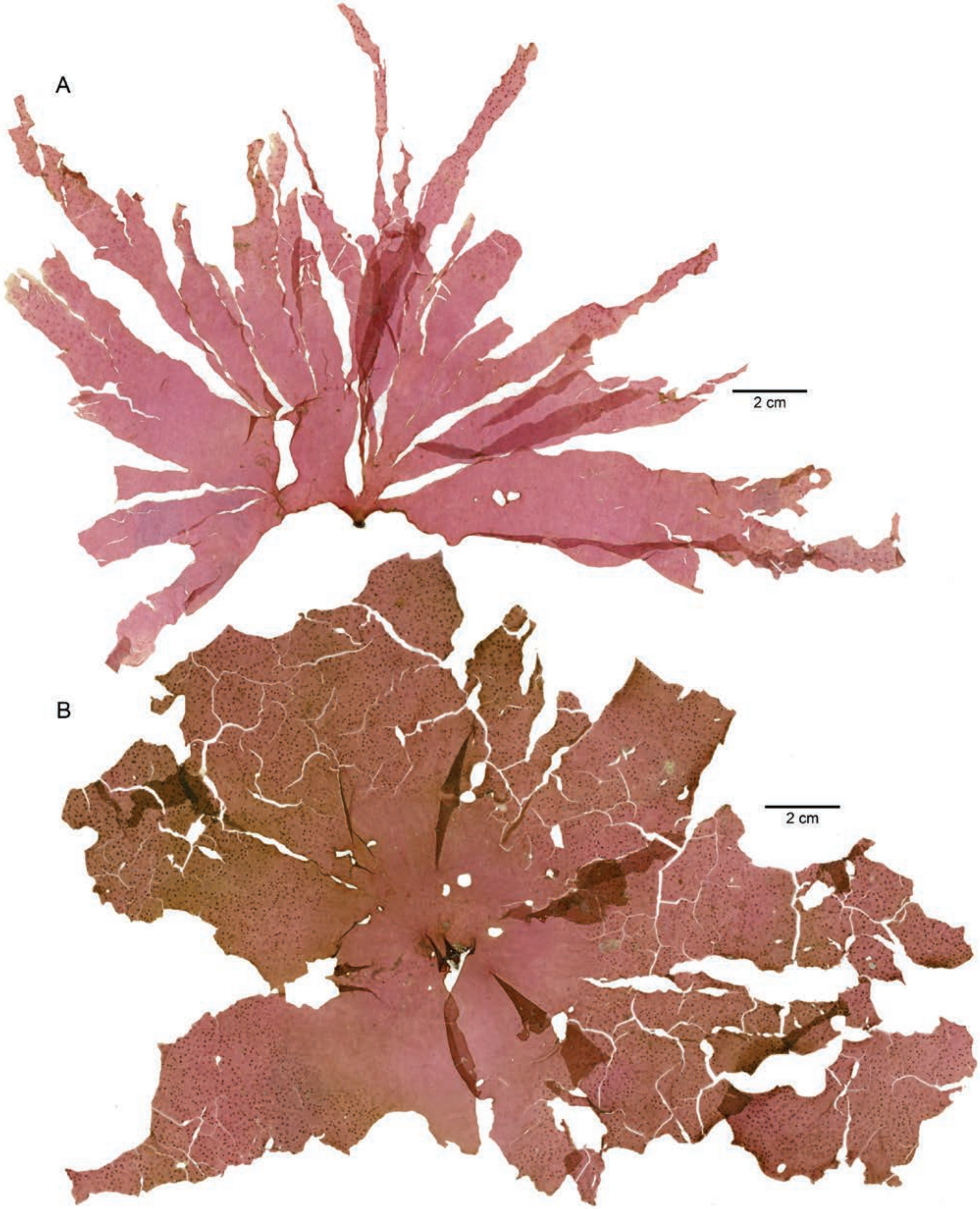

FIGURE 168. Two Gulf of California endemic species of *Kallymenia*. A. *Kallymenia baldwinii*: Holotype specimen (*EYD-25819*, US Alg. Coll.-40928). B. *Kallymenia bleckii:* Holotype specimen (*EYD-25919*, US Alg. Coll.-40927).

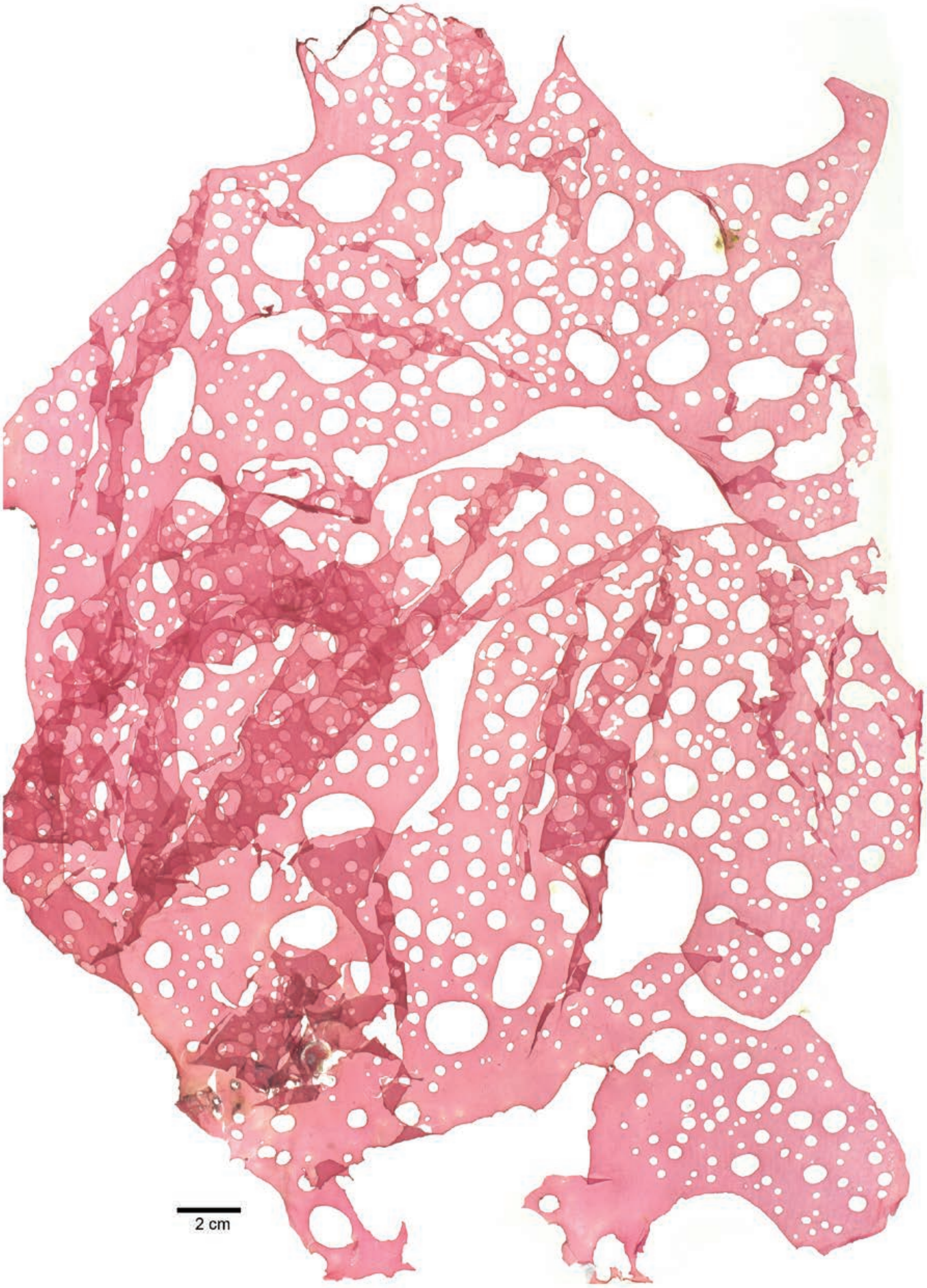

FIGURE 169. *Kallymenia pertusa*: Habit, showing the characteristic perforated blade (*JN-5667*, US Alg. Coll.-217346).

been reported in subtidal rhodolith beds (Hernández-Kantún et al., 2010). Large blades of *K. pertusa*, such as those found at Isla San Esteban and Punta La Gringa (Bahía de Los Ángeles), can become unattached or torn, perhaps because of age or size or possibly from grazing or prevailing currents, with blade fragments then drifting and becoming entangled with other algae at shallower depths (6–15 m), where they appear to continue growing.

***Pugetia* Kylin**

Pugetia Kylin, 1925:30; Norris, 1957:263, 266, figs. 3A–G, 4A–E, 5A–D [details of generitype *P. fragilissima* Kylin]; Clarkston and Saunders, 2012:43.

Algae are erect foliose blades, lack a midrib, and may be circular to wider than tall, palmately or irregular divided, or lobed. Most are entire, but at least one has holes in the surface. Blades either lack or arise above a short stipe and are attached below by one or more small discoid holdfasts. Multiaxial in structure, the medulla is pseudoparenchymatous, composed of large, round to oval, unpigmented cells that are interspersed with branching, slender filaments composed of small pigmented cells. The cortex is thin, consisting of two to three cells, with cells becoming smaller toward the surface.

Tetrasporophyte and gametophytes are isomorphic. Tetrasporangia are cruciately divided, embedded in the cortex, and scattered over the blade. Carpogonial branches are composed of three, round, oval or slightly lobed cells on a supporting cell, and usually with one or more subsidiary cells. Thalli are nonprocarpic, and the auxiliary cell systems are separate and distant from the carpogonial branch. After fertilization the dipoloid nucleus of the carpogonium is transferred to the supporting cell, which enlarges and produces lobed protuberances that issue connecting filaments to separate auxiliary cells, which in turn generate the gonimoblast filaments with terminal carposporangia. Cystocarps are relatively small, develop within the medulla and cortex, and when mature, they bulge on one side of the blade. Spermatangia are superficial on the outer cortical cells.

Remarks. Molecular, morphological, and anatomical analyses by Clarkston and Saunders (2012) revealed that one new species of *Pugetia* grouped with the generic type (*P. fragilissima* Kylin, 1925) whereas other species previously considered to be "*Pugetia*" were in two divergent clusters of the Kallymeniaceae. Some belonged in a new genus, *Salishia* Clarkston et G. W. Saunders, and one was a new species of *Beringia* Perestenko (1975) that grouped with *Erythrophyllum delesserioides* and *Kallymeniopsis oblongifructa*.

One species of *Pugetia* is known in the northern Gulf of California.

***Pugetia mexicana* E. Y. Dawson**

FIGURE 170

Pugetia mexicana E. Y. Dawson, 1966b:62, fig. 6G,H; Norris, 1973:10; Norris and Bucher, 1976:13, fig. 10; Ramírez, 1982:12, figs. 1, 18; Ramírez and Santelices, 1991:244; González-González et al., 1996:264; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:208.

Algae membranous blades, up to 20 cm tall and to 15–35 cm wide, soft and slippery in texture, rose red in color; blades (170–)250–300 µm thick, subdichotomously divided 2–5 times; upper portions often more or less palmate or sometimes irregularly to deeply divided; with entire to irregular or lobed margins and rounded terminal portions (3–5 mm wide); blades sometimes overlapping with portions often attached to each other; lowermost portion occasionally partially prostrate, attached by 1 or more small discoid holdfasts. Medulla pseudoparenchymatous; of 2(–3) layers of large parenchyma-like cells, 60–100 µm or more in diameter, and slender filaments of small, mostly elongated, pigmented cells interspersed among the large medullary cells. Cortex of 2–3 cell layers; of very small rounded cells; in surface view, about 2–3 µm in diameter; in transection oval to slightly elongate, 3–5 µm in diameter.

Tetrasporangia cruciately divided, 24–27(–30) µm long, 12–15 µm in diameter; embedded in the cortex, scattered in upper portions of blade. Cystocarps to 700 µm in diameter, without ostioles; scattered, embedded, and bulging on both surfaces. Carposporangia (10–)12–15 µm in diameter. Spermatangia superficial, derived from outer cortical cells on upper portion of thallus; spermatia about 2 µm in diameter.

Habitat. On rocks, mollusk shell fragments, and hydroids; sudtidal, 4.5–22 m depths (also dredged from 19–30 m depths; Dawson, 1966b).

Distribution. Gulf of California: Isla Mejía, Roca Blanca and Puerto Refugio, Isla Ángela de la Guarda, Isla Estanque, Isla San Esteban, and Isla San Lorenzo (Islas de la Cintura); Punta La Gringa, Bahía de Los Ángeles, to Bahía San Francisquito (Baja California). Eastern Pacific: northern Chile.

Type Locality. Off Isla San Lorenzo (Isla San Lorenzo Sur), largest of the Islas de San Lorenzo off the east coast of Baja California, southwestern Islas de la Cintura, Gulf of California, Mexico.

Remarks. There are two morphs of *Pugetia mexicana* in the northern Gulf. The subtidal specimens of Norris and Bucher (1976: fig. 10) tentatively referred to *P. mexicana* were much larger and subdichotomously to palmately divided, differing from the type specimen, a smaller irregularly shaped blade with irregular lobed margins and occasional long extensions (Dawson, 1966b: fig. 6G, H). However, both morphs have the same female reproductive systems (R. E. Norris, Friday Harbor Marine Laboratories, personal communication). Tetrasporangia (*JN-5604,* US Alg. Coll. microscope slide 4358) and spermatangia (*JN-5427,* US Alg. Coll. microscope slide 4242) are now reported for the larger, subdichotomously divided morph of *P. mexicana*. The type specimen described by Dawson (1966b) could possibly have been a fragment of a larger thallus, as similar morphologies were observed on upper parts of a Punta La Gringa specimen referred to *P. mexicana* (*JN-5427*, US Alg. Coll.-160776). The morphological differences and phylogenetic relationships of these morphs and the type need to be further

FIGURE 170. *Pugetia mexicana*: A. Habit, a large blade (*JN-5668*, US Alg. Coll.-217349). B. Small blade with scattered cystocarps (*JN-5362*, US Alg. Coll.-160774).

tested and molecular analyses performed when more material of each is collected.

Pugetia mexicana, a northern Gulf species, has also been reported from Antofagasta, Chile (Ramírez, 1982; Ramírez and Santelices, 1981).

Uncertain Record:
***Callophyllis violacea* J. Agardh**

Callophyllis violacea J. Agardh, 1885:34; Mendoza-González and Mateo-Cid, 1986:423; Gonzáles-González et al., 1996:211(in part).

REMARKS. *Callophyllis violacea* was mistakenly reported from the northern Gulf (Norris, 1973). The specimen (*JN-369*) was a gift, but the locality was apparently mislabeled and it is not from Bahía Bocochibampo. It was subsequently recorded from Guaymas (Mendoza-González and Mateo-Cid, 1986), but since then has not been reported in the northern Gulf. These specimens need to be reexamined before its presence can be verified.

CROSSOCARPACEAE

Crossocarpaceae Perestenko, 1975:1679.

Algae have entire margins and mostly simple to divided blades, with a few having stalked proliferations. Medulla is composed of large cells, relatively short-celled filaments, and slender filaments, with elongate, branched, and spinulose refractive cells. Cortex is relatively thin, with cortical cells becoming progressively smaller toward the thallus surface.

Tetrasporophytes and gametophytes, where known, are isomorphic. Tetrasporangia are irregularly cruciately divided; scattered in the cortex, attached laterally to outer cortical cells. Female reproductive structures develop within the blades or in marginal or surface proliferations (i.e., *Erythrophyllum* J. Agardh, 1872). Carpogonial branches are three-celled and borne on a clavate to lobed supporting cell along with up to four clavate to lobed subsidiary cells. Auxiliary cells, with up to four subglobose subsidiary cells, develop on a different branch system. After fertilization, the carpogonial fusion cell develops from the carpogonium, supporting cell, and subsidiary cells, initiating branched, connecting filaments that contact both auxiliary cells and specialized vegetative accessory filaments. Gonimoblast filaments appear to develop from the accessory filaments. Carposporangia are produced in clusters at the apices of gonimoblast filaments, and an embedded, large, diffuse cystocarp forms without an ostiole. Spermatangia are unknown.

REMARKS. The status of the family Crossocarpaceae has been under contention (Lobban and Wynne, 1981; Selivanova, 2002). Hansen and Lindstrom (1984; Scagel et al., 1989) treat it as a subgroup of the Kallymeniaceae, whereas others have accepted the family (Perestenko, 1986, 1996; Zinova and Gussarova, 1977; Schneider and Wynne, 2007; Guiry and Guiry, 2008–2010). The phycocolloid composition of some species of Crossocarpaceae were heterogeneous, indicating the need for their taxonomic reexamination (Chopin et al., 1999).

One genus is reported in the northern Gulf of California.

Kallymeniopsis Perestenko

Kallymeniopsis Perestenko, 1977:398; Perestenko, 1996:103, pl. 10: figs.13–21, pl. 31: fig. 6.

Kallymeniopsis Perestenko, 1975:1679, *nom. invalid.*

Foliose algae that are obovate, orbiculate, reniform, or circinate in shape, growing from a short stipe and a fleshy a discoid holdfast. Blades may be entire, lobed, or lacerated into broadly lanceolate to wedge-shaped segments; with smooth margins and a blade surface that may be smooth, undulate, or sometimes verrucose. Internal structure is composed of a filamentous medulla, with elongate, branched spiniferous refractive cells. The cortex is of mostly isodiametric cells that become smaller toward the surface.

Tetrasporophytes and gametophytes, where known, are isomorphic. Tetrasporangia are cruciately divided and scattered in the cortex over the blade. Carpogonial branch is 3-celled; each carpogonial branch is borne on the supporting cell together with up to 4 subsidiary cells. After presumed fertilization, the fusion cell develops from the carpogonium, supporting cell, and subsidiary cells. Auxiliary cells are borne on separate branch systems. Cystocarps are immersed to protruding, with sterile filaments interspersed among groups of carposporangia. Spermatangia occur in large soral areas scattered over the surface of the blade. (G. I. Hansen, Oregon State University, personal communication).

REMARKS. The generic status of *Kallymeniopsis* Perestenko may require further elucidation. Although Hansen (1997) has accepted the genus, Lindstrom (in Guiry and Guiry, 2009) suggested the genus may be congeneric with *Kallymenia*. Molecular analysis by Clarkston and Saunders (2010: fig. 2) revealed British Columbia *Kallymeniopsis oblongifructa* to be in a clade with another member of the Kallymeniaceae, *Erythrophyllum delesserioides* J. Agardh (1872; generitype; type locality: Vancouver Island), and also with *Hommersandia palmatifolia* (Tokida) Perestenko ex O. N. Selivanova et G. G. Zhigadlova (1997; basionym: *Pugetia palmatifolia* Tokida, 1948:37; type locality: Higasi-soya, Saghalien, Japan). This clade was distinct from a clade with the generitype of *Kallymenia*, i.e., *K. reniformis* (Turner) J. Agardh (1842; type locality: Isle of Wight, SE England, UK) and supports the generic separation of *Kallymeniopsis*.

Perestenko (1977) treated *Kallymeniopsis* as a member of the family Crossocarpaceae. Although this placement of the genus has been accepted by some (Perestenko, 1986, 1996; Zinova and Gussarova, 1977; Schneider and Wynne, 2007), others contend it should be treated in the Kallymeniaceae (e.g., Hansen and Lindstrom, 1984; Scagel et al., 1989; Clarkston and Saunders, 2012). In Clarkston and Saunders (2010) the *Kallymeniopsis* clade is basal in the Kallymeniaceae tree, suggesting it could be treated either way. Herein, it is tentatively treated in the Crossocarpaceae until the generitype, *Kallymeniopsis lacera* (Postels et Ruprecht) Perestenko (1977; basionym: *Iridaea lacera* Postels et Ruprecht, 1840), can be further morphologically and molecularly tested.

Kallymeniopsis is primarily a subboreal to cold-temperate genus known in the North Pacific from the Kuril Islands

("Kurile") and Okhotsk Sea (Russia) to Alaska (Perestenko, 1996). One species, *Kallymeniopsis oblongifructa*, recorded from Alaska to northern California in the northeastern Pacific (Scagel et al., 1989; Hansen, 1997), was recently reported in the northern Gulf of California (Hernández-Kantún et al., 2010, as *Kallymenia oblongifructa*).

***Kallymeniopsis oblongifructa* (Setchell) G. I. Hansen**

Iridaea oblongifructa Setchell, 1901:123; Setchell and Gardner, 1903:300.

Kallymeniopsis oblongifructa (Setchell) G. I. Hansen, 1997:194; Clarkston and Saunders, 2010:129, tbl. 1, figs. 1, 2; Clarkston and Saunders, 2012: figs. 1–4.

Kallymenia oblongifructa (Setchell) Setchell, 1912:234 [as "*Callymenia oblongifructa*"]; Abbott, 1968:197; Abbott and Hollenberg, 1976:454, fig. 402; Lindstrom, 1977:177; Scagel et al., 1989:203; Hernández-Kantún et al., 2010:2, fig. 3A–D.

Algae foliose; single or in clusters of several erect blades, 10–15(–30) cm tall; simple, obovate or broadly lanceolate and often lobed, with smooth margins; blades 100–250 μm thick; short stipe above a fleshy discoid holdfast. Medulla of periclinal filaments, 3–4 μm in diameter, and some elongate, spiniferous refractive cells running parallel to the periclinal medullary filaments. Cortex of 3–4 layers of cells, decreasing in size outwardly; inner cortical cells up to 45 μm in diameter, with projections or stellate-like extensions (as the thallus expands, subcortical cells become stretched between pit connections to form these stellate-like cells; G. I. Hansen, Oregon State University, personal communication); outer cortical cells mostly 4 μm in diameter (description after Hernández-Kantún et al., 2010).

Tetrasporangial, cystocarpic, and spermatangial thalli not known in Gulf of California.

HABITAT. Epiphytic on rhodoliths (crustose coralline nodules); rhodolith beds in subtidal channels with strong currents; 13–20 m depths.

DISTRIBUTION. Gulf of California: Isla San Pedro Nolasco. Eastern Pacific: Bering Sea and Aleutian Islands, Alaska to Mendocino County, northern California. Western Pacific: Russia.

TYPE LOCALITY. Cast ashore, on stipes of kelp; Whidbey Island ("Whidby"), Island County, Puget Sound, Washington, USA.

REMARKS. *Kallymeniopsis oblongifructa* was recently reported in the warmer subtidal waters of the northern Gulf of California by Hernández-Kantún et al. (2010, as *Kallymenia oblongifructa*). Their specimens were described as "cuneately divided," a character of *Kallymeniopsis lacera* (Postels et Ruprecht) Perestenko (1977; G. I. Hansen, Oregon State University, personal communication, 2010). This is a remarkable find since *K. oblongifructa* was previously known only in the colder subtidal waters of the northeast Pacific (Alaska to northern California). The northern Gulf *Kallymeniopsis oblongifructa* needs to be further studied and compared molecularly with type locality materials of *K. oblongifructa* and *K. lacera* and with other Gulf members of the Kallymeniaceae to elucidate their relationships.

PHYLLOPHORACEAE*

Phyllophoraceae Rabenhorst, 1863:281.

The Phyllophoraceae is a small family composed of erect, cylindrical to compressed thalli, which are mostly dichotomously branched. Most members are rather firm in texture. They are multiaxial, with growth occurring from marginal or apical meristems. Internal structure is usually pseudoparenchymatous, with a medulla that is composed of large compacted isodiametric cells or slender parallel longitudinal filaments and a cortex of similar but much smaller cells.

This family exhibits a wide diversity of reproductive adaptations and life histories, which can be isomorphic, heteromorphic, apomictic, or tetrasporoblastic. Members can be isomorphic, with erect tetrasporophytes and gametophytes; or distinctly heteromorphic, with erect gametophytes and crustose tetrasporophytes; or erect gametophytes (without separate tetrasporophytes) that produce tetrasporangia in nemathecia. There is also one genus that is parasitic. In all cases the tetrasporangia are cruciately divided and either develop in bead-like chains on an isomorphic tetrasporophyte or within nemathecia developed on a monoecious gametophyte or in a crustose thallus of those with heteromorphic tetrasporophytes and gametophytes. The female reproductive apparatus is a procarp consisting typically of a three-celled filament with a supporting cell also bearing a sterile filament. This supporting cell becomes the auxiliary cell. Cystocarps are embedded within the thallus, often filling the entire cross section of the branch. The gonimoblast filaments develop small carposporangia that are formed in dense, crowded compartments among sterile tissue. Spermatangia, where known, are developed in superficial sori but have not been convincingly described for many of the species.

There are three genera of the Phyllophoraceae represented in the northern Gulf of California.

KEY TO THE GENERA OF PHYLLOPHORACEAE IN THE GULF OF CALIFORNIA

1a. Thalli of distinctly flat, narrow blades; isomorphic; tetraspores cruciately divided, in chains within nemathecia . . . . *Petroglossum*

1b. Thalli terete or compressed to flattened branches; heteromorphic or tetrasporoblastic; tetrasporangia cruciately divided, in chains in crustose thalli, or irregularly divided in large nemathecia on branch surfaces 2

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* Contributed by James N. Norris and Suzanne Fredericq. S. Fredericq: Department of Biology, University of Louisiana at Lafayette, Lafayette, Louisiana 70504, USA.

2a. Erect gametophytes of narrow terete to compressed branches, 0.5–2.5 mm wide; life history heteromorphic, tetrasporophytes a separate crustose phase . . . . *Ahnfeltiopsis*
2b. Erect gametophytes of terete, compressed, or flattened branches; life history tetrasporoblastic, monoecious gametophyte with gonimoblasts ("tetrasporoblasts") developed from auxiliary cells within the medulla that grow outward to produce tetrasporangia within conspicuous, large, external nemathecia . . . . *Gymnogongrus*

Ahnfeltiopsis P. C. Silva et DeCew

Ahnfeltiopsis P. C. Silva et DeCew, 1992:576.

Gametophytes are upright, slightly to very rigid, of narrow, terete to flattened axes that are infrequently to repeatedly dichotomously, subdichotomously, or irregularly branched. They arise above discoid holdfasts, which are often covered with terete, rhizome-like, lowermost, prostrate branches. The medulla is pseudoparenchymatous, composed of slender, parallel longitudinal filaments. The cortex is composed of small cells in anticlinal rows.

Life histories are heteromorphic, with erect gametophytes and a fleshy crustose tetrasporophyte (Masuda et al., 1979; Masuda, 1981; DeCew and West, 1981; Fredericq and Ramírez, 1996; Masuda and Kogame, 1998; Fredericq and Lopez-Bautista, 2002; Fredericq et al., 2003). A direct life history in which the female gametophytes apomictically produce carposporophytes is also known for some species (DeCew and West, 1981; Masuda and Norris, 1994). Tetrasporophytic crusts produce cruciately divided tetrasporangia in intercalary chains. Erect female gametophytes develop a three-celled carpogonial branch on a supporting cell that is functionally an auxiliary cell. The first cell of the carpogonial branch bears a sterile cell. Cystocarps are produced internally, as they develop within the medulla the cortex thickens and protrudes, and pores (carpostomes) of short periclinal filaments are formed from the anticlinal cortical cells. Carpospores are released through the carpostomes. Spermatangia are elongate, four to five times longer than in diameter, and develop in pairs in superficial sori.

There are four species known in the northern Gulf of California.

KEY TO THE SPECIES OF *AHNFELTIOPSIS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Branched infrequently, subdichotomously, 1–3 orders; branches simple, terete to slightly compressed below, above flattened, strap shaped, up to 2.5 mm wide . . . . *A. serenei*
1b. Branched repeatedly dichotomously to subdichotomously, up to 4–8 (or more) orders 2
2a. Branches compressed to flattened, less than 1 mm wide; margins without lateral proliferations; apices forked to digitate . . . . *A. hancockii*
2b. Branches compressed to flat, wider than 1 mm, up to 2–3 mm wide; apices simple to divaricate 3
3a. Branches flattened throughout (except the very short stipe); mostly 2.0–3.0 mm wide; with few to many lateral proliferations, up to 1 cm long; branch apices divaricate, much narrowed in width, with pointed tips . . . . *A. divaricata*
3b. Branches initially compressed, becoming markedly flattened upward narrower; 1.0–1.5 mm wide . . . . . *A. leptophylla*

Ahnfeltiopsis divaricata (Holmes) Masuda

Gymnogongrus divaricatus Holmes, 1896:255, pl. 8: fig. 3a,b; Okamura, 1934a:16, pl. 310: fig. 105; Dawson, 1944a:301, pl. 71: fig. 2 [two specimens on right]; Masuda, 1987:55, figs. 10A–C [holotype], 11A–H, 12A–G; González-González et al., 1996: 220.

Ahnfeltiopsis divaricata (Holmes) Masuda, 1993:2; Masuda et al., 1994:168, figs. 6, 20, 21, 32; Yoshida, 1998:776; Abbott, 1999:160, fig. 39F.

Algae erect, up to 3(–5) cm tall, repeatedly dichotomously branched at wide angles, up to 5 or more orders; branches mostly 2.0–3.0 mm wide; initial axis more or less terete above basal attachment disc, abruptly becoming compressed upward; branches without or with few to many lateral proliferations; branch apices narrowed to about 1.0 mm wide; uppermost tips divaricate, pointed, about 5 mm wide. Medulla of large colorless cells; cortex of small, pigmented cells in anticlinal rows.

Tetrasporophytes not known in Gulf. Reproductive structures develop on margins and surfaces of upper branches and lateral proliferations. Cystocarps prominent, 550–750 µm tall, 500–1000 µm wide; with several carpostomes. Spermatangia in sori near branch apices; 1–2 develop from spermatangial parent cell; spermatia elongated, 10–12 µm tall, 2–3 µm wide (after Masuda, 1987).

Habitat. On rocks; low intertidal.

Distribution. Gulf of California: Puerto Lobos; Isla Turner (off SE end of Isla Tiburón). Central Pacific: Hawaiian Islands. Western Pacific: Japan; Philippines.

Type Locality. Shimoda, southern Izu Peninsula, Shizuoka Prefecture, central Japan (Masuda, 1987:54).

Remarks. Specimens of the northern Gulf are tentatively referred to *Ahnfeltiopsis divaricata*. These may sometimes be confused with some smaller forms of *Gymnogongrus johnstonii*. Although Dawson (1961a, as *G. johnstonii*) thought the Gulf material of these represented only one species, there appears to be two species among his collections.

The most obvious difference between them is a generic character, which can be seen in life history studies: *Ahnfeltiopsis* has a heteromorphic life history (erect gametophytes and crustose tetrasporophytes), whereas *Gymnogongrus* has a tetrasporoblastic type of life history (tetrasporangia produced in wart-like nemathecia). Thus, reproductive characters of some similar-looking specimens of Gulf *Ahnfeltiopsis divaricata* will have cystocarps, and those of smaller *Gymnogongrus johnstonii* will have nemathecia with tetraspores. Gulf material referred to *A. divaricata* should be molecularly compared with those from Japan as well as with the Gulf *G. johnstonii* to test its taxonomic status.

Specimens of *A. divaricata* from Peru (Acleto O., 1973:57, as "*G. divaricatus*," fig. 197) are probably a different species. On the basis of *rbc*L sequence analysis, *Ahnfeltiopsis divaricata* from Hawaii was found to be a distinct species from *G. johnstonii* (Fredericq and Lopez-Bautista, 2002).

Ahnfeltiopsis hancockii* (E. Y. Dawson) J. N. Norris et Fredericq, *comb. nov.

FIGURE 171

Gymnogongrus hancockii E. Y. Dawson, 1944a:300, pl. 71: fig. 2 [upper left]; 1950b:337 [in part], fig. 1 [left large specimen only]; González-González et al., 1996:221; Fernández-García et al., 2011:62.

Gymnogongrus johnstonii sensu Dawson, 1961a:250 [in part, only small "depauperate forms"], pl. 43 [lower left insert only] [non *Gymnogongrus johnstonii* (Setchell et N. L. Gardner) E. Y. Dawson, 1954c:294; basionym: *Callophyllis johnstonii* Setchell et N. L. Gardner, 1924:746].

Algae usually in clumps, 2.0–4.5 cm tall, of compressed to flattened, narrow branches, 1–3 mm wide; branching subdichotomously, often widely divaricate, at 2–5 mm intervals; branches about 300 μm in thickness, with smooth surfaces, margins usually without lateral proliferations or, if present, sparse and short, usually less than 2 mm in length, and with slightly pointed apices; branch tips divided 2 times (forked) or 3–4 times (digitate).

Tetrasporangia more or less cruciately divided; within large, irregularly shaped, globose nemathecia, up to 1.0 mm in diameter, mostly on margins, sometimes on surfaces in upper portions of the branches. Cystocarps about 450 μm in diameter; partly embedded within frond surface and protruding about 200–300 μm above surface; with several carpostomes.

HABITAT. On rocks; mid to low intertidal.

DISTRIBUTION. Gulf of California: San Felipe to Santa Rosalía; Bahía San Francisquito; Mazatlán. Eastern Pacific: Costa Rica.

TYPE LOCALITY. "Point approximately 3 miles [~4.8 km] north of Kino" (Dawson, 1944a); probably in the vicinity of Kino Nuevo (north of Kino Viejo), Bahía Kino, Sonora, Gulf of California.

REMARKS. Although the combination *Ahnfeltiopsis hancockii* is proposed, it is with some reservation that this species is reinstated. The Gulf *A. hancockii* seems to be close to *A. divaricata*, differing mostly in being sparsely branched and usually without lateral proliferations. Specimens of *A. hancockii* need to be critically compared with Gulf material referred to *A. divaricata* and to type material from Japan (cf. Masuda, 1987, 1993). Although Dawson (1961a, as *Gymnogongrus hancockii*) without comment considered *Ahnfeltiopsis hancockii* to be a

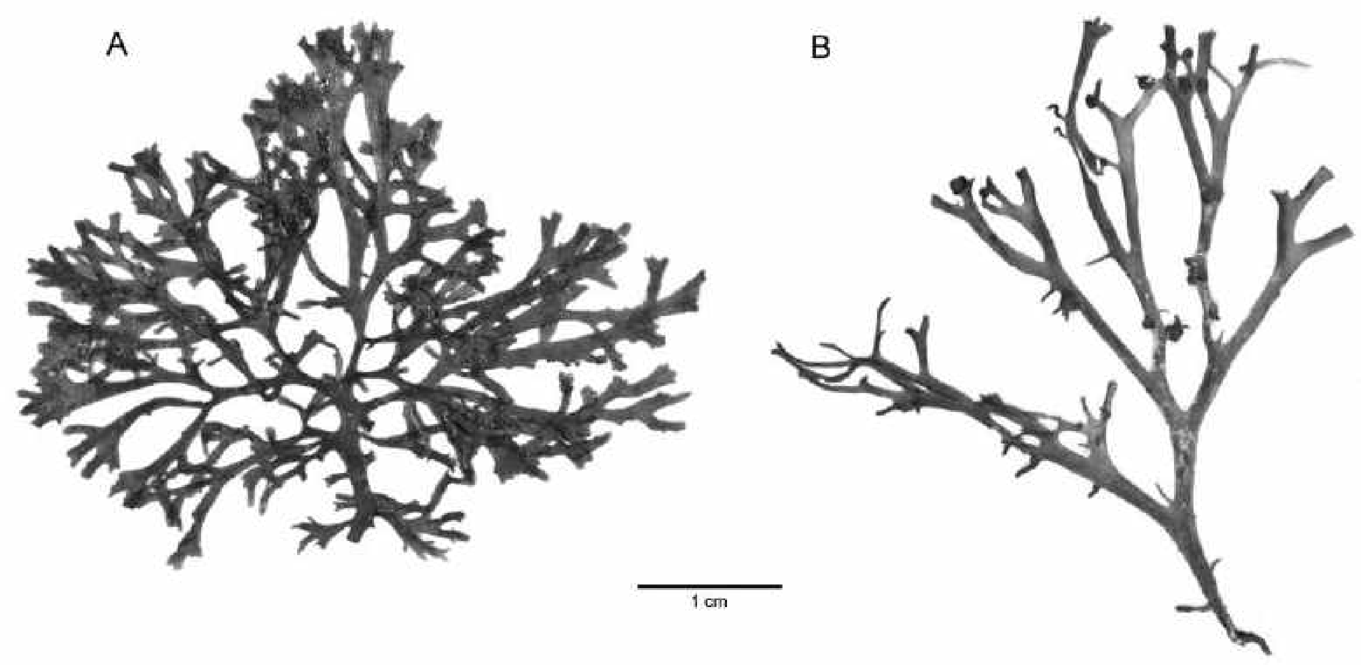

FIGURE 171. *Ahnfeltiopsis hancockii*: A. Habit (*EYD-405*, US Alg. Coll.-208111). B. Tetrasporangial nemathecia, mostly borne on margins (*JN-3228*, US Alg. Coll.-159896).

"depauperate form" conspecific with *G. johnstonii*, herein these two are separated on their habit and reproductive morphology (cystocarps in *A. hancockii* and nemathecia with tetrasporangia in *G. johnstonii*). Other Pacific Mexico records of "depauperate forms" of *G. hancockii* sensu Dawson (1961a) from Jalisco, Guerrero, Oaxaca, and Isla Socorro (Islas Revillagigedo) may also be *A. hancockii*.

Ahnfeltiopsis leptophylla (J. Agardh) P. C. Silva et DeCew

Gymnogongrus leptophyllus J. Agardh, 1876:211; Kylin, 1941:26; Smith, 1944:273, pl. 65: fig. 1; Dawson, 1945c:61; Dawson et al., 1960a:64, pl. 32: fig. 1; Dawson, 1961a:251, pl. 40: fig. 3; 1961b:431; Abbott and Hollenberg, 1976:506, fig. 453; DeCew and West, 1977b:118; Silva, 1979:322; DeCew and West, 1981:242, figs. 17–34; L. Aguilar-Rosas et al., 1982:56; Pacheco-Ruíz and Aguilar-Rosas, 1984:77; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1986:424; Scagel et al., 1989:190; R. Aguilar-Rosas et al., 1990:125; Stewart, 1991:107; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:483; R. Aguilar-Rosas and Aguilar-Rosas, 1994:522; Mateo-Cid and Mendoza-González, 1994b:40; González-González et al., 1996:221, 396; Hernández-Herrera et al., 2005:148.

Ahnfeltiopsis leptophylla (J. Agardh) P. C. Silva et DeCew, 1992:578; Stout and Dreckmann, 1993:11.

Algae in clumps, up to 6 cm tall, dark reddish brown; of few to several erect, rigid, entangled, slender, branched main axes, initially cylindrical to subcylindrical, 0.5 to 1.0 mm wide, becoming compressed to flattened and shorter upward, 0.5–1.25 mm wide; dichotomously to subdichotomously branched, up to 5 (or more) orders in more or less 1 plane; branch intervals longer in lower portions, much less in upper portions; above a spreading, discoid attachment base.

Life histories of this species are known to be heteromorphic or apomictic (DeCew and West, 1981; Silva and DeCew, 1992). Cystocarps initially develop immersed within the branches and, later, as they mature, protrude on both sides of surface; vertical elliptical in shape, about 900–1000 μm long. Spermatangia in a continuous layer, 20–25 μm thick, on surface of upper branches; spermatia borne on slender, anticlinally elongated, spermatangial parent cells (after Dawson, 1961b).

HABITAT. On rocks and tidal platforms; intertidal.

DISTRIBUTION. Gulf of California: Punta Chueca (*Socaaix* in the language of the Seri) to Segundo Cerro Prieto, Bahía Kino; Isla Pelícanos and Roca Rojo (both in Bahía Kino); Nayarit to Jalisco. Eastern Pacific: Alaska to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Islas Todos Santos (off Ensenada), Baja California; Colima to Michoacán.

TYPE LOCALITY. Santa Cruz, Santa Cruz County, California, USA.

Ahnfeltiopsis serenei (E. Y. Dawson) Masuda

FIGURE 172

Gymnogongrus serenei E. Y. Dawson, 1954a:5, pl. 3: fig. 6; 1954b:441, fig. 52d [type specimen]; 1961a:252, pl. 39: fig. 2; 1961b:431; Phạm-Hoàng, 1969:201, fig. 2.132; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:221, 396.

Ahnfeltiopsis serenei (E. Y. Dawson) Masuda, 1993:3, figs. 4–6; Masuda et al., 1994:177, fig. 5; González-González et al., 1996:382; Xia and Zhang, 1999:102, fig. 60, pl. 5: fig. 5; Serviere-Zaragoza et al., 2007:9.

Algae of several, cartilaginous, narrow, axes; sparsely, dichotomously branched up to 3 orders; initially terete, 1.0–1.2 mm in diameter, becoming compressed to flattened upward, 1.5–2.5 mm wide, 250–350(–400) μm thick; arising from a discoid attachment. Branch surfaces smooth; margins entire; apices blunt. Medulla in transection of rounded cells, 30–50 μm in diameter; lowermost portion composed of 14–18 medullary cells, upper portions of 10–12 cells; in longitudinal section of elliptical cells, with intercellular connections. Cortex in lowermost terete portion of 14 (or more) cortical cell layers thick; in upper flattened portions of 3–6 small, more or less rectangular cells, 4–5 μm in diameter, in anticlinal rows (after Masuda, 1993).

Tetrasporophyte unknown in the Gulf of California. Cystocarps central within medulla, developing outward, becoming hemispherical, 600–800 μm (or more) in diameter; markedly prominent, protruding up to 550 μm above blade surface; with multiple carpostomes in thickened cortex of 14–18 anticlinal rows of cells; 8–10 rows of cells on opposite side. Spermatangia 8–10 μm long, 2.0–2.5 μm in diameter; within elongated sori on surface of upper portion of branches (reproduction after Masuda et al., 1994).

HABITAT. On wave-exposed offshore rocks; low intertidal.

DISTRIBUTION. Gulf of California: Cabo San Lucas; Nayarit to Jalisco. Eastern Pacific: Isla San Benedicto (Islas Revillagigedo); Oaxaca. Western Pacific: China; Vietnam.

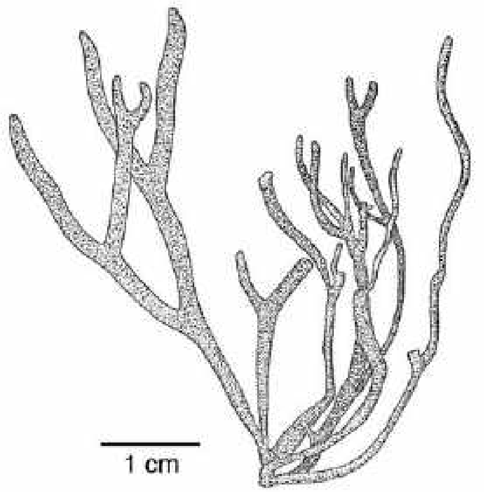

FIGURE 172. *Ahnfeltiopsis serenei*: Part of a tufted plant (*EYD-12058*; after Dawson, 1954: pl. 3: fig. 6, as *Gymnogongrus serenei*).

TYPE LOCALITY. On "roches noires" (ryolite rock); north end of Con Se Tre Island (Île de Tre), off Nha Trang, Khanh Hoa Province, south central Vietnam.

REMARKS. Described from south Vietnam, *Ahnfeltiopsis serenei* has been reported in Pacific Mexico and the southern Gulf of California; it is included since it may occur northward in the Gulf. The taxon *Gymnogongrus serenei* was published twice in 1954, first validly published by Dawson (1954a ["17 September 1954"]) and then again invalidly by Dawson (1954b ["October 1954"]).

Gymnogongrus Martius

Gymnogongrus Martius, 1833:27.

Gametophytes are erect, solitary or in clumps, and dichotomously branched (usually in one plane) above a lower terete region that usually extends only to the first or second branch dichotomy and then becomes subcylindrical to compressed upward; margins are with or without lateral proliferations and are attached by a discoid to expansive crustose base. The pseudoparenchymatous medulla is dense, composed of both large and small angular cells, often with rounded corners. The cortex consists of radial rows of compacted smaller cells.

Tetrasporangia, where known, are irregularly cruciate and found in protruding nemathecial pustules that are scattered and usually lateral on branches on the erect gametophytes. The female reproductive apparatus is a procarp consisting of a three-celled carpogonial branch. Cystocarps are globose, embedded in the branches, and have more than one ostiole. Spermatangia are superficial on the upper branches.

Three species are known in the Gulf of California, including one of questionable generic status.

KEY TO THE SPECIES OF *GYMNOGONGRUS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli somewhat flattened; mostly more or less subdichotomously or sometimes irregularly branched; branches 1.0–1.5 mm wide, without lateral proliferations . . . . ***G.? carnosus***
1b. Thalli distinctly flattened, with wider branches, 1.5 mm to more than 2 mm in width; with or without lateral proliferations 2
2a. Thalli mostly 1.5 mm wide, divaricately, dichotomously branched, mostly from lower portions of branch segments . . . . ***G. guadalupensis***
2b. Thalli dichotomously to subdichotomously branched; branches wider, 2–5 mm in width, with few to numerous simple or forked lateral proliferations, up to 1.2 cm long . . . . ***G. johnstonii***

***Gymnogongrus? carnosus* Setchell et N. L. Gardner**

Gymnogongrus carnosus Setchell et N. L. Gardner, 1924:745, pl. 22: fig. 1, pl. 47a [type specimen]; Dawson, 1944a:299; 1961a:248; 1961b:431; González-González et al., 1996:220.

Alga erect, up to 10 cm tall, slightly cartilaginous; purplish red, compressed throughout; main axis 3–5 mm wide, irregularly and more or less subdichotomously branched, 3–5 orders; branches 2–4(–5) mm wide; above a short stipitate region (to about 5 mm long), attached below by a small discoid holdfast. Medulla in transection of large, rounded, rectangular to oval, thick-walled cells; outward grading into smaller, subspherical cells of inner cortex that merge to small, thick-walled cortical cells in anticlinal rows of 6–9.

Tetrasporangia and spermatangia unknown. Cystocarps relatively small; immersed within frond (after Setchell and Gardner, 1924).

HABITAT. Known only from beach drift.

DISTRIBUTION. Gulf of California: Isla San Pedro Mártir.

TYPE LOCALITY. Cast ashore; Isla San Pedro Mártir, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. A northern Gulf endemic, *Gymnogongus? carnosus* has not again been collected and remains known only from the type collection. Setchell and Gardner (1924:745) noted that the cell walls of *G.? carnosus* were of a "very gelatinous nature" ("gelatinizing readily in freshwater after drying") and that the "combination of characters of this species" make it uncertain that it is a *Gymnogongrus*. More collections are needed to determine the generic status of *G.? carnosus* (herein with a taxonomic generic query).

***Gymnogongrus guadalupensis* E. Y. Dawson**

Gymnogongrus guadalupensis E. Y. Dawson, 1961a:249, pl. 24: fig. 3, pl. 45: fig. 1 [type specimen]; 1961b:431; 1966b:64; Stewart and Stewart, 1984:143; Mendoza-González et al., 1994:107; González-González et al., 1996:220.

Algae erect, bushy, of 1 to few branched axes, 4–5 cm tall, each becoming compressed to flattened, up to 1.5 mm wide, above a short, cylindrical stipe, 2–4 mm long; attached by a small discoid holdfast. Branching divaricately, dichotomously at intervals of 3–12 mm; become slightly twisted in various planes; branches 1.5 mm wide, about 350 μm thick, of more or less uniform width throughout, tending to narrow to 1.0 mm in width in ultimate branches, with blunt rounded apices. Medulla of thick-walled, elliptical cells, 45–70 μm in middle of medulla, becoming smaller outward, 18–25 μm.

Sporophytes unknown. Cystocarps bulging, elliptical dome-like, 0.8–1.0 mm in diameter, about 500 μm tall; scattered on axes in middle and upper portions. Spermatangia not known.

HABITAT. On rocks and in tide pools; intertidal.

DISTRIBUTION. Gulf of California: Cabeza Ballena; Mazatlán. Eastern Pacific: Isla Guadalupe.

Type Locality. Outer reef and pools; southernmost tip of Isla Guadalupe, off Baja California, Pacific Mexico.

Remarks. *Gymnogongrus guadalupensis* is reported in the southern Gulf. It is included here because of its resemblance to some of the Gulf *Ahnfeltiopsis divaricata*. More collections are needed to test their relationship and elucidate its generic status of the type.

Gymnogongrus johnstonii (Setchell et N. L. Gardner) E. Y. Dawson

FIGURE 173

Callophyllis johnstonii Setchell et N. L. Gardner, 1924:746, pl. 51: figs. A,B.

Gymnogongrus johnstonii (Setchell and N. L. Gardner) E. Y. Dawson, 1954c:294; 1959a:26, fig. 6A; 1961a:250 [in part; excluding "depauperate form"], pl. 43 [larger right specimen only]; 1961b:431; Norris, 1973:13; Huerta-Múzquiz, 1978:338; Norris, 1985d:212; Serviere-Zaragoza et al., 1993a:483; Mendoza-González et al., 1994:107; González-González et al., 1996:221; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:468; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:209; Bernecker, 2009:CD-Rom p. 63; Fernández-García et al., 2011:62.

Algae bushy, up to 25 cm tall, variable in branching and size; of few to several erect, complanate branches, 2–4(–5) mm wide; attached below by a small pseudoparenchymatous holdfast. Branching somewhat divaricate (much less so in larger thalli), much more or less dichotomously or subdichotomously branched at 3.0–12 mm intervals, secondary branches pinnate. Branches with few to numerous simple to forked lateral branchlets, mostly at 1–2 mm intervals, 3.0–11 mm long. Medulla of thick-walled cells, about 100 μm in diameter; subcortex of 3–4 layers of smaller cells, 20–25 μm in diameter; outer cortex of anticlinal rows of branched filaments of 4–5 cells, 5 μm in diameter; inner cells of cortical filament rows spherical, outermost cells elongated.

Tetrasporangia within nemathecia up to 1 mm in diameter; scattered over blade surface. Cystocarps globose, 700–800 μm in diameter, embedded within and bulging on one blade surface; scattered throughout upper portions of blade. Spermatangia superficial, covering upper portion of blade surfaces.

Habitat. On rocks; mid intertidal to shallow subtidal.

Distribution. Gulf of California: San Felipe to Santa Rosalía; Punta Arena to Cabo Pulmo; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Isla Socorro (Islas Revillagigedo); El Salvador; Costa Rica.

Type Locality. Isla de Tortuga, about 24.1 km (15 miles) northeast of Isla Marcos, off Puerto Santa Rosalía, Baja California Sur, Gulf of California, Mexico.

Remarks. *Gymnogongrus johnstonii* is especially abundant in the spring, exhibiting highly variable morphologies. The largest specimens of *G. johnstonii* are quite distinct and are mostly found in the central Gulf, particularly on Islas de la Cintura (Midriff Islands).

Petroglossum Hollenberg

Petroglossum Hollenberg, 1943:571, figs. 1–6; Schotter, 1968:75, figs. 46–50; Abbott, 1969:47.

Algae are erect and may be singular but usually have a few to several small, flat, narrow, cartilaginous, ligulate blades arising from a spreading encrusting or stoloniferous base. Each narrow blade is above a short stipe or a very narrowed basal region. Blades may be simple (unbranched) or irregularly subdichotomously branched and are with or without lateral or terminal proliferations. Medulla is composed of large, thick-walled cells and a cortex of one to two layers of smaller cells.

Tetrasporangia are cruciately divided and arranged in distinct anticlinal rows within nemathecia that are single in center of a blade. Gametangial structures are usually singular in the center of a blade, but cystocarps may also be on short laterals, and spermatangia may also be central or toward branch apices. Cystocarps are prominent, protruding on both sides of blades, with or without an ostiole. Carpospores are in groups that are separated by sterile cells. Spermatangial parent cells produce spermatangia within sori that are flush with the branch surface.

One species of *Petroglossum* is reported in the northern Gulf of California.

Petroglossum parvum Hollenberg

FIGURE 174

Petroglossum parvum Hollenberg, 1945:450; Dawson, 1949c:229; 1961a:244, pl. 40: fig. 2 [type specimens]; 1961b:431; 1966b:64, fig. 6D,E; Abbott and Hollenberg, 1976:511, fig. 458; Stewart, 1991:108; González-González et al., 1996:246; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:209.

Algae of small, narrow, ligulate blades, 1–3 cm tall, mostly strap-like 2.0–3.0(–4.0) mm wide; simple (unbranched) or divided once dichotomously (or occasionally subdichotomously) or rarely divided in threes from upper end; with rounded apices; arising from spreading prostrate axes and may also sometimes be attached by secondary discs developed along margins of prostrate growing blade (Figure 174A,B). A few blades gradually narrowing toward base; some with few short laterals. Internally of few cell layers; central portions of blade 180–190 μm thick; medulla of 1–2 large cells (Figure 174C,D); subcortex of 1–2 smaller cells; outer cortex of single layer of small, pigmented cortical cells.

Reproduction not known in the northern Gulf. Reproductive structures as reported in California (Abbott and Hollenberg, 1976) occur in center of blades. Tetrasporangia in anticlinal rows of 3–5 (Abbott and Hollenberg, 1976: fig. 458), within small rounded nemathecia, usually 1 per blade, protruding from both surfaces. Cystocarps with small, single ostiole. Spermatangia in small rounded, nemathecia.

Habitat. On rocks, pebbles, coralline rubble, and debris; subtidal, 13–18 m depths.

Distribution. Gulf of California: Isla Salsipuedes (NW of Isla Las Ánimas), Islas de San Lorenzo (SW Islas de la

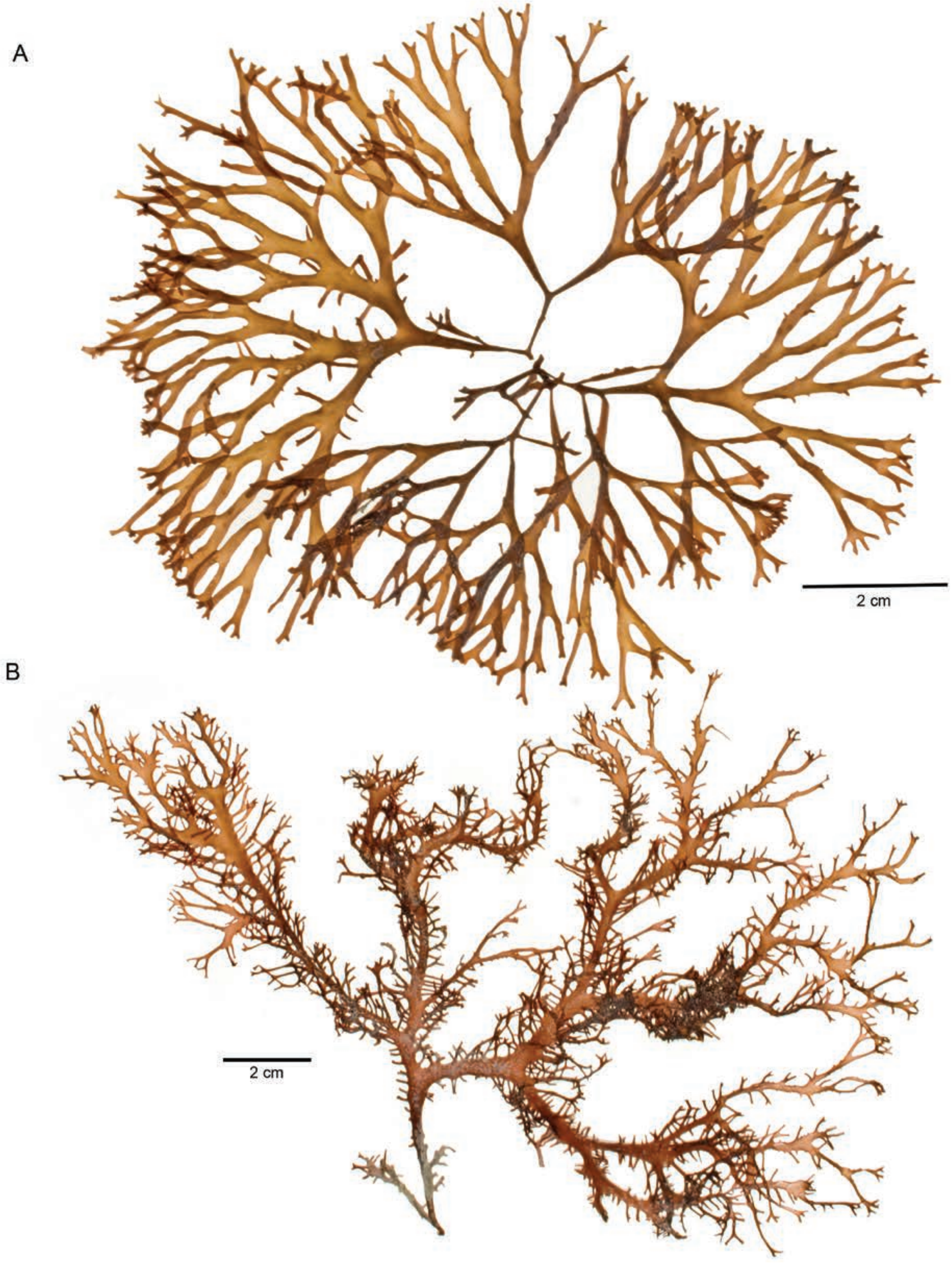

FIGURE 173. *Gymnogongrus johnstonii*, two thalli to show variation in density of spinulose branchlets: A. Specimen bearing a few short, lateral, spinulose branchlets (*JN-6205*, US Alg. Coll.-159912). B. Specimen with numerous spinulose branchlets (*JN-5736*, US Alg. Coll.-159906).

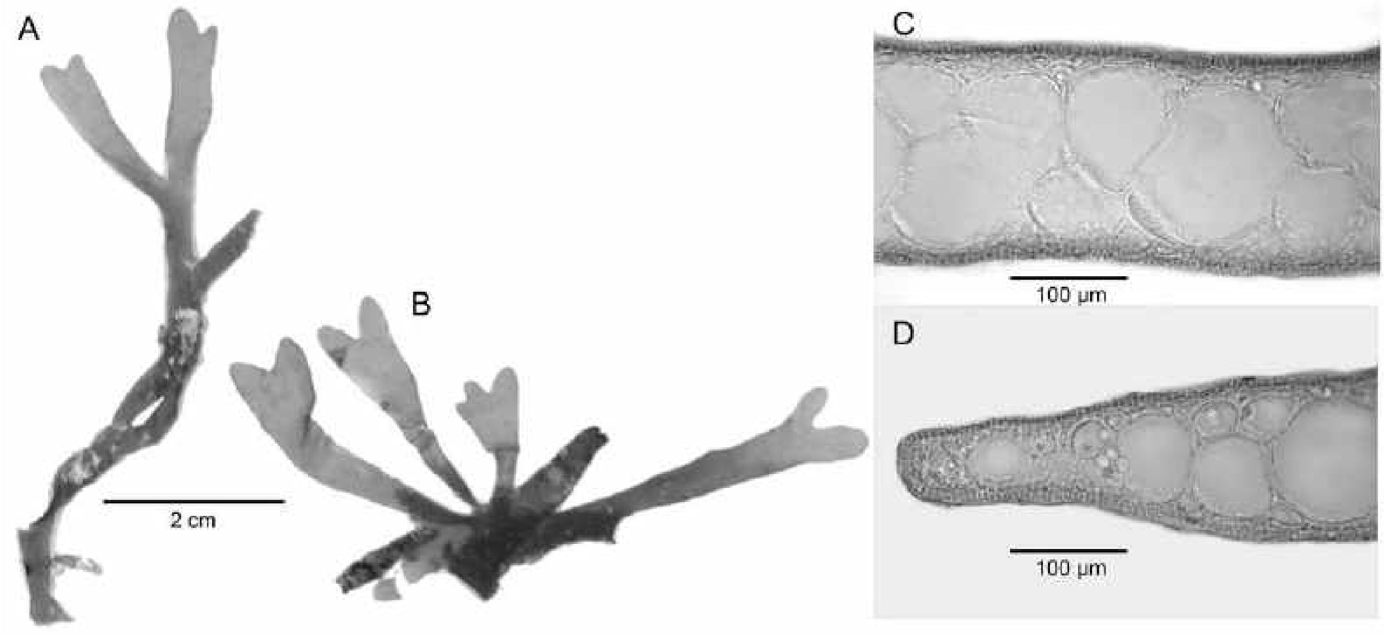

FIGURE 174. *Petroglossum parvum*: A, B. Habit variation (*EYD-26138*, US Alg. Coll.-78080). C. Transection through blade. D. Transection through thallus margin (C, D, *EYD-26138*, US Alg. Coll. microscope slide 783).

Cintura). Eastern Pacific: Santa Barbara to Laguna Beach, California; Isla Cedros, Baja California.

Type Locality. Intertidal; Laguna Beach, Orange County, southern California, USA.

Remarks. The subtidal Gulf specimens of *Petroglossum parvum* are thicker, 180–190 µm, but of only 1–2 layers of very large medullary cells in transection, whereas those of the intertidal southern California specimens are thinner, 60–120 µm thick, with 3–4 layers of comparatively smaller medullary cells. Once reproductive specimens are found in the Gulf of California, they can be compared morphologically and molecularly to type locality specimens.

Solieriaceae

Solieriaceae J. Agardh, 1876:502.

Algae of this family are mostly erect and usually large, cylindrical, compressed, flattened or foliose, and simple, branched, or lobed, attached by a discoid to crustose holdfast. One genus is a minute parasite. Thalli are multiaxial in construction with secondary pit-connections between adjacent cells. The medulla is composed of loose to dense parallel longitudinal filaments, surrounded by a subcortical layer of large cells, which grade into successively smaller, usually stellate cells outward to the outer cortex, which is composed of files of small cells at right angles to the axis.

Life histories are triphasic, with isomorphic gametophytes and sporophytes. Tetrasporangia are zonate, developed from outer cortical cells, and scattered over the thallus surface. Carpogonial branches are three (to four) celled, scattered and borne on large supporting cells in the inner cortex. Carpogonial branches are on separate cortical branches from auxiliary cells. Auxiliary cells are also scattered and borne in a similar location. The auxiliary cell systems can be identified prior to or aften diploidization (Guimarães and Oliviera, 1996). Cells surrounding auxiliary cells divide prior to gonimoblast development, and the gonimoblast filaments, at least at first, grow inward into the medulla. Cystocarps have large central fusion cells or a center of small-celled vegetative tissue and are embedded within or protruding from thallus surface, with a pericarp and an ostiole. Carposporangia develop from most or only distal gonimoblast cells. Spermatangia are in sori on thallus surface or in isolated clusters.

Remarks. There are also two genera of the Solieriaceae, both minute and parasitic: *Gardneriella* Kylin (1941) and *Tikvahiella* Kraft et P. W. Gabrielson (1983). *Gardneriella tubifera* Kylin on *Sarcodiotheca gaudichadii* is recorded in the eastern Pacific from central California to northern Baja California (Dawson, 1961a; Goff and Hommersand, 1982; Pacheco-Ruíz and Aguilar-Rosas, 1984).

Four macrophyte genera of the Solieriaceae are found in the northern Gulf of California.

KEY TO THE GENERA OF SOLIERIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes and branches compressed to flattened . . . . ***Sarcodiotheca* (in part)**
1b. Axes and branches terete to slightly compressed 2
2a. Thallus terete to slightly compressed, wiry; less than 250 µm in diameter . . . . ***Wurdemannia***
2b. Thallus terete, turgid to cartilaginous; much wider in diameter, greater than 1.0 mm (mostly 2–7 mm) 3
3a. Axes and branches with numerous conspicuous short spinose or spur-like protuberances on most surfaces; broader, 4–7(–10) mm in diameter . . . . ***Tacanoosca***
3b. Axes and branches, 1–4 mm in diameter; with smooth surfaces (without spinose or spur-like protuberances); often with short lateral branchlets 4
4a. Axes narrow, mostly less that 2 mm in diameter . . . . ***Agardhiella***
4b. Axes wider, mostly 2–4 mm in diameter . . . . ***Sarcodiotheca* (in part)**

***Agardhiella* F. Schmitz**

Agardhiella F. Schmitz in Schmitz et Hauptfleisch, 1896:371; Gabrielson and Hommersand, 1982:46.

Algae are erect, with one to many terete to slightly compressed axes, radially, distichously, unilaterally, or irregularly branched, and attached below by a discoid holdfast. Medulla is composed of parallel longitudinal filaments. Cortex is composed of rounded or angular, large cells in the inner cortex, which outwardly become successively smaller toward the surface.

Tetrasporangia are zonately divided, embedded in the cortex and scattered over branch surfaces. Cystocarps are large, embedded in the cortex and protruding beyond the branch surface, and are internally composed of a group of sterile cells, with the carposporangia formed in a ring at the periphery. Spermatangia are in small sori on branch surfaces.

One endemic species of *Agardhiella* is found in the northern Gulf of California.

***Agardhiella mexicana* E. Y. Dawson**

Agardhiella mexicana E. Y. Dawson, 1944a:288, pl. 69: fig. 1 [type collection]; González-González et al., 1996:168.

Agardhiella tenera sensu Dawson, 1961a:231 [in part; Gulf of California specimens only], pl. 34, fig. 1 [non *Agardhiella tenera* (J. Agardh) Schmitz in Schmitz et Hauptfleisch, 1897a:371, which is now *Agardhiella subulata* (C. Agardh) Kraft et M. J. Wynne, 1979:329; see also Gabrielson, 1982:93; Gabrielson, 1985:278].

Algae erect, of 1 to few terete, branched axes, up to 15 cm tall; slender, 1.0–1.5(–2) mm in diameter; branching irregularly more or less radially, 2–4(–5) orders, branches with acute apices; ultimate branchlets short, sometimes spine-like in appearance; arising from a small discoid holdfast. Medulla a small central core of longitudinal filaments; surrounded by large isodiametric cells, grading outward into cortex of small pigmented cells.

Tetrasporangia zonately divided, 15–25 µm in diameter, borne in cortical layers below surface, scattered over branches. Cystocarps and spermatangial thalli unknown.

Habitat. On rocks or shells, often partially covered by sand or fine sediment; low intertidal to shallow subtidal, 4–12 m depths (also dredged from 22–80 m depths).

Distribution. Gulf of California: Bahía La Choya (Bahía Cholla, northwest of Puerto Peñasco); Isla Ángel de la Guarda to Bahía San Luis Gonzága.

Type Locality. Dredged from 4 m depth; south shore of Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

Remarks. Apparently endemic to the Gulf of California, *Agardhiella mexicana* remains a little-known species. In the upper Gulf, growth forms of those from Bahía La Choya (vicinity of Puerto Peñasco) were noted by Dawson (1966a, as "*A. tenera*") to be the same as those he previously treated as *A. mexicana* (Dawson, 1944a).

Some investigators have followed Dawson (1961a:231, as "*Agardhiella tenera,*" now conspecific with *A. subulata* Kraft et M. J. Wynne, 1979) in considering the northern Gulf of California *A. mexicana* to be conspecific with those of the Pacific coast of North America that have been referred to "*Agardhiella coulteri*" and "*Neoagardhiella baileyii*" (e.g., Wynne and Taylor, 1973; Abbott and Hollenberg, 1976; Kraft and Wynne, 1979), but those taxa are currently recognized to be *Sarcodiotheca gaudichaudii* (Montagne) P. W. Gabrielson (1982).

However, on the basis of differences in the size of axes and branch diameters, the degree of branching, and the smaller tetrasporangia sizes, the Gulf *Agardhiella mexicana* appears to be a separate species from *Sarcodiotheca gaudichaudii*. Specimens of Mendoza-González and Mateo-Cid (1986, as "*Neoagardhiella baileyi*") from Guaymas need to be reexamined to see if they are possibly referable to *A. mexicana* or *S. gaudichaudii*.

Studies on the development of vegetative and reproductive structures of the Gulf *A. mexicana*, particularly on cystocarpic material, along with molecular phylogenetic analyses are necessary before its taxonomic status and relationship to other species can be understood.

***Sarcodiotheca* Kylin**

Sarcodiotheca Kylin, 1932:15.

Algae are erect, with one or more terete, compressed, or flattened blades, attached by a discoid holdfast. Branching is regularly or irregularly dichotomous and occasionally with proliferous branchlets. Branches are terete, compressed, or flat, gradually narrowing upward, with blunt or subacute tips. The medulla is composed of slender medullary filaments. The cortex is of large, colorless parenchymatous cells into the inner cortex and two to three outer layers of smaller, pigmented cells toward the thallus surface.

Tetrasporangia are zonately divided and borne in the outer cortex, scattered over the blade. Cystocarps project from branch surfaces and have a pericarp. Spermatangia are in irregularly shaped sori, superficial and scattered over the blade surface.

Five species of *Sarcodiotheca* are recognized from the northern Gulf of California; two are newly reported in the Gulf.

KEY TO THE SPECIES OF *SARCODIOTHECA* AND *AGARDHIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes and branches terete, branched irregularly alternately, more or less radially 2
1b. Thalli compressed to markedly flattened 3
2a. Terete axes and branches, 2–4 mm in diameter; branches constricted at base; tetrasporangia 40–42 µm in diameter . . . . ***Sarcodiotheca gaudichaudii***
2b. Terete axes and branches more slender, 1–1.5(–2) mm in diameter; tetrasporangia smaller, 15–25 µm in diameter . . . . ***Agardhiella mexicana***
3a. Blades mostly 2–7 mm wide; repeatedly dichotomously branched, margins smooth or at times with marginal proliferations; cystocarps predominately marginal . . . . ***Sarcodiotheca dichotoma***
3b. Blades mostly wider, compressed to flattened; cystocarps scattered over surface 4
4a. Thalli compressed; branching irregularly dichotomous or more or less alternate, pinnate, or opposite; up to 8 mm wide . . . . ***Sarcodiotheca taylorii***
4b. Flattened, dichotomously or irregularly branched 5
5a. Primary blades narrow, 2–6 mm wide, irregularly branched at wide intervals, 2–3(–5) times . . . . . ***Sarcodiotheca linearis***
5b. Primary blades wider, over 1 cm (up to 3.0 cm) in width; dichotomously branched, 5–7 times . . . . ***Sarcodiotheca furcata***

Sarcodiotheca dichotoma (M. Howe) E. Y. Dawson

FIGURE 175

Anatheca dichotoma M. Howe, 1911:502, pl. 29.

Sarcodiotheca dichotoma (M. Howe) E. Y. Dawson, 1944a:290; 1961a:226, pls. 28, pl. 31: fig. 4; 1961b:427; Norris, 1973:12; Gabrielson, 1982:75, figs. 2–5, 8, 11–13, 16, 18, 20, 22, 23, 27; González-González et al., 1996:268; Bula-Meyer and Norris, 2001:356: figs. 7–8; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:208.

Thalli erect, of 1 to few complanate dichotomously branched blades, to 15 cm tall or more, cuneate below to a short stipe, with a small discoid holdfast. Blades much branched in 1 plane, with 5–11 dichotomous divisions, branch angles narrow to divaricate; 0.3–1.3 mm thick, 2–7(–12) mm wide, tapering upward to forked ultimate divisions, to 1.0 mm wide; acuminate apices often conical terete; margins smooth and entire or often with numerous lateral proliferations. Medulla of central linear filaments, 10–20 µm in diameter, between large, thick-walled cells, mostly 2 layered, to 340 µm thick, these in turn abruptly adjoined to outer 2-layered cortex of small pigmented cells, 7–10 µm in diameter.

Tetrasporangia zonate, ovoid, 50–85 µm long; borne in unmodified cortex, scattered over blade. Cystocarps dome shaped, 1.3–2.0 mm in diameter; mostly restricted to blade margins or occasionally over middle portion of blade surface. Spermatangia not seen in Gulf material.

HABITAT. On rocks; shallow subtidal down to 30 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Isla San Esteban (Islas de la Cintura); El Desemboque to Bahía San Carlos; Isla La Ventana, Bahía de Los Ángeles; Puerto Escondido; Isla Carmén; Canal de San Lorenzo (off southern end of Isla Espíritu Santo); La Paz.

TYPE LOCALITY. Vicinity of La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. *Sarcodiotheca dichotoma* has also been reported in the Western Atlantic from Tobago (Taylor, 1962, as *Sarcodiotheca caribaea* W. R. Taylor; Wynne, 2011) and Caribbean Colombia (Bula-Meyer and Norris, 2001:356, figs. 7–8). On a morphological basis these seem to be one species; however, molecular comparisons of type localitiy materials of Gulf of California *S. dichotoma* and Western Atlantic *S. caribaea* and *S.dichotoma* are needed to test their relationships.

Sarcodiotheca furcata (Setchell et N. L. Gardner) Kylin

FIGURES 176, 177

Anatheca furcata Setchell et N. L. Gardner, 1903:310, pl. 23: fig. 39, pl. 24: fig. 41; Kylin, 1925:36, figs. 20, 21.

Sarcodiotheca furcata (Setchell et N. L. Gardner) Kylin, 1932:16; Dawson, 1961a:229, pl. 30: figs. 1, 2, pl. 31: figs. 1, 4; 1961b:427; Hollenberg and Abbott, 1966:85, fig. 36; Abbott and Hollenberg, 1976:488, fig. 432; Gabrielson, 1982:75, figs. 1, 6, 7, 9, 10, 14–15, 17, 19, 21, 24–26, 28; Stewart, 1991:100; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:268; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:209; Fernández-García et al., 2011:64.

Algae erect, complanate; of repeatedly, dichotomously branched blades, up to 37 cm tall; arising from a slender, cylindrical stipe, 1–2 cm in length; attached to substrate by a discoid holdfast. Blade branched in 1 plane, 5–7 times; dichotomies cuneate; segments 1.0–2.5(–3.0) cm wide, up to 1.0 mm thick

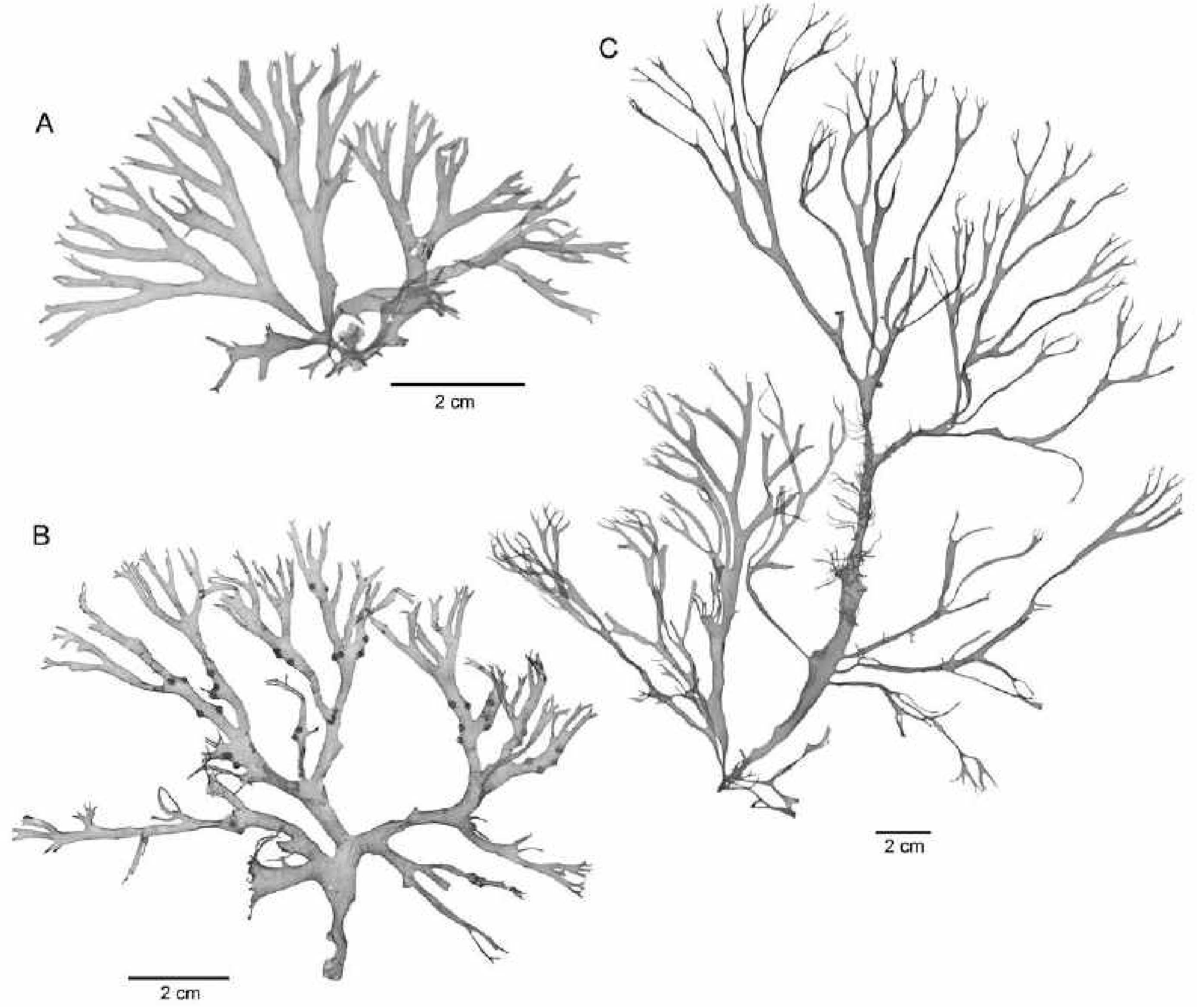

FIGURE 175. *Sarcodiotheca dichotoma*: A. Habit. B. Habit; note cystocarps borne mostly along blade margins (A, B, *JN-4432*, US Alg. Coll.-160847). C. Habit (*JN-6554*, US Alg. Coll.-160887).

when fresh; margins entire or with short proliferations or with few to numerous short to long laterals; terminal portions attenuated to subacute tips. Central medulla of interlaced filaments, surrounded on each side by 2–3 layers of large, isodiametric cells, up to 70 µm diameter. Cortex of 2 layers of small cells; pigmented cortical cells to 10 µm in diameter.

Tetrasporangia zonately divided, 70–80 µm long; scattered over thallus surface. Cystocarps dome shaped and protruding, 1–4 mm in diameter; scattered over thallus surface. Spermatangia in irregularly shaped sori, forming minute whitish mottled areas on blade surface.

Habitat. On rocks and shells; shallow subtidal, 3.3–22.7 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Isla San Esteban; Punta La Gringa, Bahía de Los Ángeles; Ensenada Grande (Bahía San Pedro, between Bahía San Carlos and Tastiota); Nayarit to Jalisco; Isla María Magdalena (Islas Marías; Islas Tres Marías). Eastern Pacific: southern Alaska to Washington; southern California; Costa Rica.

Type Locality. West coast of Whidbey (Whidby) Island, Island County, Puget Sound, Washington, USA.

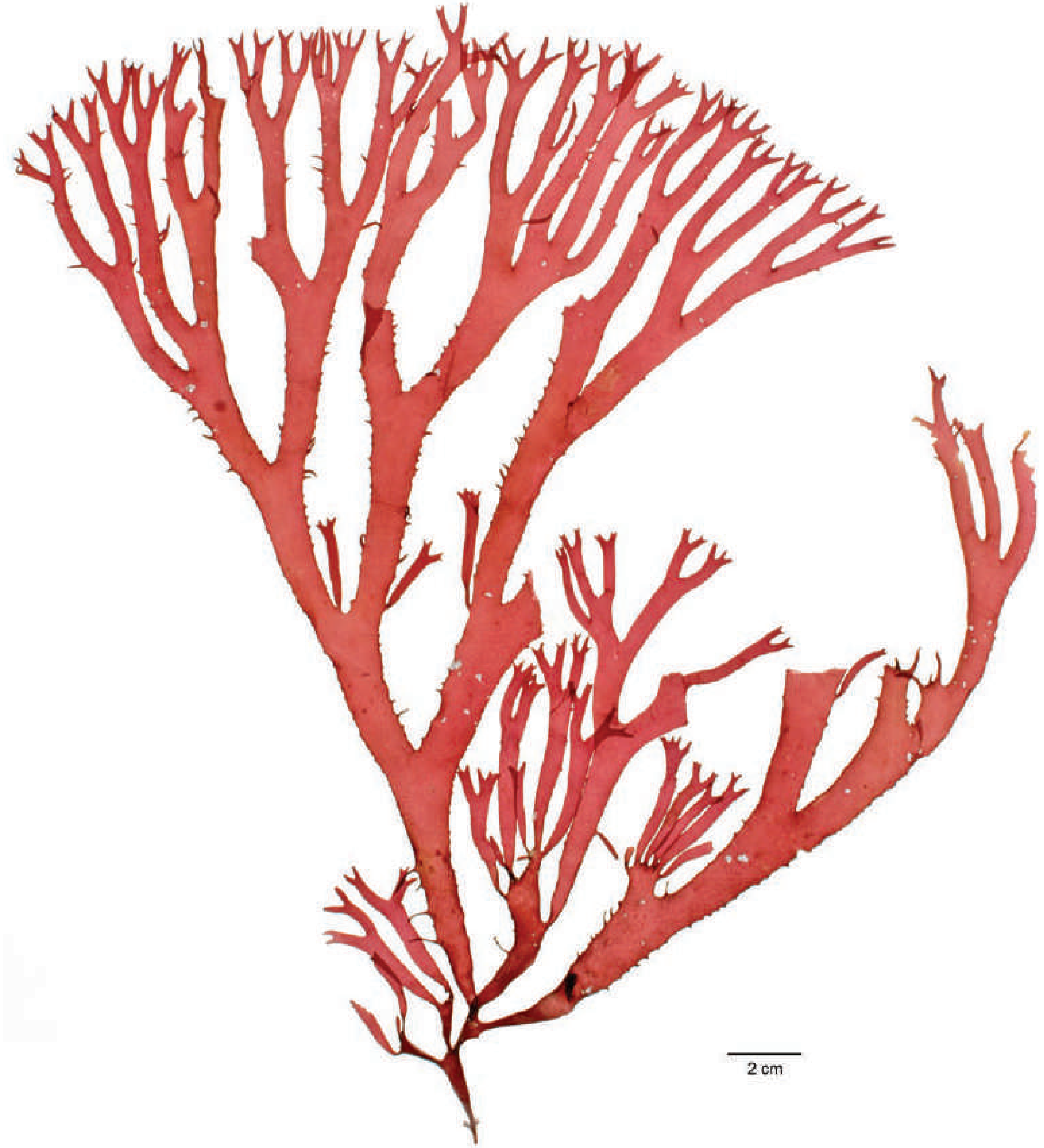

FIGURE 176. *Sarcodiotheca furcata:* Habit (*JN-5328*, US Alg. Coll.-160855).

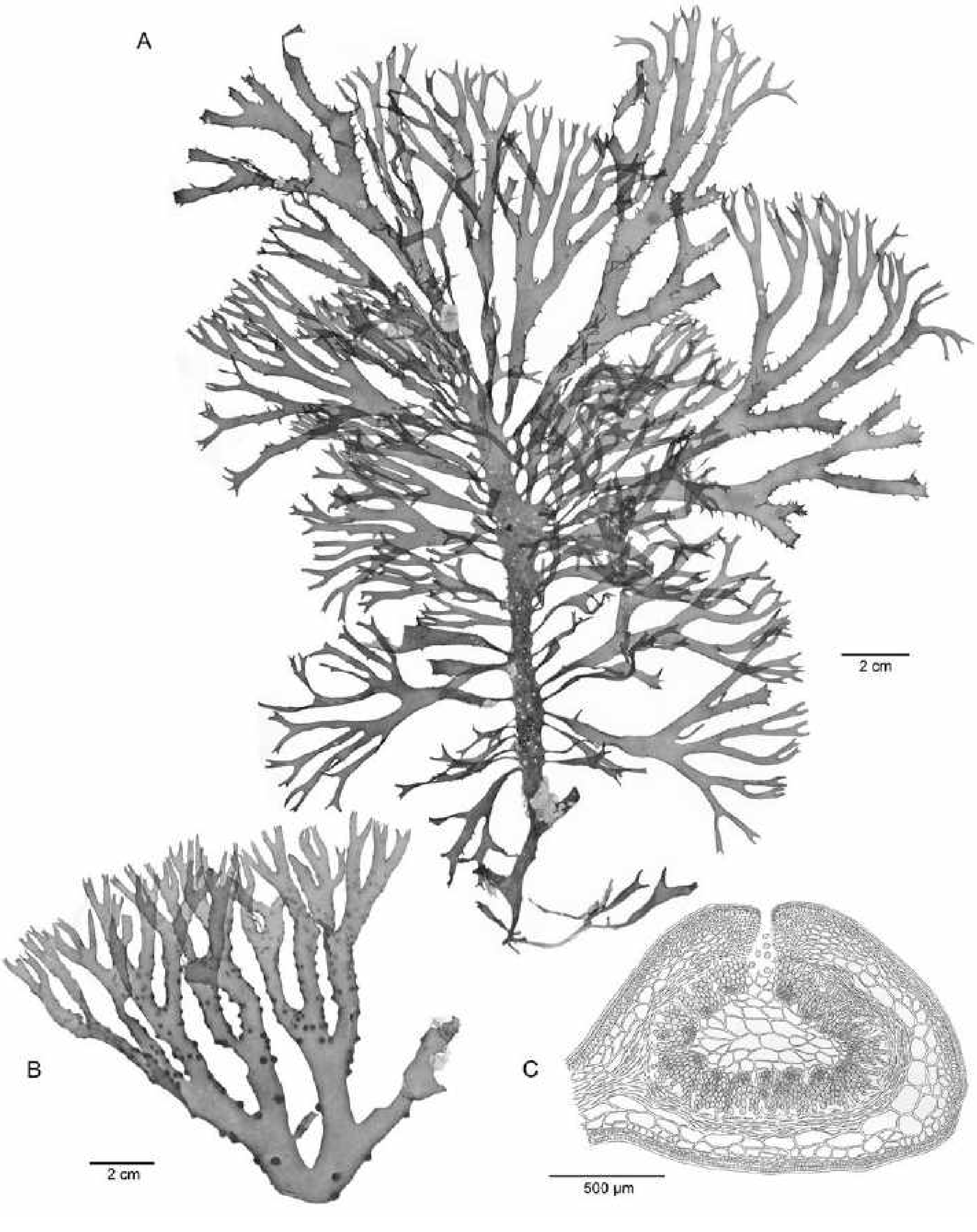

FIGURE 177. *Sarcodiotheca furcata*: A. Thallus with numerous short proliferations and short to long laterals (*JN-5349*, US Alg. Coll.-160859). B. Female gametophyte with cystocarps on thallus surface and along margins (*JN-5798*, US Alg. Coll.-160864). C. Transection of cystocarp, with large sterile cells at center, surrounded by masses of carpospores in groups (after Setchell and Gardner, 1903: pl. 24: fig. 41).

Remarks. A new distribution record, specimens of *Sarcodiotheca furcata* (US Alg. Coll.) from Puerto Refugio, Isla Ángel de la Guarda, establish it in the Gulf of California. It is distinguished from the other species of *Sarcodiotheca* in the Gulf by its larger size, deep red color, and broad, flattened, dichotomously branched blades with forked tips. In the northern Gulf, *S. furcata* is found only off some islands of Islas de la Cintura and apparently from drift at Ensenada Grande. Locally, at some locales, e.g., Puerto Refugio, Isla Ángel de la Guarda, it can be a conspicuous species in the subtidal flora. Although *S. furcata* is known from Alaska to the submarine La Jolla Canyon, southern California, it has not been found in Pacific Baja California (Stewart, 1991).

A resemblance of northern Washington *S. furcata* to the Gulf of California *S. elongata* (Setchell et N. L. Gardner) Setchell in E. Y. Dawson (1944a:289) was previously mentioned by Setchell and Gardner (1924, as *Anatheca elongata* Setchell et N. L. Gardner, 1924:747, pl. 64) in their original description. Although Dawson (1961a) later placed *S. elongata* in synonymy with another species, *S. dichotoma,* this seems to be incorrect. The type of *S. elongata* (type locality: Isla San Pedro Mártir) more closely agrees with our Gulf specimens referred to *S. furcata.* The relationship of Pacific northwest *S. furcata* and the northern Gulf *S. elongata* needs to be further comparatively tested, and their taxonomic status and relationship need to be elucidated. If different from *S. furcata*, the northern Gulf specimens could possibly be *S. elongata*.

Sarcodiotheca gaudichaudii **(Montagne) P. W. Gabrielson**

FIGURE 178

Gigartina gaudichaudii Montagne, 1842a:255; 1846a:69, pl. 143: fig. 1.

Sarcodiotheca gaudichaudii (Montagne) P. W. Gabrielson, 1982:93, figs. 1–21; Scagel et al., 1989:257; Stewart and Stewart, 1984:144; Stewart, 1991:101; Ramírez and Santelices, 1991:292; R. Aguilar-Rosas and Aguilar-Rosas, 1994:522; González-González et al., 1996:268; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Hoffmann and Santelices, 1997:310, fig. 83; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:209.

Neoagardhiella gaudichaudii (Montagne) I. A. Abbott, 1978:52.

Agardhiella gauichaudii (Montagne) P. C. Silva et Papenfuss in Silva, 1979:321.

Agardhiella coulteri sensu Kylin, 1941:18; Smith, 1944:260, pl. 62: fig. 4 [non *Agardhiella coulteri* (Harvey) Setchell in Collins et al., 1897: Exsiccate no. 333; basionym: *Hypnea coulteri* Harvey in Harvey and Bailey, 1851:371, as "*Hypriea coulteri*"; =*Rhabdonia coulteri* (Harvey) Harvey, 1853:154, pl. 23: fig. B; =*Neoagardhiella coulteri* (Harvey) P. C. Silva, 1981:487].

Agardhiella tenera sensu Dawson, 1944a:288; 1961a:231 [in part; excluding Gulf of California specimens of *Agardhiella mexicana*]; Gabrielson, 1985:275 [non *Agardhiella tenera* (J. Agardh) F. Schmitz in Schmitz and Hauptfleisch, 1897a:371, basionym: *Gigartina tenera* J. Agardh, 1841:18, which is now *Agardhiella subulata* (C. Agardh) Kraft et M. J. Wynne, 1979:329, basionym: *Sphaerococcus subulatus* C. Agardh, 1822:328].

Neoagardhiella baileyi sensu Abbott and Hollenberg, 1976:483, fig. 428 [non *Neoagardhiella baileyi* (Kützing) Wynne et Taylor, 1973:101, basionym: *Rhabdonia baileyi* Kützing, 1866:26, which is now *Agardhiella subulata* (C. Agardh) Kraft et M. J. Wynne, 1979:329].

Algae of 1 or more terete axes, up to 20 cm tall, up to 4 mm in diameter, very variable in habit morphology; branching sparse to dense, irregularly distichous or radial, mostly of only 1 order, occasionally 2(–3) orders; branches of varying length, often constricted or narrowed at base, and with acute upper tip; attached by a discoid holdfast. Medulla a central core of longitudinal filaments; surrounded by large cells that become progressively smaller toward the outer cortical layer of small pigmented cells.

Tetrasporangia zonately divided, about 70 µm long, 40–42 µm in diameter; borne in outer cortex. Carpogonial branches of 3 cells, developing in inner cortex. Cystocarps 1–2 mm in diameter, with an ostiole; prominently protruding above thallus surface. Gonimoblast with a central mass of sterile cells, bearing carposporangia terminally. Spermatangia in small patches on surface, often converging and becoming continuous on upper branches.

Habitat. On rocks and shells and partially sand-coved hard substratum; low intertidal to shallow subtidal, down to 15 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Ensenada de San Francisco; Bahía Agua Verde to Punta Los Frailes. Eastern Pacific: Alaska to Baja California Sur; Isla Clarión (Islas Revillagigedo); Peru; Chile.

Type Locality. Paita (seaport on south side of Bahía de Paita), Paita Province, northwestern Peru.

Remarks. Following the single species concept, Abbott (1978) found the correct species name for Pacific coast material referred to as "*Agardhiella coulteri*" and "*Neoagardhiella baileyii*" to be *Neoagardhiella gaudichaudii* (Montagne) I. A. Abbott (=*Agardhiella gaudichaudii* Silva et Papenfuss in Silva, 1979:321). Subsequently, Gabrielson (1982) showed *Agardhiella gaudichaudii* to belong to *Sarcodiotheca*, as *S. gaudichaudii* (Montagne) P. W. Gabrielson, an eastern Pacific species now known from southern Alaska to central Baja California, Peru and Chile, and the Galápagos Islands.

Sarcodiotheca linearis **Setchell et N. L. Gardner**

Sarcodiotheca linearis Setchell et N. L. Gardner, 1937:80, pl. 5: fig. 12a,b, pl. 15: fig. 35; Dawson, 1944a:289; 1961a:228, pl. 30: fig. 3; 1961b:427; Stewart and Stewart, 1984:144; González-González et al., 1996:268.

Algae erect, up to 10 cm tall; of narrow, flat, strap-like blades, 2–6 mm wide, 400–500 µm thick; irregularly branched to 2–3(–5) orders, branching at relatively widely separated intervals; ligulate blades gradually expanding above a short, terete stipe, 1–2 mm long, attached below by a small discoid holdfast. Medulla with a middle linear core of narrow, interlaced filaments between large, parenchymatous medullary cells that become smaller outward in subcortex. Outer cortex of 2–3 layers of small, slightly radially elongated, pigmented cells.

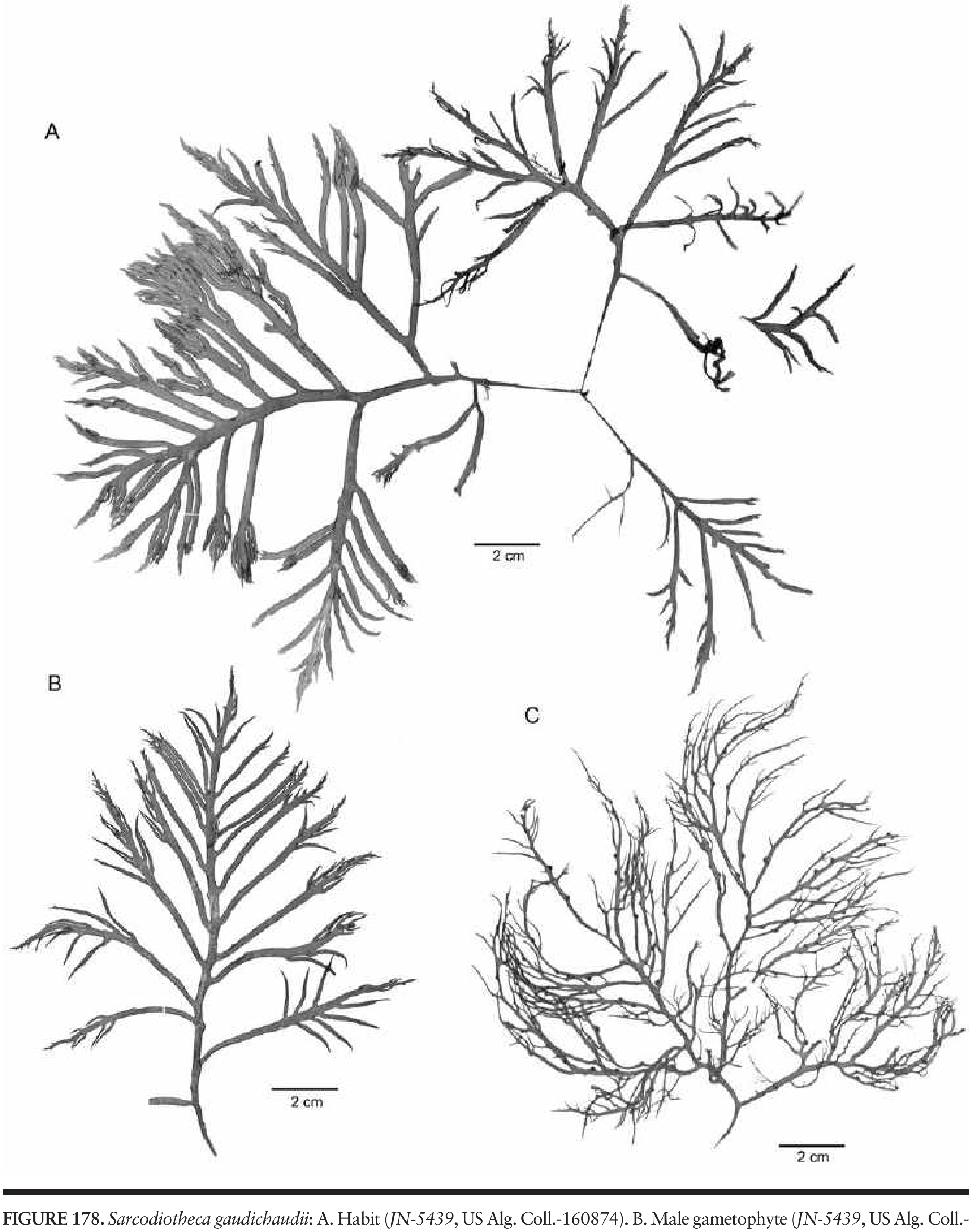

FIGURE 178. *Sarcodiotheca gaudichaudii*: A. Habit (*JN-5439*, US Alg. Coll.-160874). B. Male gametophyte (*JN-5439*, US Alg. Coll.-160875). C. Female gametophyte (*JN-6555*, US Alg. Coll.-160877).

Tetrasporangia 25–60 µm in diameter; scattered over surface. Cystocarps embedded within and protruding from both sides of blade surfaces. Spermatangia colorless, elongated; scattered over both blade surfaces.

HABITAT. On rocks; subtidal, 4–30 m depths (also dredged from 65–95 m depths).

DISTRIBUTION. Gulf of California: Isla Tiburón; Bahía de San Lucas. Eastern Pacific: Isla Guadalupe (off Baja California); Punta Entrada, Isla Magdalena to Punta Gorda (Baja California Sur).

TYPE LOCALITY. Bahía de San Lucas, southern end of Baja California Sur, Gulf of California.

REMARKS. Although recognizing *Sarcodiotheca linearis* in the southern Gulf, Dawson (1961a:229) was tentative in referring a northern Gulf specimen from off the southern end of Isla Tiburón to *S. linearis*. Thus, confirmation of *S. linearis* in the northern Gulf must await further collections.

Sarcodiotheca taylorii E. Y. Dawson

FIGURE 179

Sarcodiotheca taylorii E. Y. Dawson, 1961a:227, pl. 29; 1961b:427; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:268; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:209.

Gracilaria pinnata sensu Taylor, 1945:232 [non *Gracilaria pinnata* Setchell et N. L. Gardner, 1924:751].

Thalli erect, compressed, to 14 cm tall, and up to 8(–12) mm wide, irregularly to alternately branched in 1 plane from a more or less indistinct main axis; basal attachment unknown. Frond with entire margins; upper portions gradually attenuated; tips subulate in profile. Central medulla of slender filaments, about 9 µm in diameter; outer medulla of 3–4 layers of large isodiametric cells, 80–120 µm in diameter. Cortex composed of 2 layers of small cells; inner cortical cells 11–30 µm in diameter, outer cortical cells to 10 µm diameter.

Tetrasporangia zonate, 80–90 µm long, to 60 µm wide, scattered over thallus surface. Cystocarps dome shaped, up to 1 mm in diameter, scattered over thallus. Spermatangia not known.

HABITAT. On rocks, often partially sand covered; subtidal, 12–15 m depths.

DISTRIBUTION. Gulf of California: Isla Estanque; Isla la Ventana, Bahía de Los Ángeles; Punta Los Frailes; Nayarit to Jalisco; Isla María Magdalena (Islas Marías).

TYPE LOCALITY. Isla María Magdalena (Islas Marías; Islas Tres Marías), off Nayarit, Mexico.

Tacanoosca **J. N. Norris, P. W. Gabrielson et D. P. Cheney, *gen. nov.***

LATIN DIAGNOSIS. Algae teretes axes cum ramis plerumque radialnus et bilateralibus, et iota carrageenan ferentes. Cystocarpiis magnis, prominentibus latus secundum axes

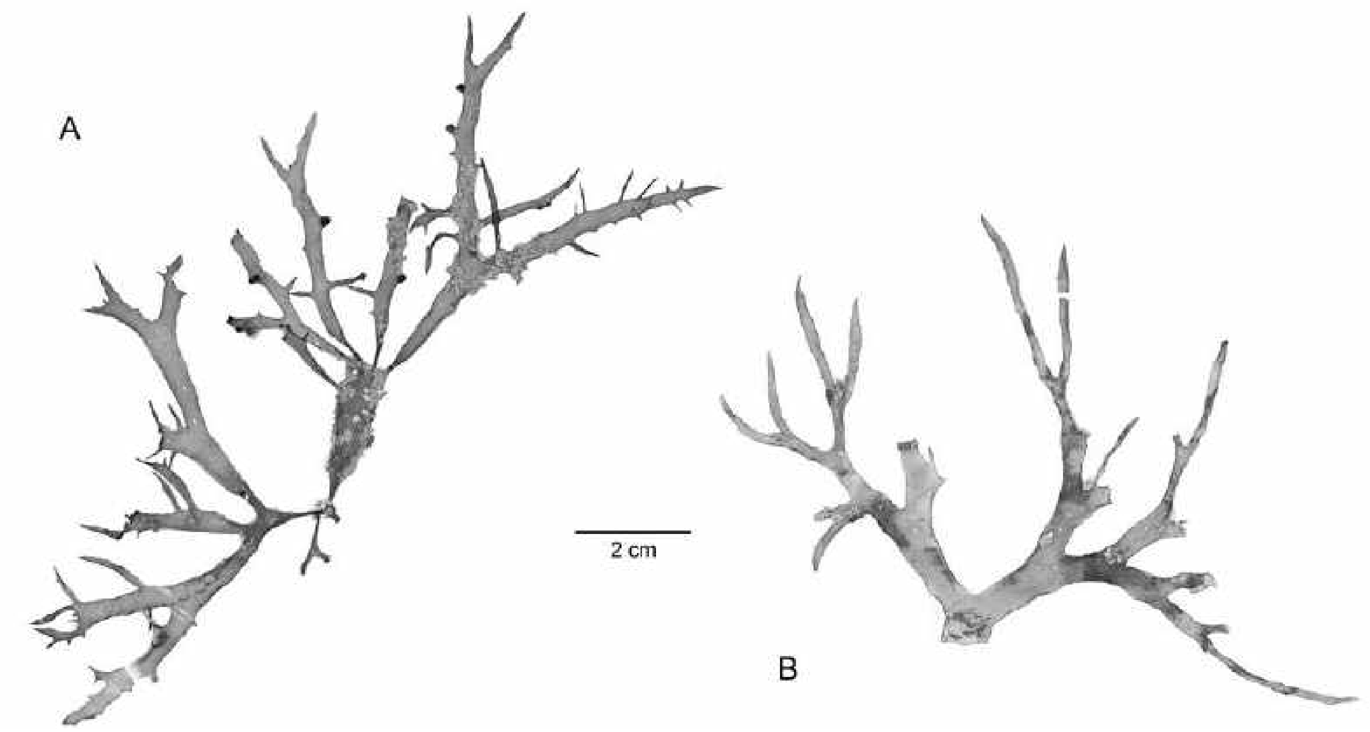

FIGURE 179. *Sarcodiotheca taylorii*: A. Female gametophyte (*JN-4460a*, US Alg. Coll.-160878). B. Tetrasporophyte (*JN-4460b*, US Alg. Coll.-160879).

ramus, vel prope basim ferri vel ramulis spinosis; pseudoparenchymatous in central sterilis tissue egens gonimoblast filamentis ca. Carposporangia produci sine cella confusionem, que vectus filamentis sterilibus botri in thalamis. Medulla axial constituendi rhizoideas coro (mediam, funis compactum litore filamentis longitudinalibus) ut cingitur cellulis pseudoparenchymatous qui fiunt successive ad exteriora minora cortex tenuis cellulis. Zonate tetrasporangiis cum utraque utrumque proprie Tetradis minores haereret corticem et ramos passim. Sori in spermatangia in ramo superficies.

Algae are erect, cartilaginous, terete; of axes that bear branches radially to bilaterally, attached below by a discoid holdfast. Axes and branches often beset with numerous papillae or spinose protuberances. One or more of these initially determinate spines may develop an indeterminate branch. Medulla composed of an axial core of rhizoids (a central cable-like strand of compacted longitudinal filaments) that is surrounded by pseudoparenchymatous cells, which become progressively smaller outward to a cortex of small cells. Species produces iota carrageenan.

Tetrasporangia zonate, with the two ends of each tetrad distinctively smaller; embedded in the cortex and scattered over the branches. Cystocarps large, protruding laterally along the branch axes, and/or borne basally near or on spinose branchlets; with a central pseudoparenchymatous, sterile tissue and lacking gonimoblast filaments. Carposporangia produced in the absence of a fusion cell and borne in clusters with sterile filaments within chambers. Spermatangia are in sori, on branch surfaces.

Generic Type. *Tacanoosca uncinata* (Setchell et N. L. Gardner) J. N. Norris, P. W. Gabrielson et D. P. Cheney (herein).

Etymology. The generic name we have chosen, *Tacanoosca*, is based on using a Latin form of the Seri language name for this species, *taca-noosc* (Norris, 1991:211). In choosing their name, we honor the Seri (*Comcáac*; "the People") of Sonora (Felger and Moser, 1973, 1991; Bowen, 1983) and their knowledge of northern Gulf of California seaweeds (Norris, 1991).

Remarks. Most of the genera related to *Tacanoosca*, i.e., *Eucheuma* J. Agardh (1847:16), *Kappaphycus* Doty (1988:159, 171), and *Betaphycus* Doty (1995:237; see also Silva, et al., 1996a:326, 919), produce kappa carrageenan and iota carrageenan, natural products of commercial value that are extensively utilized by the food and other industries (Chapman and Chapman, 1980; Abbott and Cheney, 1982; Doty and Norris, 1985; Doty, 1988; Santos, 1989; Zertuche-González et al., 1993). The Gulf of California *Tacanoosca* produce an iota carrageenan (Dawes et al., 1977); although of economic potential (Zertuche-González, 1994, 1996; Zertuche-González et al., 2006), *T. uncinata* has been only occasionally harvested and is not presently being exploited (Robledo and Freile-Pelegrín, 2011).

Barilotti and Zertuche-González (1990, as *Eucheuma uncinatum*) concluded that commercial harvesting would have significant effects on the natural populations and should not be attempted until spore propagation can be provided as part of resource management. Up until recently, efforts to produce this apparent annual species consistently in commercial quantities have been largely unsuccessful (Parker, 1974; Doty and Norris, 1985). More recent work has focused on its vegetative propagation from tissue and calluses (Gibor et al., 1981; Polne-Fuller and Gibor, 1986a, 1986b, 1987) and culture in tanks (Polne et al., 1980, 1981; Zertuche-González et al., 1987, 1993). Successful techniques for its cultivation in tanks were developed by Zertuche-González (1988, 1990); these aquaculture methods should take the strain off the need for field harvesting.

There is one known species, originally described from the northern Gulf of California.

Tacanoosca uncinata (Setchell et N. L. Gardner) J. N. Norris, P. W. Gabrielson, et D. P. Cheney, *comb. nov.*

FIGURES 8C, 180

Eucheuma uncinatum Setchell et N. L. Gardner, 1924:748, pls. 67, 68; Dawson, 1944a:288; 1961a:230, pl. 32; 1961b:427; Guzmán del Próo, 1969:689; Norris, 1973:11; Lawson et al., 1973:2177; Dawes et al., 1977:437; Huerta-Múzquiz, 1978:337; Polne et al., 1980:115; Polne et al., 1981:619; Norris, 1985a:63, figs. 1–6; Doty and Norris, 1985:55–56; Norris, 1985d:211, fig. 16.5; Zertuche-González et al., 1987:1; Doty, 1988:182, figs. 19D, 20; Dreckmann et al., 1990:27; Zertuche-González et al., 1993:601; González-González et al., 1996:201; Riosmena-Rodríquez et al., 1998:28; L. Aguilar-Rosas et al., 2000:131; Pacheco-Ruíz and Zertuche-González, 2002:468; Schubert et al., 2006:1208; Pacheco-Ruíz et al., 2008:210.

Eucheuma johnstonii Setchell et N. L. Gardner, 1924:748, pl. 25: fig. 42, pls. 65, 66.

Algae erect, cartilaginous, and cylindrical, freely branched throughout, up to 50 cm tall; attached by a discoid to conical holdfast. Primary axes, (3–)4–7(–10) mm in diameter; abundantly branched, up to 3(–4) orders, with slender, often long, branches with acute apices; axes and branches sparsely to densely beset with simple or branched, short spinose proliferations.

Tetrasporangia borne in slightly modified cortex, scattered over thallus; tetrasporangia zonately divided, 70–90 μm long, up to 33 μm wide, with the 2 end spores greatly reduced in size (see Setchell and Gardner, 1924, pl. 25: fig. 24). Cystocarps prominent, subspherical, large, 1.0–1.4 mm in diameter; either single or grouped and spread out on the thallus; borne directly on the axes and branches or often near base of short lateral (spinose) proliferations or on the spines toward the upper ends. Spermatangia narrowly elongate, anticlinally arranged in irregularly shaped superficial sori, on branch surfaces and proliferations; spermatia 2.5–3.0 μm in diameter.

Habitat. On rocks; low intertidal to shallow subtidal, down to 12 m depths.

Distribution. Gulf of California: Puerto Peñasco to Guaymas (Sonora); Puerto Refugio, Isla Ángel de la Guarda; Isla San Perdo Mártir; El Coloradito to Bahia San Francisquito (Baja California); Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Colima to Puerto Galera, Oaxaca.

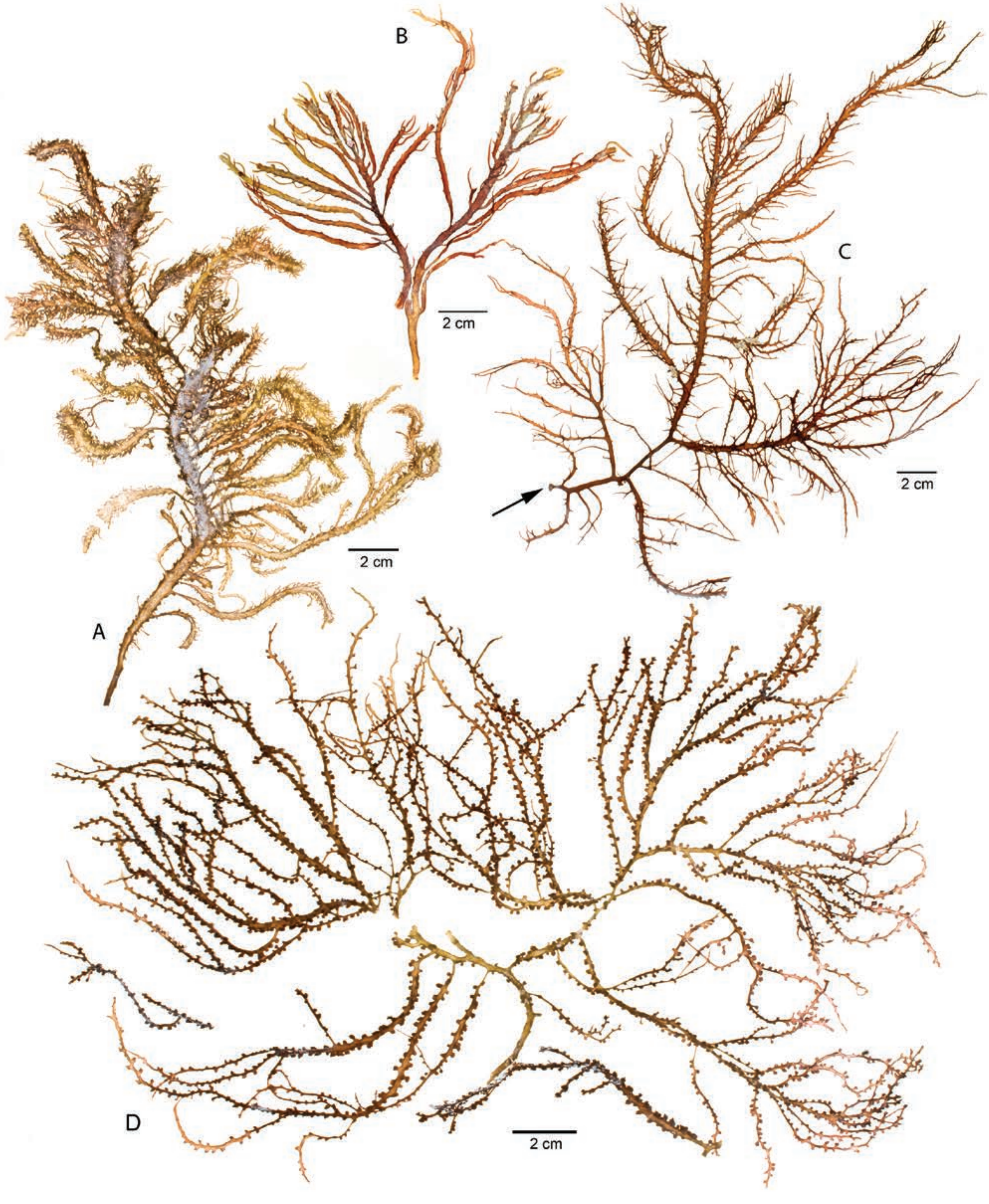

FIGURE 180. *Tacanoosca gen. nov.*, habit variation in *T. uncinata*: A. Male gametophyte (*EYD-1800a*, US Alg. Coll.-7181). B. Tetrasporophyte (*JN-238*, US Alg. Coll.-89992). C. Thallus with spinose laterals and holdfast (arrow) (*JN-5415*, US Alg. Coll.-210494). D. Female gametophyte with protuberant cystocarps (*EYD-1800b*, US Alg. Coll.-7181).

HOLOTYPE. *I.M. Johnston-86* (*Eucheuma uncinatum* Setchell et N. L. Gardner, CAS, now UC; isotype: US Alg. Coll.-56407).

TYPE LOCALITY. On rocks; Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, southwestern Islas de la Cintura, Gulf of California, Mexico.

REMARKS. *Tacanoosca uncinata* is considered to be an annual species. Small, juvenile thalli were observed in the late fall and winter (Dawson, 1961a), and the largest sizes were observed in late spring to midsummer. Stands of *T. uncinata* in Bahía de Los Ángeles underwent a huge reduction in standing crop in the fall, but some living thalli could be found year-round (Zertuche-González, 1988). As currently interpreted, *Tacanoosca uncinata* exhibits a bewildering array of morphological forms (see Norris, 1985a: figs. 1–6). Molecular analyses of these different morphological forms, including the Gulf described *Eucheuma johnstonii*, in comparison with the type of *T. uncinata*, will test if it is a single broadly defined species, or possibly more than one taxon. For example, *rbc*L analysis of Fredericq et al. (1999) found a Gulf specimen of "*E. uncinatum*" to group with some species of *Sarcodiotheca*, suggesting the possibility of more species to be elucidated.

The Puerto Peñasco specimens cited by Dawson (1966a:23, as "*Eucheuma uncinatum*") and a more recent specimen (US Alg. Coll.) collected in beach drift from Playa Las Conchas (Playa Estación), vicinity of Puerto Peñasco, have been reexamined and found not to be *T. uncinata;* they probably represent an undescribed species of *Gracilaria* in the upper Gulf.

Wurdemannia Harvey

Wurdemannia Harvey, 1853:245.

Algae are erect, forming tufts, entangled turfs, or spreading mats, and composed of slender, wiry, terete, irregularly branched axes, less than 300 µm in diameter, arising above entangled rhizomatous axes that attach to substratum. Secondary attachments may develop between branches and the lower prostrate axes. Thalli are multiaxial and nearly pseudoparenchymatous in transection. Medulla has a central core of dense, elongate (longitudinally), thin-walled medullary cells that outwardly become shorter and thicker walled to the cortical layer. Cortex is usually one layer (occasionally more) of small, rounded, thick-walled cortical cells.

Tetrasporangia are zonately divided and grouped in slightly swollen tips of fertile axes. Cystocarpic and spermatangial thalli are unknown.

REMARKS. For years *Wurdemannia* has been considered a genus of uncertain taxonomic position (e.g., Silva et al., 1996a; Abbott, 1999), or it was placed in the Gelidiaceae (e.g., Taylor, 1945; Dawson, 1953a) or the Wurdemanniaceae W. R. Taylor (1960). Saunders et al. (2004), noting their vegetative similarities, provided genetic evidence that *Wurdemannia* should be placed in the family Solieriaceae J. Agardh.

The genus is represented by one species in the northern Gulf of California.

Wurdemannia miniata (Sprengel) J. Feldmann et G. Hamel

Sphaerococcus miniatus Sprengel, 1827:340.

Wurdemannia miniata (Sprengel) J. Feldmann et G. Hamel, 1934:544, figs. 9–11; Dawson, 1944a:263; Taylor, 1945:151; Dawson, 1953a:86; 1961b:410; Chávez-Barrear, 1972b:269; Huerta-Múzquiz and Garza-Barrientos, 1975:8; Huerta-Múzquiz and Mendoza-González, 1985:48; Salcedo-Martínez et al., 1988:83; Serviere-Zaragoza et al., 1993a:484; González-González et al., 1996:326, 409; CONANP, 2002:140; Serviere-Zaragoza et al., 2007:12; Bernecker, 2009:CD-Rom p. 63; Fernández-García et al., 2011:65.

Fucus miniatus Draparnaud ex Lamarck et de Candolle, 1815:6, *nom. illeg.* [a later homonym of *Fucus miniatus* O. F. Müller, 1778:7].

Wurdemannia setacea Harvey, 1853:245.

Algae erect, short tufts or forming densely matted turfs; 1.5–3.0 cm tall, of terete to slightly compressed, wiry axes, 150–220 µm in diameter; arising from entangled, prostrate axes attached by small discs. Medulla of thick-walled, elongated cells; cells of medullary core mostly 7–8 µm in diameter, 50–800 µm in length (7–10 times longer than diameter); grading outward to cortex of smaller, thin-walled, ellipsoidal cortical cells, 3–5 µm in diameter; rhizines (hyphae, rhizoidal filaments).

Tetrasporangia zonately divided. Gametangial thalli not known.

HABITAT. On rocks and sand, pebbles, or shells, sometimes entangled with other turf algae; mostly in lagoons and protected shallow bays; intertidal to shallow subtidal, down to about 0.5 m depths.

DISTRIBUTION. Gulf of California: Bahía San Carlos; Puerto Escondido to Bahía La Paz; Nayarit to Jalisco. Eastern Pacific: Bahía Braithwaite, Isla Socorro (Islas Revillagigedo); Colima to Guerrero; El Salvador; Nicaragua; Costa Rica; Panama. Central Pacific: Hawaiian Islands. Western Pacific: China; Japan; Vietnam.

TYPE LOCALITY. Vicinity of Montpellier, Mediterranean coast, France (Lipkin and Silva, 2002).

REMARKS. *Wurdemannia miniata* is a widely reported species (Guiry and Guiry, 2009). In the field it can sometimes be confused with some of the small, terete species of the Gelidiales. Anatomically, *W. miniata* lacks rhizoidal filaments (hyphae, rhizines) in the medulla and cortex (seen in transections and longitudinal sections) of the Gelidiaceae and Pterocladiaceae, and has zonately divided tetrasporangia. The Gelidiellaceae also lack rhizoidal filaments, but along with the other Gelidiales they have tetrahedrally to decussately divided tetrasporangia.

WEEKSIACEAE

Weeksiaceae I. A. Abbott, 1968:181.

Algae are blade-like, and growth is uniaxial or, in some, initially uniaxial and becoming multiaxial. Auxiliary cells are separate from the carpogonial branch. There are usually several auxiliary cell branches on each supporting cell, some of which may be functional. Carpogonial branches have extremely large nutritive cells. Following fertilization of the carpogonium, one of the nutritive cells produces the gonimoblast. All cells of the maturing gonimoblast develop into carposporangia.

Remarks. Although the families Weeksiaceae and Dumontiaceae Bory de Saint-Vincent (1828) are sometimes considered to be a single family (e.g., Lindstrom and Scagel, 1987; see also Lobban and Wynne, 1981), others treat them as distinct (e.g., Abbott and Hollenberg, 1976; De Clerck et al., 2002).

There is one genus of the Weeksiaceae in the northern Gulf of California.

Weeksia Setchell

Weeksia Setchell, 1901:128.

Algae are entire, dissected, or lobed blades, with smooth to puckered surfaces. Growth is initially uniaxial, then becomes multiaxial. Medulla is composed of elongated, periclinal medullary filaments, with occasional anticlinal (rhizoidal) filaments from the cortical cells, and giant cells of primary axial filaments in longitudinal rows. These rows contribute to the vein-like thickenings basally. Cortex is of 3–5(–7) layers of subspherical cells; some of the larger inner cortical cells are connected to medullary filaments. Ultrastructurally, pit plugs are without cap layers (Pueschel and Cole, 1982:709, fig. 18).

Tetrasporangia are small, regularly to irregularly cruciately divided. Carpogonial branches and auxiliary cell branches have 8–15 cells. Carpogonial branches bear four to five larger, conspicuous nutritive cells. After fertilization, the gonimoblast is produced from a nutritive cell. Carposporangia are developed from all of the gonimoblast cells. Carpospores are released through a carpostome of the cystocarp. Spermatangia are in patches on blade surfaces and cut off by an oblique wall from the spermatangial parent cells.

There are two species in the northern Gulf of California.

KEY TO THE SPECIES OF *WEEKSIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades membranous, narrow to broadly lanceolate, up to 25 cm tall and to 10 cm wide; 200–500 µm thick . . . . *W. coccinea*

1b. Blades flaccid, slippery, orbicular to reniform, up to 15 cm tall, usually broader than tall; mostly 200–250 µm (rarely to 400 µm) thick . . . . *W. templetonii*

Weeksia coccinea (Harvey) Lindstrom

FIGURE 181A,B

Schizymenia? coccinea Harvey, 1862:174 [with a generic query].

Weeksia coccinea (Harvey) Lindstrom, 1986:531, figs. 1, 2 (lectotype); Lindstrom and Scagel, 1987:2228 [in part], figs. 94–97, 99; Scagel et al., 1989:263 [in part]; Saunders, 2008:784, figs. 34–37; Hernández-Kantún et al., 2009:249, tbl. 1.

Halymenia coccinea (Harvey) I. A. Abbott, 1967a:141, figs. 1–3; Abbott and Hollenberg, 1976:425, fig. 379; Pueschel and Cole, 1982:709, fig. 18; Norris, 1985d:210, fig. 16.4; González-González et al., 1996:222; Pacheco-Ruíz and Zertuche-González, 2002:467, tbl. 1.

Weeksia fryeana Setchell, 1912:254; Dawson, 1961b:411; Norris and Abbott, 1972:90; Pueschel and Cole, 1982:709.

Aeodes gardneri sensu Smith, 1944:242, pl. 54, figs. 4, 5; Abbott, 1967a:140 [non *Aeodes gardneri* Kylin, 1925:17, which is now *Halymenia gardneri* (Kylin) Parkinson, 1980:12].

Halymenia actinophysa sensu Dawson, 1954c:274 [in part; see Abbott, 1967a:144; non *Halymenia actinophysa* M. Howe, 1911:509].

Blades usually singular, membranous, narrow to broadly lanceolate, up to 25 cm tall, to 10 cm wide, thin, 200–300 µm thick; bright cherry red in color; with simple or slightly undulate margins; base of blade usually cuneate above a short, sometimes divided stipe (if divided, each with a single blade) (Figure 181A); attached below by a small discoid holdfast. Medulla filamentous (Figure 181B); sparsely traversed by a few periclinal, anticlinal, and irregularly directed filaments, up to about 75 µm long, 5–10 µm in diameter, and thin rhizoidal filaments. Outer cortex of 1(–2) layers of small, isodiametric, highly granular, pigmented cells. Inner cortex of larger cells, 25–40 µm in diameter, subtented by 2–3 cells that connect to outer medullary filaments.

Tetrasporangia cruciately divided, 30–40 µm long, 15–22 µm wide; scattered in cortex over blade surface. Cystocarps hemispherical, 200–300 µm in diameter, surrounded by few sterile filaments; scattered over and barely projecting above blade surface; carposporangia mostly 10–16 µm in diameter. Spermatangia not known in the northern Gulf (spermatangia reported from British Columbia: borne on outer layer of pigmented cortical cells; see Saunders, 2008: fig. 36).

Habitat. Apparently rare, on rocks; subtidal, down to 10–25 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Islas de Los Gemelos, Bahía de Los Ángeles; Bahía de San Lucas. Eastern Pacific: southern Alaska to northern Washington (Saunders, 2008); Oregon to Baja California (Abbott and Hollenberg, 1976).

Type Locality. Griffin Bay (south of Friday Harbor), San Juan Island, San Juan County, Washington, USA.

Remarks. Using molecular analyses, Saunders (2008) elucidated the northeastern Pacific *Weeksia coccinea*, a species with a complicated taxonomic history. Gulf specimens, tentatively referred to *W. coccinea*, are in general morphological agreement with those from Washington–British Columbia (Saunders, 2008). To confirm its identity, northern Gulf material needs to be critically molecularly compared with type locality *W. coccinea*.

Weeksia templetonii Setchell et N. L. Gardner

FIGURES 181C, 182

Weeksia templetonii Setchell et N. L. Gardner, 1937:76, pl. 10: fig. 28 [type specimen]; Dawson, 1953a:91, pl. 7: fig. 1; 1961a:91, pl. 7: fig.1;

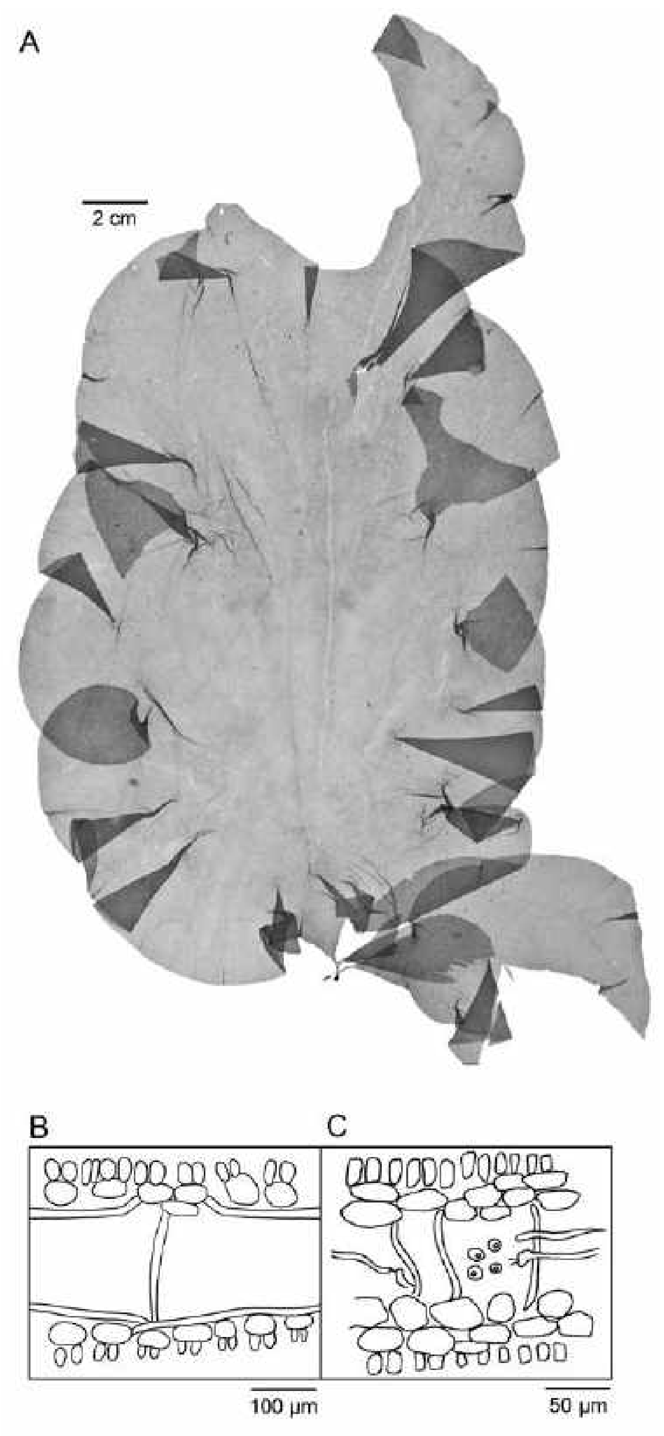

FIGURE 181. Species of *Weeksia*. A, B. *Weeksia coccinea*: A. Habit (*JN-6546*, US Alg. Coll.-159943). B. Diagrammatic transection of *Weeksia coccinea*. C. *Weeksia templetonii:* Diagrammatic transection.

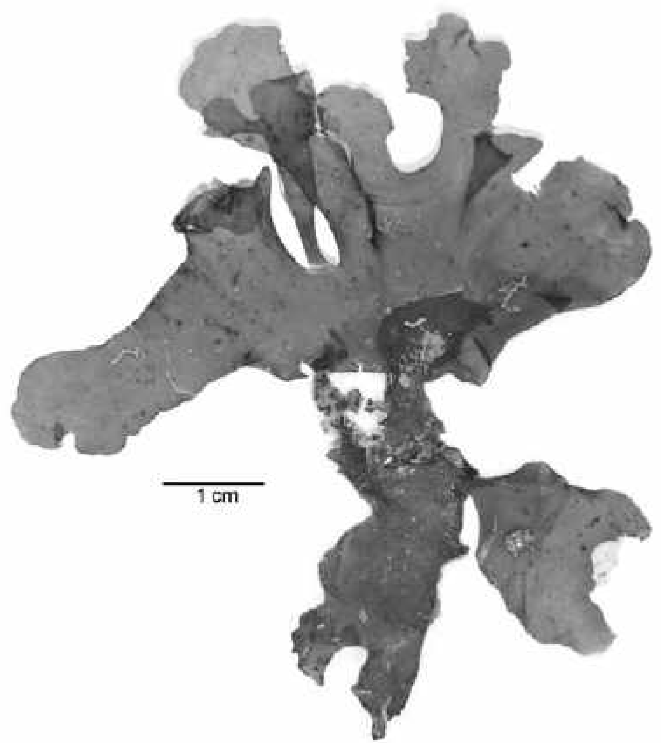

FIGURE 182. *Weeksia templetonii*: Habit of a female gametophyte (*JN-4349*, US Alg. Coll.-159945).

1961b:411; Abbott, 1968:190; Lindstrom, 1986:531, fig. 3; González-González et al., 1996:223.

Halymenia templetonii (Setchell et N. L. Gardner) I. A. Abbott, 1967a:143, fig. 7; Abbott and Hollenberg, 1976:430, fig. 382; González-González et al., 1996:223; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467, tbl. 1; Pacheco-Ruíz et al., 2008:207.

Blade mucilaginous, flaccid, orbicular to reniform (usually broader than tall), up to 15 cm tall; attached by a small discoid holdfast. Blades mostly thin, 200–250(–400) µm thick; usually with faint, false veins radiating near base (i.e., no differentiation of tissue evident in transection); with entire, irregularly lobed or lacerate margins. Medulla a network of medullary filaments composed of relatively straight cells, 40–85 µm long, 5–7 µm in diameter. Cortex of 3–4 layers of small cells.

Tetrasporangia cruciately divided, 22–26 µm long, 18–22 µm in diameter; scattered over blade. Carpogonial branch of 6–8 cells. Cystocarps up to 150 µm in diameter, embedded and scattered over blade. Spermatangia unknown.

Habitat. Rare, on rocks; subtidal, down to 20–30 m depths.

Distribution. Gulf of California: Isla Coronado (Isla Smith; off Bahía de Los Ángeles); Bahía de Loreto to Canal de San Lorenzo (off Isla Espíritu Santo); Cabo Pulmo; Punta Los Frailes. Eastern Pacific: Anacapa Island (California Channel Islands); Isla Cedros (off Baja California).

Type Locality. 38 meter depth (dredged); off Isla Cedros (Osorio-Tafall, 1948), Baja California, Pacific Mexico.

Remarks. Lindstrom (1986), investigating some species of *Halymenia* and *Weeksia,* concluded that *W. templetonii* was correctly ascribed by Setchell and Gardner (1937) to the genus *Weeksia.*

Peyssonneliales*

Peyssonneliales Krayesky, Fredericq et J. N. Norris, in Krayesky, Norris, Gabrielson, Gabriel, and Fredericq, 2009:384; Wynne and Kraft, 2010:296.

Algae are crustose, prostrate, and usually epilithic. Crusts may be noncalcified throughout, calcified throughout, or partially calcified (with hypobasal calcification between the attachment rhizoids). Calcium carbonate, if present, is in the mineral form aragonite (James et al., 1988). The lower surfaces of the crusts are partially to completely attached to the substratum, either directly (i.e., without rhizoids) or by unicellular or multicellular rhizoids. Prostrate growth is by radiating marginal rows of transversely dividing apical initials in the basal layer (multiaxial); these later divide vertically to form a single upper or lower perithallial cell. The first order of the perithallial cells gives rise to simple or branched filaments that together form a loose to compact upper-only cortex or upper and lower cortices. Cortical cells have numerous discoid or ribbon-like chloroplasts.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia are cruciately divided and borne terminally or laterally in tetrasporic nematheciathat are with or without multicellular paraphyses. Gametophytes, where known, are either monoecious or dioecious. Both the carpogonial branches and auxiliary cell branches are of three to six cells borne lateral on the erect filaments within nemathecia. Connecting filaments attach to one or often more than one auxiliary cell and develop small to sprawling fusion cells that bear the gonimoblasts. In some members, the gonimoblast may also develop directly from the connecting filament. Most cells of the gonimoblast produce carposporangia in short simple chains or branched chains. Spermatangia are apical or intercalary and develop on sympodial or apical spermatangial filaments within nemathecia.

Remarks. The molecular systematic study of Krayesky et al. (2009) clarified the taxonomy of *Peyssonnelia*, established the new order Peyssonneliales, and at that time recognized the family Peyssonneliaceae to contain only two genera, *Peyssonnelia* and *Sonderopelta* Womersley et Sinkora (1981). Members of Peyssonneliales are worldwide in distribution and are found growing on hard substratum from the intertidal to deep subtidal, down to depths of 288 m (Littler et al., 1985, 1986; Vadas and Steneck, 1988).

Currently the Peyssonniales contains one family, with some of its members occurring in the northern Gulf of California.

Peyssonneliaceae

Peyssonneliaceae Denizot, 1968:86, 308.

Squamariaceae J. Agardh, 1851:ix, 485, *nom. illeg.*

Algae of this family are usually prostrate, crustose, and dorsiventrally organized; others can have free horizontal or partially erect portions. They are partially to strongly attached to the substratum. Anatomically, there is a distinct basal hypothallium of laterally adjoined filaments, which may be calcified extracellularly in some and noncalcified in others. The lower or ventral surface of the hypothallium is without or bears rhizoidal attachments, whereas the upper hypothallium gives rise to the perithallium of vertical rows of erect filaments. Cystoliths or cell inclusions occur in some species.

Reproduction is usually by tetrasporangia, which are irregularly and cruciately divided in superficial nemathecia with slender multicellular paraphyses. Gametophytes and tetrasporophytes are isomorphic. Sexual reproductive structures are also borne in nemathecia and may be monoecious or dioecious but are apparently rare in field collections. Where known, carpogonial branches and auxiliary cells are three- to six-celled, separated by paraphyses, and borne in either superficial (on or at the surface) or elevated nemathecia above the surface. Carpogonial branches originate laterally from an intercalary cell of a nemathecial filament after the nemathcium is fully developed. Carposporangia are in unbranched to branched linear series in between paraphyses. Spermatangia are in small clusters within nemathecia and are usually without paraphyses.

Remarks. Currently 12 to 14 genera are listed in the Peyssonneliaceae (Guiry and Guiry, 2010–2011). Denizot (1968) apparently planned further studies of Mexican specimens along with other crustose groups of Pacific species. In the Gulf of California much remains to be done, and it is suspected that more taxa will be found. The finding of gametangial specimens and comparative studies of their morphologies, life histories, and DNA analyses are necessary to resolve their taxonomy.

Three genera, *Peyssonnelia*, *Metapeyssonnelia,* and *Cruoriella*, are known in the northern Gulf of California. Of these, *Metapeyssonnelia* is generally treated in this family, but molecular analyses have shown it probably belongs in Dumontiaceae complex (Krayesky et al., 2009) or possibly in the in Rhizophyllidaceae F. Schmitz, and the status of *Cruoriella* is problematic.

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* Contributed by David M. Krayesky and James N. Norris. D. M. Krayesky: Department of Biology, Slippery Rock University, Slippery Rock, Pennsylvania 16057, USA.

KEY TO THE GENERA OF PEYSSONNELIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Crusts mucilaginous and relatively soft in texture (not "hard" due to a lack of calcification); adjacent perithallial filaments nonadherent . . . . **_Cruoriella_**
1b. Crusts noncalcified to calcified (comparatively "hard"); adjacent perithallial filaments adherent 2
2a. Hypothallus (ventral view) of more or less parallel or flabellate rows of cells; perithallus (in vertical section) primarily of upwardly directed (upright) perithallial filaments . . . . **_Peyssonnelia_**
2b. Hypothallus (ventral view) of rows of cells arranged in a flabellate pattern; perithallus (in vertical section) typically of upwardly directed perithallial filaments, which in some portions of thallus changes to both upwardly and downwardly directed filaments . . . . **_Metapeyssonnelia_**

Cruoriella P. Crouan et H. Crouan

Cruoriella P. Crouan et H. Crouan, 1859:289.

Algae are thin, noncalcified crusts, usually small, up to 2 cm wide; soft and mucilaginous with the filaments of cell rows relatively easily separated under pressure; and attached to the substratum by rhizoids. In transection, the basal portion or hypothallus is of one to two cell layers. The upper portion or perithallus is composed of erect, mostly branched filaments.

Reproductive structures are developed in nemathecia. Tetrasporangia are cruciately divided and borne terminally on filaments. Carpospores are in chains, mostly terminal on filaments. Spermatangia are also borne in chains, either lateral or terminal on filaments.

REMARKS. *Cruoriella* is somewhat similar in habit, structure, and reproduction to some species of *Peyssonnelia*. *Cruoriella* is usually separated from *Peyssonnelia* on its characteristic arching to fan-shaped superficial rows of cells (especially when viewed from the bottom), soft and mucilaginous texture, and relative ease with which the rows of cells (filaments) separate under pressure. Some taxonomists (e.g., Kylin, 1956; Yoneshige, 1984, 1985; Maggs, 1990; Womersley, 1994) do not consider these features alone important enough to recognize *Cruoriella* as distinct from *Peyssonnelia*. Others (e.g., Denizot, 1968; Silva et al., 1996a; Ballantine et al., 2000; Guiry and Guiry, 2009) continue to recognize *Cruoriella*.

The generic status of the type of *Cruoriella* P. Crouan et H. Crouan (1859) is problematic. Denizot (1968) gave *Cruoriella armorica* P. Crouan et H. Crouan as the type of *Cruoriella*, and others have continued to recognize *C. armorica* (e.g., Silva et al., 1996a; Ballantine et al., 2000). Some (e.g., Taylor, 1960; Kato et al., 2005, 2006; Peña and Bárbara, 2010) have considered *Cruoriella armorica* to be a *Peyssonnelia,* as *P. armorica* (P. Crouan et H. Crouan) Weber-van Bosse (in Børgesen, 1916). If this is followed, then *Cruoriella* would be congeneric with *Peyssonnelia*, and the other species of *Cruoriella* would need to be reinvestigated to resolve their generic placement, with some species possibly needing a new type and generic name.

Denizot (1968) also considered the generitype of another crustose genus, *Cruoriopsis* L. Dufour (1864), i.e., *Cruoriopsis crucialis* L. Dufour, to be conspecific with *Cruoriella armorica* P. Crouan et H. Crouan (1859), thus reducing them to a single genus as *Cruoriella*. Abbott and Hollenberg (1976), however, recognized *Cruoriella* and *Cruoriopsis* to be separate genera. Later, Irvine (1983), noting similarities in morphology and the lateral position of tetrasporangia in both *Cruoriopsis crucialis* L. Dufour and *Plagiospora gracilis* Kuckuck (1897; generitype of *Plagiospora* Kuckuck (Gloiosiphoniaceae F. Schmitz, 1892), suggested the two may be congeneric. Thus, studies are needed to further clarify the generic status of *Cruoriella* as well as *Cruoriopsis* and *Plagiospora*.

There are two species of *Cruoriella* in the northern Gulf of California.

KEY TO THE SPECIES OF *CRUORIELLA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crust (200–)400–600 µm thick; loosely attached by a few rhizoids; tetrasporangia in elevated nemathecia, sessile or on 1-celled pedicel; spermatangia in slightly elevate nemathecia . . . . **_C. fissurata_**
1b. Crusts 80–150 µm thick; firmly attached by a few rhizoids and a dense gelatinous basal layer; tetrasporangia terminal on 2- to 6-celled filament (not in nemathecia) . . . . **_C. mexicana_**

Cruoriella fissurata E. Y. Dawson

FIGURE 183

Cruoriella fissurata E. Y. Dawson, 1953a:109, pl. 7: fig. 6, pl. 24: fig.1 [type specimen]; 1957c:18; 1960a:38; 1966b:59; Nozawa, 1969:19, figs. 1A–F, 2A–F; León-Álvarez and González-González, 1993:461; González-González et al., 1996:195; Yoshida, 1998:767; Verlaque et al., 2000:194, tbl. 1; Pacheco-Ruíz et al., 2008:208; Berneker, 2009:CD p. 62; Fernández-García et al., 2011:61.

Peyssonnelia mariti sensu Denizot, 1968:122 [in part; only *Cruoriella fissurata*; non *Peyssonnelia mariti* (Weber-van Bosse) Denizot, 1968:122; basionym: *Cruoriella mariti* Weber-van Bosse, 1921:288].

Crusts, rose red to bright red (upon drying becomes purple red), lightly calcified; up to 10 cm or more across; (200–)400–600 µm thick; growing irregularly by small fan-shaped or lobed portions, usually not overlapping; loosely attached by a few short, unicellular rhizoids. Surface in fresh specimens smooth,

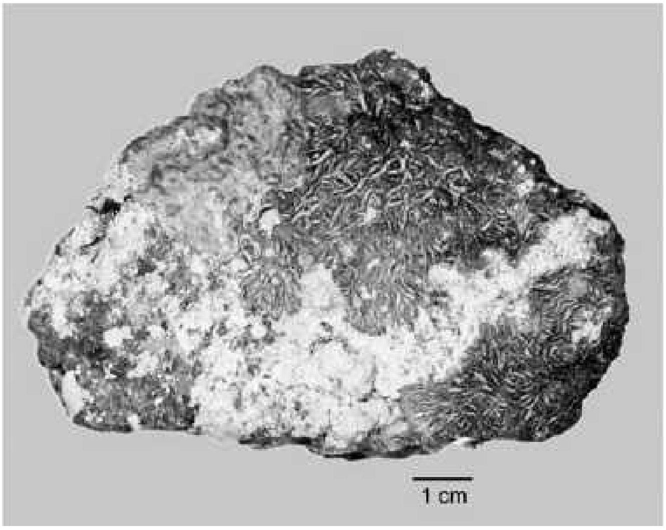

FIGURE 183. *Cruoriella fissurata*: Habit of the crust on rock (type specimen: *EYD-6830a*, AHFH, now UC).

without striations; margins wavy and more or less lobed, margins may be unattached; upon drying, crust shrinks; surface of minute mound-like elevations, which form radiating, anastomosing ridges. Hypothallus surface seen from ventral (lower) view; of cell rows converging, diverging, and anastomosing in fan-shaped arrangement. Cells of hypothallus in transection, (30–)35–50(–60) μm long, 15–20 μm in diameter; some cells dense with starch grains. Perithallus of forked (usually twice) filaments of ascending cell rows; upper cells, mostly shorter than broad, 4–5 μm tall, 12–13 μm wide.

Tetrasporangia cruciately divided, about 70–80 μm long, (30–)50–60 μm in diameter; in elevated nemathecia, 100–150 μm tall, about 650 μm wide; covering surface areas, in elongated patches up to 1.0–2.0 mm wide; tetrasporangia among slender clavate paraphyses, with apices about 9 μm in diameter (after Dawson, 1960a). Carposporangial thalli not found in the northern Gulf. Carpogonial nemathecia (as reported in southern Japan; Nozawa, 1969) 170–190 μm tall, mostly 800 μm wide; with a thin gelatinous roof. Carpogonial branch 3-celled, terminal on supporting cell; among slender, unbranched paraphyses. Gonimoblast cells cut off from secondary connecting filament near auxiliary cell; all 2–4 cells develop into globose carposporangia, 25–35 μm in diameter. Spermatangia in small, slightly elevated nemathecia, up to 220 μm or more wide and about 35 μm deep; spermatia, 2.0–2.5 μm in diameter, developed by transverse and longitudinal divisions of short, thick spermatangial parent cells.

HABITAT. On rocks, shells, coralline rubble, and worm tubes; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla San Lorenzo (southwestern Islas de la Cintura) to Guaymas; Punta Aguja (about 3.2 km SW of Punta Concepción); Cabeza Ballena. Eastern Pacific: Guerrero; Costa Rica to Panama. Western Pacific: Japan.

TYPE LOCALITY. On intertidal rocks; Cabeza Ballena, Baja California Sur, Gulf of California, Mexico.

Cruoriella mexicana **(E. Y. Dawson) Denizot**

FIGURE 184

Cruoriopsis mexicana E. Y. Dawson, 1953a:99, pl. 10: figs. 11–14; 1957c:18; 1960a:38; 1961a:193, pl. 1: figs. 2–5; 1961b:426; 1966a:21; 1966b:62; Mateo-Cid and Mendoza-González, 1992:21; Serviere-Zaragoza et al., 1993a:483; Mendoza-González et al., 1994:105; González-González et al., 1996:195; CONANP, 2002:140.

Cruoriella mexicana (E. Y. Dawson) Denizot, 1968:149, fig. 134; León-Álvarez and González-González, 1993:461; González-González et al., 1996:195, 388; L. Aguilar-Rosas et al., 2000:130; Bernecker, 2009:CD-Rom p. 62; Fernández-García et al., 2011:61.

Crusts small, thin, 80–150(–200) μm thick; attached beneath the basal cell layer by a hyaline gelatinous film and short descending rhizoids. Hypothallus of 1 layer; cells of filaments wider than tall, 8–12 μm tall by12–24 μm wide. Vertical filaments of perithallium arise from basal layer; irregularly and frequently branched; terete in tetrasporangial thalli and slightly clavate in carpogonial thalli. Cells of lower perithallium filaments more or less isodiametrical, 9–15 μm diameter; upper cells smaller, narrower, and elongated.

Tetrasporangia cruciately divided; long and slender, 70–80 μm long by 16–20 μm in diameter, borne terminally on 2- to 6-celled filaments among paraphyses. Carpospores ovate, 18–20 μm long; borne in short-branched chains, usually of 4 carpospores. Spermatangia reported by Dawson (1960a) but not described.

HABITAT. On mollusks shells and rock; low intertidal to shallow subtidal.

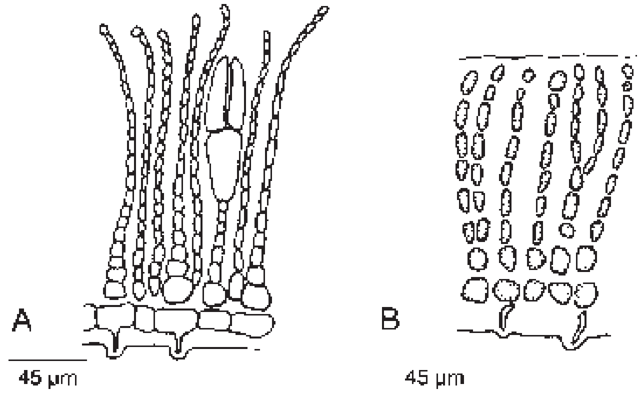

FIGURE 184. *Cruoriella mexicana*: A. Vertical section through the type specimen, a sporophytic crust; tetrasporangia terminal on filaments among paraphyses (holotype). B. Vertical section through a nonreproductive portion (A, B, after Dawson, 1953a, pl. 10: figs. 11, 12, as *Cruoriopsis mexicana*).

Distribution. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco; San Felipe; Bahía de Loreto; Laguna Agiabampo; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Islas Los Coronados (off northwest Baja California); Colima to Guerrero; Costa Rica.

Type Locality. On shells, dredged 13–15 m depths; off Isla Coronado Sur (South Island; 32°24.5′N, 117°13.8′W), Islas Los Coronados, Baja California, Pacific Mexico.

Remarks. *Cruoriella mexicana* is not well known in the northern Gulf of California. Originally described in the genus *Cruoriopsis* (Dawson, 1953a), it was subsequently transferred to *Cruoriella* by Denizot (1968). Although similar to *Peyssonnelia japonica* (Segawa) Yoneshigue (1984; basionym: *Cruoriopsis japonica* Segawa, 1941; =*Cruoriella japonica* (Segawa) Denizot, 1968), the Pacific Mexico and Gulf of California *Cruoriella mexicana* grow on shells and rocks, have a single basal layer of nontrapezoidal cells, and comparatively taller, slightly narrower tetraspores (70–80 µm tall; 16–20 µm in diameter). In contrast, *Peyssonnelia japonica* of the northern Gulf are epiphytic, have a basal layer of 1–2 trapezoidal cells, and smaller tetraspores (mostly 45–50 µm tall and 16–30 µm in diameter) (R. Aguilar-Rosas et al., 2007a). More specimens of northern Gulf *Cruoriella mexicana* are needed to evaluate its taxonomic status and phylogenetic relationship to type locality specimens and those of the northern Gulf referred to *P. japonica*. See also Remarks under *Peyssonnelia japonica*.

Metapeyssonnelia Boudouresque, Coppejans et Marcot

Metapeyssonnelia Boudouresque, Coppejans et Marcot, 1976:288.

Crusts are orbicular, spreading, and usually dark red or dark purple-red to blackish in surface view. Calcification is light to heavy, varying from complete (e.g., the type species (*M. feldmannii* Boudouresque, Coppejans et Marcot) to only partial and hypobasal in others. Most are attached by unicellular rhizoids cut off from central or distal ends of hypothallial cells, but at least one is attached by multicellular rhizoids (i.e., the Pacific Mexcio *M. mexicana*). Hypothallial cells are arranged in a flabellate or parallel pattern (in ventral view) and produce a single row of coxal (proximal perithallial) cells that nearly cover the bearing hypothallial cells or are cut off from the distal end of the hypothallial cells (seen in section views). Perithallial cells (as seen in sections) are cut off from coxal cells and regularly grow upward (mostly at angles of 45°–90°) to form the perithallus, but in some portions they can also differentiate into a superior (upper) perithallus of upward filaments and also an inferior (lower) perithallus of downward filaments. Basal hair cells are present in the upper perithallus of some species. Cystoliths may be present in the lower thallus of some species.

Tetrasporangial nemathecia may be superficial or sunken. Tetrasporangia are borne on a basal nemathecial cell (as in *M. corallipeda* Verlaque, Ballesteros et Antonius, 2000) or on cup-shaped cells cut off from basal nemathecial cell (Ballantine et al., 2014). Carposporangial nemathecia (where known) are superficial and contain elongated carposporangia in simple to occasionally branched chains of two to four cells (Ballantine et al., 2014). Spermatangia (where known) are in sori up to 50 µm high. Terminal perithallial cells cut off small squarish or triangular cells distally that produce clusters of elongate spermatangial parent cells. Spermatangia are cut off distally from spermantangial parent cells, initially in simple chains. Later, in most cases, they divide longitudinally, and each division subsequently divides transversely to form tetrads of spermatangia. Further irregular divisions result in disorganized groups of spermatangia (spermatangia after *M. milleporoides* D. L. Ballantine et H. Ruiz, 2011).

Remarks. Although *Metapeyssonnelia* is superficially very similar to *Peyssonnelia*, these genera can be distinguished by characters only seen in anatomical sections. Hypothallial cells of *Metapeyssonnelia* develop a single row of coxal cells that can produce perithallial filaments directed both upward and downward to form a lower and upper perithallus (Verlaque et al., 2000; "fountain-like" structure of Boudouresque et al., 1976). In contrast, the hypothallus of *Peyssonnelia* develops only upward (upright) perthallial filaments to form the perithallus. Some species of *Metapeyssonnelia* have been found only on nonliving substrata (e.g., rocks, tidal platforms, shells, or dead coral fragments), whereas a few Caribbean species are known to overgrow and kill corals (Verlaque et al., 2000; Ballantine and Ruíz, 2011).

There are five known species of *Metapeyssonnelia*. One, *M. mexicana,* is the only member of the genus currently known in the Pacific. It and another, possibly a new species, are known in the northern Gulf of California (and are included in the Key to *Peyssonnelia* and *Metapeyssonnelia* herein under *Peyssonnelia*).

Metapeyssonnelia mexicana (E. Y. Dawson) D. L. Ballantine et H. Ruíz

FIGURE 185

Ethelia mexicana E. Y. Dawson, 1953a:100, pl. 11: figs. 7–8; 1966a:17; 1966b:59; González-González et al., 1996:200 [non *Peyssonnelia mexicana* E. Y. Dawson, 1953a:106; non *Cruoriopsis mexicana* E. Y. Dawson, 1953a:99; =*Cruoriella mexicana* (E. Y. Dawson) Denizot, 1968:149].

Metapeyssonnelia mexicana (E. Y. Dawson) D. L. Ballantine et H. Ruíz, 2011:50, tbl. 1.

Peyssonnelia dawsonii Denizot, 1968:109, figs. 94, 95; León-Tejera et al., 1993:200; León-Álvarez and González-González, 1993:462; Verlaque et al., 2000:194, tbl. 1.

Crusts dark purple–red, closely following contour of substratum, often covering 3 cm or more, 400–1000 µm thick; lightly calcified only in basal portion; firmly attached by multicellular rhizoids along margins at first; later, thallus tissue grows downward, penetrating and filling irregularities in the substratum. Hypothallus cells arranged parallel to irregularly. Upper perithallus of laterally adjoined, branched cells in vertical rows. Lower perithallus cells irregularly arranged in some portions and stratified in other portions. Cells of lower perithallus 4–8 times

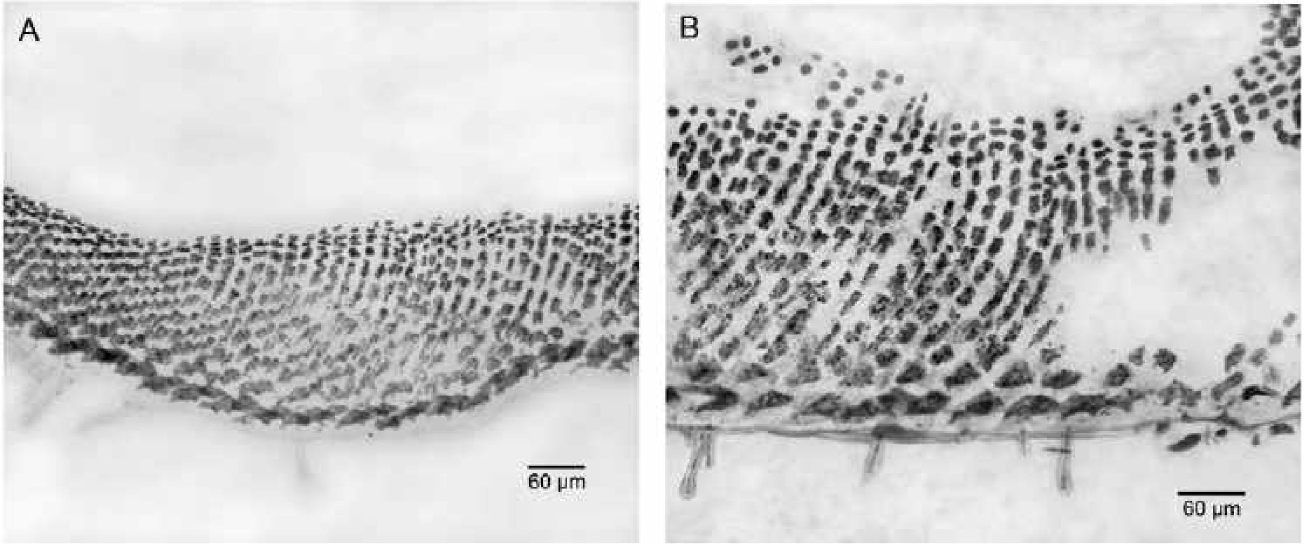

FIGURE 185. *Metapeyssonnelia mexicana*: A, B. Vertical sections, showing some unicellular rhizoids, and the perithallus of more or less assurgent filaments that become slightly more vertical near crust surface (*GJH-67-54*, US Alg. Coll. microscope slide 3109).

longer than wide, becoming smaller and shorter upward to surface cells, 4–6 µm in diameter.

Tetrasporangia elongated, 45–50 µm long by 18–20(–35) µm in diameter; within sunken sori, 1 mm (or more) wide, 120–130 µm deep. Paraphyses within sori unbranched, of 7–8 slightly clavate cells, up to 3.5 µm wide. Other reproductive structures are unknown in northern Gulf specimens.

Habitat. On rocks, tidal platform, and into crevices; high to low intertidal.

Distribution. Gulf of California: Punta Peñasco and Playa Las Conchas (Playa Estación), Puerto Peñasco; Nayarit. Eastern Pacific: Guerrero.

Type Locality. Bahía de Acapulco, Guerrero, Pacific Mexico.

Remarks. *Metapeyssonnelia mexicana* is currently the only member of the genus known in the Pacific. It has been reported in the upper Gulf of California (Dawson, 1966a, 1966b, as "*Ethelia mexicana*"), considerably northward from its type locality in Guerrero, Pacific Mexico. Other specimens cited by Dawson (1966a:17) as "*Peyssonnelia* sp.," also from the upper Gulf in Puerto Peñasco, were noted as "not specifically distinct from *Ethelia*" and thus should be reexamined.

Denizot (1968, as "*Peyssonnelia dawsonii*") examined the type specimen of *Ethelia mexicana* E. Y. Dawson (1953a), observing perithallial cells in upper parts to be in vertical rows and irregular in some portions of the lower thallus, thus lacking a generic character of *Ethelia* Weber-van Bosse (1921)—i.e., the absence of distinct cell rows. The lightly calcified *E. mexicana* has a hypothallus of parallel filaments and both ascending and descending rows of perithallial cells (Verlaque et al., 2000), characteristics recognized by Ballantine and Ruíz (2011) as occurring in *Metapeyssonnelia*.

***Metapeyssonnelia* sp. A**

Crusts thin, 146–192 µm thick; hypobasal calcification light; attached by unicellular to multicellular rhizoids. Hypothallus cells 13.5 µm tall by 32 µm wide, in a single, more or less parallel row. Upper perithallus of laterally adherent cells in vertical rows; branched near apex; occasionally with a terminal basal hair cell. Cells of perithallus longer than wide; lower perithallus cells 18 µm long by 10.8 µm in diameter, curved upward from hypothallial cells; becoming smaller and shorter upward to surface cells, about 6.3 µm long by 4.5 µm in diameter.

Reproduction not found.

Habitat. On rocks and tidal platform; intertidal.

Distribution. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco.

Remarks. This upper Gulf specimen (US Alg. Coll.) is referred to *Metapeyssonnelia* sp. A and may be an undescribed species. More collections for further morphological and molecular analyses will help clarify its taxonomic status. If found to be a *Metapeyssonnelia,* it would be the second known Pacific species.

Peyssonnelia Decaisne

Peyssonnelia Decaisne, 1841:168, 196–197, pl. 5: figs. 16, 17, 28; Decaisne, 1842a:360; Descaine, 1842b:126; Krayesky et al., 2009:374, figs. 1, 2.

Prostrate crusts that are usually more or less circular or lobed in surface view. Some species are noncalcified, whereas others contain hypobasal calcification. Crusts may be tightly adherent to loosely attached to the substratum by unicellular or multicellular, simple or branched rhizoids; some crusts with distal portions of the thallus free (unattached). Crusts are usually of 2 distinct layers: a hypothallus composed of filaments 1 layer thick and a perithallus of multilayers of filaments in vertical rows of cells; however, there are also some with a subhypothallic layer. Dorsal surface is formed by cortical cells of the perithallus, and ventral surfaces by cells of the hypothallus. Cells in some species are reported to have cystoliths or crystals as cell inclusions. Portions of the surface layer of cells develop filaments of sterile cells among which the reproductive structures are developed.

Reproductive structures develop within elevated nemathecia, scattered over the perithallus. Tetrasporangia are cruciately divided and usually terminal on filaments that are interspersed with paraphyses. Gametophytes, where known, are monoecious or dioecious, and also develop intermixed with paraphyses within nemathecia. Carpogonial branches are 3- to 6-celled. Auxiliary cells are intercalary in auxiliary cell branches of 3–6 cells. Gonimoblasts develop from the place of fusion of a segment of the connecting filament to the diploidized auxiliary cell and, as they mature, produce only a few large carposporangia. Spermatangia are borne terminally on erect spermatangial filaments, abundantly grouped in nemathecia without paraphyses.

REMARKS. In reviewing the genus *Peyssonnelia*, Maggs and Irvine (1983) elucidated reproductive characters that were not known for many of the species. More recently, Krayesky et al. (2009) clarified the genus on the basis of morphological studies and molecular analysis of *Peyssonnelia*.

There are four species reported in the southern Gulf (Dawson, 1953a, 1961b, 1966b): *Peyssonnelia squamaria* (S. G. Gmelin) Decaisne (1842a; basionym: *Fucus squamarius* S. G. Gmelin, 1768) from Isla San Ildefonso and Islas Santa Inez (Dawson, 1966b) and San José del Cabo, *P. conchicola* Piccone et Grunow (in Piccone, 1884) from Bahía Concepción and Cabo San Lucas (Dawson, 1953a, 1957a), *P. hancockii* (E. Y. Dawson) Denizot (1968; basionym: *Cruoriella hancockii* E. Y. Dawson, 1953a) from Cabeza Ballena, and *P. pacifica* Kylin (1925) from Mazatlán. Further collections and critical studies should reveal additional species in the Gulf of California.

Currently, three species of *Peyssonnelia* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *PEYSSONNELIA* AND *METAPEYSSONNELIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Crust composed of erect vertical rows of cells throughout; loosely attached to substrate by unicellular rhizoids . . . . **Peyssonnelia orientalis**
1b. Crusts partly of vertical cell rows and ascending and descending cell rows or entirely of ascending cell rows; firmly attached to substratum by multicellular or unicellular rhizoids 2
2a. Crusts with upper thallus of curving to vertical rows of cells from distinctive hypothallus, or with ascending and desending rows of cells; attached by multicellular rhizoids 3
2b. Crusts composed entirely of ascending cell rows; attached by short unicellular rhizoids 4
3a. Crust upper thallus composed of only vertical rows of cells; lower portion of ascending and descending rows of cells; firmly attached to substrate by multicellular rhizoids and by downward-growing tissue . . . . **Metapeyssonnelia mexicana**
3b. Crust with perthallus of curving rows of cells rising upward from a single row of hypothallial cells . . . . **Metapeyssonnelia species A**
4a. Crust basal layer of trapezoidal cells; attached by unicellular rhizoids from basal cells; tetrasporangia mostly 45–50 µm tall and 16–25(–30) µm . . . . **Peyssonnelia japonica**
4b. Crust basal layer of nontrapzoidal cells; firmly attached by short unicellular rhizoids; tetrasporangia longer and wider, 60–100 µm long, 22–35 µm in diameter . . . . **Peyssonnelia mexicana**

Peyssonnelia japonica (Segawa) Yoneshigue

Cruoriopsis japonica Segawa, 1941:259, fig. 7A–F; 1977:68, pl. 39: fig. 305.

Peyssonnelia japonica (Segawa) Yoneshigue, 1984:134; Yoshida, 1998:770; Kato et al., 2006:931; R. Aguilar-Rosas et al., 2007a:154, figs. 3A–D; Y.-P. Lee, 2008:363, figs. A–C.

Cruoriella japonica (Segawa) Denizot, 1968:147, 309, fig. 133; Sohn and Kang, 1980:74, pl. II: figs. 5–10.

Crusts mostly 170–180(–220) µm thick; attached by unicellular rhizoids, occasionally issued from basal cells. Hypothallus in cross section of 1–2 layers of basal cells, 2–3 times broader than tall, 8–16 µm tall, (10–)14–20 µm broad (long); trapezoidal cells above horizontal basal cells upward forms a perthallus of vertical rows of 10–16 smaller, squarish to slightly elongated cells, (4–)8–12 µm tall and mostly (4–)6–8 µm in diameter.

Tetrasporangia cruciately divided, 45–50(–90) µm tall and 16–25(–30) µm in diameter; borne on stalk of 1–5 cells, lateral on vertical filament. Sexual reproduction not described.

HABITAT. Epiphytic on *Ceratodictyon variabile* in tide pools; intertidal.

DISTRIBUTION. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco. Western Pacific: Japan; Korea.

TYPE LOCALITY. Crusts on mollusk shell (*Tegula rustica*); Sirahama, Miyake-zima, Izu Islands, Japan.

REMARKS. A western Pacific species, *Peyssonnelia japonica* was described on a mollusk shell from one of the Izu Islands south of Tokyo. It has since been reported in the eastern Pacific from upper Gulf of California as an epiphyte on *Gelidiopsis* (R. Aguilar-Rosas et al., 2007a). As we have not seen their specimens, the description is based on Segawa (1941) and in part on R. Aguilar-Rosas et al. (2007a). Comparative molecular testing of the northern Gulf *P. japonica* with those from the type locality will elucidate their relationship. Kato et al. (2006) provided molecular support that the species belongs in *Peyssonnelia* and that it was distinct from *P. armorica* (P. et H. Crouan) Weber

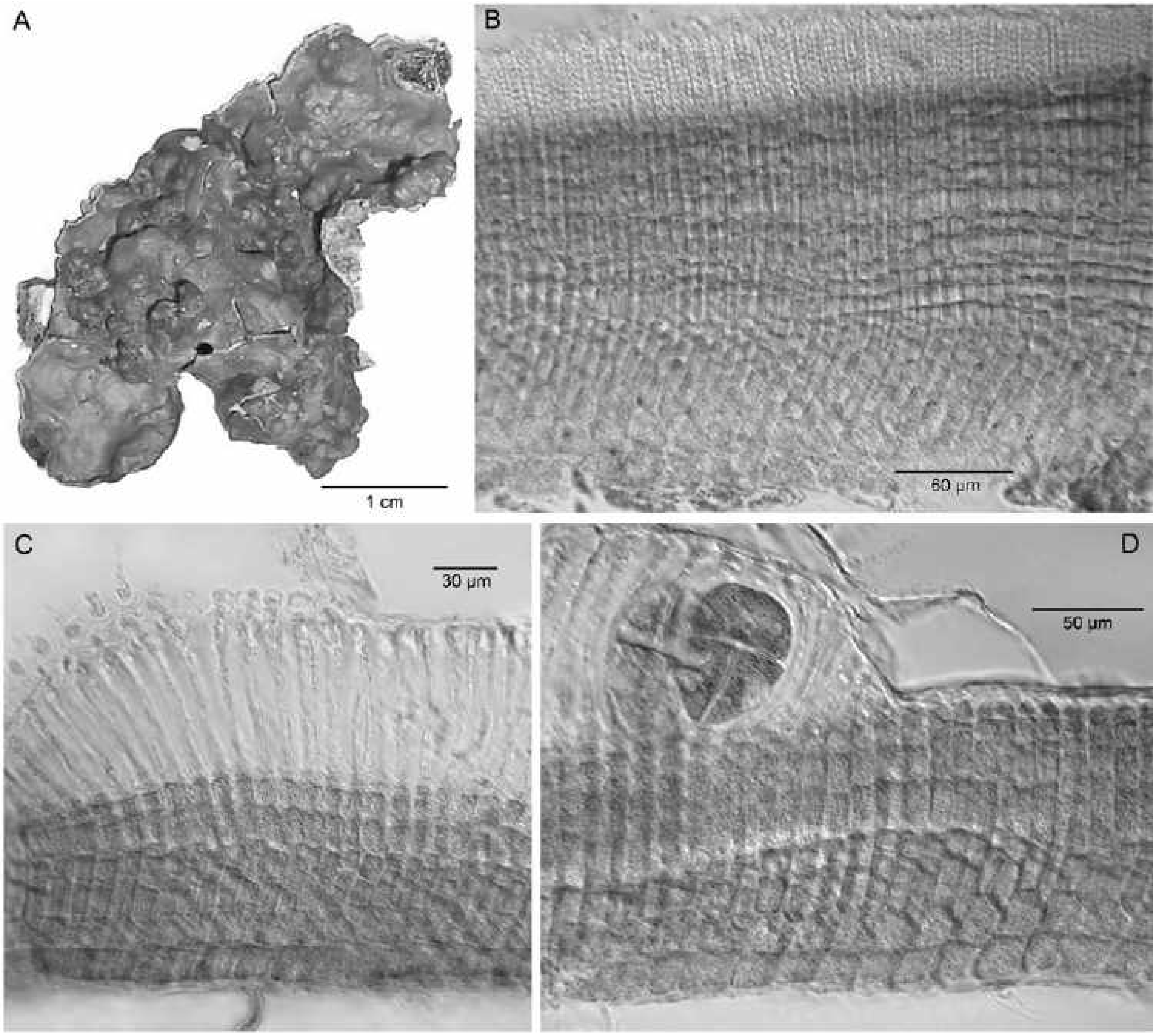

FIGURE 186. *Peyssonnelia mexicana*: A. Habit, surface view of crust (*EYD-12137*, US Alg. Coll.-12357). B. Vertical section showing thick perithallus and spermatangial nemathecia with extensive closely adjacent vertical rows of spermatangia (*EYD-26098*, US Alg. Coll. microscope slide 800). C. Section through an empty tetrasporangial nemathecia (tetrasporangia already discharged) showing slender, unbranched paraphyses arising from upper surface of crust. D. Small portion of section through elevated tetrasporangial nemathecia showing cruciately divided sporangia among unbranched paraphyses (C, D, *EYD-26099*, US Alg. Coll. microscope slide 799).

van-Bosse (in Børgesen, 1916; generitype of *Cruoriella*). See also Remarks under genus *Cruoriella* and *C. mexicana*.

Peyssonnelia mexicana E. Y. Dawson

FIGURE 186

Peyssonnelia mexicana E. Y. Dawson, 1953a:106, pl. 11: figs. 1, 2; 1961b:412; Dreckmann et al., 1990:30; Dreckmann, 1991:33; León-Tejera et al., 1993:200; León-Álvarez and González-González, 1993:462; González-González et al., 1996:247.

Crusts expanding up to 3 cm or more in width; surface relatively smooth (any irregularities reflect those of substratum), 250–550(–600) µm thick; firmly adherent to substratum by short unicellular rhizoids. Hypothallus distinct, of parallel cell rows; cells 8–15 µm tall, 25–30 µm wide, 25–30 µm high in lower surface view, with basal cuticle up to 10 µm thick. Perithallus of ascending cells, upward forming vertical rows, 1–2 times branched, usually in second to fifth tier; cells rectangular, about twice as long as wide, becoming smaller in size upward to surface layer; uppermost cells 6–8 µm in diameter.

Tetrasporangial nemathecia elevated, about 130–150 µm tall; tetraspores 60–100 µm long, 22–35 µm in diameter; among usually dense, unbranched paraphyses, of up to 7 elongate cells, from 2 to 4 µm in diameter at base, upper 2–3 cells shorter and 5 µm in diameter at apices; apical cell sometimes more or less pointed. Carpogonial not known. Spermatangia in vertical rows within elevated nemathecia.

HABITAT. On rocks; intertidal.

DISTRIBUTION. Gulf of California: Isla Las Ánimas (Isla San Lorenzo Norte), Islas de San Lorenzo (southwestern Islas de la Cintura). Eastern Pacific: Cabo Colnett, Baja California to Oaxaca.

TYPE LOCALITY. Granite rock outcrop; southeast side of Bahía Acapulco, Guerrero, Pacific Mexico.

Peyssonnelia orientalis **(Weber-van Bosse) Cormaci et G. Furnari**

FIGURE 187

Peyssonnelia rubra f. *orientalis* Weber-van Bosse, 1921:272, fig. 89.

Peyssonnelia orientalis (Weber-van Bosse) Cormaci et G. Furnari, 1987:757; Yoshida, 1998:771; Mendoza-González and Mateo-Cid, 1999:43, figs. 7–9; L. Aguilar-Rosas et al., 2000:130; Mateo-Cid et al., 2006:55; Serviere-Zaragoza et al., 2007:11; Y.-P. Lee, 2008:364, figs. A–C.

Peyssonnelia rubra var. *orientalis* Weber-van Bosse in Dawson, 1953a:104, pl. 10: figs. 8, 9; 1957a:3; 1959a:20; Dawson et al., 1960a:72, pl. 17: fig. 3; Dawson, 1961b:412; Denizot, 1968:122; Nozawa, 1972:45, fig. 2A–H; Abbott and Hollenberg, 1976:371, fig. 310; Huerta-Múzquiz, 1978:338; Stewart and Stewart, 1984:143; Mendoza-González and Mateo-Cid, 1986:422; Stewart, 1991:77; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:17; León-Álvarez and González-González, 1993:462; Serviere-Zaragoza et al., 1993a:484; Mateo-Cid et al., 1993:47; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:105; González-González et al., 1996:247; Mateo-Cid et al., 2000:64; CONANP, 2002:140; Riosmena-Rodríguez et al., 2005a:34.

Peyssonnelia orientalis (Weber-van Bosse) Boudouresque et Denizot, 1975:42, *comb. inval.*

Peyssonnelia rubra sensu Setchell et N. L. Gardner, 1930:175; Taylor, 1945:168; Huerta-Múzquiz and Garza-Barrientos, 1975:8 [non *Peyssonnelia rubra* (Greville) J. Agardh, 1851:502].

Crusts, spreading up to 8 cm wide, deep rose red to crimson, close to substratum but loosely attached by unicellular rhizoids; margins sometimes unattached. Crust lightly calcified only in basal portion, 100–300 µm thick; surface view showing longitudinal striations and sometimes faint concentric bands; margins simple or occasionally lobed. Hypothallus of cells taller than broad in transection, 25–40 µm long by 12–16 µm wide, with rounded walls, giving them the appearance of cobblestones. Perithallus of unbranched, vertical rows of cells, usually 6–10 in number; lower cells more or less isodiametric or taller than wide; upper cells flattened, 11–16 µm wide.

Tetrasporangial nemathecia elevated, 80–160 µm tall; tetrasporangia ovate to elongate, 70–110 µm long, 25–55 µm wide, in a gelatinous matrix with unbranched or single branched, slightly clavate, paraphyses. Sexual reproduction unknown in Gulf material.

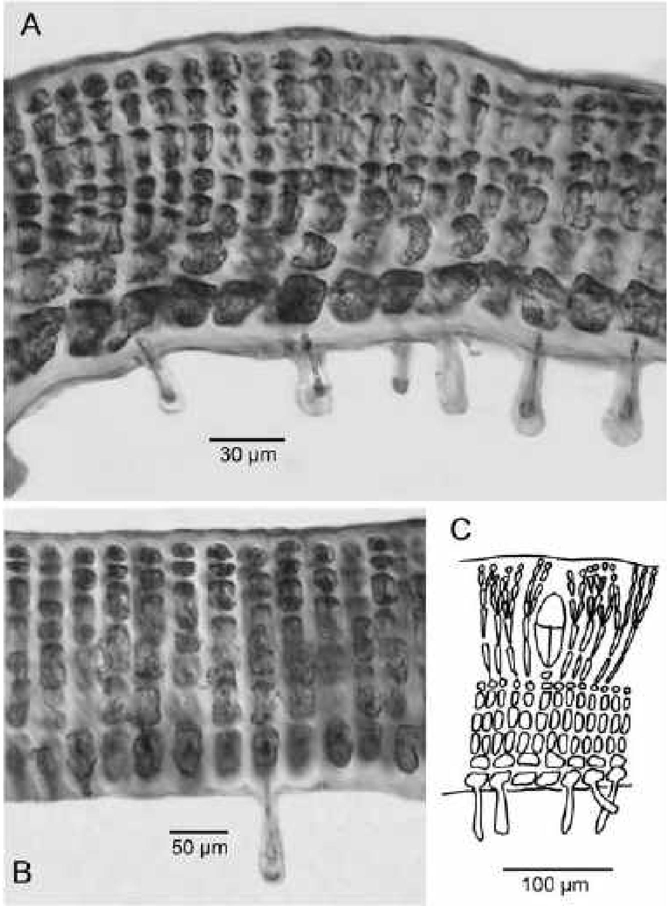

FIGURE 187. *Peyssonnelia orientalis*: A. Radial vertical section through nonreproductive crust showing the basal, single-layered hypothallus with numerous unicellular rhizoids, and erect vertical filaments forming the multilayered perithallus (6–10 cell rows high). B. Tangential section (A, B, *JN-5214*, US Alg. Coll. microscope slide 4564). C. Part of a radial vertical section through nemathecia showing cruciately divided tetrasporangia among single-branched paraphyses arising from the upper surface of the crust (after Dawson, 1953a: pl. 10: fig. 9, as *P. rubra* var. *orientalis*).

HABITAT. On rocks and shells; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla San Jorge; San Felipe to Bahía Agua Verde; Isla Cholla (NNW of Isla Carmén) to Punta Palmilla; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: California Channel Islands to Isla Guadalupe and Isla Cedros (Baja California); Isla Clarión, Isla Socorro and Isla San Benedicto (Islas Revillagigedo); Bahía de Ballenas to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Jalisco to Colima; Oaxaca; Galápagos Islands. Western Pacific: China; Korea; Japan.

Type Locality. Not specifically designated; various syntype localities are in the Philippine Islands and Indonesia (Silva et al., 1996a:213).

Remarks. Gulf of California *Peyssonnelia orientalis* are lightly calcified and relatively thin, with vertical rows of perithallial cells and elevated, more or less gelatinous tetrasporangial sori, and attached loosely by unicellular rhizoids (most notably at margins), in agreement with the Pacific concept of the species (Weber-van Bosse, 1921; Dawson, 1953a, as "*P. rubra* var. *orientalis*"). *Peyssonnelia orientalis* was reported to be in the shaded intertidal to about 20 m depths throughout Pacific Mexico (Dawson et al., 1960a). Although Denizot (1968) commented that Dawson's (1953a) material was similar to small specimens of the Atlantic *P. inamoena* Pilger (1911), the Gulf of California *P. orientalis* is different (for species comparisons, see Schneider and Reading, 1987; Womersley, 1994).

GRACILARIALES*

Gracilariales Fredericq et Hommersand, 1989a:225; Hommersand and Fredericq, 1990:138.

Algae of this order are mostly erect and free-living, with one to several cylindrical, compressed or flattened, branching or divided thalli that arise from small to large, discoid to crustose holdfasts. Cylindrical members are often wiry or stringy and mostly branched or occasionally unbranched. Other species are slightly compressed, slender, or strap-like, and some are distinctly flattened, narrow to broad, and branching to foliose. Although their anatomy appears to be multiaxial with a pseudoparenchymatous medulla, detailed examination of the uppermost apical regions reveals uniaxial growth, which becomes quickly obscure below. The cortex is composed of a few to many layers of small, pigmented cells that surround a medulla of larger hyaline cells. The outer cortical layer may have enlarged, hyaline, hair-like cells. A few members are parasitic genera that are minute, whitish, subglobose to irregularly globose thalli found growing on some of the larger pigmented members of the order.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia develop on cortical cells, become cruciately divided, and may be scattered throughout or in sori on the cortex or borne in specialized branches. Carpogonial branches are two-celled, borne laterally on cortical cells, with a supporting cell that produces two to three sterile filaments, each two cells long. After fertilization, the carpogonium fuses with its supporting cell to form a large fusion cell, and sterile filament cells fuse and transfer their contents into the fusion cell. There are no auxiliary cells. The gonimoblasts develop outward from the fusion cell, usually in rows, with the outer cells developing carposporangia. Cystocarps project from the thallus surface or along its margins. The carposporophyte is within a multilayered pericarp, with an ostiole. Traversing filaments connect to the pericarp in some members and are lacking in others. Spermatangia are formed superficially in sori or within shallow cavities to deep pits within the cortical cells.

Remarks. The Gracilariales contains two families (Fredericq and Hommersand, 1989a, 1990; Hommersand and Fredericq, 1990; Gurgel and Fredericq, 2004), the large, well-established Gracilariaceae and the smaller Pterocladiophilaceae K.-C. Fan et Papenfuss (1959).

The Gracilariaceae exhibits a high diversity of species in the Gulf of California.

GRACILARIACEAE

Gracilariaceae Nägeli, 1847:240, 254.

Most members of the family are erect and free-living and cylindrical, compressed, or flattened (in the Gulf of California, *Gracilaria* and *Gracilariopsis*). These species are of variable size and shape, more or less freely branched or divided, and range from cylindrical and stringy to sometimes slightly compressed or flattened strap-like forms and often broad, blade-like forms. The other genus in the Gulf, *Gracilariophila*, is a minute, whitish parasite on *Gracilaria*.

Growth is uniaxial and apical. In structure, all members of the family are pseudoparenchymatous, with a medulla of large, more or less isodiametric cells and a cortex of successively smaller cells to the outer cortical surface of pigmented cells. Tetrasporangia are cruciately divided. The female reproductive apparatus is a two-celled carpogonial filament on a supporting cell that bears sterile filaments. After fertilization, a large number of adjoining cells fuse with the fertile cells and produce a large fusion cell at the base of the gonimoblast cells. The gonimoblast filaments grow toward the thallus surface, with all but the center cells developing into carposporangia. Cystocarps are surrounded by a thick pericarp with an ostiole, protruding above the thallus surface. Internally, the cystocarp is with or without nutritive filaments connecting the gonimoblast cells to the pericarp. Spermatangia develop in different ways depending on the species: continuous or in patches over the thallus surface, within slightly sunken to shallow sori or patches, or developed within the cortical cell layers in shallow to deep pits or cavities.

Remarks. A large family of 13 genera (Guiry and Guiry, 2008–2010), the Gracilariaceae includes many members that are economically important, used as foods and collected and grown for the personal, commercial, or industrial use of their phycocolloids, agar, and agarose (Chen et al., 2009). When only nonreproductive thalli are found, the species can be difficult to impossible to accurately indentify on the basis of vegetative anatomical characters alone.

The Gracilariaceae is well represented in the Gulf of California by two of its free-living, macrophytic genera and one minute, parasitic genus.

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* Contributed by James N. Norris and C. Frederico D. Gurgel. C. F. D. Gurgel: University of Adelaide, School of Earth and Environmental Sciences, Adelaide, South Australia 5005, Australia.

KEY TO THE GENERA OF GRACILARIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Minute, whitish, globose parasites, less than 4 mm in diameter; growing on *Gracilaria* .... ***Gracilariophila***
1b. Free-living (nonparasitic) macrophytes, cylindrical to flat; over 2 cm and usually much taller or longer when mature (some cylindrical species up to 1 m or more in length) 2
2a. Cystocarps with traversing filaments (absorbing filaments) in pericarp floor and surrounding walls; spermatangia in pits or conceptacles within cortex .... ***Gracilaria***
2b. Cystocarps without traversing filaments (absorbing filaments) in pericarp; spermatangia superficial, produced from outer cortical cells .... ***Gracilariopsis***

Gracilaria Greville

Gracilaria Greville, 1830:iiv, 121; Fredericq and Hommersand, 1989a:213–217; Steentoft et al., 1991:663.

Algae are exceedingly variable in size; most are erect, but a few are low growing or prostrate. Thalli of most of the species are composed of one or more cylindrical, compressed, or flat fronds attached to the substrate by a discoid holdfast or prostrate branches; a few species have irregularly constricted to articulated fronds of cylindrical or irregularly shaped segments. Branching in most is pseudodichotomous or irregular, and some may have proliferous branchlets. Uniaxial growth is not easily seen because of the compact nature of the apical structure. The medulla is pseudoparenchymatous, composed of large colorless cells, with an abrupt or gradual transition to a cortex of successively smaller cells toward the outer cortex of pigmented cortical cells.

Tetrasporangia are cruciately divided, embedded in the cortex or in modified cortical cells and scattered over the thallus. Cystocarps are hemispherical to ovoid, projecting and scattered over branches. Pericarp is ostiolate, with thick walls and traversing filaments (tubular nutritive cells sensu Sjöstedt, 1926; Fredericq and Hommersand, 1990; also referred to as absorbing filaments, connecting filaments, or nutritive filaments) that connect the gonimoblast to the pericarp (Yamamoto, 1978: fig. 29; e.g., Figure 190A). Carposporangia are developed mostly in chains, but in most mature cystocarps this organization is not evident. Spermatangia are either covering the floor within shallow, cup-shaped depressions (Textorii-type; sensu Yamamoto, 1978: fig. 29; e.g., Figures 190B, 191C, 193E) or lining the inner surfaces within horse-shoe-shaped deep, ovoid to oblong pits or cavities (Verrucosa-type; sensu Yamamoto, 1978: fig. 29; e.g., Figure 196C).

REMARKS. Species of *Gracilaria* are widely distributed but are often difficult to distinguish on habit characters alone. There is often a high degree of morphological plasticity, and species limits for many are poorly known. Complexes of similar-looking species can usually be separated by comparative morphological studies, elucidation of anatomical vegetative and reproductive characters, including the ontogeny of gametophytes, pre- and postfertilization events, and comparative molecular analyses (e.g., Gurgel and Fredericq, 2004; Gurgel et al., 2003a, 2003b, 2004, 2008).

Fifteen species of *Gracilaria* and a species of uncertain taxonomic status are known in the northern Gulf of California. Two other species from the southern Gulf, *G. ascidiicola* and *G. ramisecunda* (Norris, 1985b), and two uncertain records are also included to call attention to the need for further study.

KEY TO THE SPECIES OF *GRACILARIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thallus cylindrical throughout or cylindrical to only slightly compressed or becoming oval 2
1b. Thallus distinctly complanate or flattened throughout 10
2a. Thallus cylindrical, slender; axes less than 3 mm in diameter (one species up to 4–5 mm) 3
2b. Thallus rigid and erect, cylindrical, subcylindrical to more or less compressed or oval, mostly greater than 3 mm in diameter; variously branched 5
3a. Thalli more rigid, smaller, mostly up to 15 cm tall, 1.0–1.3 mm in diameter; mostly branching from lower portions; arising from stoloniferous base .... ***G. papenfussii***
3b. Thalli usually over 25 cm in length; generally more robust, 2–4(–5) mm in diameter; branching mostly 3–5 orders; cystocarps with weakly developed traversing filaments; spermatangia in deep pits 4
4a. Thalli dark reddish brown (not black on drying); usually over 25 cm in length; mostly 2–3 mm in diameter; branching irregular, 1–2(–3) orders .... ***G. pacifica***
4b. Thalli dark brown (black upon drying); 0.3–1.0 m long; 3–4(–5) mm in diameter; branching irregular, 2–5 orders .... ***G. vermiculophylla***
5a. Axes subcylindrical to slightly compressed or oval; branching subdichotomous, subsecund, or more or less pinnate 6
5b. Axes terete, erect, and turgid; branching dichotomous, irregularly or multifariously 7
6a. Thallus crisp and usually brittle, axes slightly compressed to oval (in transection), 3–7 mm wide; branching more or less pinnate .... ***G. pinnata***
6b. Thallus not brittle, axes subcylindrical to compressed, up to 3 mm in diameter; branching subdichotomous, distichous, up to 7 orders .... ***G. subsecundata***

7a. Terete, of more or less uniform diameter throughout, 1.5–3.0 mm in diameter; dichotomously branched . . . . *G. pachydermatica*

7b. Thalli not uniform in diameter, either more robust in middle portions or in lower portions 8

8a. Dichotomously branched below, irregularly secund above; axes 1.5–2.0 mm in diameter in lower portions, becoming narrower above; cystocarps large compared to branch diameter . . . . *G. ramisecunda*

8b. Irregularly to subdichotomously branched; robust, turgid axes, 1.5–5.0 mm in diameter; cystocarps small compared to branch diameter 9

9a. Thalli usually over 8 cm tall; axes 2–5 mm diameter; infrequently, irregularly branched; cystocarps 700–900 µm in diameter, gonimoblast of large roundish cells, carpospores, 18–20 µm in diameter . . . . *G. turgida*

9b. Thalli up to 5.5 cm tall; infrequently subdichotomously branched; axes 1.5–2.0(–3.0) mm in middle portions; cystocarps 750–800 µm in diameter, gonimoblast of large, elongated cells, larger carpospores, mostly about 30 µm in diameter . . . . *G. marcialana*

10a. Thalli in unique association with a compound ascidian (tunicate) . . . . *G. ascidiicola*

10b. Thalli free-living, not closely associated with an ascidian 11

11a. Thalli with abundant short, spinose or dentate protuberances on margins and/or on blade surfaces 12

11b. Thalli either with smooth entire margins or with proliferous outgrowths on margins only (if present, outgrowths not spinose or dentate) 13

12a. Blades flat, thick (600–1500 µm thick); mostly 5.0–12.0 mm wide; with spinose protuberances on blade surface and margins . . . . *G. spinigera*

12b. Blades compressed, thin (less than 250 µm thick); less than 5 mm wide; with spinose and dentate protuberances restricted to margins . . . . *G. crispata*

13a. Thallus of narrow ligulate branches, 1.5–3.0 mm wide, upper segments tapering to subacute apices . . . . *G. tepocensis*

13b. Thallus wider, more than 3 mm in width, some over 1 cm or wider (up to 4 cm); apices mostly rounded 14

14a. Thalli less than 8 mm wide; tending to branch more than 1 plane, or with overlapping segments 15

14b. Thallus larger and wider, dichotomously divided in 1 plane; branches generally much broader (especially in middle portions of thallus), and 8.0–50 mm in width 16

15a. Thalli usually over 10 cm tall; branches ligulate, narrow, 3–8 mm wide; dichotomously to subdichotomously branched; tetrasporangia in nemathecia-like sori on surface; spermatangia in pit-like cavities . . . . *G. cunninghamii*

15b. Thallus flabellate, up to 8 cm tall, 5–7 mm wide; branched irregularly subdichotomously; tetrasporangia within unmodified cortex; spermatangia in small depressions . . . . *G. veleroae*

16a. Thalli of closely subdichotomously branched, overlapping, upper flattened branches; mostly 1.0–2.5 cm wide; margins dentate, with abundant short, finely divided marginal proliferations; ultimate segments sharply reduced in width over middle portions; cystocarps less than 900 µm in diameter . . . . *G. rubrimembra*

16b. Thalli flabellate; mostly 2.0–5.0 cm wide; margins lacking dentate or marginal proliferations; upper segments gradually reduced in width from middle portions; cystocarps larger, 1.0–1.5 mm in diameter . . . . *G. vivesii*

Gracilaria ascidiicola E. Y. Dawson

FIGURE 188

Gracilaria ascidiicola E. Y. Dawson, 1961a:203, pl. 14; 1961b:429; Norris, 1985b:124, fig. 8; González-González et al., 1996:213; CONANP, 2002:140.

Algae forming sessile lumps or ball-like shapes with a gray-white ascidian (Didemnidae), mostly entangled with and overgrown by ascidian; thalli flat, upper portions protrude about 1–4 mm above ascidian surface; much branched or a dissected, more or less contorted narrow blade, with segments 4–5 mm long, 2.5–4.0(–5.0) mm wide; margins entire, slightly lobed or undulate; apices broadly rounded. Transection 300–400 µm thick; medulla of isodiametric cells, centrally to about 100 µm in diameter, becoming smaller outward to 30–40 µm in diameter below thin cortex; cortical layer of 1–2 periclinally elongate pigmented cells, 7–16 µm long.

Reproduction unknown.

Habitat. Growing in an ascidian (tunicate, or sea squirts) on muddy bottom in ecological association with bryozoans (*Bugula* sp.) and red algae (*Ceratodictyon* sp.); shallow lagoon; 1–2 m depths.

Distribution. Gulf of California: Estero, innermost lagoon, Puerto Escondido.

Type Locality. Mud bottom, innermost lagoon; Puerto Escondido, Baja California Sur, Gulf of California, Mexico.

Remarks. Although *Gracilaria ascidiicola,* when cleaned and free of the ascidian, can resemble some forms of *G. crispata*, it differs in lacking marginal teeth and is thinner in transection, with smaller medullary cells and a thinner cortical layer. Reproductive specimens and molecular analyses of *G. ascidiicola* are needed to verify its generic placement and clarify its relationship to *G. crispata*.

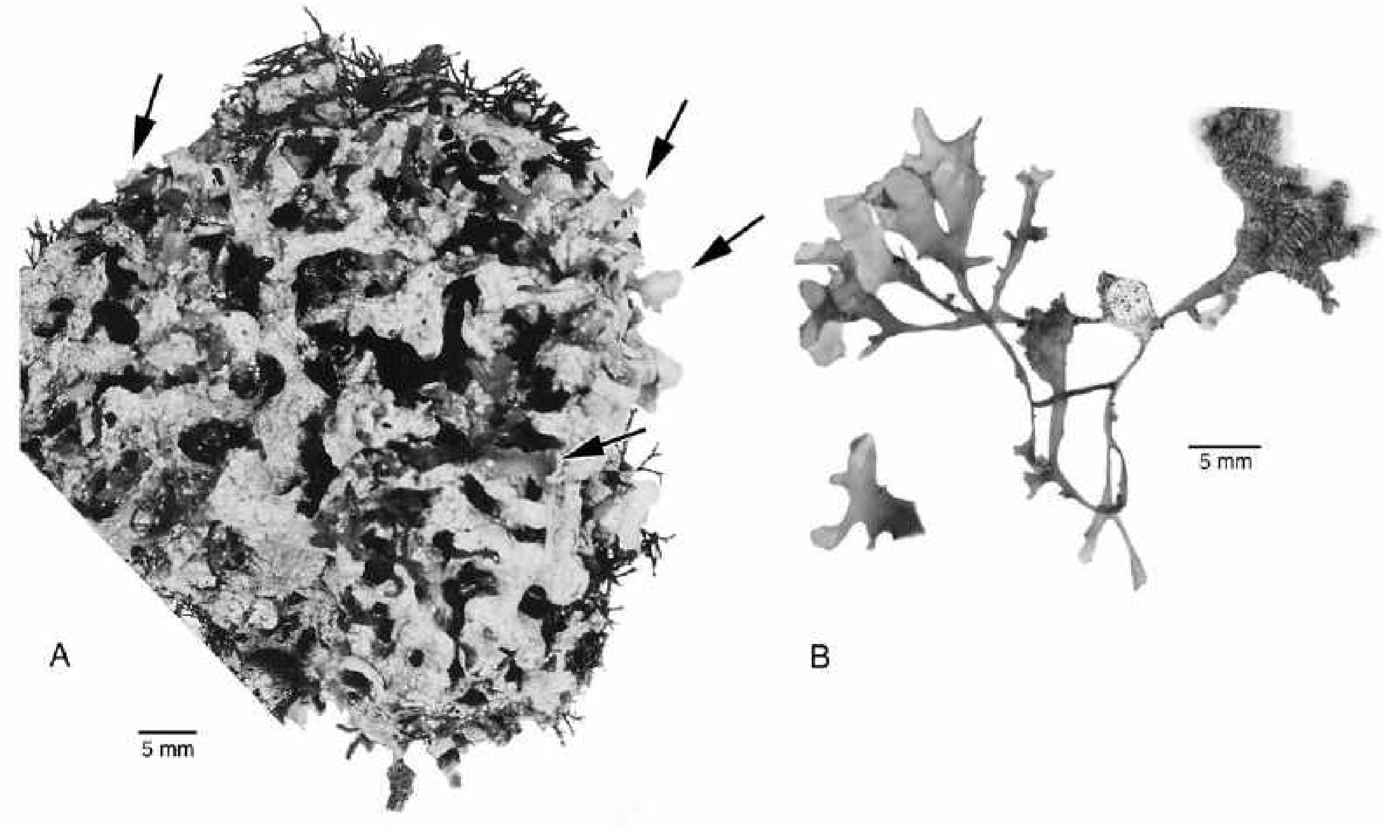


FIGURE 188. *Gracilaria ascidiicola*: A. Upper portions of *G. ascidiicola* thalli (arrows) protruding from the sessile ball that is formed in association with an ascidian, a bryozoan, and the red alga *Gelidiopsis* (isotype: photo of living specimen, *EYD-7149*, US Alg. Coll.-5690). B. Thallus detached from associated organisms (isotype, *EYD-7149*, US Alg. Coll.-41708).

Gracilaria crispata Setchell et N. L. Gardner

FIGURES 189, 190A–D

Gracilaria crispata Setchell et N. L. Gardner, 1924:753, pl. 22: figs. 7–10, pl. 44a (holotype); 1930:152; Dawson, 1944a:294; 1949a:26, pl. 8: fig. 4, pl. 9: figs. 4–10, pl. 10: figs. 5–7; 1957c:20; 1959a:26; 1961a:205, pl. 10: fig. 13, pl. 11: fig. 9, pl. 12: figs. 15, 16, pl. 15: fig. 4; 1961b:429; 1961c:415, pl. 24: fig. 2; 1966a:21; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:269; Huerta-Múzquiz, 1978:338; Norris, 1985a:93, tbls. 1, 2; 1985b:125, fig. 6; Huerta-Múzquiz and Mendoza-González, 1985:50; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:48; León-Tejera and González-González et al., 1993:497; Mendoza-González et al., 1994:107; González-González et al., 1996:213, 393; Riosmena-Rodríguez et al., 1998:27; L. Aguilar-Rosas et al., 2000:130; Cruz-Ayala et al., 2001:191; L. Aguilar-Rosas et al., 2002:234; CONANP, 2002:140; Dreckmann, 2002:95, figs.14–20; Pacheco-Ruíz and Zertuche-González, 2002:467; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:206; Bernecker, 2009:CD-Rom p. 63; Castañeda-Fernández de Lara et al., 2010:199.

Gracilaria lacerata Setchell et N. L. Gardner, 1924:755, pl. 51c; Dawson, 1944a:293; González-González et al., 1996:213.

Algae clumped, of several variably branched, narrow, flattened blades, 4–7 cm tall, somewhat “crisped” in upper portions; attached by a small discoid holdfast. Main blades divided into few to several flattened axes; these redivided into smaller segments becoming progressively shorter and narrower, attenuating upward to narrow, almost terete or spinose ultimate segments. Blade margins with minute, sharp dentition along lower portions. Medulla of 3–5 layers of isodiametric cells; up to 200 µm in diameter. Inner cortex of 2–3 layers of smaller, subcortical cells, merging somewhat abruptly with outer cortex of anticlinal rows of 2–4 cells; outermost surface layer of anticlinally elongated pigmented cells. Hairs cells, up to 500 µm long, sometimes present; extending from a basal cell within cortex.

Tetrasporangia isolated, scattered throughout cortex, over entire blade. Cystocarps protruding, dome shaped, 750–800 µm

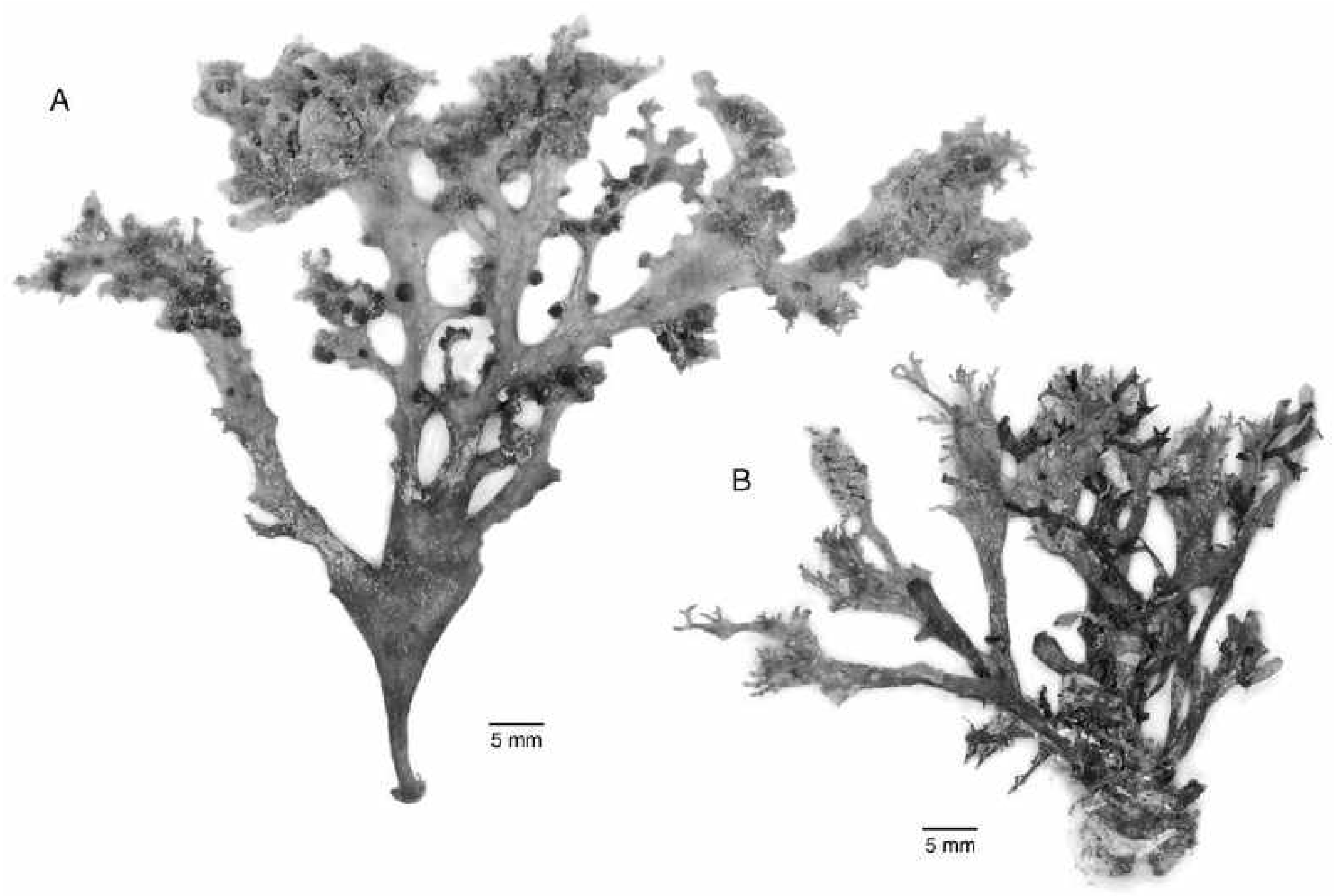


FIGURE 189. *Gracilaria crispata*: A. Flat, divided blades with distal "crisped" margins and dome-shaped cystocarps scattered in middle and upper portions of thallus (*JN-3258*, US Alg. Coll.-159559). B. Tetrasporophyte (*JN-5866*, US Alg. Coll.-159568).

in diameter, with a small rostrum; scattered over upper portions of blades. Gonimoblast of pseudoparenchymatous cells developing from a large ramified cell. Carposporangia in chains; with traversing (absorbing) filaments to pericarp. Spermatangia (Textorii-type) borne in small, shallow depressions or pits, 15–25 µm in diameter, separated by rows of elongated cortical cells; throughout upper blade segments.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Cabeza Ballena; Mazatlán and Bahía Topolobampo, Sinaloa to Jalisco. Eastern Pacific: Bahía Tortugas (inside southeast Bahía San Bartolomé), Baja California Sur; Isla Clarión (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador; Costa Rica.

TYPE LOCALITY. Rancho Eureka (near Punta Soledad), Bahía de Las Palmas, Baja California Sur, Gulf of California, Mexico.

REMARKS. Records of *Gracilaria crispata* from Peru (Acleto O., 1973, 1986) should be critically compared with those of the Gulf of California. The minute, whitish to yellowish adelphoparasite *Gracilariophila gardneri* Setchell is sometimes found on *Gracilaria crispata* in the northern Gulf (see *Gracilariophila* below).

Gracilaria cunninghamii Farlow ex J. Agardh

Gracilaria cunninghamii Farlow ex J. Agardh, 1901:93; Dawson, 1949a:11, pl. 1: figs. 1–9, pl. 2: figs. 2, 3; pl. 20: figs. 5, 6; Dawson et al., 1960a:64, pl. 28: figs. 1, 2; 1960b:13; Acleto O., 1973:52, figs. 173, 174; Acleto O., 1986:57, fig. 23; Ramírez and Santelices, 1991:248; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:213, 393.

Gracilaria textorii var. *cunninghamii* (Farlow ex J. Agardh) E. Y. Dawson, 1961a:213, pl. 10: fig. 1; 1961b:430; Abbott and Hollenberg, 1976:498, fig. 444; Abbott, 1985a:97; Mendoza-González and Mateo-Cid, 1985:30; Mateo-Cid and Mendoza-González, 1994b:40; Mendoza-González et al., 1994:107; González-González et al., 1996:216.

Tylotus cunninghamii (J. Agardh) Kylin, 1941:22, pl. 8: fig. 20 ["original exemplar"].

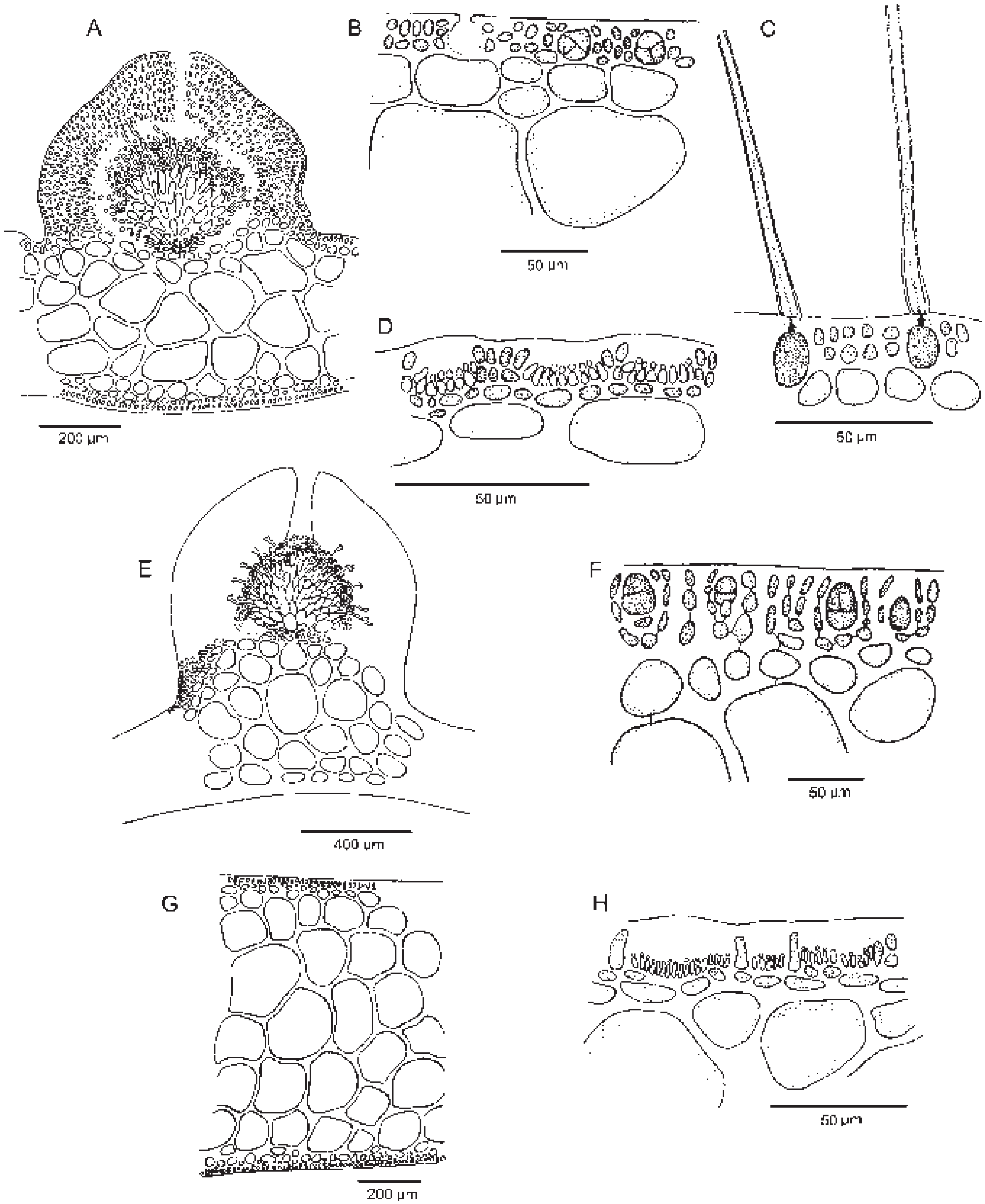


FIGURE 190. Transections of species of *Gracilaria*. A–D. *Gracilaria crispata*: A. Mature cystocarp with parenchymatous gonimoblast and traversing filaments extending into the pericarp. B. Tetrasporangia within slightly modified cortex. C. Transverse section showing basal cells in outer cortex with hairs extending above surface. D. Spermatangia in shallow depressions of outer cortex (A–D after Dawson, 1949a: pl. 9: figs. 6, 7, 10; pl. 10: fig. 7). E–G. *Gracilaria rubrimembra*: E. Mature cystocarp with parenchymatous gonimoblast and numerous traversing filaments extending into the pericarp (after Dawson, 1949a: pl. 13: fig. 7). F. Tetrasporangia in modified outer cortex. G. Transection of nonreproductive thallus showing large medullary cells and cortex of small cells (E–G after Dawson, 1949a: pl. 13: figs. 2, 8). H. *Gracilaria veleroae*: Spermatangia in small depressions separated by modified cortical cells (after Dawson, 1949a: pl. 10: fig. 4).

Algae 10–20 cm tall, of flattened, ligulate, irregularly subdichotomously branched fronds; axes and branches 3–8 mm wide, 400–600 µm thick; frond narrowly cuneate above a short stipitate region, attached below by small discoid holdfast. Medulla of large, thin-walled cells (becoming slightly thicker in older lower portions); in transection, inner medullary cells rectangular, with rounded corners, up to 200 µm wide; outer medulla of subcuboidal cells, (15–)20–40 µm in diameter. Cortex of 1–2(–3) layers of small, subcuboidal, pigmented cells, 5.0–12 µm in diameter.

Tetrasporangia cruciately divided; borne within irregularly shaped, swollen, nemathecoid sori on the blade surfaces. Cystocarps sessile, globose (sometimes slightly constricted at base), with an ostiole; gonimoblast of large cells developed above a basal floor of small cells, with traversing (absorbing) filaments connecting to pericarp. Spermatangia within deep pit-like cavities within thallus; cavities separated by modified cortical cells.

Habitat. On rocks; low intertidal to shallow subtidal.

Distribution. Gulf of California: San Felipe to Guaymas; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: San Luis Obispo, central California to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Ecuador; Peru.

Type Locality. Santa Barbara, Santa Barbara County, southern California, USA.

Remarks. A few Gulf of California specimens are tentatively referred to *Gracilaria cunninghamii,* but the presence of this species in the Gulf needs to be molecularly confirmed. These specimens could be confused with some smaller specimens of *G. vivesii*. *Gracilaria cunninghamii* is flattened, ligulate, and subdichotomously branched, with comparatively narrow segments, 3–8 mm wide, 400–600 µm thick, Whereas the somewhat similar *G. vivesii* is flabellate (not ligulate) and usually larger, with much wider segments, (8–)10–50 mm broad, 350–750 µm thick. Dawson (1949a) described growth in *G. cunninghamii* by a terminal region of apical filaments (difficult to distinguish a single apical cell) that, just a few cells below the apices, develop a medulla of compact cells, with the medullary cells attaining maximum size within a few millimeters below the apices.

Gracilaria marcialana E. Y. Dawson

Gracilaria marcialana E. Y. Dawson, 1949a:15, pl. 24: fig. 6, pl. 25: figs. 1–6; 1961a:205, pl. 10: fig. 15, pl. 11: figs. 4, 5, pl. 12: fig. 1; 1961b:429; Norris, 1985b:126; Mendoza-González and Mateo-Cid, 1986:424; González-González et al., 1996:214; Cruz-Ayala et al., 2001:191; CONANP, 2002:140.

Algae of 1 to few (up to 6) erect, turgid, cylindrical axes; up to 5.5 cm tall, 1.5–2.0(–3.0) mm in diameter; infrequently, subdichotomously branched, 1–2 orders, with terete apices; often with few short, sometimes spine-like branchlets; attached by a somewhat conical holdfast, irregularly shaped, with short prostrate laterals. Cystocarpic thalli more robust and turgid than tetrasporangial or spermatangial thalli. Medulla in transection broad, of large, thin-walled cells, 250–300 µm in diameter; outward merging with smaller subcortical cells, 40–70 µm in diameter. Cortex of 1–2 cell layers, of small irregularly shaped, pigmented cortical cells, about 10 µm in diameter (these cells sometimes further divided by cell walls in various planes). Hair cells deciduous, often only base of hair cell seen in cortical layer.

Tetrasporangia ovate, cruciately divided, 30–35 µm in diameter; scattered throughout a very slightly modified cortex. Cystocarps protruding, globose, sometimes with a slight basal constriction, 750–800 µm in diameter; gonimoblast of large elongate cells radiating from fusion cell, connected to pericarp by numerous traversing (absorbing) filaments; carposporangia about 30 µm in diameter, with a conspicuous stellate central body. Spermatangia in irregular shallow depressions (Textorii-type), 20–40 µm in diameter, separated by 1–2 rows of elongated cortical cells; spermatia 3–4 µm in diameter; produced on slender, clavate spermatangial parent cells arising from concave floor of depression (after Dawson, 1949a, 1961a).

Habitat. Growing on shell and coral fragments in reef habitats; subtidal (dredged from 8–30 m depths).

Distribution. Gulf of California: Roca Rojo, Bahía Kino; Punta San Marcial, Bahía Agua Verde to Canal de San Lorenzo, Isla Espíritu Santo; Bahía de La Paz.

Type Locality. Dredged from 16–30 m depths; reef, vicinity of Roca San Marcial, about 2.0 km (~1.25 miles) north-northeast of Punta San Marcial (south of Bahía Agua Verde), Baja California Sur, Gulf of California, Mexico.

Remarks. *Gracilaria marcialana* is an endemic species in the Gulf of California. The report of *G. marcialana* in Pacific Mexico from Colima (Mateo-Cid and Mendoza-González, 1991) was considered doubtful by Dreckmann (2002).

Although distinctive, the Gulf of California endemic *G. marcialana* remains known from only a few specimens. It somewhat resembles *G. turgida* in habit, but each is known from different ecological habitats: *G. marcialana* grows in the subtidal on offshore reefs, and *G. turgida* grows in the intertidal on very shallow, muddy, fine-sediment bottom of lagoons and esteros. Morphologically, *G. marcialana* is smaller, up to 5.5 cm tall, mostly 1.5–2.0 mm in diameter, with 2–6 axes arising from a spreading, irregular discoid to somewhat conical base, infrequently subdichotomously branched, and has cystocarps with gonimoblasts of large, elongated cells and larger carposporangia, about 30 µm in diameter. In contrast, *G. turgida* is larger, mostly 8–15 cm tall, 2.0–5.0 mm in diameter, with 1 to few axes arising from a small discoid base, irregularly to subsecundly branched, and has cystocarps with gonimoblast cells of large, vacuolated cells and smaller carposporangia, 18–20 µm in diameter.

Gracilaria pachydermatica Setchell et N. L. Gardner

FIGURE 191

Gracilaria pachydermatica Setchell et N. L. Gardner, 1924:753, pl. 24: figs. 30, 31; Dawson, 1944a:294; 1949a:18, pl. 4: figs. 3–6, pl. 5: figs. 3–5, pl. 6: figs. 1, 2; 1954e:338; 1957b:26; 1961a:206, pl. 10: fig. 7, pl. 12: figs. 9, 10, pl. 15: figs. 1, 2; 1961b:429; 1966a:22; Norris, 1985a:93, tbls. 1, 2; 1985b:125, 127, figs. 3, 6; Huerta-Múzquiz and Mendoza-

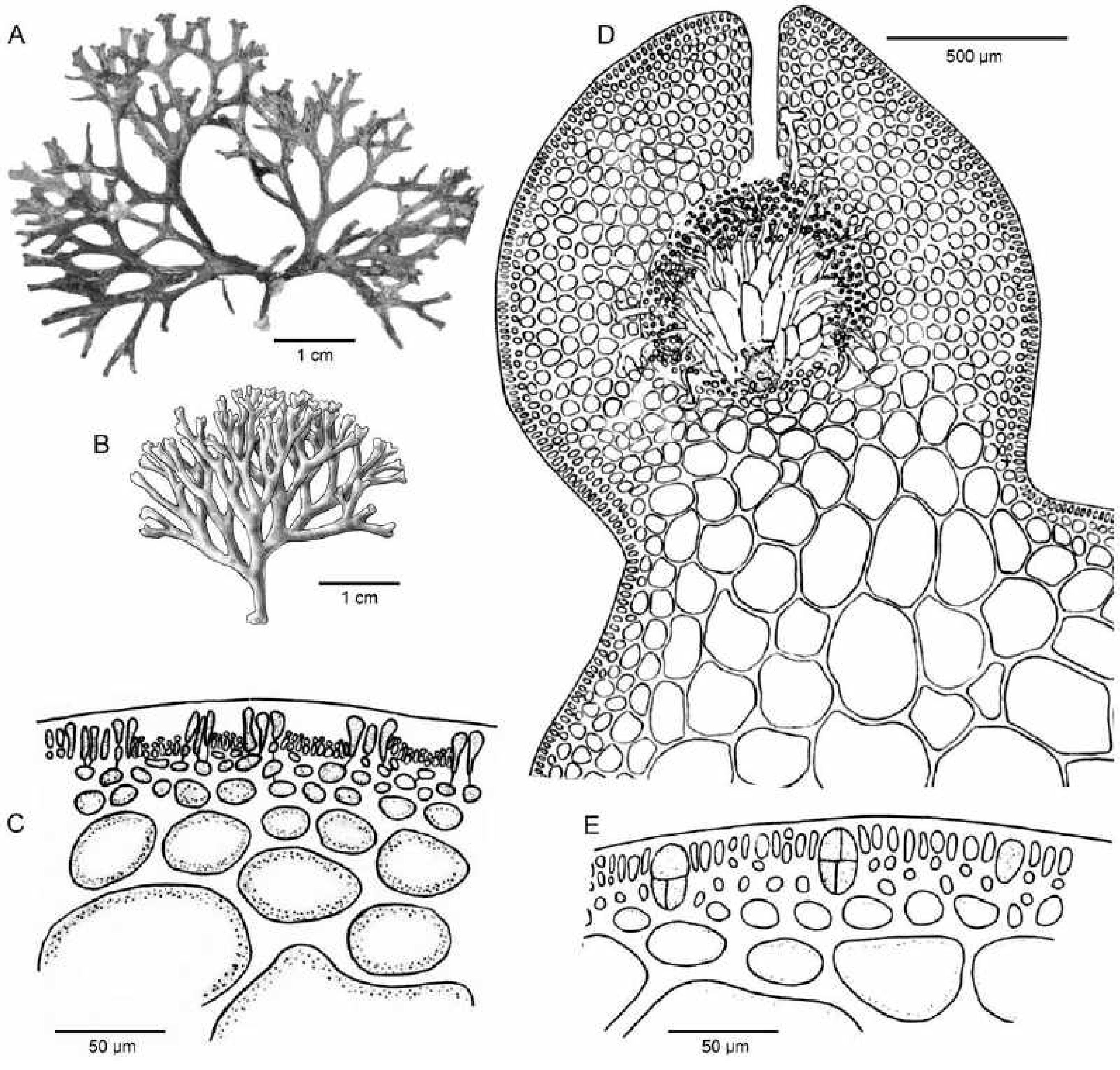


FIGURE 191. *Gracilaria pachydermatica*: A. Habit (*JN-3953*, US Alg. Coll.-159595). B. Cylindrical and cartilaginous axes (holotype; modified after Setchell and Gardner, 1924: pl. 24: fig. 30). C. Transection showing spermatangia in broad depressions in cortex (after Dawson 1949a: pl. 4: fig. 4). D. Cystocarp with traversing filaments (after Dawson 1949a: pl. 5: fig. 5). E. Tetrasporangia in outer cortex (after Dawson, 1949a: pl. 6: fig. 2).

González, 1985:50; Mendoza-González and Mateo-Cid, 1986:424; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:48; Mateo-Cid and Mendoza-González, 1994b:40; González-González et al., 1996:214, 393; Mateo-Cid and Mendoza-González, 1997:57: pl. 2: figs. 8, 9, pl. 9: fig. 36; Riosmena-Rodríguez et al., 1998:27; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:130; Cruz-Ayala et al., 2001:191; Dreckmann, 2002:101, figs. 21–26; CONANP, 2002:140; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:55; Pacheco-Ruíz et al., 2008:207.

Gracilaria guaymasensis E. Y. Dawson, 1944a:298, pl. 70, fig. 2 [lower right]; González-González et al., 1996:213.

Gymnogongrus sinicola E. Y. Dawson, 1944a:300, pl. 71, fig. 2 [lower left].

Thalli clumped, of few to several rigid, terete axes, 1.5–3.0 mm in diameter; regularly, repeatedly, dichotomously branched, up to 5 times; arising from a discoid holdfast. Branch intervals shorter upward; surfaces smooth (without proliferations). Medulla of large, thin-walled, rotund cells to 200 µm in diameter, becoming successively smaller outward to subcortex of small cells, 10 µm in diameter; outer cortical layer a single row of anticlinally elongated, pigmented cells, about 10 µm long by 5 µm wide. Nonpigmented hairs, often present extending from outer cortex; basal cell of hairs, larger and different shape than other surface cells.

Tetrasporangia ovoid, 30–35 µm long, borne in little-modified cortex; scattered over upper branches. Cystocarps spherical, 750–1000 µm in diameter, with slight basal constriction, ostiolate, rostrate, and borne on upper branches. Carposporangia 13–15 µm in diameter; gonimoblast of pseudoparenchymatous cells, with abundant traversing (absorbing) filaments to pericarp, developing from a large fusion cell (which remains visible in mature cystocarp). Spermatangia borne in sunken confluent cavities (Textorii-type) separated by elongated cortical cells; over thallus surface.

Habitat. On rocks; mid intertidal to shallow subtidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Cabeza Ballena; Sinaloa to Jalisco. Eastern Pacific: Isla Cedros (off Baja California); Bahía Sebastián Vizcaino to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Oaxaca.

Type Locality. Isla de Tortuga, off Puerto Santa Rosalía (about 24.1 km or15 miles NE from Isla San Marcos), Baja California Sur, Gulf of California, Mexico.

Gracilaria pacifica I. A. Abbott

Gracilaria pacifica I. A. Abbott, 1985b:116, figs. 2–8; 1985a:97; Scagel et al., 1989:187; Stewart, 1991:105; Mendoza-González et al., 1994:107; R. Aguilar-Rosas and Aguilar-Rosas, 1994:522; Abbott, 1995:191; González-González et al., 1996:217; Cruz-Ayala et al., 2001:191; Pacheco-Ruíz et al., 2008:207.

Gracilaria confervoides sensu Dawson, 1949a:13, pl. 15: fig. 9 [non *Gracilaria confervoides* (Linnaeus) Greville, 1830:123; =*Gracilaria gracilis* (Stackhouse) Steentoft, L. M. Irvine et Farnham, 1995:115].

Gracilaria verrucosa sensu Dawson, 1961a:214 [in part; only some Gulf of California material]; 1966a:22 [non *Gracilaria verrucosa* (Hudson) Papenfuss, 1950:195, which is now *Gracilaria gracilis* (Stackhouse) Steentoft, L. M. Irvine et Farnham, 1995:115; =*Fucus gracilis* Stackhouse, 1802:xxx, 100].

Algae of cylindrical, simple to branched axes, 30–100 cm long; arising from a small conical holdfast. Habits of two forms: (1) in protected habitats, axes 0.5–1.0(–2.0) mm in diameter and irregularly branched to 3 orders and (2) differing in exposed coastal habitats, with axes 1.5–3.5 mm in diameter and usually unbranched or sparsely branched to 1–2 orders (Abbott, 1985b). Medulla of large colorless cells, 150–250 µm in diameter, with thick cell walls (3.0–10 µm thick); an abrupt transition from medulla to cortex of 2 layers of small pigmented cells.

Tetrasporangia oval, 30–33 µm long by 20–30 µm diameter, borne in modified cortex, scattered over thallus surface of main axes and lateral branches. Cystocarps dome shaped to globose, protruding, usually less than 1.0 mm (occasionally up to 2.0 mm) in diameter. Gonimoblast of very large, thin-walled columnar cells, with somewhat weakly developed traversing (absorbing) filaments lateral to carposporangial mass; pericarp of brick-like cells. Spermatangia in obovate to somewhat oval pits, to 125 µm deep (description after Abbott, 1985a).

Habitat. Usually growing on sandy, fine-sediment bottoms; shallow subtidal.

Distribution. Gulf of California: Bahía Kino; Bahía San Carlos to Bahía Empalme; Santa Rosalía to Bahía de La Paz; Mazatlán. Eastern Pacific: southern British Columbia to Baja California.

Type Locality. Intertidal (0.0 ft. tide level); midway to southwest end of Stillwater Cove, Pebble Beach, Monterey County, California, USA.

Remarks. Records of *Gracilaria pacifica* in the Gulf of California are based on the reports of Mendoza-González et al. (1994:107), González-González et al. (1996), Cruz-Ayala et al. (2001), and Pacheco-Ruíz et al. (2008).

Comparative studies indicated several species may be involved in the "*G. verrucosa* complex" of similar-looking terete taxa (Bird et al., 1982), particularly in the Pacific (Abbott et al., 1985). "*Gracilaria verrucosa*" (a name not valid anymore) as known from the northeastern Pacific Coast from Alaska to California (Abbott and Hollenberg, 1976) has been shown to correspond to *G. pacifica* I. A. Abbott (1985b; Scagel et al., 1989; Hansen, 1997). Abbott (1985a) noted that in central California *G. pacifica* can be found growing intermixed with northeast Pacific "*Gracilaria lemaneiformis,*" which is now *Gracilariopsis andersonii* (see Gurgel et al., 2003a).

The four species of similar-looking cylindrical specimens of *Gracilaria* and *Gracilariopsis* from the northern Gulf can be difficult to separate. Two that have spermatangia in pits are species of *Gracilaria*: *G. pacifica* is generally more robust, with cystocarps having traversing filaments, and *G. papenfussii* is usually shorter and more slender, with weakly developed traversing filaments (sensu Abbott, 1985b:116). In contrast, the spermatangia of the other two, *Gracilariopsis andersonii* and *G. animasensis,* are in superficial shallow depressions and have cystocarps that lack traversing filaments.

Gracilaria papenfussii I. A. Abbott

Gracilaria papenfussii I. A. Abbott, 1983:562, figs. 1 [holotype], 2, 3; Abbott, 1985a:97; Stewart, 1991:105; Abbott, 1995:191; González-González et al., 1996:217; Cruz-Ayala et al., 2001:191; Riosmena-Rodríguez et al., 2005a:33.

Gracilaria andersonii sensu auct. Kylin, 1941:21 [his cited specimens only, not including the type; non *Gracilaria andersonii* (Grunow) Kylin, 1941:21; in part, only the type specimen of *Cordylecladia andersonii* Grunow (in Piccone, 1886:63) and none of the other specimens cited].

Gracilariopsis andersonii sensu Dawson, 1949a:43 [in part; only his specimens cited]; 1961a:216 [in part; only his specimens cited; non *Gracilariopsis andersonii* (Grunow) E. Y. Dawson, 1949a:43, only the type of *Cordylecladia andersonii* Grunow (in Piccone, 1886:63), and none of the other specimens he cited].

Algae of cylindrical, erect axes up to 15(–18) cm tall, 0.5–1.0(–1.3) mm in diameter, usually abundantly branched, but irregularly and often unilaterally; above a compact stoloniferous base, attached by discoid holdfast. In transection, medulla of large, more or less uniform-sized cells; cortex of 2 layers of small pigmented cells.

Tetrasporangia oval, scattered in cortex; over thallus surface. Cystocarps protruding, globose to dome shaped, slightly rostrate; scattered over thallus; without traversing filaments to pericarp. Gonimoblast of very large cells (a character more typical of *Gracilaria* sensu stricto and *Hydropuntia* Montagne, 1842d), developing from a conspicuous fusion cell, carposporangia about 20 µm long. Spermatangia within deep pits within slightly swollen upper branches.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de La Paz. Eastern Pacific: San Francisco Bay; Santa Barbara, southern California to Bahía de Ballena, Baja California Sur.

TYPE LOCALITY. La Jolla, San Diego County, California, USA.

REMARKS. *Gracilaria papenfussii* has been recorded in the Gulf of California by Cruz-Ayala et al. (2001). Specimens that were misidentified as “*Gracilaria andersonii*” by Kylin (1941), i.e., only the specimens of Kylin cited in this publication and not the type specimen of *Cordylecladia andersonii*, were considered to be distinct from “*Gracilaria andersonii*” and were described as a new species, *Gracilaria papenfussii,* by Abbott (1983). On the other hand, the type material of *Cordylecladia andersonii* Grunow is now *Gracilariopsis andersonii* (Grunow) E. Y. Dawson.

The taxonomic status of *Gracilaria papenfussii* is problematic, as there appears to be a reported mixture of spermatangial and cystocarpic generic characters. The spermatangia of *G. papenfussii* were described to be in deep pits, as in *Gracilaria* (Abbott, 1983:562), but the cystocarps of *G. papenfussii* were later reported (Abbott, 1985a:118) to lack traversing filaments (a character of *Gracilariopsis*), with a gonimoblast of very large cells (a character more typical of *Gracilaria* sensu stricto and *Hydropuntia*). Either this was in error or perhaps the male and females were individuals of more than one species or possibly specimens of the invasive *Gracilaria vermiculophylla* were inadvertently included.

Gracilaria (*Gracilariopsis?*) *papenfussii* can be confused with *Gracilariopsis lemaneiformis* and *Gracilariopsis andersonii* (see also Remarks under *Gracilaria pacifica*). Although at one time another common North American terete species, *Gracilariopsis sjoestedii* (Kylin) E. Y. Dawson (basionym: *Gracilaria sjoestedtii* Kylin), was considered to be identical with *Gracilaria lemaneiformis* (Abbott, 1983), Gurgel et al. (2003b), using morphological and molecular analyses, showed *Gracilariopsis lemaneiformis* (Bory) Weber-van Bosse to be restricted in distribution to Pacific South America and showed that the similar-looking *Gracilariopsis andersonii* (including *G. sjoestedii* as a synonym) was a separate species found on the northwest Pacific coast of North America. It is difficult to distinguish some northern Gulf *Gracilaria papenfussii* from *Gracilaria pacifica* or some *Gracilariopsis andersonii.* Abbott (1983, as “*G. lemaneiformis*”) noted *G. andersonii* to usually be 4–8 times longer than *G. papenfussii*, with much longer lateral branches of similar diameter. When similar morphologies of these species are encountered, they can be separated with gametangial thalli. The spermatangia are borne in deep pits in *G. papenfussii* and in pyriform pits (about 100 µm deep) in California *G. pacifica* and are distinctly superficial and continuous over the thallus surface in *Gracilariopsis andersonii.* Further, cystocarps of *Gracilaria papenfussii* lack nutritive filaments, but in *G. pacifica* the traversing filaments are few, weakly developed, and usually lateral to carposporophyte. Cystocarps in *Gracilariopsis andersonii* also completely lack any traversing filaments but have superficial spermatangia (characters of *Gracilariopsis*), which is very different from the reported spermatangial pits of *Gracilaria papenfussii.*

Polne-Fuller and Gibor (1987) showed that southern California *Gracilaria papenfussii* could be induced to produce calluses of undifferentiated tissue for culture (see also Aguirre-Lipperheide et al., 1995).

For now, the northern Gulf specimens can only be tentatively referred to *G. papenfussii* until they can be critically compared to the Gulf’s other cylindrical species and its presence can be confirmed. Further, the taxonomic status and generic position of the type and type locality specimens of *G. papenfussii* need to be molecularly tested and elucidated.

Gracilaria pinnata Setchell et N. L. Gardner

FIGURE 192

Gracilaria pinnata Setchell et N. L. Gardner, 1924:751, pl. 61; Dawson, 1944a:294; Norris, 1985a:93, tbl. 1, 2; Norris, 1985b:125, fig. 6; González-González et al., 1996:214; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; L. Aguilar-Rosas et al., 2000:130; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Gracilaria subsecundata sensu Dawson, 1949a:20 [in part]; 1961a:209 [in part; non *Gracilaria subsecundata* Setchell et N. L. Gardner, 1924:755].

Algae rose red, pinnately branched from more or less distinct axes, up to 25 cm tall or more; when fresh, slightly compressed to oval in transection, cartilaginous, brittle in texture; 3–4(–7) mm wide; branch segments narrowing upward to acuminate apices, short marginal laterals present; attachment unknown. Medulla of large, thick-walled, colorless cells, grading gradually outward

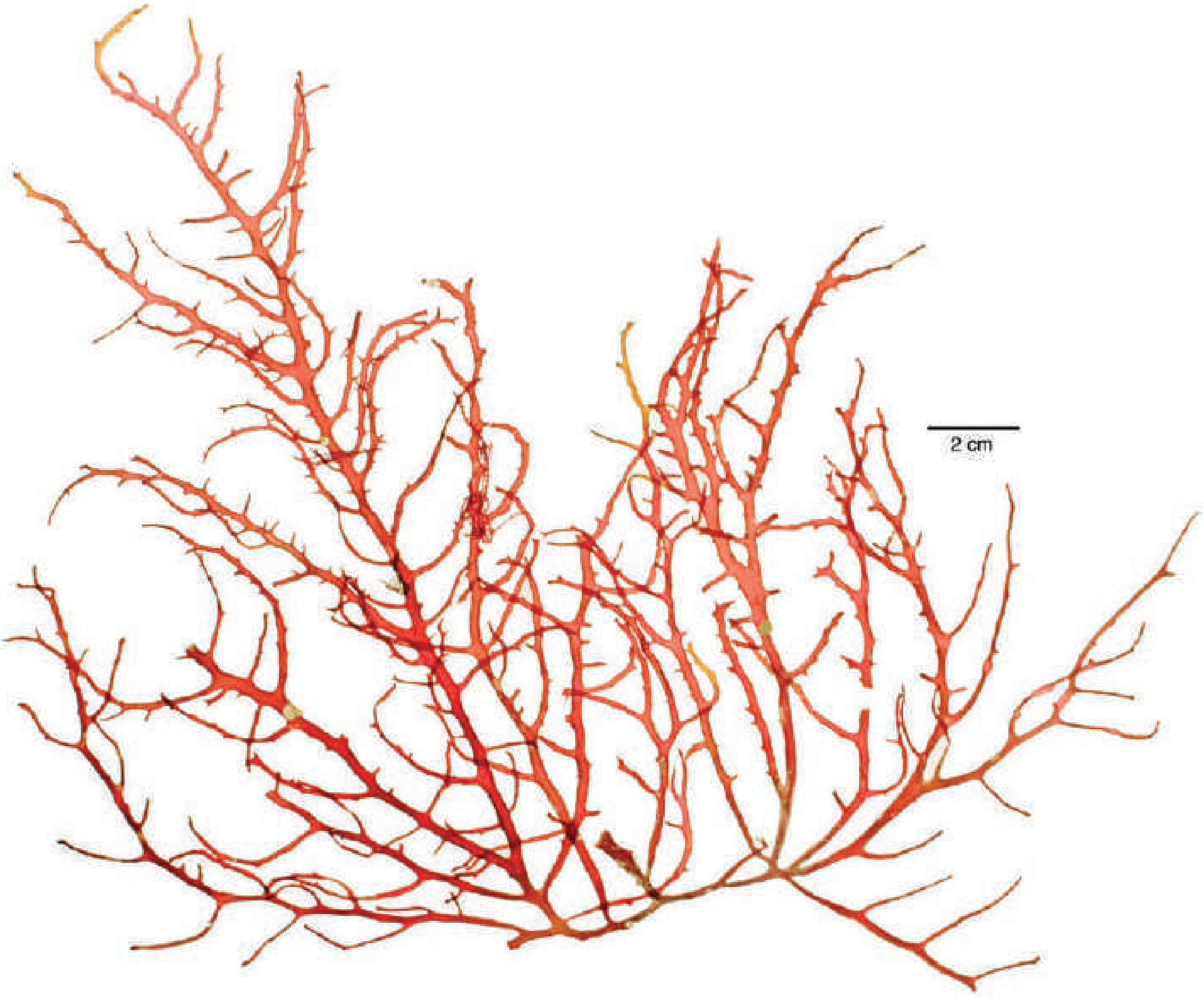


FIGURE 192. *Gracilaria pinnata*: Habit (*JN-5334*, US Alg. Coll.-159632).

to a 2-layered cortex of small cuboidal to anticlinally elongated cells, 10–12 µm long by (3–)5–10 µm in diameter.

Tetrasporangia ovoid, (30–)40–65 µm long by 25–40 µm wide; borne deep within subcortex and surrounded by 3–4 anticlinally elongated cortical cells. Cystocarps dome shaped, prominent, up to 1.0 mm in diameter, scattered over thallus; carposporangia (18–)22–30 µm in diameter; gonimoblast of pseudoparenchymatous cells, with traversing (absorbing) filaments to pericarp. Spermatangia in shallow depressions (Textorii-type), 20–22 µm wide by 12–15 µm deep, and separated by anticlinally elongated cells; scattered over upper portions of branches.

HABITAT. Clumps of entangled fronds found free-living on sand plains and sandy bottoms; subtidal, 5–23 m depths.

DISTRIBUTION. Gulf of California: El Coloradito; Puerto Refugio, Isla Ángel de la Guarda to Bahía de Las Ánimas; Cabo Pulmo to Los Frailes.

TYPE LOCALITY. Bahía de Los Ángeles, Baja California, Gulf of California, Mexico.

REMARKS. Dawson (1949a) mistakenly concluded that *Gracilaria pinnata* was conspecific with *G. subsecundata* Setchell et N. L. Gardner. However, later comparative morphological analyses of newer subtidal collections from Puerto Refugio, Isla Ángel de la Guarda (Norris and Bucher, 1976), that were identical with the type specimen and topotype specimens (US Alg. Coll.) have shown *G. pinnata* to be a distinct species. Setchell and Gardner (1924) probably described their alga from dried herbarium material because freshly collected subtidal specimens are not flat as they noted, but rather slightly compressed and oval in transection, 3–4(–7) mm wide. The pinnate branching, bright rose red color when fresh, oval transection of the axis, and the rigid but brittle nature (easily breaking into pieces when placing specimens into collecting bags) serve to distinguish *G. pinnata* from all other Gulf species.

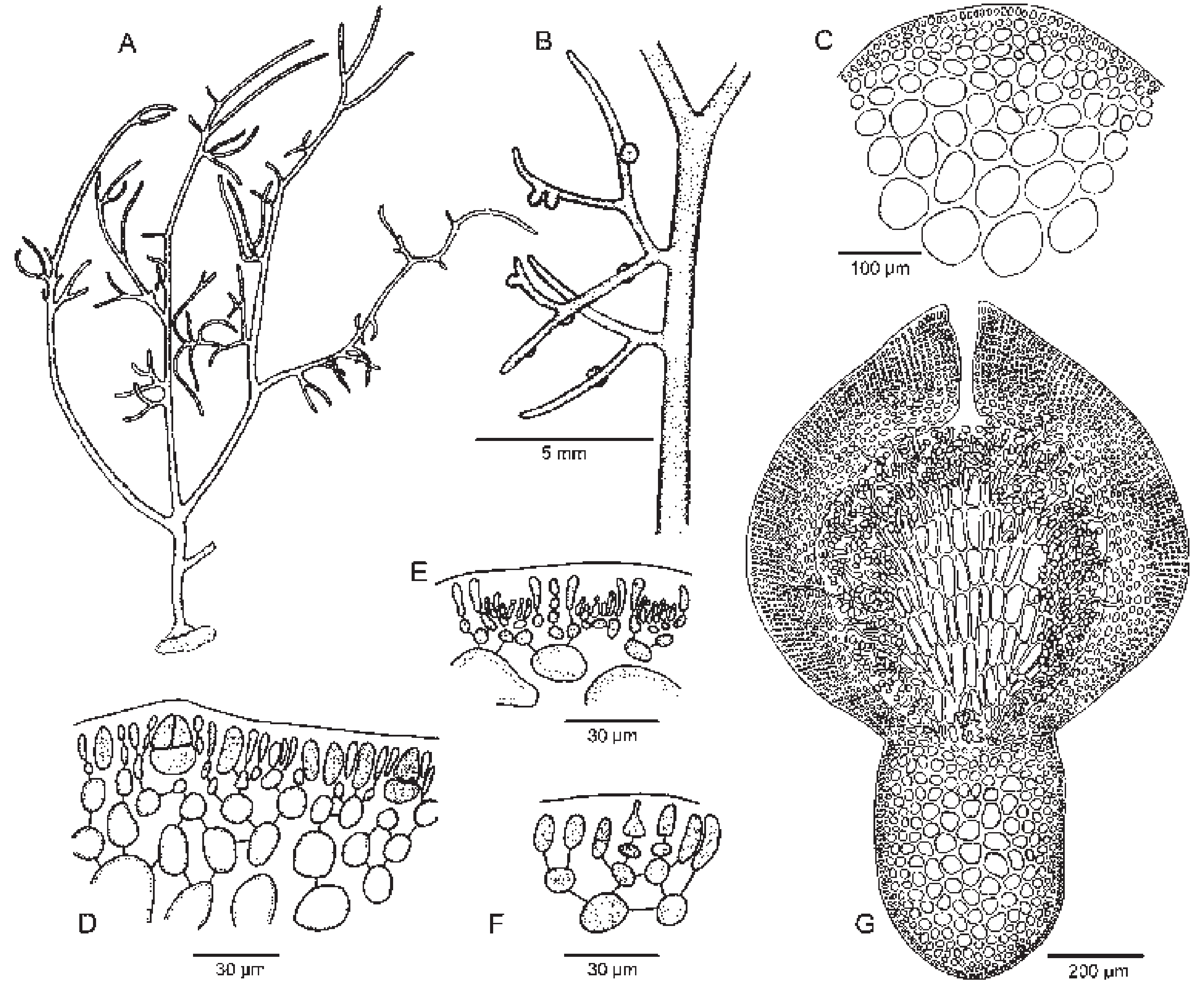


FIGURE 193. Type collection of *Gracilaria ramisecunda*: A. Habit of tetrasporangial alga (after Dawson 1949a: pl. 3: fig. 1). B. Part of a cystocarpic thallus (after Dawson 1949a: pl. 4: fig. 1). C. Transection of axis showing gradual transition from cortex to medulla. D. Transection of a tetrasporic branchlet showing modified cortex. E. Transection of spermatangial thallus showing spermatangia in shallow pits. F. An example of a carpogonial branch; others may bear more or fewer branches off carpogonial branch cells (C–F after Dawson 1949a: pl. 3: figs. 4–6, 8). G. Transection of bearing branch and mature cystocarp showing the fusion cell, pseudoparenchymatous gonimoblast, and numerous traversing filaments to the pericarp (After Dawson, 1949a: pl. 5: fig. 2).

Pacific Mexico specimens (AHFH, now UC) identified as "*Gracilaria pinnata*" (Taylor, 1945) were later found to be a new species: *Sarcodiotheca taylorii* E. Y. Dawson (1961a).

Gracilaria ramisecunda E. Y. Dawson

FIGURE 193

Gracilaria ramisecunda E. Y. Dawson, 1949a:17, pl. 3: figs. 1–8; pl. 4: figs. 1, 2; pl. 5: figs. 1, 2; 1959b:26; 1961a:207, pl. 10: fig. 12, pl. 12: fig. 2, pl. 15: fig.3; 1961b:429; 1966b:64; Norris, 1985b:128, fig. 14; González-González et al., 1996:214; Mendoza-González and Mateo-Cid, 1999:43, figs. 10–13; CONANP, 2002:140.

Algae erect, usually a single main axis, cylindrical to slightly compressed, robust and rigid, mostly 6–8 cm tall; basal portion 1.5–2.0 mm in diameter and up to 7 mm long, tapering upward to upper portions of 400–1000 µm in diameter, with blunt apices; branching mostly 3–4 orders; first 2 orders irregularly subdichotomous, usually with long intervals between branches; second 2 orders irregular, tending to secund, with intervals of about 0.5–1.5 cm; attached by discoid holdfast. Medulla in transection of 8–10 rotund to ovoid cells, 40–60(–100) µm in diameter; subcortex of 2 layers of cells about 12–22 µm in diameter. Outer cortex a single layer of anticlinally elongate cortical cells, (6–)10–15 µm in diameter; with some basal cells of hairs. In longitudinal section, 2-layer subcortex of isodiametric cells very distinct from longitudinally elongated medullary cells.

Tetrasporangia cruciately divided, ovoid, 30–40 µm tall, 15–25(–35) µm in diameter; in slightly modified cortex of anticlinal elongate cells; scattered in upper branches. Cystocarps subglobose, (550–)600–1200 µm in diameter, sessile with a slight basal constriction; ostiolate; scattered, protruding on branches in upper thallus; gonimoblast of pseudoparenchymatous cells above a conspicuous fusion cell, with traversing (nutritive) filaments to pericarp; carposporangia 14–17 µm in diameter. Spermatangial thalli compressed; spermatangia (Textorii-type) in small sunken depressions separated by anticlinally elongated cortical cells.

HABITAT. On rocks and in tide pools; low intertidal.

DISTRIBUTION. Gulf of California: Puerto Escondido to Cabeza Ballena. Eastern Pacific: Oaxaca.

TYPE LOCALITY. Intertidal; Cabeza Ballena, Baja California Sur, Gulf of California, Mexico.

Gracilaria rubrimembra E. Y. Dawson

FIGURES 190E–G, 194

Gracilaria rubrimembra E. Y. Dawson, 1949a:32, pl. 13: figs. 1–8; 1961a:208, pl.10: fig. 11, pl. 13: fig. 2 [type collection]; 1966a:22; 1966b:64; Norris, 1985a:93, tbls. 1, 2; Norris, 1985b:129, fig. 2; González-González et al., 1996:215, 350: fig. 29, 394; Riosmena-Rodríguez et al., 1998:27; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Algae of 1 to few dull red, complanate, subflabellate, membranous blades, up to 2.5 cm in width (broadest in middle portions of thallus); irregularly subdichotomously to polychotomously branched in 1 plane; lower portions of blade narrowing basally to a short, compressed stipe, 1.0 mm in diameter, attached below by a discoid holdfast. Upper portions congested and overlapping; margins with numerous short, divided, pointed or lobed, lateral proliferations. Transection 700–850 µm thick. Medulla of large, thin-walled cells, 120–160 µm in diameter, grading to smaller inner cortical cells, 20–25 µm in diameter, and outward to outer cortex of 1–2 layers of small, variously shaped pigmented cells, 8.0–15 µm in diameter.

Tetrasporangia 20–30 µm in diameter, embedded within inner cortex, surrounded by 2–4 filamentous cells (which are modified inner and outer cortical cells). Cystocarps dome shaped, projecting, up to 900 µm in diameter, ostiolate, slightly rostrate; scattered over upper portion of blade surfaces. Gonimoblast developing from a branched fusion cell; composed of pseudoparenchymatous cells above a dome of medullary cells, with numerous traversing (absorbing) filaments to pericarp. Spermatangia unknown.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; Isla San Pedro Mártir.

TYPE LOCALITY. South side of Ensenada de San Francisco, near Puerto San Carlos, Sonora, Gulf of California, Mexico.

REMARKS. *Gracilaria rubrimembra* is another endemic species in the Gulf of California. Dreckmann (2002) noted the report of *G. rubrimembra* from Nayarit to Jalisco (Serviere-Zaragoza et al., 1993a) needs to be verified.

Gracilaria spinigera E. Y. Dawson

FIGURES 195, 196

Gracilaria spinigera E. Y. Dawson, 1949a:24, pl. 8: figs. 1–3, pl. 9: figs. 1–3; 1959a:26, fig. 5; 1961a:208, pl. 12: fig. 6, pl. 16; 1961b:429; Norris, 1985b:129, fig. 15; Mateo-Cid and Mendoza-González, 1992:20; Serviere-Zaragoza et al., 1993a:483; González-González et al., 1996:214, 394; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:27; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467; Hernández-Herrera et al., 2005:147.

Algae of several branched, complanate blades, up to 15 cm tall; blades (3.5–)5.0–12.0 mm in width (broadest in upper portions), narrowing downward to a cuneate base above a stipe-like or abruptly contracted basal portion; attached by a small discoid holdfast. Primary branching subdichotomous, often closely set; apical portion with several spinose terminal segments. Secondary branches short, marginal spinose branchlets, 4–12 mm long. Transection 600–1500 µm thick. Medulla of large cells, 150–180 µm in diameter, grading into subcortical layer of cells, 25–50 µm in diameter; outer cortex a single layer of small, anticlinally elongated cells.

Tetrasporangia 20–25 µm in diameter, embedded in little-modified cortex of anticlinal oblong cells, 10–14 µm long; scattered over blade. Cystocarps globose, barely rostrate, 1.2–1.5 mm in diameter, individually scattered on blade surfaces; or clustered and congested among spines of branchlets and 400–600 µm in diameter. Gonimoblast of large pseudoparenchymatous cells, with numerous traversing (absorbing) filaments to thick-walled pericarp. Spermatangia in closely spaced ovoid cavities (Verrucosa-type), 35–60 µm deep by 28–45 µm wide, with a surface opening up to 20 µm in diameter.

HABITAT. On rocks; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles to Guaymas; Puerto Escondido; Isla Carmen; Bahía de La Paz; Cabo Pulmo to Los Frailes.

TYPE LOCALITY. Ensenada de San Francisco (vicinity Puerto San Carlos), Sonora, Gulf of California, Mexico.

REMARKS. *Gracilaria spinigera* is distinguished from other Gulf species of *Gracilaria* by its flattened, "gigartinoid-chondracanthoid" appearance and its deep spermatangial cavities. Dawson (1961a) suggested smaller specimens from Isla Santa

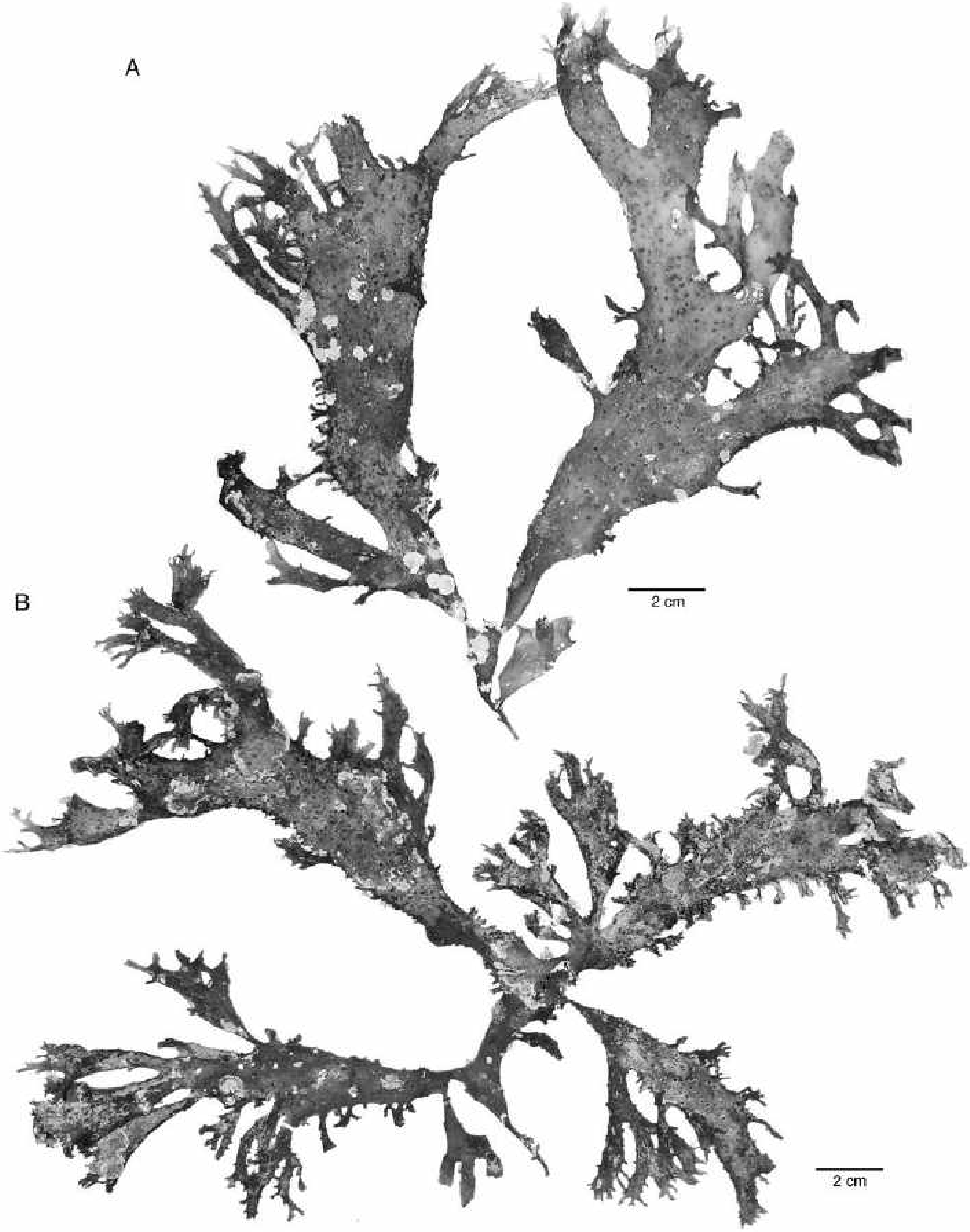


FIGURE 194. *Gracilaria rubrimembra*, two specimens showing morphological variability: A. Flat and wide thallus. B. Thallus with numerous finely divided and somewhat dentate marginal proliferations (A, B, both *JN-3032*: A, US Alg. Coll.-159638; B, US Alg. Coll.-159637).

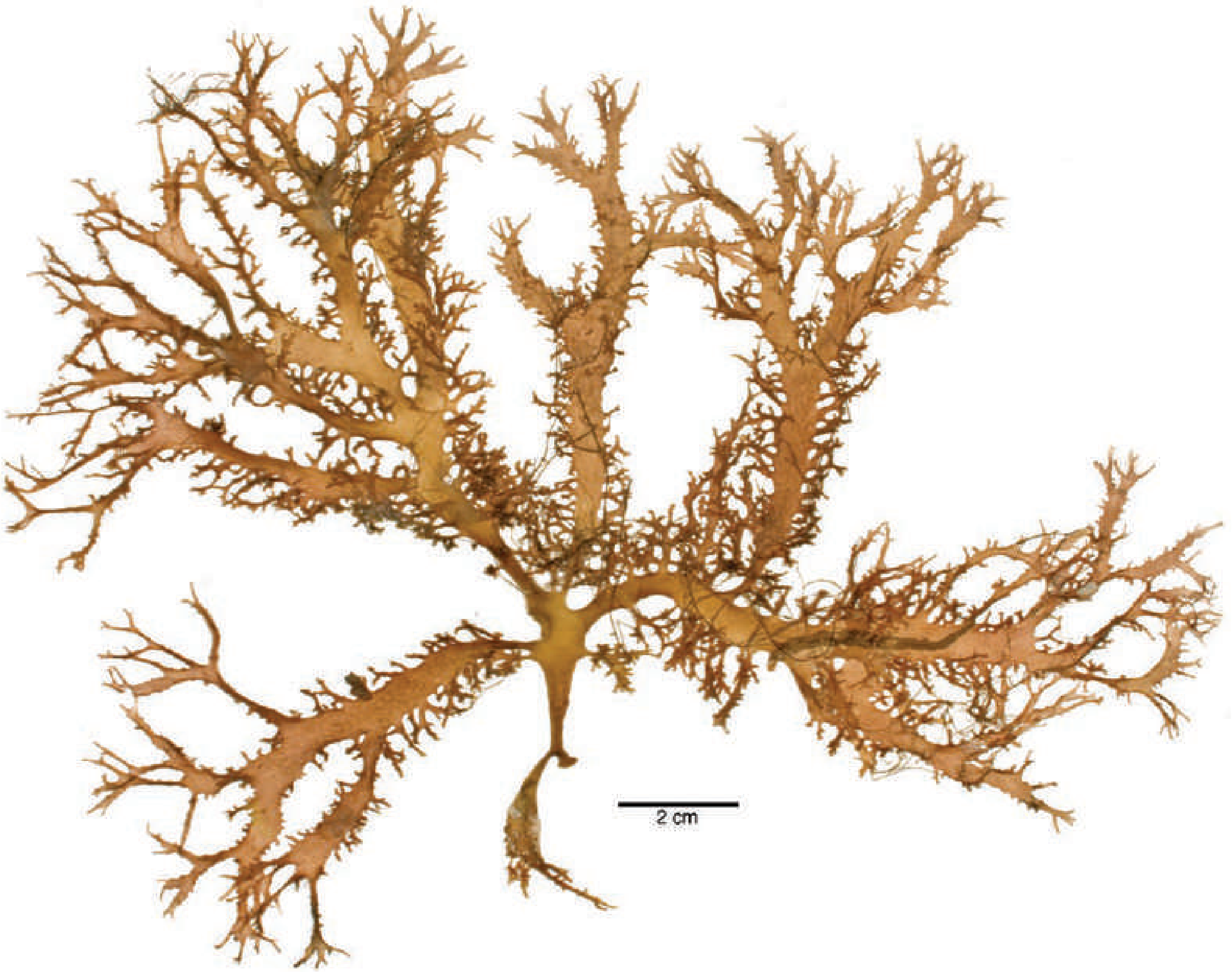


FIGURE 195. *Gracilaria spinigera*: Habit (*EYD-10986*, US Alg. Coll.-7536).

Margarita (Pacific Mexico) may also be this species, but Dreckmann (2002) stated that the Pacific Mexico reports of "*G. spinigera*" from Nayarit (Mateo-Cid and Mendoza-González, 1992) and Jalisco (Serviere-Zaragoza et al., 1993a) corresponded with other species. The reports from Pacific Costa Rica (Bernecker and Wehrtmann, 2009; Fernández-García et al., 2011) and the Philippines (Silva et al., 1987) should also be reinvestigated to confirm their identifications.

Gracilaria subsecundata Setchell et N. L. Gardner

FIGURE 197A,B

Gracilaria subsecundata Setchell et N. L. Gardner, 1924:755, pl. 23: figs. 26, 27, pl. 59; Dawson, 1944a:294; 1949a:20, pl. 6: figs. 3–11, pl. 7: figs. 1–9; 1959a:26; 1961a:209, pl. 10: fig. 10, pl. 11: figs. 1, 6, pl. 12: figs. 3, 4, pl. 17; 1966a:22; Norris, 1973:13; Huerta-Múzquiz, 1978:336; Norris, 1985a:93, tbls. 1, 2; Norris, 1985b:131, fig. 7; Mendoza-González and Mateo-Cid, 1986:424 [with a query]; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:47; González-González et al., 1996:215, 394; Riosmena-Rodríguez et al., 1998:27; L. Aguilar-Rosas et al., 2000:130; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Gracilaria compressa sensu Dawson, 1944a:296 [in part; non *Gracilaria compressa* (C. Agardh) Greville, 1830:125; =*Gracilaria bursa-pastoris* (S. G. Gmelin) P. C. Silva, 1952:265].

Gracilaria pinnata sensu Dawson, 1961a:209 [in part; non *Gracilaria pinnata* Setchell et N. L. Gardner, 1924:751].

Algae bushy when small, becoming more or less laxly branched with growth; subcylindrical to compressed branches, up to 25 cm tall, (2–)3 mm in diameter; branching sparse to

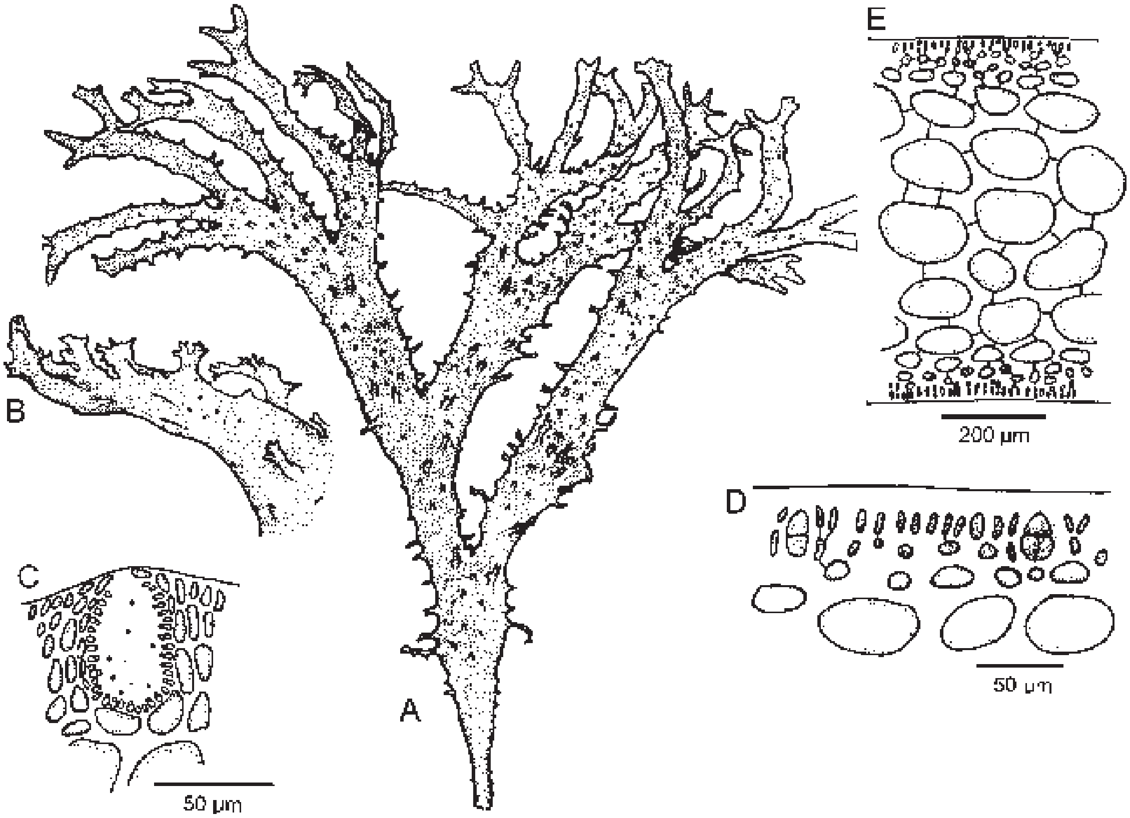


FIGURE 196. *Gracilaria spinigera*: A. Habit. B. Branching in terminal portion of specimen (A, B after Dawson 1949a: pl. 8: figs. 1, 2). C. Longitudinal section of spermatangial cavity (holotype; after Dawson 1949a: pl. 8: fig. 5). D. Transection of tetrasporangial thallus. E. Transection of dried specimen (D, E after Dawson, 1949a: pl. 9: figs. 2, 3).

dense, usually subdichotomous, up to 6–7 orders; can become more or less alternate, pinnate, or secund with growth; arising from a small discoid holdfast. Branches attenuating upward to acute tips; branch internodes variable with size and age, from about 3 mm in small or densely branched thalli, and 1–6 cm in larger thalli. Medulla of large rotund cells, about 200 or more µm in diameter, grading into radially elongate subcortical cells, 25 µm in diameter. Outer cortex of 2–3 angular to elliptic pigmented cells, mostly up to 10 µm long by 5–8 µm wide; tending to be anticlinally arranged. Hairs sometimes present, conspicuous; or only the basal cells of hairs within outer cortex.

Tetrasporangia ovoid, cruciately divided and, 25–30(–45) µm in diameter, but some sporangia divided periclinally to produce bispores; within modified cortex of irregular, small cells organized in anticlinal rows of 3–4 cells (outermost cell elongated); scattered over branch surfaces. Carpogonial branch 2-celled. Cystocarps dome shaped (not constricted), ostiolate, scattered over upper portions of thallus. Gonimoblast broad based, of pseudoparenchymatous cells, developed from a large fusion cell, with many traversing (absorbing) filaments to pericarp. Spermatangia in sunken depressions (Textorii-type), 14–17 µm in diameter, containing 8–20 spermatangial parent cells; depressions separated by bands of cortical cells, usually in groups over branch surfaces.

HABITAT. On rocks or sand-covered substrate, often found in bays and estuaries; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Piedras del Burro (Gulfo de Santa Clara) to Bahía Agua Verde; Isla Espiritu Santo to Bahia de La Paz; Bahía Topolobampo.

TYPE LOCALITY. Guaymas, Sonora, Gulf of California, Mexico.

REMARKS. Collection and examination of tetrasporangial *Gracilaria subsecundata* will be helpful to determine if the reported bispores (Dawson, 1949a) are viable or if they are immature tetrasporangia. *Gracilaria subsecundata* is probably endemic in the Gulf of California. Dreckmann (2002) noted that reports of *G. subsecundata* from Nayarit (Serviere-Zaragoza et al., 1993a) and in Pacific Mexico from Colima (Mateo-Cid and Mendoza-González, 1991) were doubtful.

Gracilaria tepocensis (E. Y. Dawson) E. Y. Dawson

FIGURE 198A

Rhodymenia? *tepocensis* E. Y. Dawson, 1944a:307 [with generic query], pl. 65: fig. 1.

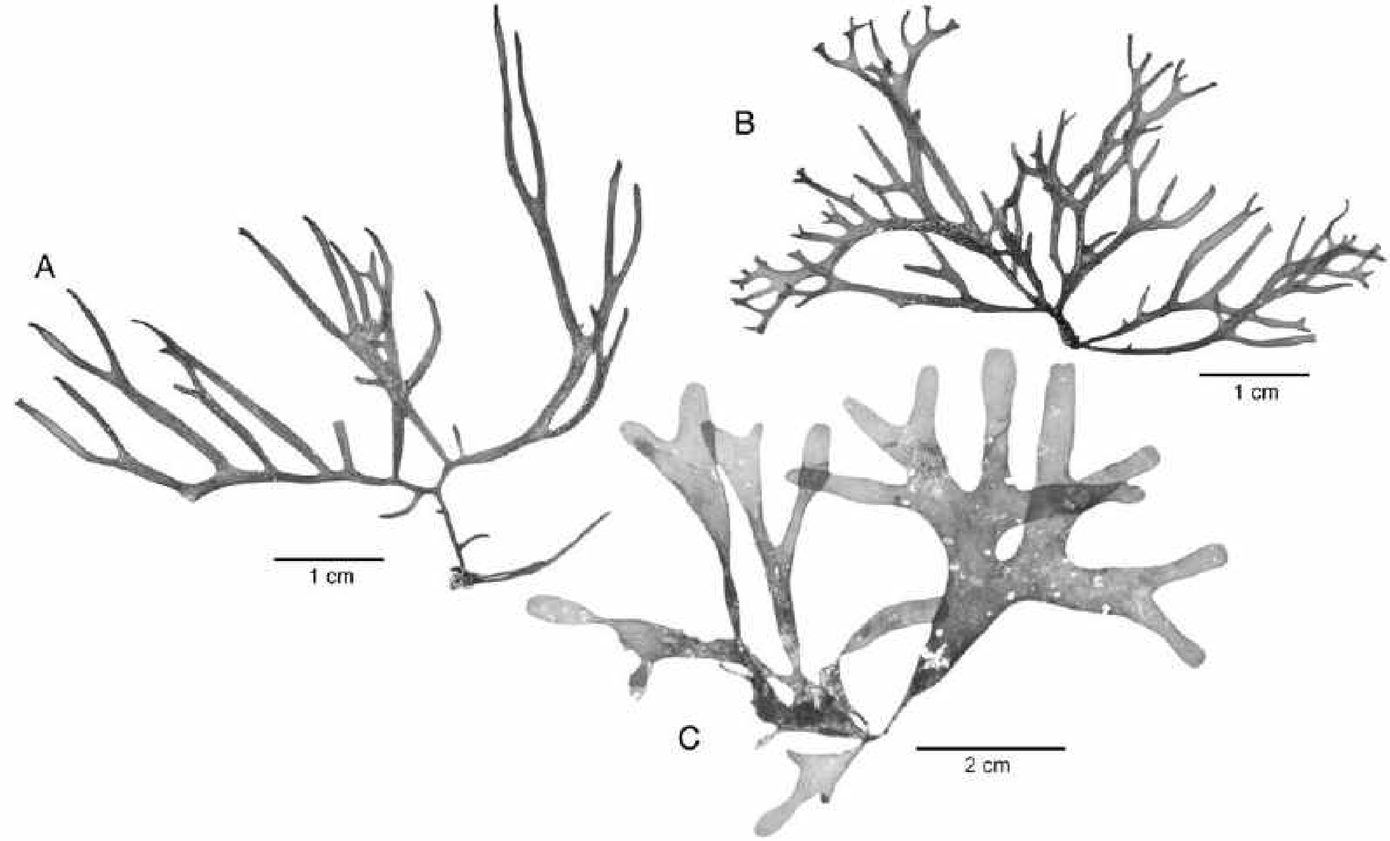


FIGURE 197. Species of *Gracilaria*. A, B. *Gracilaria subsecundata*: A. Habit of male gametophyte. B. Habit, a nonreproductive thallus (A, B, *JN-4990*, US Alg. Coll.-159647). C. *Gracilaria veleroae*: Habit, specimen from the type collection (*EYD-141a-40*, AHFH-37, now UC).

Gracilaria tepocensis (E. Y. Dawson) E. Y. Dawson, 1961a:211; 1961b:430; 1966b:64; Norris and Bucher, 1976:17; Huerta-Múzquiz, 1978:339; Norris, 1985b:131, fig. 13; Mendoza-González and Mateo-Cid, 1985:30; González-González et al., 1996:215, 394; Aguilar-Rosas et al., 2000:130; Pacheco-Ruíz et al., 2008:207.

Algae lax, of few to several narrow, complanate, subdichotomously branched fronds, up to 25.5 cm long and 2.0–3.0(–5.5) mm wide, attached by a small discoid holdfast. Fronds repeatedly branched in 1 plane, up to 3–4 orders, at intervals of 1–2(–6) cm; margins entire, smooth; upper branches reduced in width upward to either a blunt apex or to apices of two or more digitate segments. Transection (150–)200–300 µm thick. Medulla narrow, of 2 layers of large cells, 100–200 µm in diameter, abruptly adjoined to a thin, completely or partially developed subcortical layer of smaller cells. Outer cortex usually a single layer of periclinally elongated, pigmented cells, 7–10(–20) µm in diameter.

Tetrasporangia about 20 µm in diameter; borne in slightly modified cortex of 2-celled anticlinal filaments (not always evident); scattered over thallus. Cystocarps globose, up to 500 µm in diameter, rostrate; borne on thallus margins or over surface. Gonimoblast of radially elongated pseudoparenchymatous cells, developing from a large fusion cell; with numerous traversing (absorbing) filaments to pericarp. Spermatangia (Textorii-type) in small, partially sunken, irregularly confluent sori, bordered by little-modified to anticlinal elongate cortical cells; spermatia 3–4 µm in diameter.

Habitat. On rocks; subtidal, down to 4.5–21 m depths.

Distribution. Gulf of California: San Felipe to Puertecitos; Bahía Tepoca to Bahía Agiabampo; Puerto Refugio, Isla Ángel de la Guarda to Isla Estanque (Islas de la Cintura); Bahía de Los Ángeles.

Type Locality. Bahía Tepoca, Sonora, Gulf of California, Mexico.

Remarks. *Gracilaria tepocensis* was originally known only from dredged material from Bahía Tepoca, Isla Estanque (Dawson, 1944a, 1961a), and Agiabampo, Sonora (Dawson, 1966b). Our diving surveys yielded numerous collections of *G. tepocensis* from the shallow subtidal to 11 m depths, Puerto Refugio, Isla Ángel de la Guarda (Norris and Bucher, 1976). The reported depths of the dredged specimens (Dawson, 1961a), particularly the one from 113 m, are doubtful for attached, growing

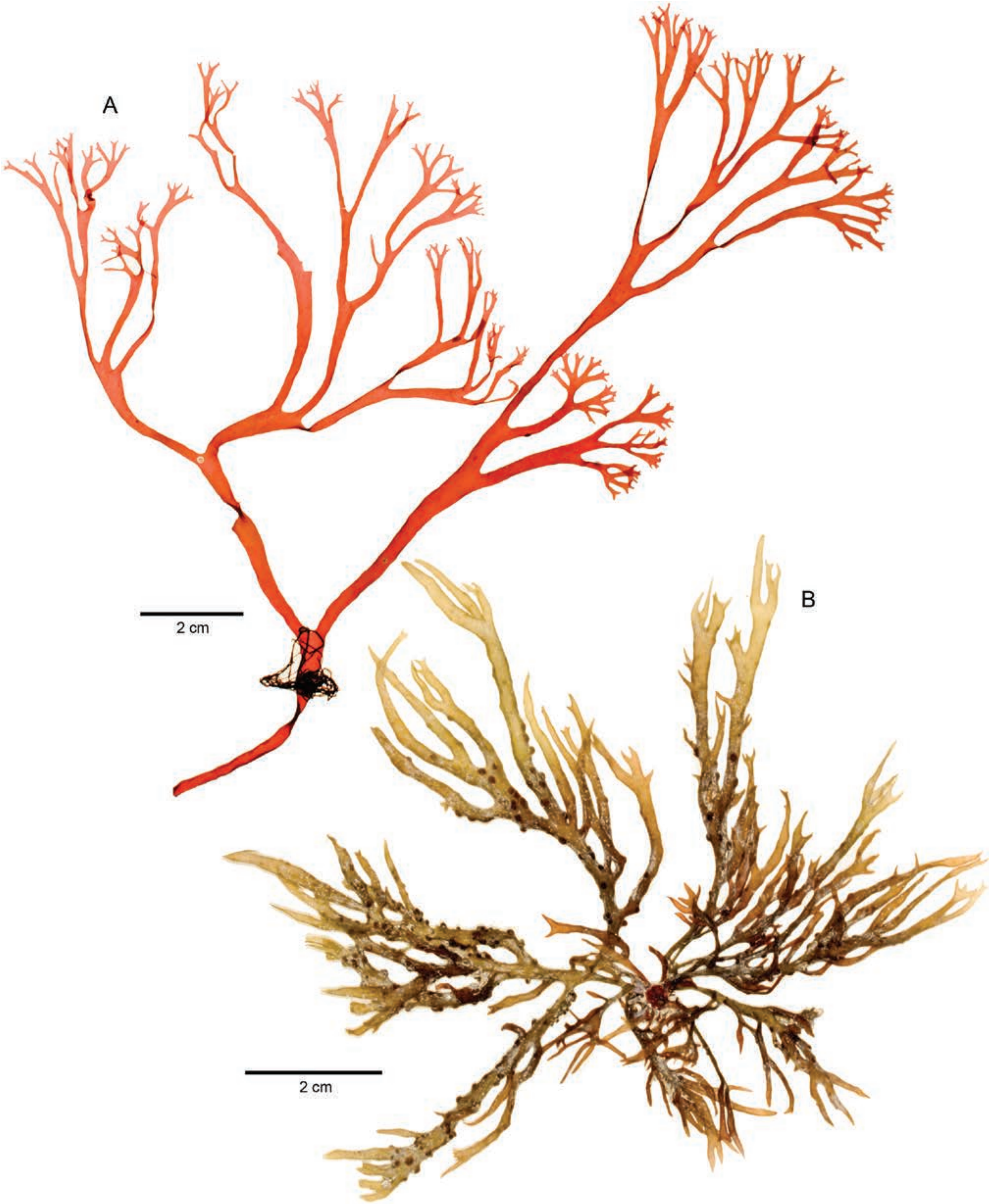


FIGURE 198. Species of *Gracilaria*. A. *Gracilaria tepocensis:* Habit (*JN-5356*, US Alg. Coll.-156380). B. *Gracilaria turgida:* Habit of female gametophyte with cystocarps (*JN-3212*, US Alg. Coll.-159687).

intact specimens. It is possibly an endemic in the Gulf of California, but this awaits molecular and morphological comparisons.

Although the Pacific Costa Rican *G. crockeri* E. Y. Dawson (1949a) has been considered conspecific (Dawson, 1961a), its relationship to the northern Gulf *G. tepocensis* needs to be reinvestigated. Reports of *G. tepocensis* from Pacific Mexico (Pedroche and González-González, 1981; Mateo-Cid and Mendoza-González, 1991) were noted by Dreckman (2002) as doubtful. Those of León-Tejera and González-González (2000, as "*Gracilaria* aff. *tepocensis*"), as well as records from El Salvador (Fernández-García et al., 2011), Costa Rica (Bernecker, 2009), and Peru (Acleto O., 1973, 1986) should also be reexamined to verify their identity.

Gracilaria turgida E. Y. Dawson

FIGURE 198B

Gracilaria turgida E. Y. Dawson, 1949a:14, pl. 21: figs. 1–11, pl. 24: fig. 1; 1961a:213, pl. l0: figs. 5, 6, pl. 12: fig. 11, pl. 24: fig. 1; 1966a:22; 1966b:63; Abbott and Hollenberg, 1976:498, fig. 445; R. Aguilar-Rosas, 1982:84; Norris, 1985a:94, tbls. 1, 2; Norris, 1985b:132, fig. 5; Huerta-Múzquiz and Mendoza-González, 1985:50; Ortega et al., 1987:72, pl. 3: fig. 18, pl. 4: figs. 19, 20; Sánchez-Rodríguez et al., 1989:44; González-González et al., 1996:216; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:130; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:467; Riosmena-Rodríguez et al., 2005a:33; Pacheco-Ruíz et al., 2008:207; R. Aguilar-Rosas et al., 2009:6, fig. 2e.

Algae cylindrical, robust, turgid and succulent; sometimes somewhat brittle and light brown to pale brownish red when fresh; of 1 to several axes, up to 15 cm tall, 2–5 mm in diameter; sparsely, irregularly branched, 1–2(–3) times, with terete, blunt apices; attached below by a discoid holdfast. Medulla of large, thin-walled cells, grading outward to the cortex of small, rotund cells; outer cortex usually a single layer of smaller, somewhat anticlinally elongated, pigmented cells; often with numerous, deciduous hairs present in cortical layer.

Tetrasporangia borne in more or less modified cortex, scattered throughout thallus. Cystocarps globose, (500–)700–900 µm in diameter, prominent, ostiolate, to some extent basally constricted, scattered on upper thallus; carposporangia 18–20 µm diameter. Gonimoblast of large vacuolated cells, with numerous traversing (absorbing) filaments to pericarp. Spermatangia within shallow, cup-shaped depressions (Textorii-type) separated by modified anticlinally elongated cortical cells; in cortical layer.

Habitat. On shells or rocks, in mudflats, lagoons, and estuaries, often in tidal drainage channels; intertidal.

Distribution. Gulf of California: Punta Gorda (Gulfo de Santa Clara) to Bahía La Choya (Bahía Cholla, vicinity of Puerto Peñasco); El Coloradito; Estero de Bahía de Las Ánimas to Cabo Pulmo; Laguna de Agiabampo; lagunas from Navachiste to Santa María–La Reforma. Eastern Pacific: southern California; Estero de Punta Banda, Baja California to Bahía Magdalena, Baja California Sur.

Type Locality. Mudflat, upper Newport Harbor, Newport–Balboa, Orange County, California, USA.

Remarks. *Gracilaria turgida* seems to prefer, or is possibly restricted to, the protected habitats of lagoons, esteros, mudflats, and salt marshes.

Gracilaria veleroae E. Y. Dawson

FIGURES 190H, 197C

Gracilaria veleroae E Y. Dawson, 1944a:297, pl. 70: fig. 2 [left: type specimen]; Dawson, 1946:83; 1949a:28, pl. 2: figs. 7, 8, pl. 10: figs. 1–4; 1961a:214, pl. 10: figs. 2, 3, pl. 12: fig. 5, pl. 19: fig. 1; 1961b:430; Abbott and Hollenberg, 1976:499, fig. 446; L. Aguilar-Rosas, 1981:94; Huerta-Múzquiz and Mendoza-González, 1985:50; Abbott, 1985a:98; Norris, 1985b:132; Sánchez-Rodríguez et al., 1989:44; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:48; González-González et al., 1996:216, 394; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:130; León-Tejera and González-González, 2000:327 [as *G.* aff. *veleroae*]; CONANP, 2002:140; Dreckmann, 2002:104, figs. 27–32; Serviere-Zaragoza et al., 2007:10; Pacheco-Ruíz et al., 2008:207; Castañeda-Fernández de Lara et al., 2010:199.

Gracilaria tenuifolia W. R. Taylor, 1945:234, pl. 78: fig. 1.

Gracilaria johnstonii sensu Taylor, 1945:9 [in part; non *Gracilaria johnstonii* Setchell et N. L. Gardner, 1924:752 9, which is now *Gracilaria vivesii* M. Howe, 1911:503].

Algae of compressed, membranous, flabellate blades, up to 8 cm tall; dichotomously to subdichotomously branched, 3–5 orders; branches 5–7 mm wide, with entire smooth margins and rounded apices, narrowing downward, becoming more or less cuneate above a small discoid holdfast. Transection usually less than 250 µm thick (occasionally 300– 400 µm thick). Cortex a single layer of periclinally flattened, pigmented cells, 5(–9) µm tall by 12–13 µm wide.

Tetrasporangia spherical, 25–35 µm in diameter, borne within barely modified cortex; scattered over thallus. Cystocarps dome shaped, up to 1000 µm in diameter, ostiolate, slightly rostrate; usually near blade margins. Gonimoblast of large pseudoparenchymatous cells, developing from a large fusion cell, with numerous traversing (absorbing) filaments to pericarp. Spermatangia in small, shallow depressions (Textorii-type), sometimes becoming partially confluent; depressions separated by anticlinally elongate cells; scattered over blade surfaces; spermatia 2.5–3.0 µm in diameter.

Habitat. On rocks; subtidal 4–30(–79) m depths.

Distribution. Gulf of California: Punta Peñasco to Cabeza Ballena; Nayarit. Eastern Pacific: La Jolla, southern California to Bahía Magdalena, Baja California Sur; Isla Socorro and Isla Clarión (Islas Revillagigedo); Guerrero; Galápagos Islands.

Type Locality. Dredged 4–30 m depths; near Isla Turner, off the southern shore of Isla Tiburón (Islas de la Cintura), Gulf of California, Mexico.

Remarks. Some specimens of *Gracilaria veleroae* can superficially resemble smaller specimens of *G. cunninghamii*, but these can be easily separated anatomically. *Gracilaria* *veleroae* is typically much thinner in transection (mostly less than 250 µm thick) and membranous, whereas *G. cunninghamii* is thicker (400–600 µm) and coriaceous. The tetrasporangia of the *G. veleroae* are borne in a barely modified cortex and are spherical and larger (25–35 µm in diameter) compared to those of *G. cunninghamii,* which are in a modified cortex and smaller, 15–22 µm in diameter (Dawson, 1949a, 1961a; Norris, 1985b).

***Gracilaria vermiculophylla* (Ohmi) Papenfuss**

Gracilariopsis vermiculophylla Ohmi, 1956:271, figs. 1–4, pls. 1, 2; 1958:46.

Gracilaria vermiculophylla (Ohmi) Papenfuss, 1967:101; Yamamoto, 1978:130, pl. 28: figs. 1–7, pl. 29: figs. 1–6, pl. 47: figs. 2, 3; Xia and Yamamoto, 1985:69; Yamamoto, 1985:77, tbls. 1, 2, fig. 12; Abbott, 1995:194; Yoshida and Yamamato, 1998:825, fig. 3-73B,C; Terada and Yamamoto, 2002:215, figs. 1 (holotype), 2 (isotype), 3–13; Bellorin et al., 2004:70, figs. 1–24; Piñón-Gimate et al., 2008:116; Orduña-Rojas et al., 2008:503; M.-S. Kim et al., 2010:393, 398, figs. 21–26.

Gracilaria asiatica Zhang et B.-M. Xia, 1985:175, figs. 1–2; Nguyên, 1992:207; Terada and Yamamoto, 2002:216.

Gracilariopsis rhodotricha sensu Ohmi, 1958:47, fig. 2, pl. 10; Nguyên, 1992:207 [non *Gracilariopsis rhodotricha* E. Y. Dawson, 1949a:47].

Gracilaria pacifica sensu R. Aguilar-Rosas et al., 1993:219; Pacheco-Ruíz et al., 1993:491; Garza-Sánchez et al., 2000:205 [non *Gracilaria pacifica* I. A. Abbott, 1985b:116].

Algae of slender, cylindrical axes, dark brown (drying black), up to 30(–100) cm long, 1–2(–3) mm in diameter; branching unilaterally or alternately at irregular intervals, 2–5 orders; branches tapering near apices; attached by small discoid holdfast or unattached. In transection, cell size transition from medulla to cortex gradual. Medulla 4–5(–12) layers of large elliptical cells, 34–410 µm by 12–25 µm, with abundant starch grains and thick cell walls, 12–20 µm. Cortex mostly of 3–4 layers of pigmented cells (up to 8 layers in tetrasporangial and spermatangial basal regions); inner cortex 3–5 layers of radially elongated cells; outer cortical cells, 7–18 µm tall, 3–8 µm wide. Cortical hairs, usually near apices, deciduous; hair basal cell persistent, multinucleate.

Asexual reproduction by fragmentation. Tetrasporangia elongate, decussate-cruciately or irregularly divided; up to 65 µm long, 30–45 µm in diameter; produced within cortex; surrounded by anticlinally elongated cortical cells. Carpogonial branches 2-celled, with short trichogynes; developed from outer cortical cell, supporting 2 short sterile filaments. Fusion cell "star-like" (seen only in early development stages), produces gonimoblast initials. Gonimoblast large, of small, densely protoplasmic cells. Cystocarp floor bears carposporangia initials and a few traversing (absorbing) filaments. Pericarp of 3–4 outer layers of rounded cells, with terminal cells radially elongated, 7–17 µm long, 5–10 µm in diameter, without secondary pit connections; middle layer of 6–10 cells, star shaped because of abundant secondary pit connections; innermost layer of 1–4 rounded cells in chains, each with only a single pit connection. Spermatangial conceptacles usually single, sometimes coalescing; initially, conceptacles may initially be shallow depressions with spermatangia restricted to cavity floor; later, as development continues, becoming deeper, to 90(–120) µm in depth, 60–80 µm in diameter (Verrucosa-type), with spermatangia on both floor and walls of cavity. Spermatangium cut off by oblique division of a spermatangial parent cell. (Reproduction after Bellorin et al., 2004:73.)

Habitat. On rocks, pebbles, and shells, usually partially covered in fine sediments or mud, or may be unattached and free-floating; in coastal rivermouths, lagoons, esteros, and protected shallow bays; intertidal.

Distribution. Gulf of California: Laguna Ohuira and Bahía de Navachiste to Teacapán, Sinaloa. Eastern Pacific: Elkhorn Slough, central California to Estero de Punta Banda, northern Baja California. Western Pacific: China; Korea; Japan; Vietnam.

Type Locality. Gomejima, Akkeshi-ko Lagoon (shallow estuary connected to shore of Akkeshi Bay), Kushiro Province (now Kushiro Subprefecture), Hokkaidō Island, Japan.

Remarks. The Japanese *Gracilaria vermiculophylla* (Ohmi) Papenfuss is an agarophyte known in the northwestern Pacific (Yamamoto, 1985; Yoshida, 1998; Tseng and Xia, 1999; M.-S. Kim et al., 2010). It was apparently introduced over 30 years ago to the northeastern Pacific as early as 1981 in Elkhorn Slough, Monterey Bay, California (e.g., US Alg. Coll.-094794). Within the last 20 years, *G. vermiculophylla* has been recorded in the northeastern Pacific from northern Baja California and central California (Bellorin et al., 2004; Miller et al., 2011) and British Columbia (Saunders, 2009). It is recognized to be an invasive species introduced in the Eastern Pacific and Eastern and Western Atlantic on numerous occasions by the shipping and importation of Japanese oysters to North America and Europe (e.g., Bellorin et al., 2004; Rueness, 2005; Thomsen et al., 2006; Freshwater et al., 2006; S.-Y. Kim et al., 2010), or possibly as a component of seaweed/seagrass mixture used as commercial soil conditioner (Abreu et al., 2011). Its success as an invasive species and known habitat modifier (Wallentinus and Nyberg, 2007; Williams and Smith, 2007) has raised ecological and environmental concerns. Genetic data support the hypothesis that the Sea of Japan (East Sea) populations of *G. vermiculophylla* were the probable source of the invasive species to Pacific North America (S.-Y. Kim et al., 2010).

Gracilaria vermiculophylla has been recently reported in the southern Gulf from Ohuira, Navachiste, and Santa María-La Reforma, Sinaloa (Orduña-Rojas et al., 2008; Piñíon-Gimate et al., 2008, 2012). The highest biomass of this nonnative species was found in laguna Santa María-La Reforma, with high nutrient concentrations attributed to sewage affulents and where it increased from the dry to rainy seasons with the highest temperatures and decreased during the cold season (Piñón-Gimate et al., 2008, 2012). The highly invasive *G. vermiculophylla* needs to be monitored as it may also be elsewhere in the Gulf of California.

Although cystocarps of *Gracilaria vermiculophylla* were originally described by Ohmi (1956, as *Gracilariopsis vermiculophylla*) as lacking traversing filaments, these were observed to be generally rare but present in type locality material (Yamamoto, 1978); this was similarly observed in southern Gulf of

California material by Bellorin et al. (2004). In the Akkeshi-ko lagoon (type locality) *G. vermiculophylla* grows sympatrically with Japanese "*G. verrucosa*," a species with which it shares similar spermatangial conceptacles, and also with *Gracilariopsis chorda* (Holmes) Ohmi (1958), which has similar cystocarps (but very different spermatangial structures). Yamamoto (1985:131) suggested that *G. vermiculophylla* may possibly be a hybrid between these two. However, molecular phylogenetic analyses based on *rbc*L gene sequences conducted by Gurgel and Fredericq (2004) clearly demonstrated that *G. vermiculophylla*, together with *G. tenuistipitata* C. F. Chang et B.-M. Xia (1976) and *G. chilensis* C. J. Bird, McLachlan et E. C. Oliveira (1986), formed a distinct evolutionary lineage, showing that they need to be recognized as a new and distinct genus.

All cylindrical species of *Gracilaria* reported in the northern Gulf, i.e., *G. vermiculophylla, G. pacifica,* and *G. papenfussii,* are in need of further morphological comparisons and clarification based on molecular analyses with type locality specimens of each species. *Gracilaria vermiculophylla*, although often difficult to identify solely by morphology, can be accurately identified using molecular techniques. The mtDNA barcode marker *cox*1 enables analysis of intraspecific genetic diversity and haplotype richness (Gulbransen et al., 2012) and for comparing native and non-native species.

Gracilaria vivesii M. Howe

FIGURE 199

Gracilaria vivesii M. Howe, 1911:503, pls. 30, pl. 33: figs. 1–5; Setchell and Gardner, 1924:750; Dawson, 1949a:34, pl. 2: figs. 4–6, pl. 14: figs. 1–6, pl. 15: figs. 1–6; Salcedo-Martínez et al., 1988:83; Hoyle, 1994:93; González-González et al., 1996:216.

Gracilaria johnstonii Setchell et N. L. Gardner, 1924:752, pl. 22: figs. 11–14, pl. 60; Dawson, 1944a:293; González-González et al., 1996:213.

Gracilaria sinicola Setchell et N. L. Gardner, 1924:752, pl. 62; González-González et al., 1996:215.

Gracilaria vivipara Setchell et N. L. Gardner, 1924:750, pl. 24: figs. 28, 29, pl. 63; González-González et al., 1996:217.

Gracilaria textorii sensu [in part; for the following citations] Dawson, 1959a:26; 1961a:211; Norris, 1973:13; Huerta-Múzquiz, 1978:338; Littler and Littler, 1981:151; Norris, 1985a:94, tbls. 1, 2; 1985b:132, fig. 1; 1985d:212; Huerta-Múzquiz and Mendoza-González, 1985:50; Mendoza-González and Mateo-Cid, 1985:30; Mateo-Cid et al., 1993:48; González-González et al., 1996:216; Riosmena-Rodríguez et al., 1998:27; L. Aguilar-Rosas et al., 2000:130; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207 [non *Gracilaria textorii* (Suringar) Hariot, 1891:223; basionym: *Sphaerococcus textorii* Suringar, 1868:259, pl. 23; J. Agardh, 1876:426].

Algae flabellate, of 1 to few irregularly subdichotomously branched, flat, broad blades, light rose red to darker red, tending to be coriaceous; up to 35 cm tall; branches (1.5–)2.0–5.0 cm wide; (350–)400–600(–750) µm thick in transection; attached below by a discoid holdfast. Blades branched in 1 plane, up to 6 times; margins usually smooth and entire, but some with simple, divided, or branched lateral proliferations; upper divided segments, narrower, up to 10 mm wide, with ultimate segments 4–5 mm wide, terminating in rounded to attenuate apices. Medulla of large, thin-walled ovoid cells, 250–500 µm in width; outer medulla cells smaller, subglobose to oval, about 15–50(–100) µm in diameter. Cortex usually a single layer of small pigmented cells, about 5 µm in diameter; cortex becoming 2 layers of cortical cells in larger, older portions.

Tetrasporangia ovate to elongate, 15–22 µm in diameter; borne in modified cortex, surrounded by anticlinally elongated cortical cells; scattered over surface. Carpogonial branches 2-celled; in terminal portions of thallus. Cystocarps globose, large, 1200–1600 µm in diameter, prominent, ostiolate, slightly rostrate; scattered over thallus. Gonimoblast of pseudoparenchymatous cells, developed from a large fusion cell, with numerous traversing (absorbing) filaments to pericarp. Spermatangia in individual to confluent, cup-shaped cavities (Textorii-type) surrounded by modified cortical cells.

Habitat. On rocks; lowermost intertidal to shallow subtidal, down to 20 m depths.

Distribution. Gulf of California: San Felipe to Guaymas; Isla San Esteban (Islas de la Cintura); Bahía Concepcíon to Bahía de La Paz, including Isla Carmén, Isla Espíritu Santo, and La Paz.

Type Locality. La Paz, Baja California Sur, Gulf of California, Mexico.

Remarks. *Gracilaria vivesii,* a species originally described from the southern Gulf (Howe, 1911; Dawson, 1949a), is recognized in the field by its broad, flabellate, dichotomously divided frond, usually without lateral proliferations. Apparently only occasionally collected in the southern Gulf, *G. vivesii* is more frequently found in the subtidal of the northern Gulf of California and Islas de la Cintura. The rose red to dark red or greenish red divided blades of Gulf *G. vivesii* are very variable in size; this high degree of phenotypic variation makes it difficult to define the species limits.

Dawson (1949a, as *G. vivesii*) and Ohmi (1955) noted many Gulf specimens were similar to *G. textorii* from Japan. Ohmi (1955) observed *G. vivesii* to be coriaceous and *G. textorii* to be usually membranous, also noting *G. vivesii* to be less proliferous and less dissected than *G. textorii*, but then he concluded they were conspecific. Most of the Gulf of California specimens referred to "*Gracilaria textorii*" sensu Dawson (1961a) are, for now, referred to *Gracilaria vivesii* M. Howe (1911). Molecular analyses will help clarify the taxonomic status of Gulf of California *G. vivesii* and its relationship to Japanese *G. textorii*. Records of *G. vivesii* from tropical Pacific Mexico (Salcedo-Martínez et al., 1988) and Peru (Acleto O., 1973, 1986; Ramírez and Santelices, 1991) should be reexamined to verify their identification.

Uncertain Record:
Gracilaria hancockii E. Y. Dawson

Gracilaria hancockii E. Y. Dawson, 1944a:297, pl. 65: fig. 2; 1949a:39; González-González et al., 1996:213; Pacheco-Ruíz et al., 2008:206.

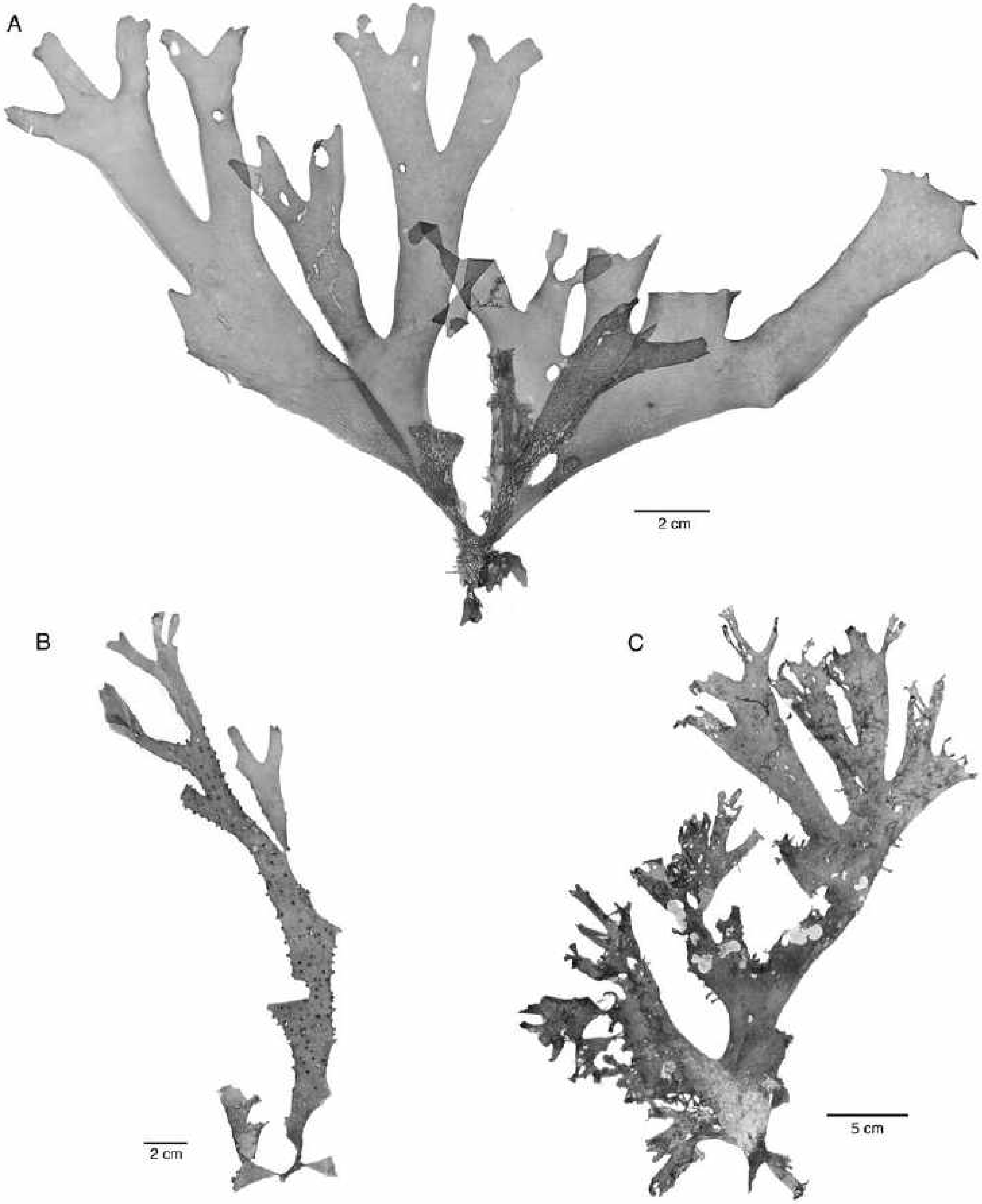


FIGURE 199. *Gracilaria vivesii*: A. Habit (*JN-5252*, US Alg. Coll.-159675). B. Female gametophyte, with the largest cystocarps of the species of *Gracilaria* in the Gulf of California (*JN-2966*, US Alg. Coll.-159659). C. Habit of a large specimen (*JN-6198*, US Alg. Coll.-159683).

Algae of several slender axes, cylindrical at base, 800–1200 μm in diameter, becoming compressed to flattened above, up to 2 mm wide; axes loosely, multifariously branched; apices acute, attenuated; attached directly to or by a very short stipe above a discoid holdfast. Medulla of large, thin-walled cells; cortex of 2–3 layers of much smaller cells (after Dawson, 1944a).

Tetrasporangia not originally described (Dawson, 1944a); tetrasporophytes were later noted to be either a species of *Gracilaria* or *Gracilariopsis* (Dawson, 1949a). Cystocarps as originally described (Dawson, 1944a) were later found to be a species of *Agardhiella* (see Dawson, 1949a). Spermatangia not known.

HABITAT. Known only from dredged material; subtidal.

DISTRIBUTION. Gulf of California. Islas de la Cintura: off "South Shore Beach," Puerto Refugio, Isla Ángel de la Guarda; southern end of Isla Tiburón.

TYPE LOCALITY. Dredged 4–32 m depths; off southern shore of Isla Tiburón near Isla Turner (Turners) (Islas de la Cintura), Gulf of California, Mexico.

REMARKS. Dawson's (1949a:39) reexamination of the type collection of *Gracilaria hancockii* (Dawson, 1944a: pl. 65: fig. 2; AHFH, now UC) found it to contain at least three mixed elements: (1) sterile *Gracilaria subsecundata*, (2) tetrasporophytic specimens of either a *Gracilaria* or a *Gracilariopsis*, and (3) cystocarpic material of a species of *Agardhiella*. At the time, Dawson (1949a) considered *G. hancockii* a "*nomen confusum.*" Since the newer Botanical Codes (e.g., McNeill et al., 2006, 2012) no longer recognize "*nomen confusum,*" *G. hancockii* could be based on the selection of the sterile specimen that Dawson (1949a) referred to *G. subsecundata*. This would make *G. hancockii* conspecific with *G. subsecundata* until molecular analyses can be done on the type material to further elucidate its taxonomic status.

Uncertain Record:
***Gracilaria textorii* (Suringar) Hariot**

Sphaerococcus textorii Suringar, 1868:259, pl. 23; 1870:135; J. Agardh, 1876:426.

Gracilaria textorii (Suringar) Hariot, 1891:223.

Gracilaria textorii (Suringar) De Toni, 1895:27, *nom. illeg.*; [remaining citations in part only, excluding Gulf of California *Gracilaria vivesii*:] Ohmi, 1955:320, pls. 1–6; 1958:40, figs. 20, 21; Dawson, 1959a:26; Dawson et al., 1960b:21; Dawson, 1961a:211; Yamamoto, 1978:123, pls. 12–14, pl. 42: figs. 5–7, pl. 43: figs. 1–4; González-González et al., 1996:216; M.-S. Kim et al., 2010:394, 395, figs. 13–20.

REMARKS. The presence of the Japanese *Gracilaria textorii* in the northern Gulf of California seems unlikely and requires further study. Most of the specimens of Gulf "*G. textorii* sensu Dawson (1961a)" are referred to *G. vivesii.* Although the two species were proposed to be conspecific by Ohmi (1955), a conclusion that was later followed by Dawson (1961a), Yamamoto (1978), and most others since then, their relationship remains to be tested. The two are suggested herein to be separate species. There is also the possibility that Japanese *G. textorii* has been introduced in the Gulf of California, but if so, it is not easily recognized, and comparative molecular analyses will be necessary to elucidate its presence and relationship to the Gulf of California *G. vivesii.* For now, *Gracilaria textorii* (Suringar) Hariot (1891; type locality: Okinawa Prefecture, west coast of Hokkaido, Sea of Japan) is recognized as a western Pacific species from Japan (Inagaki, 1933; Ohmi, 1958; Yamamoto, 1978; Yoshida, 1998; M.-S. Kim et al., 2010), China (Xia and Yamamoto, 1985), Korea (M.-S. Kim et al., 2006), and Vietnam (Nguyên, 1992).

In a molecular systematic study, M.-S. Kim et al. (2006) found western Pacific *G. textorii* from Korea and Japan to be identical and both to be genetically distinct from *Gracilaria incurvata* Okamura (1931:41, pl. 73: figs. 1–6). They also noted that Japanese "*G. textorii*" sensu Gurgel and Fredericq (2004, GenBank accession number AY049325, from Gobogahana, Japan) was molecularly the same as the Japanese *G. incurvata.* Some forms of *G. textorii* and *G. incurvata* can be confused. *Gracilaria incurvata* is a species characterized by narrower blades, 0.5– 1.5 cm wide, 3–5 medullary cell layers, a fleshy texture, and incurved upper portions (Yamamoto, 1978, 1985; M.-S. Kim et al., 2006). Smaller, narrower Gulf of California forms that were referred to "*G. textorii*" (sensu Dawson, 1961a) need to be critically compared, morphologically and genetically, to the Japanese *G. incurvata* Okamura, southern California *G. cunninghamii,* southern Gulf of California *G. vivesii*, and Japanese *G. textorii* to resolve the taxonomic status of Gulf material.

Gracilaria textorii has also been reported in Pacific Mexico on the west coast of Baja California Sur from Bahía Tortugas (inside southeast Bahía San Bartolomé) to Punta Pequeña (north of Bahía San Juanico) and the Chester Islets (NE of Punta Falsa) (Dawson, 1961a), and the Galápagos Islands (Taylor, 1945, as "*G. johnstonii*"). Dreckmann (2002) observed that the Pacific Mexico "*G. textorii*" from Islas Revillagigedo (Taylor, 1945), Colima (Mateo-Cid and Mendoza-González, 1991), and Guerrero (Salcedo-Martínez et al., 1988) differed from the original description as well as from those of the Gulf of California. These collections should also be reexamined and compared with material of Gulf *G. vivesii* and Japanese *G. textorii*.

Excluded Species:
Gracilaria verrucosa

Gracilaria verrucosa (only Gulf of California collections) sensu Dawson, 1961a:214, pl. 20; 1961b:43: 1966a:22; Norris, 1973:13; Huerta-Múzquiz and Mendoza-González, 1985:50; Norris, 1985c:133; Mendoza-González and Mateo-Cid, 1986:424; González-González, 1996:315; Riosmena-Rodríguez et al., 1998:27 [non *Gracilaria verrucosa* (Hudson) Papenfuss, 1950:195, *nom. rej.,* basionym: *Fucus verrucosus* Hudson, 1762:470*, nom. rej.*; see Irvine and Steentoft, 1995; this taxon is now *Gracilariopsis longissima* (Gmelin) Steentoft, L. Irvine et W. Farnham, 1995:117, basionym: *Fucus longissimus* Gmelin, 1768:134].

REMARKS. All Gulf of California specimens identified as "*Gracilaria verrucosa*" need to be reexamined and, once identified to genus, compared to the narrow, cylindrical species of *Gracilaria* (*G. pacifica*, *G. papenfussii*, and *G. vermiculophylla*) and *Gracilariopsis* (*G. andersonii*, *G. animasensis*, *G. megaspora,* and *G. rhodotricha*) that are known or reported in the Gulf of California.

Gracilariopsis E. Y. Dawson

Gracilariopsis E. Y. Dawson, 1949a:40; Fredericq and Hommersand, 1989b:228–241.

Algae are erect and exhibit varying degrees of branching, with most species being cylindrical, elongated, and often stringy, but a few are flattened. All are attached by a small discoid holdfast.

Tetrasporophytes are as for the family. Carpogonial branches and development of the primary fusion cell are also as for the family. The mature fusion cell is composed of the carpogonium and up to six adjacent sterile cells. Anatomically, the cystocarps of *Gracilariopsis* notably lack traversing (absorbing) filaments that in *Gracilaria* connect the gonimoblast to the pericarp. Instead, the cystocarp has a broad-based gonimoblast of small cells linked to the basal cells of the carposporophyte by specially modified cells on the cystocarp cavity floor by secondary pit connections through gonimoblast conjunctor cells. Carposporangia are formed in chains at the periphery of the gonimoblast cells. Spermatangial parent cells are in pairs or threes on the outer cortical cells, with each cutting off a single spermatangium by a transverse division. Spermatangia are superficial and may cover the thallus surface or are in sori flush with outer cortical cells (Chorda-type; Yamamoto, 1978).

REMARKS. Species of *Gracilariopsis* are generally cylindrical and considered less diverse in habit than those of *Gracilaria* (Gurgel and Fredericq, 2004). The first flat species of *Gracilariopsis* was recognized and described by Gurgel et al. (2003a).

Without male or female gametophytes, or molecular evidence, the genera and species of *Gracilariopsis* and *Gracilaria* with similar habits can be difficult to distinguish. The two genera are separated primarily by characteristics of the sexual reproductive structures. In describing *Gracilariopsis,* Dawson (1949a) included species that lacked traversing (absorbing) filaments between the gonimoblast and the pericarp. Fredericq and Hommersand (1989a, 1989b, 1990) emphasized four differences between the two genera: (1) fusion cells in *Gracilariopsis* incorporate only the cells closely flanking the carpogonium compared to *Gracilaria*, where additional cells are later added; (2) traversing filaments (absorbing filaments or nutrient tubular cells) between the gonimoblast and pericarp within the cystocarp are present in *Gracilaria* but absent in *Gracilariopsis*; (3) the carposporangial chains of *Gracilariopsis* are straighter and more regularly organized; (4) spermatangial parent cells develop from superficial (surface) cortical cells in *Gracilariopsis*, whereas in *Gracilaria* they are developed from adventitious filaments arising on subsurface (intercalary) cortical cells, forming depressions, cavities, or deep pits.

One species, *Gracilariopsis longissima* (S. G. Gmelin) Steentoft, L. M. Irvine et Farnham (1995), is reported in the southern Gulf from Bahía de Navachiste, Sinaloa (Orduña-Rojas et al., 2008). Three cylindrical species of *Gracilariopsis*, including one new species, are recorded in the northern Gulf of California.

KEY TO THE SPECIES OF *GRACILARIOPSIS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Branches slender, less than 500 μm in diameter; thalli up to 20 cm long; cystocarps smaller, about 500 μm in diameter; carposporangia larger, about 50 μm in diameter . . . . ***G. megaspora***

1b. Branches broader, mostly 0.6–1.5 mm (or more) in diameter; thalli usually longer, more than 20 cm long (sometimes very long to 1.0 m or more); carposporangia 15–35 μm in diameter 2

2a. Thalli mostly very long, up to 1.2 m; main axes 0.5–1.5 mm in diameter; lateral branches narrow, 300–600 μm in diameter, generally shorter; cystocarps 0.8–1.6 mm in diameter; carposporangia 20–30 μm in diameter . . . . ***G. animasensis***

2b. Thalli usually shorter, mostly up to 20 cm; main axes 1.5–3.5 mm in diameter; lateral branches usually broader, 0.5–1.5 mm in diameter, usually longer; cystocarps mostly over 1 mm diameter; carposporangia about 28 μm in diameter . . . . ***G. andersonii***

Gracilariopsis andersonii (Grunow) E. Y. Dawson

Cordylecladia andersonii Grunow in Piccone, 1886:62 [in part].

Gracilariopsis andersonii (Grunow) E. Y. Dawson, 1949a:43, pl. 16: figs. 1–4; 1961a:216, pl. 10: fig. 16, pl. 11: fig. 13, pl. 19: fig. 2; 1961b:430; González-González et al., 1996:217; Gurgel et al., 2003a:64, 66, fig. 37, tbls. 1, 2; Gurgel et al., 2003b:154, 161, figs. 2, 3b, tbl. 1; Gurgel and Fredericq, 2004:139, 148, fig. 1, tbl. 1.

Gracilaria sjoestedtii Kylin, 1930:55, figs. 40E,F, 41, 43; Smith, 1944:267, pl. 63: fig. 4; Dawson, 1944a:296; Norris, 1973:12 [in part]; Abbott and Hollenberg, 1976:498,fig. 443; Silva, 1979:322 [in part]; R. Aguilar-Rosas, 1982:84; Sánchez-Rodríguez et al., 1989:43; Fernández-García et al., 2011:62.

Gracilariopsis sjoestedtii (Kylin) E. Y. Dawson, 1949a:40 [in part], pl. 15: fig. 10, pl. 16: figs. 5–8, pl. 17: figs. 1–9, pl. 18: fig. 4; Dawson and Beaudette, 1959:15; Dawson, 1961a:218 [in part], pl. 10: fig. 14, pl. 11: fig. 10, pl. 23: figs. 1–6; 1961b:430; Hollenberg and Abbott, 1966:86; Dawson, 1966a:22; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Fernández-García et al., 2011:62.

Gracilaria lemaneiformis sensu Abbott, 1983:561, fig. 4 [left specimen only]; Abbott, 1985a:97; R. Aguilar-Rosas and Aguilar-Rosas, 1994:522; Mendoza-González and Mateo-Cid, 1996b:66, pl. 5: figs. 16, 17; Pacheco-Ruíz et al., 1999:509; L. Aguilar-Rosas et al., 2000:130; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz et al., 2008:207; Pérez-Estrada et al., 2012:191 [non *Gracilaria lemaneiformis* (Bory de Saint

Vincent) Greville, 1830:liv; *Gracilaria lemaneiformis* (Bory de Saint Vincent) Weber-van Bosse, 1928:435, now =*Gracilariopsis lemaneiformis* (Bory de Saint-Vincent) E. Y. Dawson, Acleto O., et Foldvik, 1964:59, and restricted in distribution to Pacific South America; see Gurgel et al., 2003a:64, 66].

Algae erect, in the northern Gulf mostly 15–18 cm long (but also reported up to 1 m, as "*G. sjoestedii*"); of few to several, cylindrical axes, 1.5–3.5 mm in diameter; sparingly to abundantly, irregularly branched; arising from stoloniferous prostrate branches and a discoid holdfast. Branches narrower than axes, mostly 0.5–1.0 mm in diameter. Medulla of large cells, grading into cortex of 3–4 layers of small, pigmented, cortical cells.

Tetrasporangia oblong, 30–38 µm long, embedded in modified cortex of anticlinally elongated cells; borne in the upper branches. Cystocarps protruding, globose to dome shaped, 800–1800 µm in diameter; scattered over branch surfaces; carposporangia to about 28 µm in diameter, borne in chains. Gonimoblast of small cells, broad based; lacking traversing (absorbing) filaments between pericarp and gonimoblast. Spermatangia in superficial layer (Chorda-type) arising from the cortex and covering branch surface.

HABITAT. Growing on rocks, sometimes partially sand covered or in fine sediment; intertidal to shallow subtidal, down to 2 m depths.

DISTRIBUTION. Gulf of California: El Tornillal (Gulfo de Santa Clara); Bahía La Choya (Bahía Cholla, vicinity of Puerto Peñasco) to Guaymas; San Felipe; Bahía Topolobampo (with query). Eastern Pacific: British Columbia to California; Punta Descanso (Baja California) to Bahía Magdalena (Baja California Sur); Oaxaca to Chiapas; El Salvador; Costa Rica.

TYPE LOCALITY. Santa Cruz, Santa Cruz County, California, USA (Gurgel et al., 2003b).

REMARKS. Northern Gulf of California specimens morphologically similar to the northeastern Pacific *Gracilariopsis andersonii* are tentatively referred to this species. Molecular systematic studies on northern Gulf *G. andersonii* are needed to test its taxonomic identity in comparison with the California *G. andersonii* from its type locality. Specimens identified as "*Gracilariopsis sjoestedii*" sensu Dawson (1961a) from Ensenada de San Francisco are *Gracilariopsis animasensis*. Other northern Gulf specimens referred to "*Gracilaria lemaneiformis*" (cited above) and to "*Gracilaria sjoestedii*" from Punta Cheuca and Guaymas (Mendoza-González and Mateo Cid, 1985) and Laguna Agibampo, Sonora and Sinaloa (Ortega et al., 1987), should also be reexamined to determine if they too belong here or are another cylindrical species.

Gracilariopsis animasensis Gurgel et J. N. Norris, *sp. nov.*

FIGURES 200–202

"*Gracilariopsis* sp. 1" sensu Gurgel et al., 2003a:59–60, 64–66, tbl. 1; 2003b:154, figs. 1, 2, tbl. 1 [as "*Gracilariopsis lemaneiformis* Mexico" and "*G. lemaneiformis* Australia"]; Gurgel and Fredericq, 2004: fig. 1, tbl. 1 [as "*Gracilariopsis* sp. Australia"].

Cordylecladia lemaneiformis sensu Setchell and Gardner, 1924:759 [non *Cordylecladia lemaneiformis* (Bory de Saint-Vincent) M. Howe, 1914:128, which is now *Gracilariopsis lemaneiformis* (Bory de Saint-Vincent) E. Y. Dawson, Acleto O. et Foldvik, 1964:59].

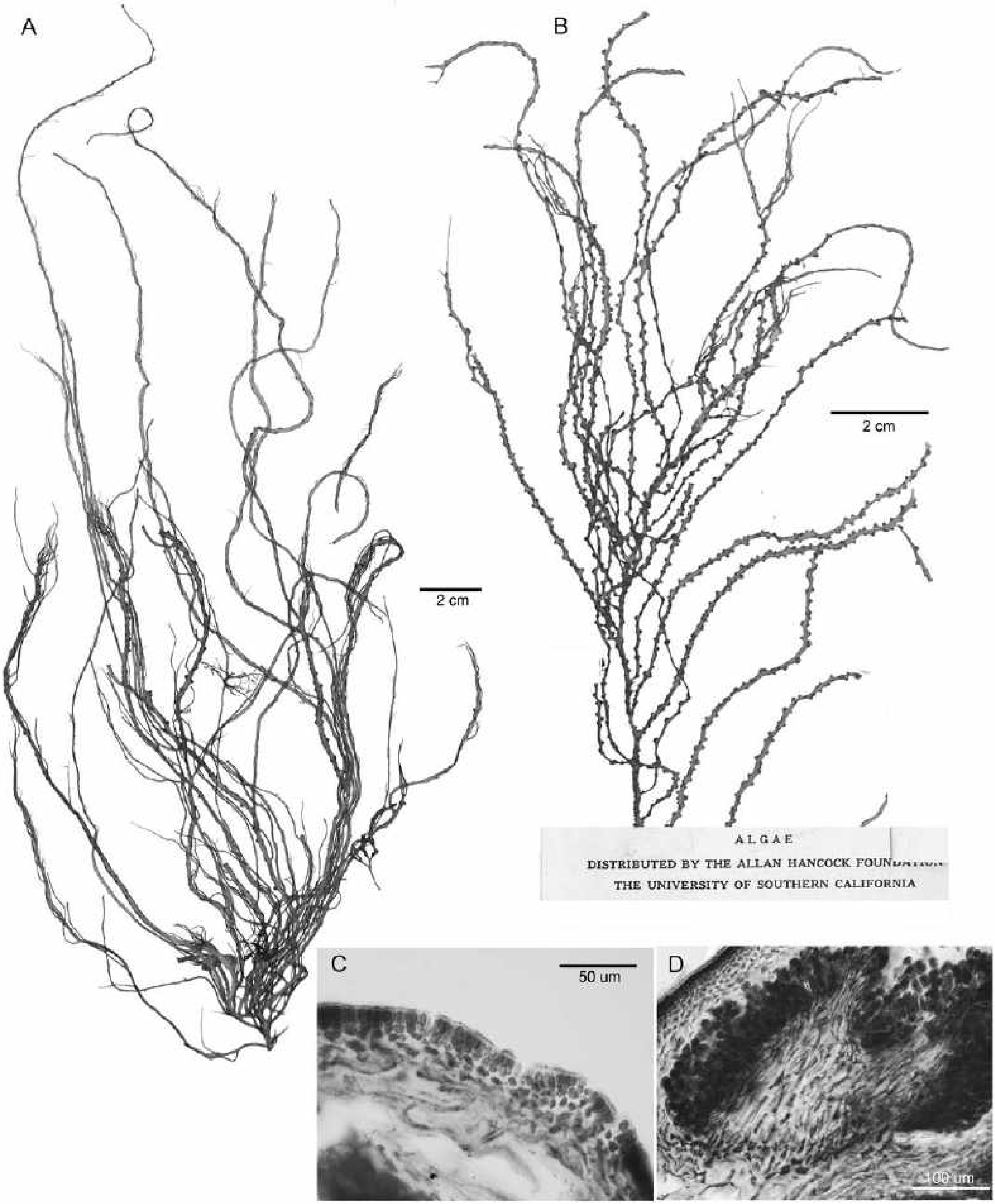
Gracilaria lemaneiformis sensu Dawson, 1961a:415 [in part], pl. 23: figs. 1–6; 1966a:22; Norris, 1985a:93, tbls. 1, 2, fig. 33; Norris, 1985b:125, figs. 9, 10 [non *Gracilaria lemaneiformis* (Bory de Saint-Vincent) Weber-van Bosse, 1928:151, 435].

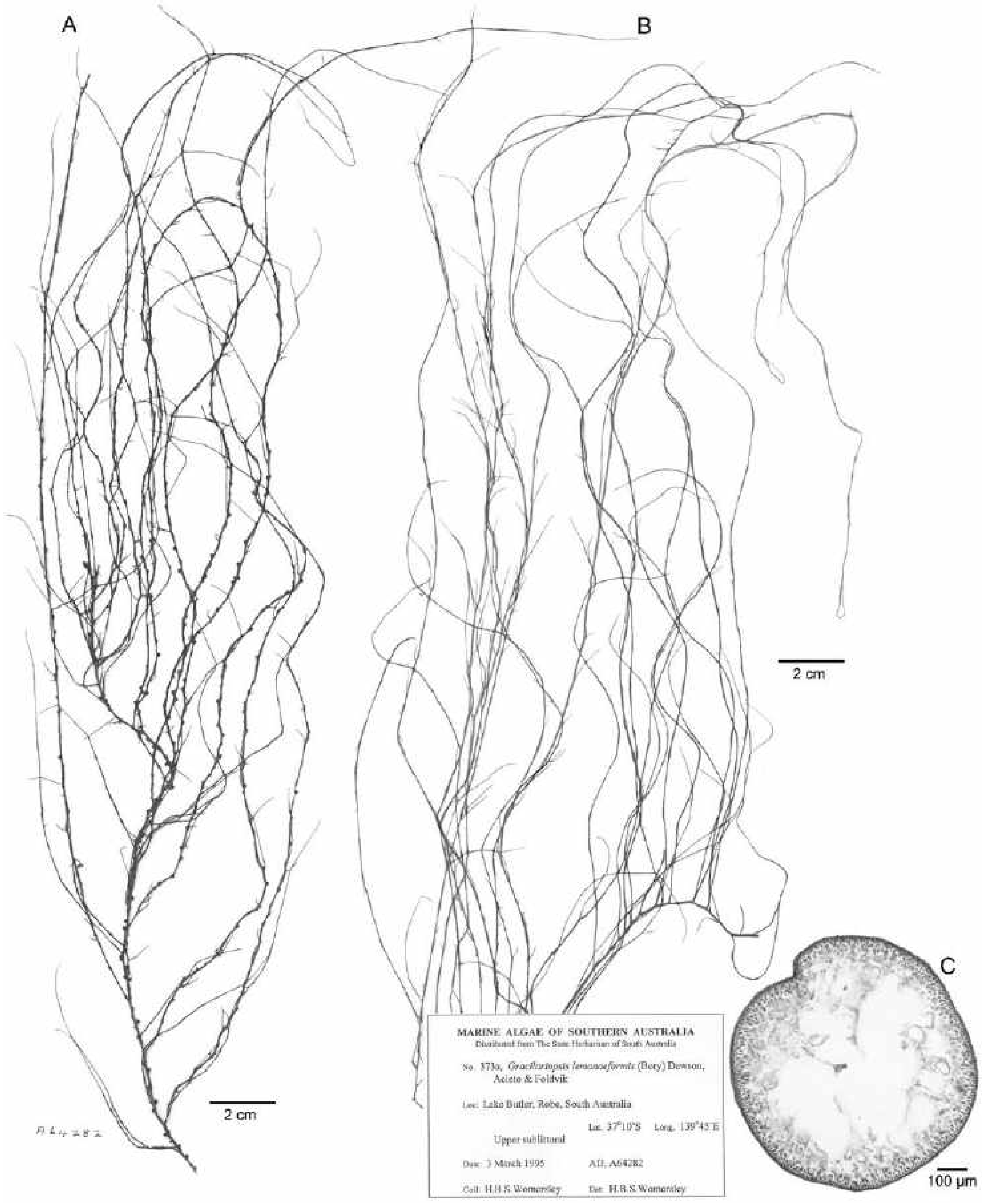
Gracilariopsis lemaneiformis sensu Womersley, 1996:30, fig. 8A–F; Arellano-Carbajal et al., 1999:51; Pacheco-Ruíz and Zertuche-González, 2002:467 [non *Gracilariopsis lemaneiformis* (Bory de Saint-Vincent) E. Y. Dawson, Acleto O., et Foldvik, 1964:59; basionym: *Gigartina lemaneiformis* Bory de Saint-Vincent, 1828:151].

Gracilariopsis sjoestedii sensu Dawson, 1949a:42, and Dawson, 1961b:218 [both in part; only the Ensenada de San Francisco specimens]; Norris, 1973:12, and Huerta-Múzquiz, 1978:337 [both in part; only Bahía de Las Ánimas specimens; non *Gracilariopsis sjoestedii* (Kylin) E. Y. Dawson, 1949a:40, basionym: *Gracilaria sjoestedii* Kylin, 1930:55, which is now *Gracilariopsis andersonii* (Grunow) E. Y. Dawson, 1949a:43; see Gurgel et al., 2003b:154].

LATIN DESCRIPTION. Algae graciles, omnino ramis paucis ad pluribus longis teretibus, ad 1.2 m longae, e hapterono discoideo plerumque ramulis prostratis consociato orientes; axes principales conspicui, (0.5–)0.7–1.5 mm diametro, ubique irregulariter ramosi, parci ad abundantes, ramis brevibus, plerumque gracilioribus; rami laterales 300–600 µm diametro; ramuli ultimi 150–200 µm diametro, acuminati sed saepe effracti. Medulla stratis 3–5 cellularum; cellulis magnis, 200–500 µm diametro.

FIGURE 200. (Opposite) *Gracilariopsis animasensis* Gurgel et J. N. Norris, *sp. nov.*: A. Holotype (*JN-3215* ♀; US Alg. Coll.-89276). B. Cystocarpic specimen from Ensenada San Francisco, Gulf of California (*EYD-1813,* AD-A6283). C. Transection though middle part of the main axis detailing the gradual transition between medulla and cortex and radially elongated cortical cells (*EYD-1813,* AD-A6283, microscope slide 21062). D. Longitudinal section through cystocarp; note the absence of traversing filaments and the presence of elongated cells that connect the gonimoblast to cells on the floor of the carposporophyte, with the irregular shape of the gonimoblast mass containing well-defined, large gonimoblast cells in the middle, well-defined pericarp composed of small, laterally compressed cells, and carposporangia organized in short chains (*EYD-1813,* AD-A6283, microscope slide 21061). (For C and D, note that Gulf of California specimens collected in 1946 did not expand when immersed in water, hence the compressed aspect of the sections).


A
B
2 cm
2 cm
ALGAE
DISTRIBUTED BY THE ALLAN HANCOCK FOUN
THE UNIVERSITY OF SOUTHERN CALIFORNIA
C
50 um
D
100 um



MARINE ALGAE OF SOUTHERN AUSTRALIA
Distributed from The State Herbarium of South Australia

No. 373a, *Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto & Foldvik

Loc: Lake Butler, Robe, South Australia

Lat. 37°10'S Long. 139°45'E

Upper sublittoral

Date: 3 March 1995 AD, A64282

Coll: H.B.S. Womersley Det: H.B.S. Womersley

FIGURE 201. *Gracilariopsis animasensis* from South Australia: A. Cystocarpic specimen. B. Nonreproductive specimen (A, B, from Lake Butler, Robe, AD-A64282c). C. Transection of thallus showing vegetative structure (AD-A63430, microscope slide 14314).

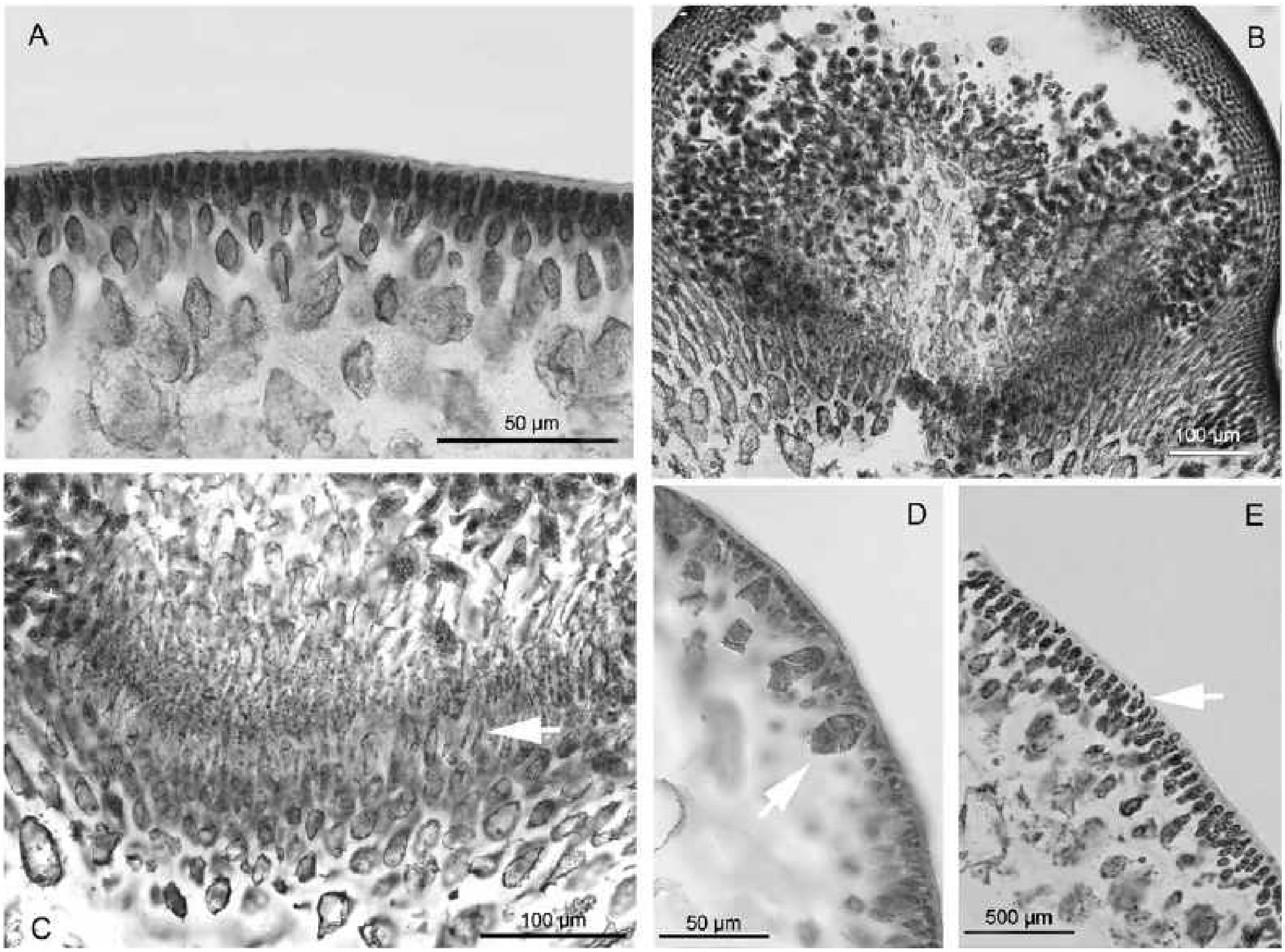


FIGURE 202. *Gracilariopsis animasensis* from South Australia: A. Transection through middle part of main axis showing gradual transition between medulla and cortex and radially elongated cortical cells (AD-A63430, microscope slide 14316). B. Longitudinal section through a cystocarp depicting the absence of traversing nutritive filaments, well-formed medullary cell layer at the base of the carposporophyte, and irregular shape of the gonimoblast mass, which contains well-defined, large gonimoblast cells in the middle and a well-defined pericarp composed of small laterally compressed cells. C. Detail of elongated cells connecting gonimoblast cells and gametophyte cells at the base of the cystocarp (arrow); note the well-developed layers of medullary cells at the base of the carposporophyte (B, C, AD-A63430, microscope slide 14317). D. Transection through middle of a tetrasporophyte showing decussate-cruciately divided tetrasporangia (arrow) flanked by slightly modified cortical cells (AD-A63430, microscope slide 14320). E. Transection through the middle part of a male gametophyte showing Chorda-type spermatangia and spermatium cut off from cortical spermatangial parent cell (arrow) (AD-A63430, microscope slide 14319).

Tetrasporangia decussate divisa, ovoidea ad ellipsoidalia, 38–55 µm longa, 15–35 µm diametro. Cellulae corticales radiatim elongatae. Carposporophytum base lata, cellula conjunctionum persistenti sed parva, sine filamentis peragrantibus (bibulis) pericarpium ad gonimoblastum jungentibus. Cellulae inferae gomnioblasti ovoideae (non ampliatae), 20–40 µm diametro, foveis ad cellulas soli cystocarpi extense conjungentes. Cellulae carposporophytum ad solum cystocarpi conjungentes elongatae, conspicuae. Gonimoblastus cellulis majoribus distinctis consistens, irregulariter formatus. Spermatangia in strato superficiali (ut in Chorda).

Algae slender, of a few to several long, cylindrical branches throughout, up to 1.2 m long; arising from a discoid holdfast usually associated with prostrate branches. Main axes conspicuous (Figures 200A,B, 201A,B), (0.5–)0.7–1.5 mm in diameter, branched irregularly, sparingly to abundantly, along their entire length, with short, usually more slender, lateral branches, 300–600 µm in diameter; ultimate branchlets 150–200 µm in diameter, acuminate but commonly broken. Medulla of 3–5 cell layers; of large colorless cells, 200–500 µm in diameter, with numerous secondary pit connections and thick cell walls, 10–20 µm; cells becoming progressively smaller outward and grading into subcortex of 3–5 cells; outer cortex, 1–2(–4) cell layers of small, radially elongated (subpalisade), pigmented cortical cells; cortical cells sometimes ovoid to more or less isodiametric (in both transverse and longitudinal sections), 6.0–17.5 µm long, 4–7 µm in diameter (Figures 200C, 201C, 202A); diagonal cortical cell division evident. Cortex often with intact hairs above conspicuous basal cells.

Tetrasporangia decussately divided, ovoid to ellipsoidal, 38–55 µm long, 15–35 µm in diameter; within slightly modified cortex of anticlinally elongated cells (Figure 202D); pit connected to inner cortical cells; scattered throughout the cortex of branches. Cystocarps protruding, hemispherical to conical, usually dome shaped, with a broad base or sometimes slightly constricted at base; 1.0–1.6 mm in basal diameter, 800–1600 µm in height; with or without beaked rostrum; irregularly scattered over branch surfaces, primarily occurring on main axes and thicker branches, rarely on thin terminal branchlets. Pericarp 100–200 µm thick, of 8–14 small, isodiametric cells with secondary lateral pit connections, all compacted and well organized in files (Figures 200D, 202B). Carposporophyte broad based, with a persistent but inconspicuous fusion cell and without traversing (absorbing) filaments connecting the pericarp to the gonimoblast. Gonimoblast of well-defined larger cells, irregular in shape; lower cells of gonimoblast, ovoid (not enlarged), 20–40 µm in diameter, extensively pit connected to cells of the cystocarp floor (Figures 202B–C). Cells connecting carposporophyte to the floor of the cystocarp, elongated and conspicuous (Figures 200D, 202B–C). Carposporangia more or less ovoid, 20–30 µm in diameter; developed in chains, usually unbranched or occasionally branched. Spermatangia in superficial layer (Chorda-type) arising from the cortex and covering branch surface; cut off from elongated initials by transverse walls; spermatia 2–3 mm in diameter (Figure 202E).

Etymology. The name of the type locality, Bahía de Las Ánimas (“bay of lost souls”), is based on ánima (Spanish, feminine noun), which means soul. We name this species *G. animasensis* not only for its type locality, one of the locales where we obtained specimens, but also to loosely reflect the meaning of a “lost soul” of *Gracilariopsis* since initially it was unclear whether the species was native or exotic (non-indigenous).

Holotype. Coll. J. N. Norris and K. E. Bucher, *JN-3215* (cystocarpic), 23 May 1972, US Alg. Coll.-089276 (Figure 200A).

Isotypes. US Alg. Coll.-89274, US Alg. Coll.-156378 (Norris, 1985b: fig. 9), and US Alg. Coll.-159743.

Type Locality. Growing in fine–sediment sand, intertidal to 1.0 m depths; in shallow channel near entrance to mangrove estero, inside Bahía de Las Ánimas (28°48′28″N, 113°21′39″W), east coast of Baja California, Gulf of California, Mexico.

Paratypes. Gulf of California, Mexico: Bahía de Las Ánimas, Baja California, from aquaculture tanks, Coll. J .A. Zertuche-González, June 1998 (*rbc*L GenBank accession number AY049416 [*C.F.D. Gurgel-211*], specimen in silica gel). Ensenada de San Francisco (~7 km east of Bahía San Carlos and ~15.7 km NW of Heroica Guaymas), Sonora: Coll. E. Y. Dawson (*EYD-1813* [♀], 17 May 1946, AD-A6283 (Figure 200B–D), including microscope slides 21061 and 21062 [Figure 200B–D], and *EYD-1813* [♀, ♂, and tetrasporophyte], AHFH, now UC, and *EYD-1814*, AD-A6262).

South Australia, Australia: Lake Butler (small lake used as harbor for fishing fleet; Womersley, 1996:31), Robe (37°9′47.61″S, 139°45′4.83″E], Coll. H. B. S. Womersley, 15 April 1994: AD-A63430a (3 specimens; Figures 201C, 202B,C), AD-A63430b (2 specimens), AD-A64745, AD-A64775, and AD-A64404; 3 March 1995: AD-A64282a (3 specimens; ♀ on left side), AD-A64282b (2 specimens; Figure 201A–B), and AD-A64282c (2 specimens; Figure 201A); and 1 December 2007: AD-A47259, AD-A47260, and AD-A74304a-h (9 specimens on 8 herbarium sheets, all nonreproductive). Middle Beach (mangrove area), north of metropolitan Adelaide: Coll. C. F. D. Gurgel, AD-A89218 and AD-A89219.

Habitat. Mostly growing in fine–sediment sand and on small, sand-covered rocks, pebbles, and shells in shallow, protected waters of esteros, estuaries, marinas, lagoons, and bays; intertidal to very shallow subtidal, 0–3 m depths (habitats are similar in both the northern Gulf of California and South Australia).

Distribution. Gulf of California: Bahía de Los Ángeles, Baja California, to Punta Trinidad, Baja California Sur; Ensenada de San Francisco (between Bahía San Carlos and Guaymas), Sonora. Southern Ocean: Lake Butler, Robe, and Middle Beach mangrove area, north of metropolitan Adelaide, both South Australia, Australia.

Remarks. *Gracilariopsis animasensis* has a wide, disjunct distribution, known only from the northern Gulf of California and two locales in South Australia. Northern Gulf of California specimens collected by E. Y. Dawson on 17 May 1946 (Dawson, 1949a, as “*Gracilariopsis sjoestedii*”; *EYD-1813* [♀], AD-A6283, and *EYD-1814* [♀, tetrasporic], AD-6262, and AHFH, now UC) from the Sonoran coast at Ensenada de San Francisco (NW of Guaymas) are now identified to be *Gracilariopsis animasensis*. Specimens of *G. animasensis* have been found growing attached from the Baja California coast of the northern Gulf since 1969 in the intertidal of the estero (small lagoon into which the tide flows) at Bahía de Las Ánimas (*JN-387*, MLML; Norris, 1973, as “*G. sjoestedii*”; 1985b, as “*G. lemaneiformis*”) and on intertidal, sand-covered rocks at Bahía San Francisquito (*JN-277*, US Alg. Coll.-090173). In South Australia it was first collected by H. B. S. Womersley in 1994 from Lake Butler, Robe (Womersley, 1996, as “*Gracilariopsis lemaneiformis*”), indicating it to be an introduced species.

Sequence analysis of the *rbc*L gene of northern Gulf specimens from Bahía de Las Ánimas revealed them to be an undescribed species of *Gracilariopsis* (Gurgel et al., 2003a, as

"*Gracilariopsis* sp. 1"). The Gulf of California *Gracilariopsis animasensis* can be superficially similar to some larger specimens of the northeastern Pacific *Gracilariopsis andersonii* (Grunow) E. Y. Dawson and to the Pacific South American *Gracilariopsis lemaneiformis* (Bory de Saint Vincent) E. Y. Dawson, Acleto O. et Foldvik (1964) from Peru to Chile (Gurgel et al., 2003b). The latter two species are typically more slender and have fewer, but usually longer, lateral branches, whereas *Gracilariopsis animasensis* is generally larger, more robust and succulent, and heavier, often with more abundant, but shorter, lateral branches.

The works of José A. Zertuche-González and Isaí Pacheco-Ruíz and their collaborators (e.g., Arellano-Carbajal et al., 1999; Pacheco-Ruíz et al., 1999, 2003) have described important aspects of the biology and ecology of this species in the Gulf of California. Pacheco-Ruíz et al. (1999, as "*Gracilariopsis lemaneiformis*") studied seasonal variation in biomass of *G. animasensis* along the Baja California coast of the northern Gulf. Agar from *G. animasensis* was reported to be of high quality, and since 1995, it has been exploited commercially in the Gulf of California from Bahía de Los Ángeles (east coast of Baja California) to Punta Trinidad (east coast of Baja California Sur), with an estimated 46,000 dry tons available for harvest (Pacheco-Ruíz et al., 2003). Biomass production is reportedly massive, and individual alga growth rates up to 12% per day have been observed, peaking when the water temperatures and the nutrient concentrations are highest (spring and summer in the northern Gulf of California (Pacheco-Ruíz et al., 1999, as "*G. lemaneiformis*)." In South Australia, Lake Butler is situated in an upwelling region where during the spring-summer season, temperatures are the lowest while light and nutrient concentration are the highest, quite similar to the best growing photoperiod conditions of *Gracilariopsis animasensis* as described for the Gulf of California populations.

Gracilariopsis megaspora E. Y. Dawson

Gracilariopsis megaspora E. Y. Dawson, 1949a:45, pl.18: figs.1–3; 1961a:217, pl. 11: fig. 3, pl. 22: fig. 2; 1961b:430; González-González et al., 1996:217; Gurgel et al., 2003a:61, tbl. 2.

Gracilaria megaspora (E. Y. Dawson) Papenfuss, 1967:100; Chang and Xia, 1976:145, figs. 40, 41; Norris, 1985b:127; Abbott, 1995:191; González-González et al., 1996:214; Xia and Zhang, 1999:60, fig. 36, pl. 5: fig. 6; Pacheco-Ruíz et al., 2008:206.

Algae cylindrical, up to 20 cm long, thin, less than 500 µm in diameter throughout; main axes abundantly branched to 2–3 orders; branches 5.0–35 mm long; attached by a small discoid holdfast. Medulla of large cells, up to 100 µm wide, with an abrupt change to subcortex of 2–3 layers of subcortical cells 20–35 µm in diameter; outer cortex of 1 layer of anticlinally arranged pigmented cells, about 10 µm in diameter, often with abundant short hairs above their basal cells.

Tetrasporangia unknown. Cystocarps projecting, globose, about 500 µm in diameter, slightly constricted at their base and barely rostrate. Gonimoblast of small, densely massed cells, rich in protoplasm, arising from a distinct fusion cell; lacking any nutritive filaments. Carposporangia in chains, ovoid, unusually large, to 50 µm long; each with a distinct central stellate body. Spermatangia unknown.

HABITAT. Floating in shallow, sandy lagoon and probably attached to sand-covered rocks in shallows bays and lagoons; intertidal.

DISTRIBUTION. Gulf of California: Bahía San Carlos. Western Pacific: China.

TYPE LOCALITY. Lagoon, Bahía San Carlos (north of Guaymas), Sonora, Gulf of California, Mexico.

REMARKS. In the Gulf of California, *Gracilariopsis megaspora* is only known from the type collection, a small, not very informative specimen. It has since also been reported in China (Chang and Xia, 1976; Xia, 1985; Xia and Zhang, 1999) and in India (Umamaheswara Rao, 1974; Silva et al., 1996a). It differs from *Gracilariopsis andersonii* and *G. animasensis* in generally having thinner axes, with abundant, short, stubby basal hairs in the cortex and smaller cystocarps with very large carpospores. The described cystocarps of *G. megaspora* support its placement in *Gracilariopsis*. Future Gulf collections, particularly from the type locality, should reveal tetrasporangial and spermatangial specimens necessary to elucidate this species. Additional cystocarpic material will allow genetic testing to determine its relationship to other terete Gulf species.

Uncertain Record:
Gracilariopsis rhodotricha E. Y. Dawson

Gracilariopsis rhodotricha E. Y. Dawson, 1949a:47, pl. 19, figs. 3–7; 1961a:317, pl. 10: fig. 9, pl. 11: figs. 11–12, pl. 21: fig. 1(holotype); 1961b:430; González-González et al., 1996:217.

Gracilaria rhodotricha (E. Y. Dawson) Papenfuss, 1967:100.

DISTRIBUTION. Eastern Pacific: Isla Clarión and Isla Socorro, Islas Revillagigedo (Dawson, 1949a; Serviere-Zaragoza et al., 2007).

TYPE LOCALITY. Dredged from 56–102 m; off Isla Clarión, Islas Revillagigedo, Colima, Pacific Mexico.

REMARKS. One specimen from Bahía de San Lucas, Baja California Sur (*E. Y. Dawson-6847*; US Alg. Coll.) was tentatively referred to *G. rhodotricha* (Norris, 1985c:133, fig. 12). Further collections and the finding of gametophytes of *G. rhodotricha* in the Gulf of California are needed to verify its presence. Additional type locality collections are needed for molecular testing of its generic and taxonomic status. Terada and Yamamoto (2002) referred the Japanese "*G.rhodotricha*" of Ohmi (1958) to *Gracilaria vermiculophylla*. Other records of *G. rhodotricha* from Vietnam (Phạm-Hoàng, 1969) and Queensland (Lewis, 1984) should also be reexamined.

Gracilariophila Setchell et H. L. Wilson

Gracilariophila Setchell et H. L. Wilson in Wilson, 1910:81; Fredericq et al., 1989:167, figs. 1–36; Gerung and Yamamoto, 2002:209.

Algae are minute, colorless to whitish (lacks pigments, including chlorophyll), and more or less globose to postulate. They grow as adelphoparasites on some species of *Gracilaria* and *Gracilariopsis* on the host's surface, with elongated rhizoidal filaments (cellular processes) that penetrate into its host's tissue. The medulla is composed of large, thick-walled, somewhat angular cells that grade into the cortex of small cells.

Tetrasporangia are isolated, embedded in the cortex, and scattered over the thallus. Cystocarps are ostiolate and either embedded within the thallus or borne on the tuberculate surface. Spermatangia are superficial on the outer cortex.

One species of *Gracilariophila* is known from the northern Gulf of California.

Gracilariophila gardneri Setchell

Gracilariophila gardneri Setchell, 1923:393; Dawson, 1949a:51, pl. 23: figs. 4–7; 1961a:218; 1961b:430; 1966a:22; Abbott and Hollenberg, 1976:500, fig. 448; Abbott, 1983:562; Norris, 1985b:125; González-González et al., 1996:217.

Algae a minute, more or less wart-like pustule, 3.0–3.5 mm in diameter; an adelphoparasite appearing whitish to yellowish on host species of *Gracilaria* and *Gracilariopsis*. Cellular processes penetrate host's tissue and grow endophytically, often surrounding or isolating algal host cells and forming connections with them.

Tetrasporangia elongate to elliptical, 28–34 μm long, irregularly cruciately to partially zonately divided (see Dawson, 1949a: pl. 23: fig. 5); borne over pustule surface. Cystocarps hemispherical, nonrostrate, obscurely ostiolate, either isolated or grouped; carposporangia 11–13 μm in diameter. Spermatangia superficial, in outer tissue (up to 50 μm thick) of densely packed slender, anticlinal filaments, 6–17 μm long by 1.5–2.5 μm in diameter; spermatia about 3 μm in diameter.

HABITAT. Found parasitic on *Gracilaria crispata*; on rocks and tidal platform; mid intertidal.

DISTRIBUTION. Gulf of California: Playa Las Conchas (Playa Estacíon), Puerto Peñasco; Bahía Bocochibampo. Eastern Pacific: Santa Monica to La Jolla, southern California.

TYPE LOCALITY. On *Gracilaria cunninghamii* Farlow ex J. Agardh; Santa Monica, Los Angeles County, southern California, USA.

REMARKS. *Gracilariophila gardneri* can sometimes be found on *Gracilaria crispata* growing on the tidal platform, Playa Las Conchas, Puerto Peñasco (Dawson, 1966a; *JN-3163*, US Alg. Coll.), in the upper Gulf and in the southeast Gulf from Bahía Bocochibampo (Dawson, 1949a, 1961a). Dawson (1961a) noted *Gracilariophila*-like tubercles on Gulf "*Gracilaria textorii*" but concluded they were not sufficient for identification.

Gracilariophila gardneri is morphologically similar to the generitype, *G. oryzoides* Setchell et H. L. Wilson (in Wilson, 1910; see Fredericq et al., 1989), an adelphoparasite found on *Gracilariopsis andersonii* (Abbott, 1983:562, as "*G. sjoestedtii*") of the Pacific Coast from British Columbia to Baja California (Dawson, 1961b; Scagel et al. 1989) and on *G. cunninghamii* from Baja California Sur (Mateo-Cid and Mendoza-González, 1994b). The Gulf *G. gardneri* differs only in tetrasporangia, which are irregularly divided versus being strictly, regularly, cruciately divided in *G. oryzoides*. Further investigations of the anatomy, host specificity, and DNA are needed to test the relationship of these two species.

PTEROCLADIOPHILACEAE

Pterocladiophilaceae K.-C. Fan et Papenfuss, 1959:38.

Parasitic algae that are minute, generally more or less spherical, and basally penetrating the tissue of the host and protruding above the host's surface.

Tetrasporangia are cruciately divided. Carpogonial branch is 2-celled. Spermatangia are produced in chains, cut off transversely at upper end of spermatangial parent cell.

REMARKS. The Pterocladiophilaceae is represented in the Gulf by *Gelidiocolax*, a minute parasitic alga growing on species of the Gelidiales (Fan and Papenfuss, 1959).

Gelidiocolax N. L. Gardner

Gelidiocolax N. L. Gardner, 1927c:340.

Parasitic algae that are diminutive, whitish, pale pink or colorless, subspherical to hemispherical tubercules, up to 5 mm in diameter, on host species of *Gelidium* and *Pterocladia*. Thalli are composed of basal-penetrating rhizoids that apparently either form or lack secondary pit connections to the host tissue and outwardly develop a solid mass of isodiametric cells.

Tetrasporangia are cruciately divided and scattered over the thallus surface. The initial stages of gonimoblast development are unknown, but the carposporophytes apparently consist of a small basal fusion cell and radiating chains of carposporangia developed in conceptacle-like chambers in the thallus that have an ostiole at the surface. Carposporophytes are surrounded by a thick pericarp and grouped in lobes of the thallus. Spermatangia are produced from the spermatangial parent cells in rows of 3–4 and can cover the entire surface.

REMARKS. On the basis of significant anatomical and morphological similarities to the Gracilariales, Fredericq and Hommersand (1990) removed the genera *Gelidiocolax* and *Pterocladiophila* K.-C. Fan et Papenfuss (1959; parasites on members of the Gelidiales) and *Holmsella* Sturch (1926; on some Gracilariaceae) from the family Choreocolacaceae Sturch (1926) and transferred them to the Pterocladiophilaceae. The molecular data of Zuccarello et al. (2004a) supported the placement of *Holmsella* in the Gracilariales, but they noted that parasitic algae rarely infect members outside their family and concluded that molecular data are needed to test the family placement of the other genera.

There is one species of this diminutive parasite in the northern Gulf of California.

Gelidiocolax microsphaericus N. L. Gardner

Gelidiocolax microsphaericus N. L. Gardner, 1927c:341; Dawson, 1953a:61; 1954a:323; Fan and Papenfuss, 1959:33; Dawson, 1961b:410; Stewart, 1976:342, fig. 285; 1991:97; González-González et al., 1996:204; L. Aguilar-Rosas et al., 2000:130; Mateo-Cid et al., 2000:64.

Minute parasites, subspherical to hemispherical mounds, white to pinkish white, 175–230 μm in diameter, found on some members of Gelidiaceae; internally of filaments, dichotomously to trichotomously branched, terminating in long, narrow apical, surface cortical cells.

Tetrasporangia 22–28 µm in diameter; scattered over surface. Carpogonial branch 2-celled. Cystocarps within thallus; carposporangia in dense clusters. Spermatangia, 1.5–2.0 µm in diameter; 3–4 seriate on upper ends of outer cortical cells; covering surface of thallus.

HABITAT. Adelphoparasite on *Gelidium pusillum*; intertidal.

DISTRIBUTION. Gulf of California: El Coloradito to Puertecitos; Punta Arena. Eastern Pacific: Balboa, southern California to Punta Descanso, Baja California; Isla San Martín (northwest of San Quintín, Baja California).

TYPE LOCALITY. On *Gelidium pulchrum* N. L. Gardner (1927b; =*Gelidium purpurascens* N. L. Gardner, 1927b); ~3.2 km south of Balboa Beach, Orange County, southern California, USA.

CRYPTONEMIALES

Cryptonemiales F. Schmitz, 1892:21.

Halymeniales G. W. Saunders et Kraft, 1996:730.

Algae are low growing, repent, or erect and exhibit a wide range of morphologies. Species may be narrow to broad, unbranched or branched, or foliose blades. Thalli are multiaxial in structure. The medulla is filamentous, and the cortex is pseudoparenchymatous. In one family, the Halymeniaceae, secondary pit connections are common between cells in the medulla and inner cortical layers.

Member algae have a triphasic life history with isomorphic gametophytes and tetrasporophytes. Tetrasporangia are usually cruciately or decussately cruciately divided. Carpogonial branches and auxiliary cells are located in separate branch systems (nonprocarpic), and carpogonial branches are from two- to four-celled. After presumed fertilization, carpogonia produce multiple septate, branched connecting filaments that transfer the zygote nucleus to auxiliary cells. Diploidized auxiliary cells issue a single gonimoblast initial, directed thallus outward. The carposporophyte is multilobed with a small fusion cell, and the bulk of gonimoblast cells convert to carposporangia.

REMARKS. The distinction of the Cryptonemiales and Gigartinales has long been debated (e.g., Kraft and Robbins, 1985; Abbott, 1999). Saunders and Kraft (1996) clarified the two orders and proposed a new name, the Halymeniales, for this order, restricting it to two families. Thus, two names are in current use for this order, Cryptonemiales F. Schmitz (1892) and Halymeniales G. W. Saunders et Kraft (1996), and there has been much discussion on which of these ordinal names should be used (e.g., Kraft and Saunders, 2000; Silva, 2002; Gavio et al., 2005). At present, the Botanical Code (McNeill et al., 2006, 2012: Art. 11.10) does not require priority for use of taxon names above the rank of family. Therefore, although either name could be used, the ICBN does recommend using priority. For now, following Recommendation 16A, "in choosing among typified names for a taxon above the rank of family, authors should generally follow the principle of priority," the name Cryptonemiales is used for this order.

The order is represented by two families in the marine flora of the northern Gulf of California.

KEY TO THE FAMILIES OF CRYPTONEMIALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Gulf species membranous (not gelatinous), generally slippery in texture; some cortical filament cells with secondary pit connections; carpogonial branch 2- to 4-celled; most genera with separate clusters of accessory sterile filaments (ampullae) for each carpogonial branch or auxiliary cell; carposporophyte cupped or surrounded by involucres derived from ampullary filaments, in some genera with additional involucres derived from medullary filaments .... **Halymeniaceae**

1b. Gulf species gelatinous; cortical filament cells without secondary pit connections; carpogonial branch 3-celled; auxiliary cells intercalary in normal cortical filaments; female reproductive structures not in ampullary filament clusters .... **Tsengiaceae**

HALYMENIACEAE

Halymeniaceae Bory de Saint-Vincent, 1828:158 [as "Halymeniae"]; Guiry, 1978a:192; Silva, 1980:82.

Cryptonemiaceae Harvey, 1849b:75, 132; Papenfuss, 1955:188; Silva, 1980:82.

Grateloupiaceae F. Schmitz, 1892, *nom. illeg.*:18, 21; Schmitz and Hauptfleisch, 1897c:508, fig. 274; Kylin, 1956:213 [see Silva, 1980:82].

Algae are generally erect and simple, divided, or branched, with species displaying great variation in habit, being cylindrical, compressed, flattened, or blade-like. Thalli are multiaxial in construction, with a filamentous medulla and a cortex of cells that become successively smaller toward the surface.

Gametophytes isomorphic with tetrasporophytes. Tetrasporangia are cruciately divided, embedded in the cortex, and either (1) scattered over the thallus surface, (2) grouped in sori, or (3) borne in modified areas of tissue (nemathecia). Sexual thalli are monoecious or dioecious. The carpogonial branch is generally two-celled; this branch and the auxiliary cell branch are separate from each other (nonprocarpic), and in most genera, each is surrounded by a cluster of special ampullary filaments (accessory sterile filaments) that arise from inner cortical cells. Connecting filaments develop from fertilized carpogonia and these contact and diploidize the auxiliary cell, which then develops the carposporophyte. Cystocarps are embedded in the thallus and in most genera are cupped or surrounded by sparse to conspicuous involucres derived mostly from the ampullary filaments (ampullae); in some genera, however, additional involucres are derived from medullary filaments. Spermatangia are superficial on the thallus, cut off from terminal cortical cells.

The Halymeniaceae is represented by four genera in the northern Gulf of California.

KEY TO THE GENERA OF THE HALYMENIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli ranging from narrow, branching fronds to foliose blades; medulla with predominantly periclinal filaments, anticlinal medullary filaments rare to absent 2
1b. Most thalli foliose blades; medulla with some conspicuous anticlinal filaments . . . . ***Halymenia***
2a. Thalli of thin, flattened blades; blades entire (unbranched), divided, or lobed; cortex thin, 1–3(–6) cell layers; medulla of loose periclinally directed filaments, some with dense and refractive contents (these generally wider) . . . . ***Cryptonemia***
2b. Thalli flat, usually thicker; of narrow strap-like branches or subcylindrical and narrow in diameter or compressed, flattened blades; cortex of 4 or more cell layers; medulla with lax to congested filaments, filaments without refractive contents 3
3a. Texture rigid or cartilaginous; fronds of narrow, strap-shaped branches, usually with few to many laterals; cortex thick, of 5–12 cells in anticlinal file; medulla packed with filaments; tetrasporangia grouped in sori in outer cortex . . . . . . ***Prionitis***
3b. Thalli lubricous to leathery; of compressed to flattened blades or subcylindrical narrow axes and branches; cortex of 4–8 cells in anticlinal file; medulla lax to dense throughout (1 species with sparse filaments and a hollow center); tetrasporangia scattered in cortex . . . . ***Grateloupia***

***Cryptonemia* J. Agardh**

Cryptonemia J. Agardh, 1842:100.

Algae are erect, flattened blades that vary in form from lanceolate to ovoid or broad and are unbranched or branched, lobed or irregularly divided above a stipe that is attached by a small discoid holdfast. Some have proliferous branchlets along blade margins or the stipitate portion. In at least one species, the stipe is perennial and exhibits growth rings. The thallus is typically relatively thin, usually 300 µm or less thick. The medulla is composed of predominately periclinally directed filaments; some of the medullary filaments may have dense and highly refractive contents. The cortex is thin, usually composed of one to four layers of more or less spherical to ellipsoid small cells that become progressively smaller toward the surface.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia are generally small (<25 µm) and cruciately divided, embedded in the cortex, and scattered over the blade surface. Female reproductive structures are borne in ampullae, with ampullary filaments branched up to four orders. Carpogonial branches are two-celled, borne on a primary or secondary ampullar filament. The hypogynous cell may develop a sterile filament. Auxiliary cell ampullae are slightly more complex; the auxiliary cell is a basal or suprabasal cell of a second- or third-order ampullary filament in a branch system separate from those of the carpogonial branches. After fertilization, connecting filaments are issued by the carpogonia and contact auxiliary cells, where a small auxiliary fusion cell is formed. A single gonimoblast initial arises from the diploidized auxiliary cell and produces a compact carposporophyte of many small carposporangia. The surrounding pericarp is slight, formed by elongated ampullary filament cells. Cystocarps are embedded and scattered, slightly distending the blade surface. Spermatangia, where known, are superficial over the thallus.

REMARKS. One Pacific Mexico species, *Cryptonemia decolorata* W. R. Taylor (1945; type locality: Isla María Magdalena, Islas Marías) described from the southernmost entrance to the Gulf off Nayarit, has been also reported in the southern Gulf, from Bahía Concepción (Mateo-Cid et al., 1993).

There are five species of *Cryptonemia* in the northern Gulf of California, two of which are endemic to the Gulf.

KEY TO THE SPECIES OF *CRYPTONEMIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades generally smaller; lobed, pseudodichotomously or irregularly branched; up to 15 mm wide 2
1b. Blades larger, ovate to obovate or broadly lanceolate; simple, lobed, or divided; more than 15 mm wide 4
2a. Blade with distinctively lobed, orbicular-shaped bladelets from margins of central blade (resemble *Opuntia* cactus pads), up to 9 mm in diameter; up to 50 µm thick . . . . ***C. opuntioides***
2b. Blades divaricately, pseudodichotomously or irregularly branched 3
3a. Blades irregularly dividing, often becoming much lacerated; up to 15 mm wide; 80–90 µm thick . . . . ***C. veleroae***
3b. Blades distinctly and divaricately pseudodichotomously branched, at times repeatedly; (2.0–)3–15 mm wide; 40–70(–110) µm thick . . . . ***C. guaymasensis***
4a. Blades ovate to obovate, entire or only once or twice lobed; membranous; 4–30 cm tall and wide; 120–300(–450) µm thick . . . . ***C. obovata***
4b. Blades ovate to broadly lanceolate, usually divided (rarely entire), or dichotomously or pinnately branched; 5–14 cm tall, 2–6 cm wide; more delicate, thinner; 35–100 µm thick; margins sometimes with small lateral bladelets . . . . ***C. angustata***

***Cryptonemia angustata* (Setchell et N. L. Gardner) E. Y. Dawson**

FIGURE 203

Kallymenia angustata Setchell et N. L. Gardner, 1937:77 [as "*Callymenia angustata*"], pl. 3: fig. 6b, pl. 12: fig. 32; Dawson, 1944a:285, pl. 68: fig. 1.

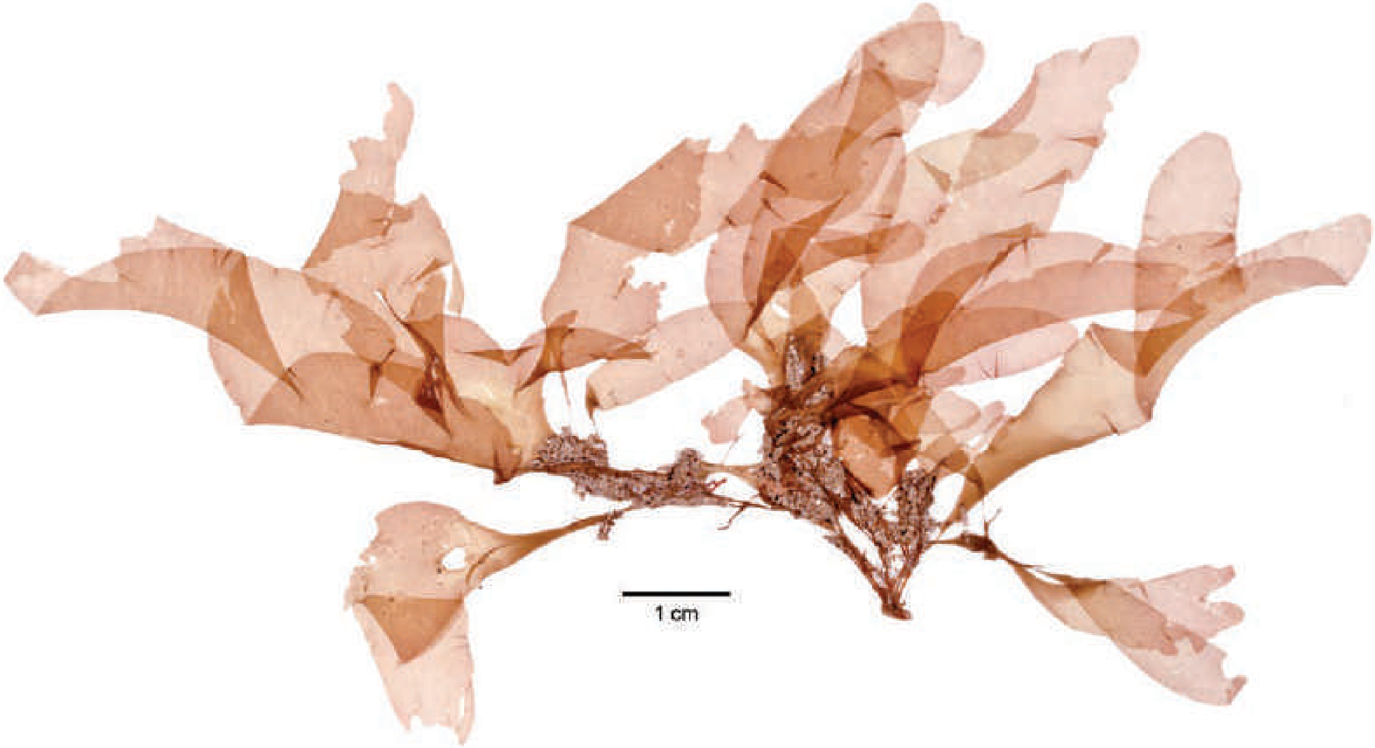


FIGURE 203. *Cryptonemia angustata:* Habit of a tetrasporophyte (*JN-4500*, US Alg. Coll.-158994).

Cryptonemia angustata (Setchell et N. L. Gardner) E. Y. Dawson, 1954c:261, pl. 2: figs. 11–14; 1960a:45; Dawson et al., 1960a:56, pl. 24: fig. 3; Dawson, 1961b:422; 1961c:413, pl. 19: fig.3; Dawson et al., 1964:50, pl. 56: fig. B; Dawson, 1966a:21; Abbott, 1967a:147 [in part], figs. 9, 10; Abbott and Hollenberg, 1976:437 [in part], fig. 387; Stewart, 1991:89; Ramirez and Santelices, 1991:229; González-González et al., 1996:195; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:52; Dreckmann et al., 2006:155; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:207; Bernecker, 2009:CD-Rom p. 63; Fernández-García et al., 2011:61.

Kallymenia tenuifolia W. R.Taylor, 1945:214 [*nom. illeg.*], pl. 72: figs. 1–4 [non *Kallymenia tenuifolia* Feldmann, 1935:368].

Algae membranous, ovate to broadly lanceolate blades, rose red, 5–14 cm tall, 2–6 cm wide; arising from a short distinct stipe; attached below by a small discoid holdfast. Blades simple or pinnately divided, sometimes with irregular proliferations; blades stipitate. Blades 35–60 μm thick in smaller blades and can be up to 90(–100) μm thick in larger thalli. Medulla of a few, slender, longitudinally aligned filaments, some thicker and with dense refractive contents. Cortex of (1–)2–3 cell layers; outer cortical cells 3–8(–10) μm in diameter; inner cortical cells slightly larger.

Tetrasporangia cruciately divided, 20 μm or less in diameter in surface view; scattered in cortex over blade. Cystocarps up to 200 μm in diameter, surrounded by a few sterile (ampullary) filaments; embedded within thallus and bulging blade surface; scattered over blade. Spermatangia not seen.

HABITAT. Occasional on shaded rocks and tide pools, low intertidal, down to 10 m depths; dredged from 30–84 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía Tepoca to Punta La Gringa, Bahía de Los Ángeles; Bahía de San Lucas. Eastern Pacific: Monterey Bay, central California, and La Jolla, southern California; Isla Magdalena, Bahía Magdalena (Baja California Sur); Isla Socorro (Islas Revillagigedo); Chiapas; El Salvador; Costa Rica; Peru.

TYPE LOCALITY. Bahía Santa María, west coast of Isla Magdalena (outside Bahía Magdalena), Baja California Sur, Pacific Mexico.

REMARKS. *Cryptonemia angustata*, described from Pacific Baja California Sur, is predominately a warm-temperate to subtropical species. Gabrielson et al. (2004) noted that as reported in colder waters of the northeast Pacific, *C. angustata, C. obovata* J. Agardh (1876), and *C. borealis* Kylin (1925) can be difficult to separate and are in need of reinvestigation. The northern California *C. obovata* and the Washington *C. borealis* are both cool- to cold-temperate species. Morphologically, Gulf of California specimens referred to *C. angustata* are close to *C. veleroae* (E. Y. Dawson) E. Y. Dawson (see also Remarks under *C. veleroae*) and should be critically compared.

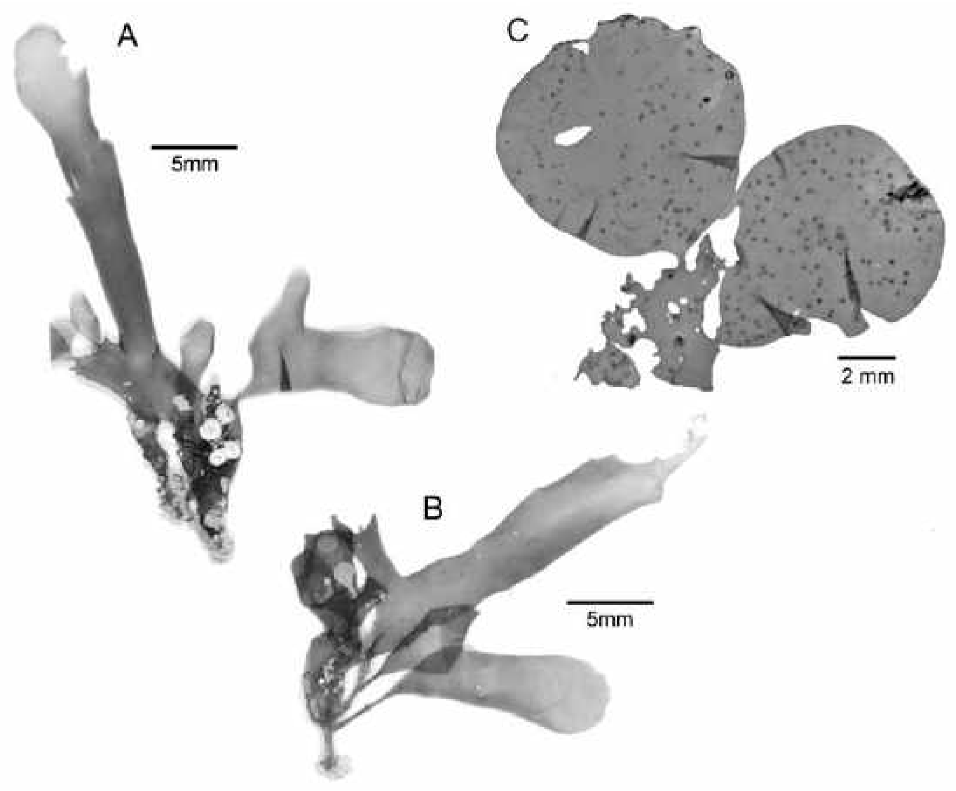


FIGURE 204. Species of *Cryptonemia*. A, B. *Cryptonemia guaymasensis*: Habits of two thalli (*EYD-27492*, US Alg. Coll.-40772). C. *Cryptonemia opuntioides*: Habit of holotype (*EYD-26126*, US Alg. Coll. microscope slide 786).

***Cryptonemia guaymasensis* (E. Y. Dawson) E. Y. Dawson**

FIGURE 204A,B

Kallymenia guaymasensis E. Y. Dawson, 1944a:286, pl. 68: fig. 2 [as "*Callymenia guaymasensis*"].

Cryptonemia guaymasensis (E. Y. Dawson) E. Y. Dawson, 1954c:263; 1960a:45; 1961b:422; 1966a:21; Lewis, 1990: fig. 6 [holotype]; González-González et al., 1996:195; L. Aguilar-Rosas et al., 2000:130; CONANP, 2002:139; Mateo-Cid et al., 2006:52.

Algae of strap-like axes in lower portion, subdichotomously divided above, usually branched; dark rose red, mostly 5–7 cm tall, 5.0–15 mm wide; smaller in intertidal, up to 3 cm tall and (2.0–) 3.0 mm wide; arising from subcylindrical to compressed stipes, 2–5 mm long; attached by a small discoid holdfast. Axes with round apices, margins sometimes undulate. Intertidal algae up to 110 μm thick, with stipe sometimes extending into base of blade as a midrib, occasionally extending to first division. Subtidal algae 40–70 μm thick; midrib lacking. Branching divaricately subdichotomous in 1 plane; sometimes secondary proliferations from margins. Medulla narrow, of branched interwoven filaments; some with dense refractive contents. Cortex of 2–3(–4) cell layers; subcortex 1–2 layers of rotund cells, 8–12 μm in diameter; outer cortex of 1 layer (rarely 2) of small pigmented cells, 4–6 μm in diameter.

Tetrasporangia unknown. Cystocarps 200–250 μm in diameter; embedded, bulging (more prominent on side with ostiole); scattered over blade surface; carposporangia in compact mass, appearing pedicellate (borne on persisting auxiliary cell). Spermatangia unknown.

HABITAT. On sides of rocks, in crevices, and on side walls of deeper tide pools; low intertidal to shallow subtidal, down to 6 m depths; also dredged from 8–37 m depths (Dawson, 1954c).

DISTRIBUTION. Gulf of California: Playa Las Conchas (Playa Estacíon), Puerto Peñasco to Guaymas; El Coloradito to Santa Teresa; Bahía de Loreto to Bahía de San Lucas. Eastern Pacific: Costa Rica.

TYPE LOCALITY. On muddy bottom, 4–6 m depths; outer harbor, Guaymas, Sonora, Gulf of California, Mexico.

REMARKS. Intertidal specimens identified as *Cryptonemia guaymasensis* from Puerto Peñasco (Dawson, 1966a) are 3–4 mm wide and 1–3 cm tall, smaller overall than those reported elsewhere in the Gulf (Dawson, 1954c). Once thought to be a Gulf endemic (Dawson, 1954c), *Cryptonemia guaymasensis* has also been reported from Pacific Costa Rica (Dawson, 1960a; Bernecker, 2009 [CD-Rom], as "*C. limensis*"; Fernández-García et al., 2011, as "*C. limensis*") and in the western Atlantic from Brazil (Pinheiro-Joventino, 1977; Creed et al., 2010). Lewis (1990) included *C. guaymasensis* as a synonym of *C. limensis* (Sonder ex Kützing) J. A. Lewis (basionym: *Euhymenia limensis* Sonder ex Kützing, 1849), a species from Peru and northern Chile (Ramírez and Santelices, 1991, as "*Sebdenia limensis* (Sonder ex Kützing) M. Howe, 1914"). After more fertile specimens from the Gulf of California are collected, especially from the type locality, a critical morphological and molecular systematic study is needed to evaluate the taxonomic status of Gulf *C. guaymasensis* and its relationship to South American *C. limensis*.

Cryptonemia obovata J. Agardh

FIGURE 205

Cryptonemia obovata J. Agardh, 1876:681; Kylin, 1925:10, fig. 8a; Dawson, 1954c:260, pl. 1: figs. 9, 10; Dawson et al., 1960a:56, pl. 25: figs. 3, 4; 1960b:18; Dawson, 1961b:422; Hollenberg and Abbott, 1966:68, figs. 26, 27; Abbott, 1967a:145; Acleto O., 1973:41, 124, 127–128; Abbott and Hollenberg, 1976:438, fig. 389; Silva, 1979:318; Norris, 1985d:210; Scagel et al., 1989:171; Stewart, 1991:89, fig. 6; González-González et al., 1996:308.

Algae membranous, ovate to obovate blades, 4–30 cm tall, arising from a short-branched stipe; attached below by a small conical holdfast. Blades mostly reddish brown, simple or divided or torn, sometimes with secondary blades; firm in texture, margins entire; (65–)100–250(–450) µm thick. Medulla of intertwined predominately periclinally directed filaments; some medullary filaments with highly refractive contents. Cortex of 3–6 rows of cells; inner cortical cells oval, gradually becoming smaller outward; outer cortical cells slightly elongated.

Tetrasporangia cruciately divided, scattered in outer cortex over thallus. Cystocarpic and spermatangial plants unknown in Gulf material.

Habitat. Rare, attached to shells or rocks, mud-sand bottom; subtidal, 14 m depth.

Distribution. Gulf of California: Canal de Infiernillo (between Isla Tiburón and El Desemboque, Sonora); Isla San Esteban. Eastern Pacific: Alaska to Cabo Tórtolo (off south entrance to Bahía Tortugas [Bahía San Bartolomé]), Baja California Sur; Peru; Chile.

Type Locality. San Francisco Bay entrance (probably Fort Point, vicinity of Golden Gate Bridge), San Francisco, San Francisco County, northern California, USA.

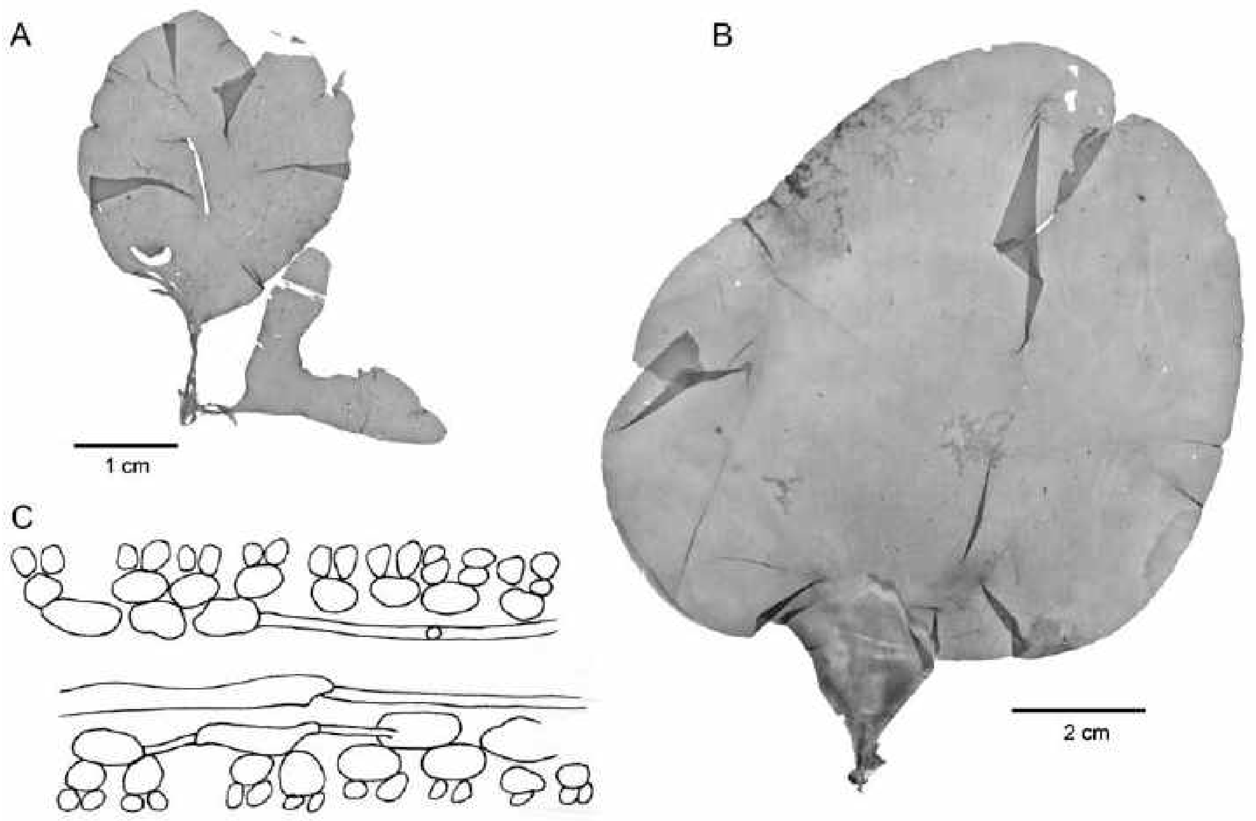


FIGURE 205. *Cryptonemia obovata*: A. Habit of small blade (*JN-4729*, US Alg. Coll.-158996). B. Habit of large blade (*EYD-21577*, US Alg. Coll.-7069). C. Diagrammatic transection of *C. obovata*.

Remarks. *Cryptonemia obovata* is generally recognized by its reddish brown color and larger and thicker blades than other *Cryptonemia* species in the Gulf.

Cryptonemia opuntioides E. Y. Dawson

FIGURE 204C

Cryptonemia opuntioides E. Y. Dawson, 1966b:59, fig. 6F; González-González et al., 1996:195; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Algae up to 1.5 cm tall, with orbicular blades originating from margins of a central blade, attached below by a small discoid holdfast. Secondary orbicular blades, up to 9 mm in diameter (shaped like *Opuntia* cactus pads); borne on short stipes from eroded or grazed margins of primary blade; blades very thin, about 50 µm thick. Medulla of a few slender, mostly periclinally directed filaments, many with dense refractive contents. Cortex mostly 2 rows of cells; inner cortex of rotund cells, up to 11 µm in diameter; outer cortex a single layer of small cells, to 7 µm in diameter.

Tetrasporophytes unknown. Cystocarps 250–275 µm in diameter, to 225 µm thick, prominently bulging on both sides of blade, scattered throughout blade. Spermatangia unknown.

Habitat. Poorly known, subtidal, 12–18 m depths.

Distribution. Gulf of California: Isla La Ventana, Bahía de Los Ángeles; Isla Salsipuedes.

Type Locality. Isla Salsipuedes, Islas de San Lorenzo (Islas de la Cintura), off Baja California, Gulf of California, Mexico.

Remarks. *Cryptonemia opuntioides* is apparently a northern Gulf endemic and restricted to the subtidal.

Cryptonemia veleroae (E. Y. Dawson) E. Y. Dawson

Kallymenia veleroae E. Y. Dawson, 1944a:285 [as "*Callymenia veleroae*"], pl. 45: fig. 1; Hernández-Kantún et al., 2010:1.

Cryptonemia veleroae (E. Y. Dawson) E. Y. Dawson, 1954c:262; 1961b:423; González-González et al., 1996:196; Silva et al., 1996b:233.

Blades up to 4 cm tall; initially simple and entire, obovate to oblanceolate, becoming split (divided) and forming additional divisions; lower portion of blades up to 8 mm wide, cuneate at the short, narrow, flattened stipe; upper portions up to 15 mm wide. Blades mostly 80–90 µm thick; medulla of longitudinal filaments, 5–6 µm in diameter, 30–65 µm long; inner cortex of 1–2 layers of periclinally elongated cells, 10–20 µm tall; outer cortex a single layer of small pigmented cells, 5–7 µm in diameter.

Tetrasporophytes unknown. Cystocarps not described. Spermatangia grouped together and separated by sterile cells in superficial sori (see Dawson, 1954c).

Habitat. Subtidal, 10–20 m depths.

Distribution. Gulf of California: Rocas Consag; Guaymas.

Type Locality. Outside Guaymas Harbor entrance, Guaymas, Sonora, Gulf of California, Mexico.

Remarks. Although poorly known, *Cryptonemia veleroae* is apparently close to *C. angustata* (Dawson, 1944a, 1954c), and later, the two were considered to be conspecific (Abbott, 1967a). Recognition of *C. veleroae* as a distinct species is problematic, primarily on the basis of differences seen in comparably sized blades: in *C. veleroae* they are deeply divided and show progressive lacerations and thicker blades (80–90 µm), whereas those of *C. angustata* are simple ovate and later divided blades with broadly lanceolate segments and are thinner (35–60 µm). For now, both taxa are recognized in the northern Gulf, until their taxonomic status can be elucidated with molecular evidence.

Grateloupia C. Agardh

Grateloupia C. Agardh, 1822:221.

Algae are erect, terete (at least basally in some), compressed or flattened, and lanceolate, linear, or foliose, above a cylindrical to compressed stipe that is attached below by a discoid holdfast. Thalli are simple, entire, lobed, or much divided or irregularly, dichotomously, subdichotomously, pinnately, or palmately branched in one or more planes. Some occasionally have proliferous branchlets. Surfaces are lubricous to leathery in texture and are usually mostly smooth, although some have short surface proliferations. Multiaxial in structure, the medulla is relatively sparse, composed of colorless filaments (mostly periclinal), sometimes with rhizoidal filaments. Some cells have long processes, called stellate or ganglionic cells, especially in the outer medulla and inner cortex. The cortex varies in thickness among the species, with an inner cortex of rounded to rotund cells and an outer cortex composed of anticlinal rows of progressively smaller cells toward the surface.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia are cruciately divided, embedded in the outer cortex, and scattered over the thallus. Gametophytes are monoecious or dioecious. Carpogonial branches and auxiliary cells are in separate accessory branch systems (ampullae). Ampullary filaments are sparingly branched, usually only to one or two orders. Auxiliary cell ampullae consist of a primary filament and one to three unbranched secondary filaments. Carpogonia are terminal on a two-celled carpogonial branch on a primary ampullar filament. After fertilization, connecting filaments develop and can fuse with a succession of auxiliary cells located in separate ampullae. A small auxiliary fusion cell is formed, and a single, outwardly directed gonimoblast initial produces a compact cystocarp of many small carposporangia, embedded within the thallus, surrounded by moderate involucres derived from both medullary and ampullary filaments. Cystocarps are usually conical in outline with a small ostiole. Spermatangial parent cells formed from surface cells and spermatangia are borne superficially in whitish sori or scattered over the blade surface.

Remarks. The species of *Grateloupia* in the Gulf of California have a firm, but slippery, lubricous texture and often are quite elastic when fresh. In the Gulf, the foliose *Grateloupia* can be distinguished from other foliose red species by their smooth or proliferous surface, slippery texture, and darker color, often iridescent, brown-mahogany, greenish purple, or deep violet. The exception to this is the very large foliose, *G. violacea,* that is a distinctive iridescent rose red when fresh.

Grateloupia species are economically important as a food (Kumari et al., 2010), producers of carrageenan (Critchley and Ohno, 1998; Critchley et al., 2006), and bioactive natural products (Wang et al., 2007). Those of the Gulf of California, such as *G. violacea*, warrant further investigations. However, once introduced into marine habitats, nonnative species of *Grateloupia* are among the most invasive (Inderjit et al., 2006). Japanese *Grateloupia turuturu* Yamada (1941; shown by Gavio and Fredericq, 2002, to be correct name for Altantic "*G. doryphora*") has been found in major shipping ports in the North Atlantic (Miller et al., 2011), most likely introduced via ship ballast waters (Villalard-Bohnsack and Harlin, 2001), hull fouling and aquaculture (Hewitt et al., 2007), and also possibly transported by boats and yachts. In the Pacific, *G. turuturu* was discovered in the port of Ensenada, Baja California, in 2008 (Aguilar-Rosas in Miller et al., 2011), and in California in 2009 at Santa Barbara Harbor (Hughey et al., 2009) and 2010 in Half Moon Bay (Miller et al., 2011). The potential introduction of nonnative *Grateloupia* could cause problems in the Gulf of California, and the ports and harbors, including those of Puerto Peñasco, Bahía San Carlos, Guaymas, La Paz, and Mazátlan, should be monitored by methods such as those given by Meinesz (2007).

The genus, *Sinotubimorpha* W.-X. Li et Z.-F. Ding (1998; generitype: *S. porracea* (Mertens ex Kützing) W.-X. Li et Z.-F. Ding; basionym: *Grateloupia porracea* Mertens ex Kützing, 1843) was distinguished from *Grateloupia* by its hollow thallus, secondary filaments in the ampullae, one- to three-celled carpogonial branches, and one- to four-celled sterile filaments on the carpogonium. Subsequently, Wang et al. (2000) and Sheng et al. (2012) found no morphological or genetic support for the separation of these genera.

With seven species, *Grateloupia* is well represented in the northern Gulf of California.

KEY TO THE SPECIES OF *GRATELOUPIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Large, long and wide, flat blades; more than 1 cm in width, mostly 3–8 cm (up to 20 cm wide); up to 30–55 (or more) cm in length; rose red to dark violet or brownish 2
1b. Fronds much narrower, less than or only up to 1(–2) cm in width; shorter, up to 12(–20) cm tall; compressed or flattened (some more or less terete in portions), more or less lanceolate or linear and much branched; red to dark red or greenish purple 3
2a. Thalli with smooth surfaces and entire margins; rose red; up to 55 cm long (largest to 230 cm), more than 5 (up to 20) cm wide . . . . ***G. violacea***
2b. Thalli surfaces and margins with numerous spine-like proliferations or short papillose branchlets; brownish mahogany to dark brownish black; up to 30 cm long, usually less than 8 cm wide . . . . ***G. howei***
3a. Axes mostly 10(–20) mm wide, branching in 1 plane, predominately and abundantly pinnate; axes surface smooth or with slender short proliferous branchlets . . . . ***G. prolongata***
3b. Axes mostly less than 5 mm wide, branching in 1 plane (distichous) or more than 1 plane (multifarious) 4
4a. Branching in more than 1 plane 5
4b. Branching in 1 plane or dichotomous to subdichotomous 6
5a. Mostly over 8 cm tall; medulla filaments very sparse and loose; central portion of medulla hollow; ultimate branchlets catenate . . . . ***G. catenata***
5b. Mostly less than 4 cm tall; medulla filaments not sparse; medulla solid (without a hollow center); ultimate branchlets not catenate . . . . ***G. hancockii***
6a. Branched dichotomous to subdichotomous; branches up to 2.5 mm wide . . . . ***G. dactylifera***
6b. Branching partly pinnate to irregular; branches up to 4 mm wide; variegated dark greenish purple, usually iridescent . . . . ***G. versicolor***

Grateloupia catenata Yendo

FIGURE 206

Grateloupia catenata Yendo, 1920:9; Wang et al., 2000:228–234, figs. 1 [lectotype], 2–19; De Clerck et al., 2005b:392, tbl. 1.

Sinotubimorpha catenata (Yendo) W.-X. Li et Z.-F. Ding in Xia, 2004:141, fig. 83, pl. 13: fig. 1.

Grateloupia filicina var. *lomentaria* M. Howe, 1924:142, pl. 1: figs. 2–4, pl. 2: figs. 1–5; Okamura, 1936:540; Dawson, 1950b:155, fig. 29; 1954c:253; 1966a:20; Dawson and Neushul, 1966:177; González-González et al., 1996:218; Mateo-Cid et al., 2006:51.

Grateloupia filicina var. *porracea* f. *lomentaria* (M. Howe) Okamura, 1936:540.

Lomentaria drouetii E. Y. Dawson, 1944a:309, pl. 46: figs. 1, 2, pl. 74: fig. 2; González-González et al., 1996:242.

Sinotubimorpha porracea sensu Li and Ding, 1998:1 [in part, Chinese specimens only; non *Sinotubimorpha porracea* (Mertens ex Kützing) W.-X. Li et Z.-F. Ding, 1998:1; which is now *Grateloupia porracea* Mertens ex Kützing, 1843:397 (type locality: West Indies)].

Grateloupia filicina sensu Dawson, 1954c:252; 1961b:422 [non *Grateloupia filicina* (J. V. Lamouroux) C. Agardh, 1822:223; basionym: *Delesseria filicina* J. V. Lamouroux, 1813:125].

Algae of 1 to several terete to compressed axes, 8–12(–20) cm tall; multifariously, or pinnately branched, 2–5 orders; arising from a small discoid holdfast. Axes mostly 1.5–2.0(–3.0) mm in diameter, with narrower branches, 700–1000 μm in diameter; ultimate branchlets short, more slender, less than 200 μm in diameter, usually with 1 or 2 constrictions (catenate proliferations), attenuated upward. Internally with a medulla of sparse, slender,

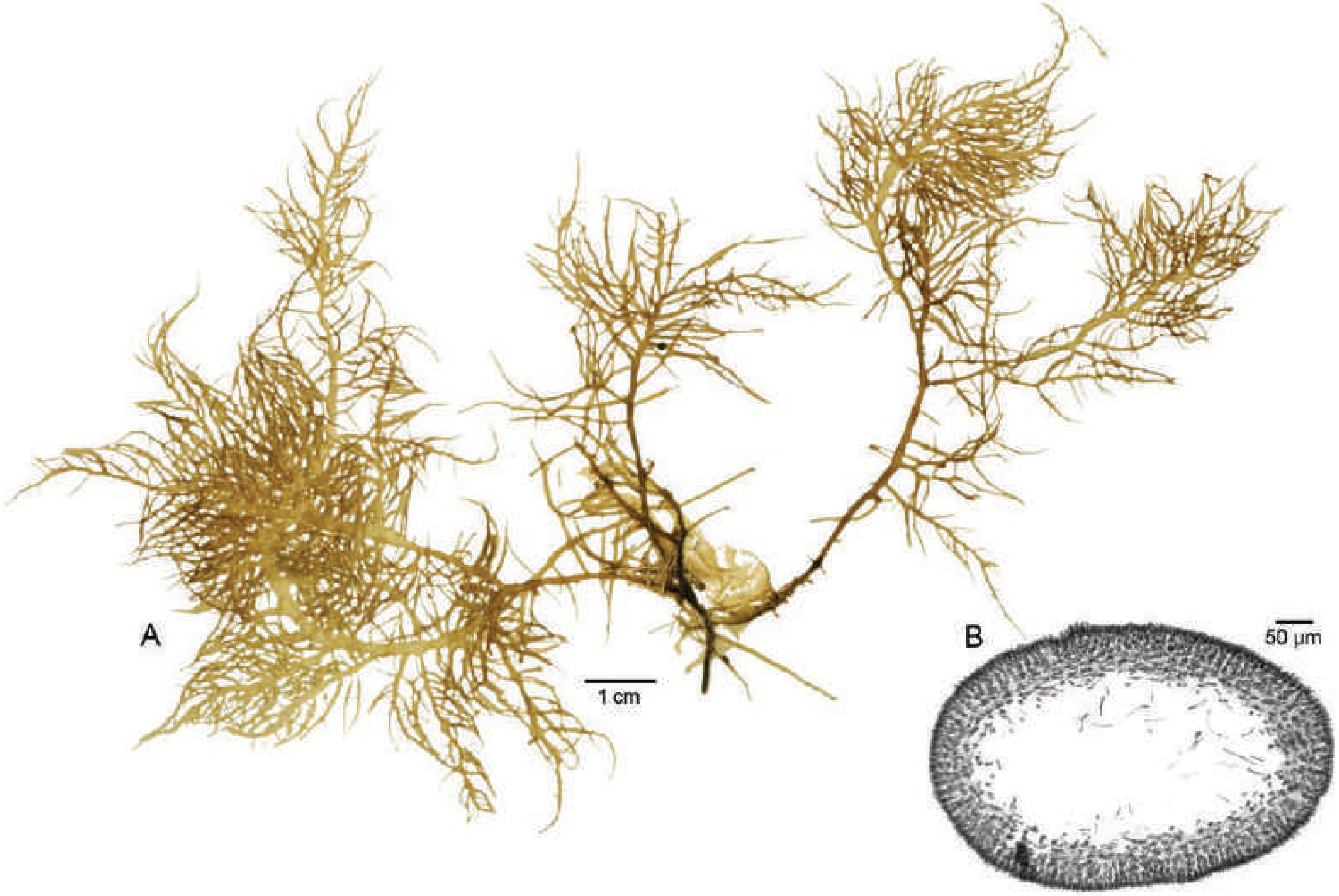


FIGURE 206. *Grateloupia catenata*: A. Habit. B. Transection of compressesd axis showing hollow medulla (center) (A, B, *JN-6058*, US Alg. Coll.-159869, microscope slide 8684).

branched filaments, 7–8 µm in diameter; inner medulla often partly or entirely hollow. Inner cortex of (1–)2 layers, sometimes partially incomplete, of more or less rotund cells; outer cortex of anticlinal rows of 2–3 smaller cells.

Tetrasporangia scattered in cortex; 35–40 µm tall, 18–20 µm in diameter. Cystocarps immersed in cortex, scattered over thallus. Spermatangia not observed in Gulf specimens.

HABITAT. On rocks and tidal platforms; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de Topolobampo; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Anacapa Island (California Channel Islands); northern Baja California. Western Pacific: China; Japan; Korea.

TYPE LOCALITY. Syntype localities of Yendo (1920:10); Japan: Honshū Island: Tsugaru and [Cape] Tappizaki, Shimofuro and Ajigasawa (Aomori Prefecture), and Fukuyama (Hiroshima Prefecture); and Hokkaidō Island (Hokkaidō Prefecture): Hokodate. Lectotype locality: Ajigasawa, Aomori Prefecture (northern Honshū Island), Japan (Wang et al., 2000: fig. 1).

REMARKS. Gulf specimens tentatively referred to *Grateloupia catenata* are in agreement with the interpretation of Dawson (1950b, 1954c), who concluded that most Gulf material closely resembled *G. filicina* var. *lomentaria* (Howe, 1924). The latter, described from China (type locality: Pei-tai-ho (Beidaihe), Hebei Province), is now considered to be a synonym of the Japanese *G. catenata* Yendo (Wang et al., 2000; De Clerck et al., 2005b).

H.-W. Wang et al. (2000) found no basis for the generic separation of *Sinotubimorpha* W.-X. Li et Z.-F. Ding (1998) from *Grateloupia*. Although *S. porracea* was considered to be conspecific with *S. catenata* (Yendo) W.-X. Li et Z.-F. Ding (in Xia, 2004), this was not supported by Wang et al. (2000), who recognized the western Pacific *G. catenata* and the western Atlantic *G. porracea* as distinct species.

The Gulf *Grateloupia catenata* also resembles *G. avalonae* E. Y. Dawson (1949b) from the California Channel Islands in habit but differs from it primarily in being centrally hollow. Morphological and molecular systematics of these taxa should clarify their taxonomic status and the identification of Gulf *G. catenata*.

Grateloupia dactylifera E. Y. Dawson

Grateloupia dactylifera E. Y. Dawson, 1954c:257, pl. 10: fig. 53; 1961b:422; González-González et al., 1996:217.

Algae solitary or in clumps, up to 4 cm tall, of 1 or more flat, branched fronds, axes up to 2.5 mm wide, 200–300 μm thick; with or without a very short stipe above a small irregularly shaped disc. Branching dichotomously to subdichotomously divaricate, up to 9 orders; widest near base, narrowing in width upward; ultimate branches somewhat "hand-like." Medulla of loose to moderately dense periclinal filaments, up to 5 μm in diameter. Inner cortex of angular to "arachnoid" cells; outer cortex of anticlinal rows of 3–4 small cells, 3–4 μm in diameter.

Tetrasporangia not known. Cystocarps 120–130 μm in diameter, embedded and bulging from either side in middle to upper portions of thallus; carposporangial mass subglobose to reniform and "pedicellate" on modified auxiliary cell; carposporangia up to 14 μm in diameter. Spermatangia unknown.

HABITAT. On rocks; mid to low intertidal.

DISTRIBUTION. Gulf of California: Ensenada de San Francisco; Bahía San Gabriél, Isla Espíritu Santo.

TYPE LOCALITY. Ensenada de San Francisco, vicinity of Guaymas, Sonora, Gulf of California, Mexico.

REMARKS. Apparently a Gulf endemic, *Grateloupia dactylifera* is known from only a few specimens. More specimens, particularly reproductive ones, are need to evaluate its taxonomic status.

Grateloupia hancockii E. Y. Dawson

FIGURE 207

Grateloupia hancockii E. Y. Dawson, 1944a:280, pl. 69: fig. 2; 1950b:155; 1954c:254, pl. 1: figs. 7, 8; 1961b:422; Dreckmann et al., 1990:30; González-González et al., 1996:218; Pacheco-Ruíz et al., 2008:207.

Algae clumps, 2–3(–7) cm tall, of several abundantly branched, mostly nonpercurrent axes arising from a small discoid holdfast. Axis compressed, narrow, to 1 mm wide, 300–400(–700) μm thick; multifariously branched throughout, mostly irregularly, but appearing pinnate, to 2–3 orders; ultimate branchlets sometimes attenuated to acute tips. Medulla of slender, branched filaments; sparse and interlaced toward center; dense and mostly longitudinally aligned, adjoining inner cortex. Cortex 7–8 cells thick; inner cortex of 1–2 layers of large cells, 12–15 μm in diameter, giving rise to anticlinal filaments of small cells, to 5 μm in diameter.

Tetrasporangia embedded in cortex and scattered over thallus. Cystocarps embedded and scattered throughout thallus. Spermatangia superficial on thallus surface.

HABITAT. On rocks; mid to low intertidal, shallow subtidal down to 1 m depth.

DISTRIBUTION. Gulf of California: Bahía La Choya (Bahía Cholla, vicinity of Puerto Peñasco) to Guaymas; Isla Estanque, off southeast end of Isla Ángel de la Guarda (Islas de la Cintura). Eastern Pacific: Michoacán.

TYPE LOCALITY. "Rocky headland about 3 miles north of Kino," Bahía Kino, Sonora, Gulf of California, Mexico (Dawson, 1944a).

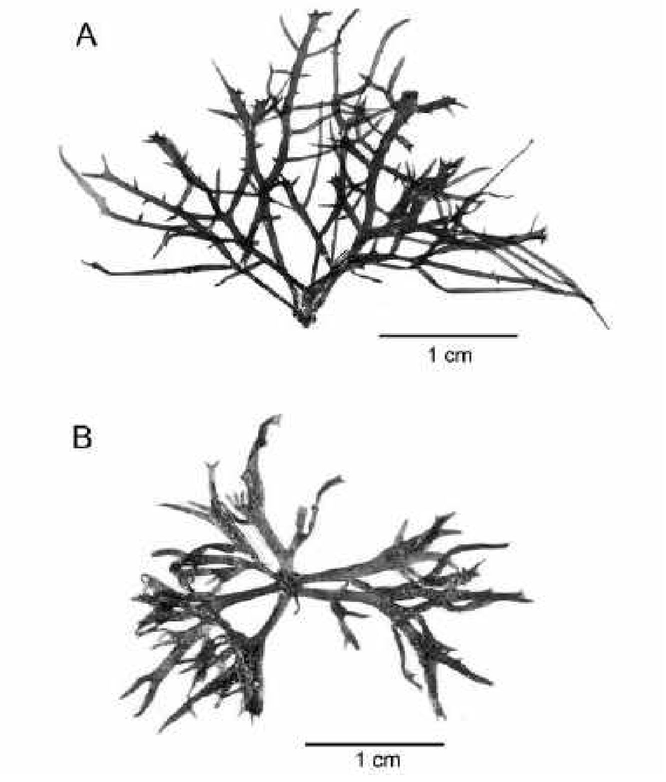


FIGURE 207. *Grateloupia hancockii*: A, B. Habit variations (A, *JN-5597*, US Alg. Coll.-159781; B, *JN-5894*, US Alg. Coll.-159782).

REMARKS. *Grateloupia hancockii* forms dark greenish red to brownish red clumps on intertidal rocks. In the northern Gulf G. *hancockii* can be distinguished from the similar-sized, clumped forms of *G. catenata* by its distinctly solid (nonhollow) medulla and stiffer branches (Dawson, 1954c). A northern Gulf species that was originally thought to be restricted in distribution to Sonora (Dawson, 1954c), *G. hancockii*'s distribution is now extended northward to Bahía La Choya (*JN-5894*, US Alg. Coll.-159782) and is also reported from the south end of Isla Estanque (Islas de la Cintura) (*JN-5597*, US Alg. Coll.-159781). Dreckmann et al. (1990) report *G. hancockii* from Michoacán, indicating its presence south of the Gulf of California in Pacific Mexico.

Grateloupia howei Setchell et N. L. Gardner

FIGURE 208

Grateloupia howei Setchell et N. L. Gardner, 1924:782 [as "*G. howeii*"], pl. 83; Dawson, 1944a:281; 1950b:153, fig. 28; 1954c:246, pl. 1: fig. 2, pl. 6: fig. 47; 1959a:6, 22; Dawson et al., 1960a:64, pl. 25: fig.1; 1960b:10; Dawson, 1961b:422; Chávez-Barrear, 1972b:269; Huerta-Múzquiz, 1978:335; Stewart and Stewart, 1984:144; Mendoza-González and Mateo-Cid, 1992:17; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid et al., 1993:47; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:106; González-González et al.,

FIGURE 208. Habits of *Grateloupia howei*: A. Mature thallus with numerous spinose papillae on surface and margins, and proliferous bladelets along margins (*JN-5519*, US Alg. Coll.-159785). B. Juvenile thallus (*JN-5920*, US Alg. Coll.-159790).

1996:218, 354: fig. 33; Riosmena-Rodriguez et al., 1998:27; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Gigartina eatoniana sensu Dawson, 1944a:301 [not *Gigartina eatoniana* J. Agardh, 1899:15].

Thalli of 1 to several complanate blades, lubricous in texture, up to 30 cm tall; arising from a discoid holdfast. Blades simple, divided, or pinnately branched; 450–800 μm thick; margins usually with proliferous bladelets; surface covered in varying degrees with few to numerous short papillate and spinose outgrowths. Medulla a loose network of slender, branched filaments, 2.5–3.0 μm in diameter. Cortex of 8–10 cell layers; the outer 4–5 cells small and in anticlinal filaments.

Tetrasporangia 32–40 μm long, 9–14 μm in diameter, embedded in cortex and scattered over upper portions of blades. Cystocarps embedded and slightly raising thallus surface, scattered over blade and appearing as minute warts among spinose outgrowths. Spermatangia superficial on blade surface.

Habitat. On rocks, low intertidal to shallow subtidal, down to 15 m depths.

Distribution. Gulf of California: Puerto Lobos to Roca El Solitario (off northern Bahía Agua Verde); Isla San Pedro Mártir; Isla San Esteban; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Isla Guadalupe; Isla Cedros; Isla San Benito; Punta María, Baja California, to Todos Santos, Baja California Sur; Guerrero.

Type Locality. Isla San Esteban (Islas de la Cintura), Gulf of California, Mexico.

Remarks. Variable in size and shape, some specimens of *Grateloupia howei* superficially may look "*Chondracanthus*-like." In the field, blades of *G. howei* can be distinguished from *Chondracanthus* by their lubricous texture, mahogany (brownish reddish) color, and short proliferations on both surfaces and margins of the blades.

Grateloupia prolongata J. Agardh

FIGURE 209

Grateloupia prolongata J. Agardh, 1847:10; Kützing, 1867:7, pl. 24: figs. a,b; Setchell and Gardner, 1924:780, pl. 80; Dawson, 1944a:279; 1945b:24; 1954c:248, pl. 7: fig. 49; 1959a:10, 22; 1961b:422; Abbott and Hollenberg, 1976:435, fig. 385; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 76; Stewart, 1991:91; R. Aguilar-Rosas and Aguilar-Rosas, 1994:521; González-González et al., 1996:218; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467; López et al., 2004:11; Xia, 2004:125, fig. 72 (1–6), pl. 12: fig. 2; Hernández-Herrera et al., 2005:147; Pacheco-Ruíz et al., 2008:207.

Grateloupia prolongata Liebmann ex Kützing, 1849:730, *nom. illeg.* [later homonym].

Algae of compressed to flattened, ligulate fronds, up to 20(–50) cm long, expanding above a stipitate portion from cuneate lower portion; upward to 1–2(–3) cm in width; 250–400 μm thick; arising from a small discoid holdfast. Frond margins usually with numerous, pinnate lateral branchlets, narrow (less than 10 mm) and up to 15 cm long; these often with abundant secondary pinnate bladelets. Blade surfaces smooth or sometimes with scattered, short, slender proliferations. Medulla of loose slender filaments; sometimes very sparse. Inner cortex of 1–2 layers of large cells adjoining an outer cortex of small pigmented cells in anticlinal rows, 5–6 cells in length.

Tetrasporangia embedded in cortex and scattered over thallus. Mature tetrasporangia 40–50 μm long, 10–15 μm in diameter, among somewhat elongate cortical cells. Cystocarps embedded, slightly bulging, and scattered over thallus. Spermatangia unknown in Gulf material.

Habitat. On rocks; low intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Lobos to Guaymas; Isla San Pedro Nolasco; Bahía de Los Ángeles to Bahía de Loreto. Eastern Pacific: Goleta, southern California to Salina Cruz, Oaxaca. Western Pacific: China.

Type Locality. In describing *Grateloupia prolongata,* J. Agardh (1847:10) gave the locale as "Pochetti"; Dawson (1954c) later listed this locality with the added comment "probably on the coast of Oaxaca." Kützing (1849:730) stated the locale as "Guatulco (Mexico)," probably Huatulco, Oaxaca. De Clerck et al. (2005b:392) gave the locale as "Pochutla" (Oaxaca), Pacific Mexico (note that Pochutla is Spanish for the place of pochotes; pochote is the Spanish name for the Mexican tree species of *Ceiba* [Malvaceae]).

Grateloupia versicolor (J. Agardh) J. Agardh

FIGURE 210

Grateloupia sternbergii var. *versicolor* J. Agardh, 1847:10.

Grateloupia versicolor (J. Agardh) J. Agardh, 1851:181; De Toni, 1905:1565; Dawson, 1954c:256, pl. 6, fig. 48; 1959a:7, 22; 1961b:422; 1961c:423, pl. 20: fig. 3; 1962b:208, fig. 101; 1966a:20; 1966b:59; Huerta-Múzquiz, 1978:338; Mendoza-González and Mateo-Cid, 1986:423 [with a query]; Salcedo-Martínez et al., 1988:83; González-González et al., 1996:219; Ramírez and Santelices, 1991:234; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:17; Serviere-Zaragoza et al., 1993a:483; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:47; Stout and Dreckmann, 1993:10; Mateo-Cid and Mendoza-González, 1994b:39; Mendoza-González et al., 1994:106; Mateo-Cid et al., 2000:64; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; López et al., 2004:11; Mateo-Cid et al., 2006:51; Serviere-Zaragoza et al., 2007:10; Gabrielson, 2008:94–96, fig. 3 [type of *Grateloupia versicolor*]; Pacheco-Ruíz et al., 2008:207; Fernández-García et al., 2011:62.

Grateloupia filicina sensu Taylor, 1945:204 [non *Grateloupia filicina* (J. V. Lamouroux) C. Agardh, 1822:223; see Dawson, 1954c:253].

Prionitis sternbergii sensu Kylin, 1941:10 [in part], pl. 2: figs. 6, 7; Dawson, 1944a:282 [non *Prionitis sternbergii* (C. Agardh) J. Agardh, 1851:190; basionym: *Sphaerococcus sternbergii* C. Agardh, 1822:275; see Dawson, 1954a:256; Gabrielson, 2008:95].

Thalli of several erect narrow, compressed, branched fronds, up to 4.5 cm tall; dull purple to purple-green; arising from a discoid holdfast. Axes up to 4 mm wide; 300–500 μm thick; branched pinnately, subdichotomously, or irregularly, up to 4(–5) orders. Branches lanceolate, usually with short, lateral branchlets. Medulla dense, of branched filaments, mostly periclinally

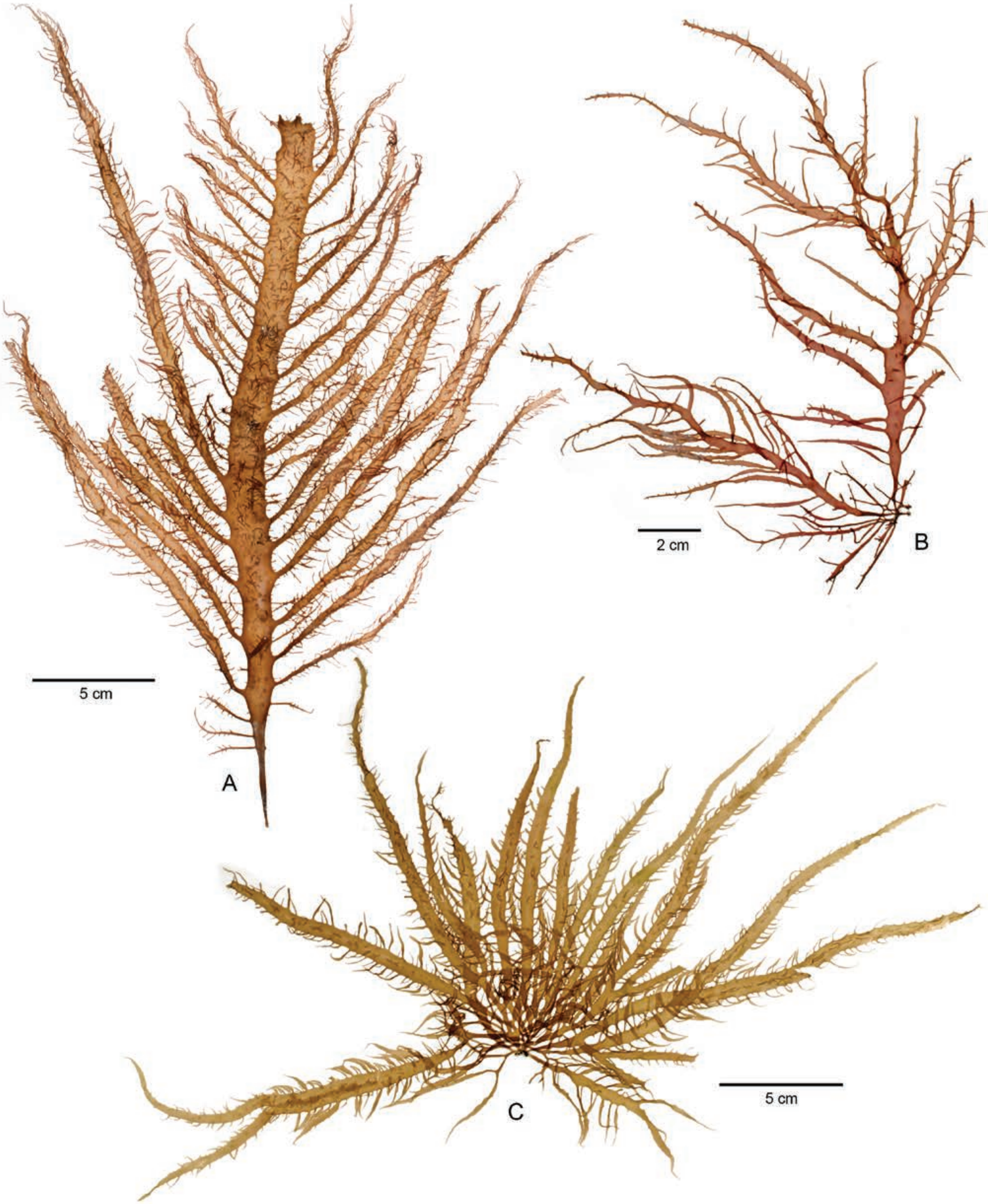


FIGURE 209. Habit variation in *Grateloupia prolongata.* A. *JN-5167*, US Alg. Coll.-159794. B. *JN-5351*, US Alg. Coll.-159796. C. *JN-5898*, US Alg. Coll.-159804.

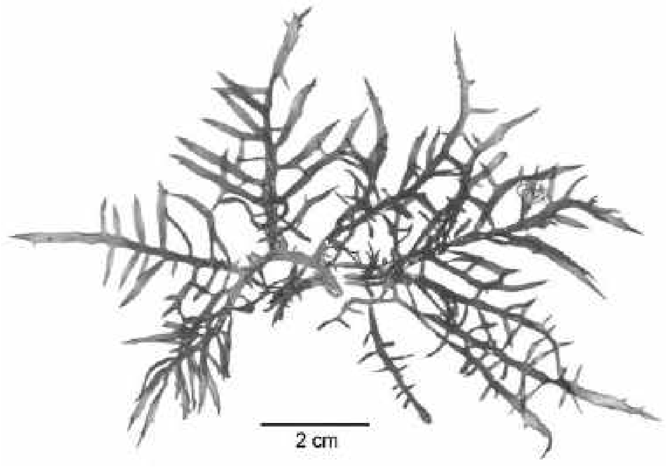


FIGURE 210. *Grateloupia versicolor*: Habit (*JN-5720*, US Alg. Coll.-159814).

aligned near the center; outer medulla of inflated stellate cells, grading into cortex of anticlinal filaments of 4–5 small cells.

Tetrasporangia 30–35 µm long, 10–12 µm wide, embedded in cortex and scattered over thallus surface. Cystocarps embedded and more or less aggregated or scattered over upper branch surfaces. Spermatangia not observed.

Habitat. On rocks or hard substrata, tidal platforms, and tidal pools; mid to low intertidal.

Distribution. Gulf of California: Puerto Peñasco to Bahía San Francisquito; Bahía Concepción to Cabeza Ballena; Mazatlán, Sinaloa to Jalisco. Eastern Pacific: Isla Magdalena (Bahía Magdalena) to Todos Santos, Baja California Sur; Isla San Benedicto (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador; Chile. Western Pacific: China.

Type Locality. "St. Augustín in littore Mexicano Oceani Pacifici, Liebman" (J. Agardh, 1851); "St. Augustín, probably Oaxaca" (Dawson, 1954c), which is San Agustín, Bahías de Huatulco, Oaxaca, Pacific Mexico.

Remarks. A variety, *Grateloupia versicolor* var. *prostrata* E. Y. Dawson (1954a), was described from Isla San Benedicto (Islas Revillagigedo) and has been reported elsewhere in Pacific Mexico (Dawson, 1957a; Chávez-Barrear, 1972b; Huerta-Múzquiz and Garza-Barrientos, 1975) and El Salvador (Dawson, 1961c).

Grateloupia violacea (Setchell et N. L. Gardner) E. Y. Dawson

FIGURE 211

Schizymenia violacea Setchell et N. L. Gardner, 1924:786, pl. 25: figs. 37, 38, pl. 87.

Grateloupia violacea (Setchell et N. L. Gardner) E. Y. Dawson, 1961a:200, pl. 8; 1961b:422; Norris, 1973:10; González-González et al., 1996:219; Pacheco-Ruíz and Zertuche-González, 2002:467; Pacheco-Ruíz et al., 2008:207.

Schizymenia johnstonii Setchell et N. L. Gardner, 1924:786, pl. 88; Dawson, 1944a:287.

Thalli of 1 or more membranous blades, rose red, slippery in texture, up to 230 cm long and up to 80 cm wide, arising above a short stipe; attached below by a small discoid holdfast. Blades broadly lanceolate to broadly ovate; 150–400 µm thick; simple, entire, or sometimes deeply cleft, occasionally lacerated or eroded; with undulate margins. Broad medulla of loosely interwoven slender filaments. Cortex relatively thin, of anticlinal filaments composed of 3–4 small ovoid cells.

Tetrasporangia cruciately divided, ellipsoidal, 28–32 µm long, 14–16 µm in diameter; scattered over blade surfaces above basal portion. Cystocarps embedded and bulging out from blade surface, nonostiolate; scattered over blade; carposporangial mass 100–160 µm in diameter. Spermatangia unknown.

Habitat. On rocks; subtidal, 5–15 m depths.

Distribution. Gulf of California: Isla Patos (off north end of Isla Tiburón) to Bahía San Francisquito.

Type Locality. Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

Remarks. *Grateloupia violacea* is a Gulf endemic, apparently restricted to the central Gulf. Recent collections suggest that *G. violacea* is an annual or perhaps a perennial with a persistent holdfast. Although occasional in distribution, where found, *G. violacea* can be abundant, reaching its largest sizes and population numbers in late spring.

Uncertain Record:
***Grateloupia abreviata* Kylin**

Grateloupia abreviata Kylin, 1941:10; Mendoza-González and Mateo-Cid, 1986:423 [with query].

Remarks. *Grateloupia abreviata* is generally considered to be conspecific with *G. doryphora* (Montagne) M. Howe (1914), e.g., by Abbott and Hollenberg (1976), but others have recognized it in Pacific Mexico from Michoacán (Dreckmann et al., 1990). Its reported presence in the northern Gulf of California by Mendoza-González and Mateo-Cid (1986, with a query) needs to be verified.

Uncertain Record:
***Norrissia setchellii* (Kylin) Balakrishnan**

Grateloupia setchellii Kylin, 1941:10; Mendoza-González and Mateo-Cid, 1986:432.

Norrissia setchellii (Kylin) Balakrishnan, 1980:284.

Remarks. Specimens of *Norrissia setchellii* from Segundo Cerro Prieta, Bahía Kino (Mendoza-González and Mateo-Cid, 1986, as "*Grateloupia setchellii*") need further study to verify its presence in the northern Gulf of California.

Halymenia C. Agardh

Halymenia C. Agardh, 1817:xix.

Algae are erect, usually lubricous, with one or more simple, lobed or dichotomously to irregularly branched fronds, attached by a discoid holdfast. Multiaxial in structure, the medulla is

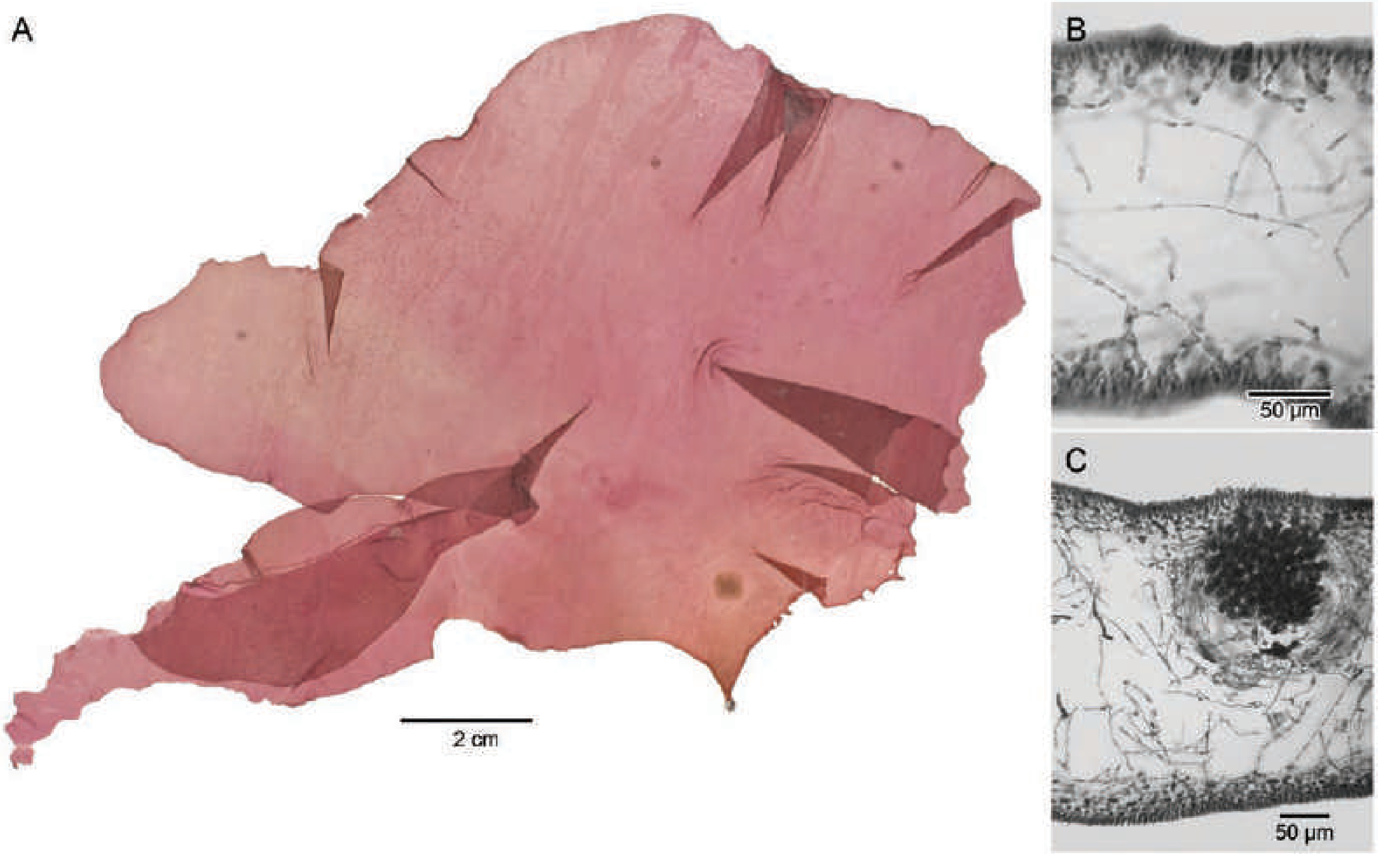


FIGURE 211. *Grateloupia violacea*: A. Habit (*JN-3053*, US Alg. Coll.-159831). B. Transection showing a relatively wide medulla of sparse, irregularly oriented filaments, and a thin cortex, bearing a tetrasporangium (*JN-3053-III*, US Alg. Coll. microscope slide 4332). C. Transection through a cystocarp showing the basal fusion cell and involucres derived from medullary and ampullary filaments (*JN-3053-IX*, US Alg. Coll. microscope slide 4521).

composed of loosely interwoven slender filaments, with a number of anticlinally directed filaments from one side of the cortex to the other and also some periclinally oriented filaments. Filaments may radiate from stellate or refractive (deeply staining) ganglionic cells in the outer medulla and inner cortex. The cortex is relatively thin (three to six cells) and consists of large subcortical cells, becoming progressively smaller to an outer layer of small cells.

Tetrasporangia are cruciately divided, embedded in the outer cortex, and scattered over the thallus surface. Gametophytes are monoecious or dioecious. Carpogonial branches and auxiliary cells are borne singly on separate branch systems, both surrounded by ampullary filaments that arise from inner cortical cells. The carposporophyte has an auxiliary cell that remains distinct at its base and is surrounded by a loose network of slender involucres branching to the third order, derived from elongation and expansion of the ampullary filaments (without contribution from medullary filaments), and an ostiole is usually present. Cystocarps are embedded and scattered over the thallus. Spermatangia are borne in whitish sori at the cortical layer surface.

Currently, *Halymenia* is represented by five species in the northern Gulf of California.

KEY TO THE SPECIES OF *HALYMENIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli composed of several stipitate, linear to lanceolate blades; simple or 1–2 times dichotomously branched; with acute or bifurcate apices; generally less than 1.5 cm wide . . . . ***H. bifida***
1b. Thalli obovate to broadly lanceolate foliose blades; not dichotomously branched; greater than 1.5 cm wide (wider than the above species) 2

2a. Thalli of several broadly lanceolate, sometimes falcate blades; cystocarps with prominent ostiole; blades 400–500 µm thick and tall (20 cm or more) . . . . *H. californica*
2b. Blades obovate to broadly lanceolate or elliptical, orbicular, or reniform; cystocarps with inconspicuous ostioles; blades thinner, less than 400 µm thick, and typically less than 20 cm tall 3
3a. Blades obovate to lanceolate . . . . *H. gardneri*
3b. Blades elliptical, orbicular (wider than tall), or reniform 4
4a. Blades nearly sessile (only a very short "peg" to attachment disc); blades broader than tall; carposporangia large, 20–30 µm in diameter . . . . *H. megaspora*
4b. Blades above a short stipe; carposporangia smaller, 9–12 µm in diameter . . . . *H. actinophysa*

Halymenia actinophysa M. Howe

FIGURE 212

Halymenia actinophysa M. Howe, 1911:509, pl. 34; Dawson, 1944a:277; Taylor, 1945:206 [in part]; Dawson, 1954c [in part]:273, pl. 4: figs. 29–34, pl. 15: figs. 59, 60, pl. 16: fig. 61; 1961b:423; 1966a:20; Abbott, 1967a:144; L. Aguilar-Rosas et al., 2000:130; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:55; Pacheco-Ruíz et al., 2008:207; Hernández-Kantún et al., 2009:248, figs. 1–12, tbls. 1–3; Bernecker, 2009:CD-Rom p. 63; Fernández-García et al., 2011:62.

Sebdenia actinophysa (M. Howe) Soler-Onís in de Jong, 1998:114, *nom. illeg.*; Serviere-Zaragoza et al., 2007:11; Littler and Littler, 2010.

Halymenia refugiensis E. Y. Dawson, 1944a:278 [with a generic query], pl. 44: figs. 2, 3; Littler and Littler, 2010; Fernández-García et al., 2011:62.

Algae of 1 or more membranous, usually lubricous blades, light to dull rose red in color, arising from a small stipe; attached by a small discoid holdfast. Blades elliptical or irregularly orbicular, 4–12(–30) cm tall, 4–10(–20) cm wide; (50–)150–300 µm thick in transection; margins simple or sinuate or irregularly dentate or lacerate. Medulla of anticlinal, sparingly branched filaments, occasionally with a few irregularly placed periclinal filaments. Medullary filaments, 7–19(–24) µm in diameter, 135–240 µm long, arising from capituliform (stellate) cells of the subcortical layer. Ganglioid (stellate) cells with dense refractive contents. Inner cortex of spherical cells, 8–15 µm in diameter; subcortex of capituliform ("stellate") cells with up to 8 stout filamentous arms radiating out. Outer cortex thin, of 1–2 cell layers; outermost cells 5–8 µm in diameter.

Tetrasporangia cruciately divided, ovoid to subspherical, 9–14 µm in diameter; embedded in outer cortex, scattered over blade. Gonimoblast is "pedicellate" on elongated auxiliary cell. Cystocarps 100–180 µm in diameter, embedded and scattered over thallus; carposporangia 6–12 µm in diameter, in a compact, subspherical mass, surrounded by slender involucral filaments derived from elongated ampullary filament cells, inconspicuously ostiolate. Spermatangia developed by division of outer cortical cells.

HABITAT. Occasional on rocks; subtidal, down to 25 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to La Paz. Eastern Pacific: Isla Clarión and Isla Socorro (Islas Revillagigedo); Costa Rica; Panama. Central Pacific: Hawaiian Islands (Abbott, 1999).

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. The internal structure of Gulf *Halymenia actinophysa*, seen in transection, has characteristic large, subcortical capituliform cells ("arachnoid" or "stellate ganglia" of Dawson, 1954c, and "mace-like" of Abbott, 1999).

There has been a difference of opinion as to the generic placement of *Halymenia actinophysa*. Soler-Onís (in [de] Jong, 1998:114) proposed the transfer of *H. actinophysa* to *Sebdenia,* but since the basionym was not cited, that combination was invalid. However, recent morphological studies of Hernández-Kantún et al. (2009) of *Halymenia actinophysa* collected in the vicinity of La Paz (type locality) included reproductive specimens that revealed characteristics that confirm it should be included in *Halymenia*. Smaller, thicker specimens of *H. actinophysa* (4–10 cm tall, 4–9 cm wide, and 150–300 µm thick) from the southern Gulf were elucidated by Hernández-Kantún et al. (2009). Larger and thinner specimens (up to 30 cm tall, to 20 cm wide, and 70–130(–220) µm thick) that were referred to *H. actinophysa* by Dawson (1954c) and Norris (1975, US Alg. Coll.) should be morphologically and molecularly reinvestigated to work out their taxonomic status. Their difference in thickness could represent phenotypic or habitat variation or could be an artifact of air-drying and pressing versus freshly collected or liquid-preserved specimens or could possibly reflect differences in different parts of the blades where sections were made or may possibly represent another taxon.

Another species also described from the Gulf of California, *Halymenia refugiensis* E. Y. Dawson (1944a), was considered to be conspecific with *H. actinophysa* by Dawson (1954c; Abbott, 1967a). More recently, Littler and Littler (2010) recognized *H. refugiensis* as a distinct species when reporting it from Pacific Panama. The taxonomic status of northern Gulf *H. refugiensis* (type locality: Puerto Refugio, Isla Ángel de la Guarda) should be reinvestigated and tested in comparisons with the southern Gulf *H. actinophysa.*

Halymenia bifida E. Y. Dawson

Halymenia bifida E. Y. Dawson, 1954c:269, pl. 2, figs. 19–21, pl. 12, fig. 56; 1961b:423; 1966a:27; 1966b:59; Mateo-Cid et al., 2006:52; Hernández-Kantún et al., 2009:249, 253: tbls. 1, 3.

Algae composed of several lanceolate, membranous stipitate blades, up to 8 cm tall, 4–13 mm wide, simple or dichotomously branched once or twice, 150–260 µm thick; arising from a short, slender, compressed, simple or branched stipe; attached by a small discoid holdfast. Blade margins entire

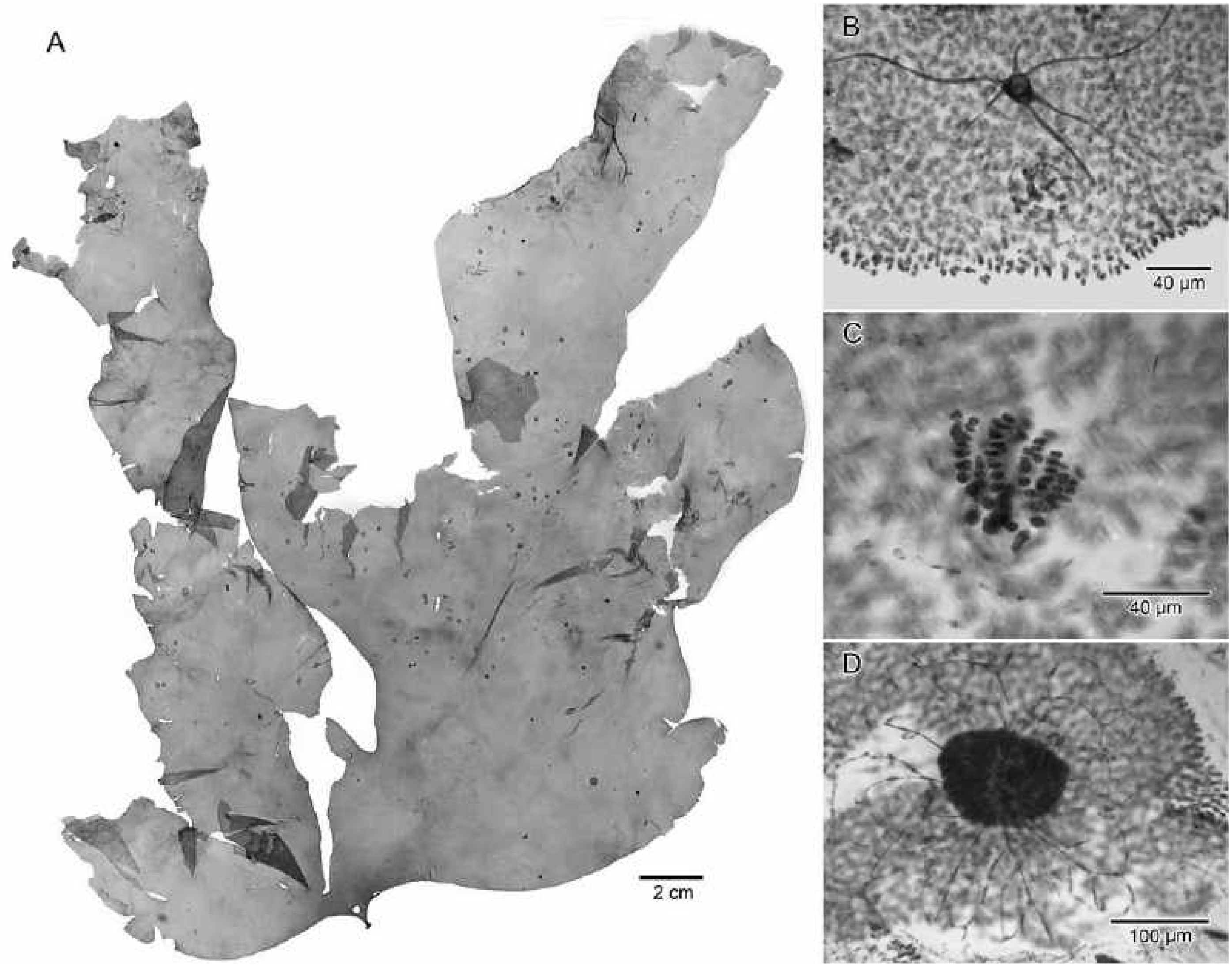


FIGURE 212. *Halymenia actinophysa*: A. Habit (*JN-5137*, US Alg. Coll.-159936). B–D. Squash preparations of female gametophyte: B. Ganglionic cell and developing ampulla. C. Young ampulla. D. Elongated ampullary filaments around carposporophyte (B–D, *JN-4501c*, US Alg. Coll. microscope slide 4399).

or occasionally sparsely beset with short pinnate bladelets, 1–2 mm long; apices acute, usually bifurcate; lowermost portion cuneate above stipe. Medulla of sparse, branched filaments (4–5 µm in diameter), irregularly and loosely cross from one side to the other, with some stellate or arachnoid cells adjoining the subcortex. Inner cortex of 2 layers of large, rotund cells, 9–16 µm in diameter. Outer cortex 1 layer of ovoid cells, 5–7 µm in diameter.

Tetrasporangia cruciately divided, ovoid, 15–18 µm long; borne in cortex, scattered over blade surfaces. Cystocarps 100–150 µm in diameter, surrounded by a loose network of involucres derived from elongation of the ampullary filament cells, embedded and scattered over thallus. Spermatangia unknown.

HABITAT. On rocks, lowermost intertidal to subtidal; dredged from 8–19 m depths.

DISTRIBUTION. Gulf of California: Punta Pelícano (vicinity of Puerto Peñasco); Punta Los Frailes; Bahía de San Lucas.

TYPE LOCALITY. Punta Los Frailes, Baja California Sur, Gulf of California, Mexico.

Halymenia californica G. M. Smith et Hollenberg

Halymenia californica G. M. Smith et Hollenberg, 1943:216, figs. 18, 19; Smith, 1944:243, pl. 54: fig.6, pl. 55: fig. 4; Dawson, 1954c:270, pl. 13: fig. 57; 1961b:423; Hollenberg and Abbott, 1966:70; Abbott, 1967a:140, fig. 13; Abbott and Hollenberg, 1976:425, fig. 378; L. Aguilar-Rosas, 1981:93; Anaya-Reyna and Riosmena-

Rodríguez, 1996:864, tbl. 1; CONANP, 2002:140; Hernández-Kantún et al., 2009:249, 253: tbls. 1, 3; Fernández-García et al., 2011:62.

Halymenia abyssicola E. Y. Dawson, 1944a:278 [with generic query]; 1954c:271, pl. 3: figs. 22–25; 1961b:423; Fernández-García et al., 2011:62.

Halymenia actinophysa sensu Dawson, 1954c:273 [in part; non *Halymenia actinophysa* M. Howe, 1911:509].

Thalli of usually 1 (rarely more) membranous blade, up to 30 cm tall, to 18 cm wide; dark rose red in color; arising from a short, broad stipe; attached by a discoid holdfast. Blades broadly lanceolate, sometimes falcate, 400–500 µm thick; margins entire; base cuneate. Medulla traversed by many slender anticlinal filaments from one side to the other and also contains some loosely arranged periclinal filaments (2–4 µm in diameter). Outer cortex of branched anticlinal filaments, 3–4 cells long; inner cortex and outer medulla of 2–4 layers of periclinal irregularly shaped filaments.

Tetrasporangia cruciately divided, elongate, 22–25 µm long, 12–14 µm in diameter; borne in cortex, scattered over thallus surface. Cystocarps hemispherical, ostiolate; scattered throughout blade. Spermatangia unknown in Gulf material.

Habitat. On rocks; subtidal, 5–30 m depths.

Distribution. Gulf of California: Isla San Esteban; Isla Tiburón; Bahía de Loreto to Isla Partida (off north end of Isla Espíritu Santo); Cabo Pulmo to Punta Los Frailes. Eastern Pacific: northern British Columbia to central Baja California; Panama.

Type Locality. Moss Beach, San Mateo County, central California, USA.

Remarks. In the Gulf of California, *Halymenia californica* is found in the northern Gulf from Islas de la Cintura and in the southern Gulf from Isla Partida (off north end of Isla Espíritu Santo) to Punta Los Frailes.

Halymenia gardneri (Kylin) P. G. Parkinson

Aeodes gardneri Kylin, 1925:17, fig. 7a; Smith, 1944:241, pl. 54: figs. 4, 5.

Halymenia gardneri (Kylin) P. G. Parkinson, 1980:12; Lindstrom, 1986:532; Scagel et al., 1989:192; Stewart, 1991:92; Spalding et al., 2003:277; Pacheco-Ruíz et al., 2008:208.

Algae foliose, of 1 or more obovate to lanceolate, usually undivided, blades, bright cherry red in color, central California sizes up to 50 cm tall and to 25 cm wide (Smith, 1944; note that sizes were not reported for northern Gulf specimens by Pacheco-Ruíz et al., 2008); arising above a discoid holdfast. Medulla of interwoven filaments. Cortex of 3–6 layers of similar-sized cells.

Reproductive structures not reported for northern Gulf material. In California specimens, cystocarps loosely surrounded by a few sterile filaments, ostiolate (after Kylin, 1925; Smith, 1944, 1969).

Habitat. On rocks; subtidal.

Distribution. Gulf of California: Bahía de Los Ángeles. Eastern Pacific: southern British Columbia to southern California.

Type Locality. Whidbey Island ("Whidby"), Island County, Puget Sound, Washington, USA.

Remarks. *Halymenia gardneri* has been reported from Bahía de Los Ángeles by Pacheco-Ruíz et al. (2008). Since I have not seen their specimens, the description of the species is based on Smith (1944).

Halymenia megaspora E. Y. Dawson

FIGURE 213

Halymenia megaspora E. Y. Dawson, 1954c:272, pl. 3: figs. 26 [type specimen], 27, 28, pl. 14: fig. 58; Dawson, 1961b:423; González-González et al., 1996:223; Hernández-Kantún et al., 2009:249, 253: tbls. 1, 3.

Blades irregularly orbicular to reniform, membranous, lubricous, 10–15 cm high (wider than tall), 200–400 µm thick; lobed or lacerate; with smooth margins; cuneate in lower portion to a short stipe; attached below by a small discoid holdfast. Medulla sparse, of irregular, more or less anticlinal filaments (in transection, mostly from one side to the other); medullary filaments 6–7 µm in diameter, 150–163 µm long. Some stellate cells connected by periclinal filaments occur in the subcortex. Cortex of 3–4 layers of ovoid cells, 9–10 µm in diameter; outermost cortical cells slightly elongated, 10–12 µm long, 9–10 µm in diameter.

Tetrasporangia unknown. Cystocarps 100–150 µm in diameter, scattered over blade; carposporangia large, 20–30 µm in diameter (longer than wide), not angular, in a loose mass. Spermatangia unknown.

Habitat. On rock and sand bottom; subtidal, from 8.0 to 18 m depths.

Distribution. Gulf of California: Canal de San Lorenzo (off southern end of Isla Espíritu Santo) to Bahía Los Frailes.

Type Locality. Rock-sand bottom, 8–15 m depths; Bahía Los Frailes (south side of Punta Los Frailes), Baja California Sur, Gulf of California, Mexico.

Remarks. *Halymenia megaspora* was described with its blade as "almost sessile" above a small fleshy peg and discoid attachment (Dawson, 1954c). Later Hernández-Kantún et al. (2009) in referring to this species, noted the base was cuneate above a short stipe. *Halymenia megaspora* is known in the southern Gulf, but it likely may be found in subtidal collections elsewhere in the Gulf. Although it was included as a synonym of *W. templetonii* (Abbott, 1967a, as "*Halymenia templetonii*"), it is currently considered a separate species. The type of *H. megaspora* E. Y. Dawson and additional collections are needed for critical study to clarify its taxonomic status.

Prionitis J. Agardh

Prionitis J. Agardh, 1851:185.

Algae are erect and cartilaginous, with one or more axes that are terete throughout, or terete to slightly compressed in the lowermost portions and become compressed to flattened upward. These axes are pinnately, dichotomously, or irregularly branched often from the margins, and attached by a discoid holdfast. Branches are compressed or flat and can rebranch, often

FIGURE 213. *Halymenia megaspora*: Habit (paratype: *EYD-6904A*, US Alg. Coll.-206130).

with a few to numerous proliferous branchlets. The medulla is composed of tightly interwoven periclinal filaments. The cortex is composed of dense, compacted cells, which become progressively smaller toward the thallus surface or have an abrupt size difference between the inner and outer cells.

Tetrasporangia are cruciately divided, scattered and embedded beneath the surface or borne in nemathecia. Carpogonial branches and auxiliary cells are formed singly in separate clusters of filaments (ampullae). Cystocarps are embedded in the thallus, surrounded by slender filaments, and have a carpostome. Spermatangia are borne in whitish sori on flattened branch surfaces.

Remarks. Wang et al. (2001) suggested that *Prionitis* was congeneric with *Grateloupia*. Whereas their analyses included the generitype, *Prionitis lanceolata* (Harvey) Harvey (1853; basionym: *Gelidium lanceolata* Harvey in Hooker and Arnott, 1833), their California specimens were from Pigeon Point, San Mateo County, not from the type locality (Monterey, Monterey County; Silva, 1979). [Note: if accepted, the name would be *Grateloupia americana* Kawaguchi et H.-W. Wang (in Wang et al., 2001) to avoid being a homonym of *G. lanceolata* (Okamura) Kawaguchi (1997).] However, Gabrielson (2008) considered the proposed generic merger premature until morphological and molecular studies of *Prionitis* species from the Gulf of California, the Southeast Pacific, and eastern tropical Pacific can be completed. He also noted it is likely that there is more than one genus in the circumscribed *Grateloupia* sensu lato. There have been four species of *Prionitis*, one with two varieties, recorded for the northern Gulf of California. One additional species, *Prionitis mexicana* E. Y. Dawson (1944a), occurs in the southern Gulf from Cabeza Ballena to San Jose del Cabo (type locality) and Pacific Mexico from Baja California Sur (Dawson, 1954c, 1961b).

KEY TO THE SPECIES OF *PRIONITIS* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli thin, up to 1 mm wide; branching irregular or dichotomous and irregular in mid portions 2
1b. Thalli mostly broader, 2.0–4.0 mm wide; taller; primary branching dichotomous to subdichotomous 3
2a. Thalli up to 15 cm tall; subcylindrical to compressed, axes and branches wiry, mostly less than 1mm in diameter; primary branching irregular . . . . *P. delicatula*
2b. Thalli shorter, up to 4 cm tall; compressed to flattened, axes and branches, narrow, 0.5–1.0 mm wide; branching primarily dichotomous (can become irregular in middle thallus) . . . . *P. acroidalea*
3a. Pinnate laterals on axes and branches, usually long, 10–15 mm in length . . . . *P. abbreviata* var. *guaymasensis*
3b. Pinnate laterals on axes and branches shorter, mostly less than 3 mm long 4
4a. Young branches spatulate; thalli usually 8 cm or less tall . . . . *P. abbreviata* var. *abbreviata*
4b. Young branches not spatulate; thalli taller, up to 12(–20) cm tall . . . . *P. cornea*

Prionitis abbreviata Setchell et N. L. Gardner var. *abbreviata*

FIGURE 214A

Prionitis abbreviata Setchell et N. L. Gardner, 1924:785, pl. 25: fig. 39, pl. 50b; Dawson, 1944a:283; Taylor, 1945:211; Dawson, 1959a:25; 1961b:423; 1966a:20; Norris, 1973:19; Huerta-Múzquiz, 1978:338; Ramírez, 1982:13, figs. 3, 20; Littler and Littler, 1981:tbl. 3, fig. 4; Huerta-Múzquiz and Mendoza-González, 1985:50; Ramírez and Santelices, 1991:237; González-González et al., 1996:259; Riosmena-Rodríguez et al., 1998:27; Mateo-Cid et al., 2000:64; L. Aguilar-Rosas et al., 2000:130; Cruz-Ayala et al., 2001:191; CONANP, 2002:140; Pacheco-Ruíz and Zertuche-González, 2002:467; Mateo-Cid et al., 2006:51, 55.

Zanardinula abbreviata (Setchell et N. L. Gardner) G. De Toni, 1936b:[2]; Dawson, 1954c:279, pl. 19: fig. 64, pl. 20: figs. 65,–66; González-González et al., 1996:273; Pacheco-Ruíz et al., 2008:208.

Thalli of 1 or more branched flattened fronds, to 8 cm tall, often forming loose and irregularly shaped clumps, attached below by a small discoid holdfast. Fronds linear-lanceolate, cartilaginous, dark brownish red to black; axes to 4 mm wide; 250–500 µm thick; branched irregularly, primary branches more or less dichotomous, ultimate segments spatulate with blunt apices. Secondary branching more or less pinnate and sometimes rebranched in a pinnate manner; mostly branched in 1 plane at irregular intervals along margins of primary branches. Adventitious foliar proliferations occasionally on faces of primary branches. Medulla of densely packed filaments. Cortex of inner 3 layers of rotund cells, 10–18 µm in diameter, grading into outer cortex of small cells, 3.5–5.0 µm in diameter, in anticlinal rows.

Tetrasporangia cruciately divided, 45–50 µm long, 9–12 µm wide, borne in nemathecial sori, on secondary branchlets. Cystocarps up to 250 µm in diameter, embedded, ostiolate, aggregated on secondary branchlets, often bulging out of surface. Spermatangia unknown.

Habitat. On rocks, in tide pools, along ledges and crevices in slightly shaded areas; mid to lowermost intertidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena. Eastern Pacific: Galápagos Islands; Chile.

Type Locality. Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

Remarks. Two varieties of *Prionitis abbreviata* are found in the Gulf of California. One, *P. abbreviata* var. *abbreviata*, has broader primary axes that are mostly dichotomously branched, with spatulate ultimate segments, similar to the type described by Setchell and Gardner (1924). The other variety, originally described as *P. guaymasensis* E. Y. Dawson (1944a), is *P. abbreviata* var. *guaymasensis* (E. Y. Dawson) E. Y. Dawson (1954c). This variety typically has narrower and longer,

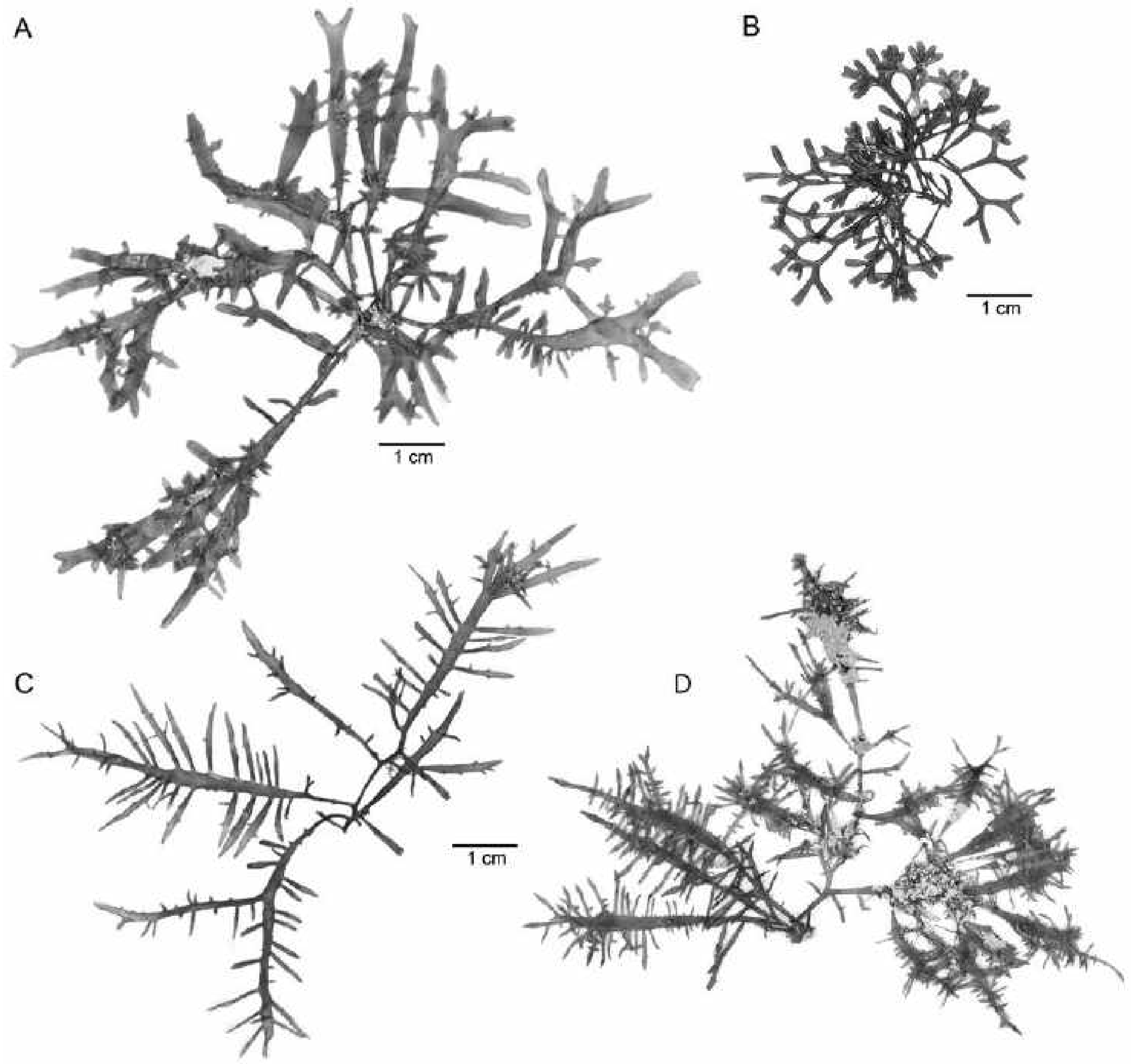


FIGURE 214. Species of *Prionitis*. A. *Prionitis abbreviata* var. *abbreviata*: Habit (JN-7059, US Alg. Coll.-160707). B. *Prionitis acroidalea*: Habit (*EYD-961*, US Alg. Coll.-12842). C, D. *Prionitis abbreviata* var. *guaymasensis*: Habit variation (C, *EYD-27341*, US Alg. Coll.-40742; D, *JN-4051*, US Alg. Coll.-160679).

more abundant pinnate secondary lateral branchlets. There are some thalli that are intermediate between these two varieties, but in agreement with Dawson (1954c) I find it useful to recognize these two rather commonly occurring, usually distinct, varieties.

Prionitis abbreviata var. *guaymasensis* (E. Y. Dawson) E. Y. Dawson

FIGURE 214C,D

Prionitis guaymasensis E. Y. Dawson, 1944a:283, pl. 66: figs. 1, 2.

Prionitis abbreviata var. *guaymasensis* (E. Y. Dawson) E. Y. Dawson, 1959a:25; 1961b:423; 1966a:20; González-González et al., 1996:259; Mateo-Cid et al., 2006:51.

Zanardinula guaymasensis (E. Y. Dawson) E. Y. Dawson, 1945e:93; González-González et al., 1996:273.

Zanardinula abbreviata var. *guaymasensis* (E. Y. Dawson) E. Y. Dawson, 1954c:279; González-González et al., 1996:273.

Thalli cartilaginous, up to 7 cm tall; a single to few erect, narrow main axes; 1.5–2.0 mm wide, occasionally divided, usually in one plane; with numerous lateral, long secondary branchlets, 5–18 mm long, 0.7–1.0 mm wide, narrowed at branch origin; with subacute apices (attenuated); thalli attached by discoid holdfast.

Habitat. On rocks, tidal platforms, and tide pools; intertidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas; Isla San Pedro Nolasco; Puerto Refugio, Isla Ángel de la Guarda.

Type Locality. Punta San Pedro, about 41 km north of Guaymas, Sonora, Gulf of California, Mexico.

Prionitis acroidalea (Setchell et N. L. Gardner) E. Y. Dawson

FIGURE 214B

Grateloupia acroidalea Setchell et N. L. Gardner, 1924:781, pl. 26: figs. 45–46; Dawson, 1944a:281.

Prionitis acroidalea (Setchell et N. L. Gardner) E. Y. Dawson, 1961a:424; Mendoza-González and Mateo-Cid, 1986:423 [with a query]; González-González et al., 1996:259.

Zanardinula acroidalea (Setchell et N. L. Gardner) E. Y. Dawson, 1954c:277, pl. 5: figs. 37–39 [from type of *Prionitis kinoensis*]; González-González et al., 1996:273.

Prionitis kinoensis E. Y. Dawson, 1944a:284, pl. 67: fig. 1; Taylor, 1945:210; Huerta-Múzquiz and Mendoza-González, 1985:50; González-González et al., 1996:260.

Zanardinula kinoensis (E. Y. Dawson) E. Y. Dawson, 1945e:94; González-González et al., 1996:273.

Algae forming short clumps, up to 4 cm tall; of few to several dark purple or greenish red compressed to flattened, cartilaginous, usually densely branched fronds; very narrow, up to 1 mm wide (more or less uniform width throughout), 280–480 μm thick; attached by a small discoid holdfast. Branching mostly dichotomous and more or less divaricate, becoming irregular in middle portions; short secondary branchlets, 1–4 mm long; apices blunt, as wide as lower portion of branch or somewhat swollen in fertile thalli. Medulla of densely interwoven, compacted filaments. Cortex with an inner cortical layer of 2–3 large cells with "intercellular connections" (Dawson, 1954c: 278, pl. 5: fig. 39, as *Zanardinula acroidalea*); outer cortical layer of anticlinal filaments composed of 5–6 small, pigmented cells.

Tetrasporangia 40–50 μm long, 8–13 μm wide, borne in nemathecial sori on secondary branchlets and terminal in branches. Cystocarps about 150 μm in diameter, ostiolate, embedded in branchlets and terminal portions. Spermatangia borne in sori, superficial on branchlets and terminal portions.

Habitat. On rocks, high to mid intertidal.

Distribution. Gulf of California: Bahía Kino to Guaymas; Isla Turner (off SE end of Isla Tiburón); Isla de Tortuga; Bahía de La Paz. Eastern Pacific: Galápagos Islands.

Type Locality. Upper intertidal; Isla de Tortuga, about 24.1 km [15 miles] northeast of Isla San Marcos, off Puerto Santa Rosalía, Baja California Sur, Gulf of California, Mexico.

Prionitis cornea (Okamura) E. Y. Dawson

Grateloupia cornea Okamura, 1913:63, pl. 118: figs. 1–11; Kawaguchi, 1989:226, figs. 22–25; Wang et al., 2001:253, figs. 1–3.

Prionitis cornea (Okamura) E. Y. Dawson, 1958:71; Dawson et al., 1960a:76, pl. 26: fig. 1; Dawson, 1961b:424; Dawson and Neushul, 1966:177; Guzmán del Proó et al., 1972; Abbott and North, 1972:76; Abbott and Hollenberg, 1976:445, fig. 395; L. Aguilar-Rosas, 1981:93; Pacheco-Ruíz and Aguilar-Rosas, 1984:72, 77; Scagel et al., 1989:244; R. Aguilar-Rosas et al., 1990:125; R. Aguilar-Rosas and Aguilar-Rosas, 1994:521; Perestenko, 1996:97, pl. 9: fig. 5; Riosmena-Rodríguez et al., 1998:27; Yoshida, 1998:729, fig. 3-57B; Schubert et al., 2006:1212, tbl. 1; Pacheco-Ruíz et al., 2008:208; Castaneda-Fernández de Lara et al., 2010:200, tbl. 1.

Carpopeltis cornea (Okamura) Okamura, 1936:553.

Zanardinula cornea (Okamura) E. Y. Dawson, 1954c:282, pl. 22: fig. 68.

Algae cartilaginous, up to 20 cm tall; of 1 or more narrow, strap-like main axes and branches, (1–)2 mm wide, more or less equal width throughout; 280–500 μm thick; primarily subdichotomously branched, up to 3–4 orders, at intervals of 1–4 cm, secondary branching pinnate, usually sparse from the margins, mostly 2–3 mm long (up to 10 mm long); apices slightly tapered; attached by spreading irregularly discoid holdfast. Medulla dense, of intertwined compact filaments, 4–10 μm in diameter; subcortex of irregular layers of rotund cells, to 25 μm in diameter, becoming progressively smaller to surface of small, pigmented cells.

Tetrasporangia cruciately divided, 30–43 μm long, 8–12 μm in diameter; in elongated elevated sori on ultimate branches. Cystocarps ostiolate, embedded within secondary branches and ultimate branchlets; carposporangial mass 130–150 μm in diameter, pedicellate above an auxiliary cell. Spermatangia not observed.

Habitat. On rocks; low intertidal.

Distribution. Gulf of California: Bahía de Los Ángeles; Mulegé. Eastern Pacific: Vancouver Island, British Columbia to Bahía Asuncíon, Baja California Sur; California Channel Islands; Islas Todos Santos (off Ensenada), Baja California. Western Pacific: Russia; China; Korea; Japan.

Type Locality. Kadzusa, Chiba Prefecture, Honshū Island, Japan.

Remarks. *Prionitis cornea* has been reported in the northern Gulf from Bahia de Los Ángeles by Pacheco-Ruíz et al. (2008). Because I have not seen their specimens, the description is after Dawson (1954c).

Prionitis delicatula (W. R. Taylor) E. Y. Dawson

Prionitis filiformis var. *delicatula* W. R. Taylor, 1945:210, pl. 66: fig. 1.

Prionitis delicatula (W. R. Taylor) E. Y. Dawson, 1961a:424; 1966a:20; 1966b:59; González-González et al., 1996:260; Mateo-Cid et al., 2006:51.

Zanardinula filiformis f. *delicatula* (W. R. Taylor) E. Y. Dawson, 1945e:94; González-González et al., 1996:273.

Zanardinula delicatula (W. R. Taylor) E. Y. Dawson, 1954c:284; González-González et al., 1996:273.

Thalli bushy in appearance, of several branched, very narrow subcylindrical to compressed, sometimes flattened, axes, up to 15 cm tall; arising from a broad, discoid holdfast. Axes wiry, cartilaginous, brown to purple-black, up to 1 mm wide, 180–300 μm thick, of more or less uniform width throughout; primary branching irregular; secondary branching more or less pinnate, branches relatively long, up to 3 cm, branching more dense in upper portions; branches tapering toward their basal portion; apices subacute. Medulla of densely packed filaments. Inner cortex of 2–3 irregular layers of rotund cells, to 12 µm in diameter; outer cortex of anticlinal rows of 3–4 small cells, to 4 µm in diameter.

Reproductive material unknown.

HABITAT. On rocks; mid intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco. Eastern Pacific: Isla San Benitos; Isla Cedros; Bahía Asuncion to Isla Magdalena (Bahía Magdalena), Baja California Sur.

TYPE LOCALITY. On rocks; Bahía Sur ("South Bay"), Isla Cedros ("Isla Cerros"), off Baja California, Pacific Mexico.

REMARKS. Dawson (1966a) in reporting *Prionitis delicatula* in the upper Gulf, noted the Puerto Peñasco specimens had fewer determinate laterals; and thalli of his specimens (US Alg. Coll.) were subcylindrical to slightly compressed, whereas those of Pacific Baja California Sur were flattened (cf. Taylor, 1945: pl. 66: fig. 1).

Uncertain Record:
***Prionitis australis* (J. Agardh) J. Agardh**

Prionitis australis (J. Agardh) J. Agardh, 1851:188; Mendoza-González and Mateo-Cid, 1986:432.

REMARKS. *Prionitis australis*, a California species (Abbott and Hollenberg, 1976), was recorded from Segundo Cerro Prieta, Bahía Kino, by Mendoza-González and Mateo-Cid (1986) and González-González et al. (1996). Collection of more material, as well as reexamination of their specimens, will be helpful in order to verify its presence in the northern Gulf.

TSENGIACEAE*

Tsengiaceae G. W. Saunders et Kraft, 2002:1259; Schneider and Wynne, 2007:227.

Members are multiaxial in structure, with a filamentous medulla and a cortex of branched filaments forming cortical fascicles, without gland cells, and secondary pit connections between cells are lacking.

Life histories, where known, are an alternation of isomorphic generations. Tetrasporangia are scattered on fronds and regularly to irregularly cruciately divided. Gametophytes have a three-celled carpogonial branch, and connecting filaments are septate and branched, arising directly from an undivided fertilized carpogonium. Auxiliary cells are intercalary in cortical filaments and are diploidized (fertilized) by lateral fusion with a connecting filament, the connecting filaments often proceeding on to diploidize additional auxiliary cells. A gonimoblast is issued directly from the diploidized auxiliary cell. The carposporophyte develops thallus outward, with one to three gonimolobes.

REMARKS. A monotypic family, members of the Tsengiaceae strongly resemble those of the Nemastomataceae (Nemastomatales) in habit and vegetative structure. Saunders and Kraft (2002, as Halymeniales) provided morphological data, supported by molecular evidence, that *Tsengia* is closer to members of the Cryptonemiales and belonged in its own family.

Tsengia is now reported in the northern Gulf of California.

Tsengia K.-C. Fan et Y.-P. Fan

Tsengia K.-C. Fan et Y.-P. Fan, 1962:191; Womersley and Kraft, 1994:274.

Algae are erect, firm to soft and flaccid, and often lubricous or gelatinous. Species may be foliose, simple to divided, or laciniate, or others are terete or compressed and subdichotomously to irregularly branched. Thalli may also have many laterals or proliferations. Thalli are multiaxial with a medulla composed of entangled filaments. The cortex is formed by subdichotomously (to trichotomously) branched anticlinal filaments that are without gland cells or secondary pit connections.

Life histories, where known, are triphasic, involving isomorphic tetrasporophytes and gametophytes (Umezaki, 1974, as *Nemastoma nakamurae*). Tetrasporangia are regularly to irregularly cruciate to obliquely divided; borne laterally off a cortical filament cell, scattered over the thalli. Gametophytes are monoecious or dioecious. Carpogonial branches 3(–4)-celled, borne on a supporting cell in the inner portions of cortical fascicles, with straight, curved, or coiled trichogynes. Auxiliary cells are borne in similar locations on inner cells of cortical fascicles. Fertilized carpogonia develop one to four connecting filaments that grow to an auxiliary cell (Umezaki, 1967). Connecting filaments may diploidize several auxiliary cells in succession (Dixon and Irvine, 1977b, as *Platoma bairdii*). Gonimoblasts arise directly from auxiliary cells and develop thallus outward. The carposporophyte is borne among the cortical filaments, with all of its cells (except the gonimoblast initial) developing into carposporangia. Spermatangia are developed from the outer cells of the cortical filaments (after Womersley and Kraft, 1994).

One species of *Tsengia* occurs in the northern Gulf of California.

Tsengia abbottiana (J. N. Norris et Bucher) J. N. Norris et Bucher, *comb. nov.*

FIGURES 215, 216A,B

Platoma abbottianum J. N. Norris et Bucher, 1977:157 [as "*P. abbottiana*"], figs. 1–9; González-González et al., 1996:248; Pacheco-Ruíz et al., 2008:210; Gabriel et al., 2010:4, tbl. 1.

Algae erect foliose blades, up to 27 cm tall, flattened, rose red, gelatinous and slippery but firm in consistency; arising from a short stipe attached by a discoid holdfast, branching somewhat dichotomously to irregularly. Young blades often with forked blunt apices; blades thicken and expand, becoming irregularly lobed with age. Internally, blades composed of loosely aggregated filaments in a gelatinous matrix. Medulla consists of slender, septate, sparingly branched, longitudinally arranged

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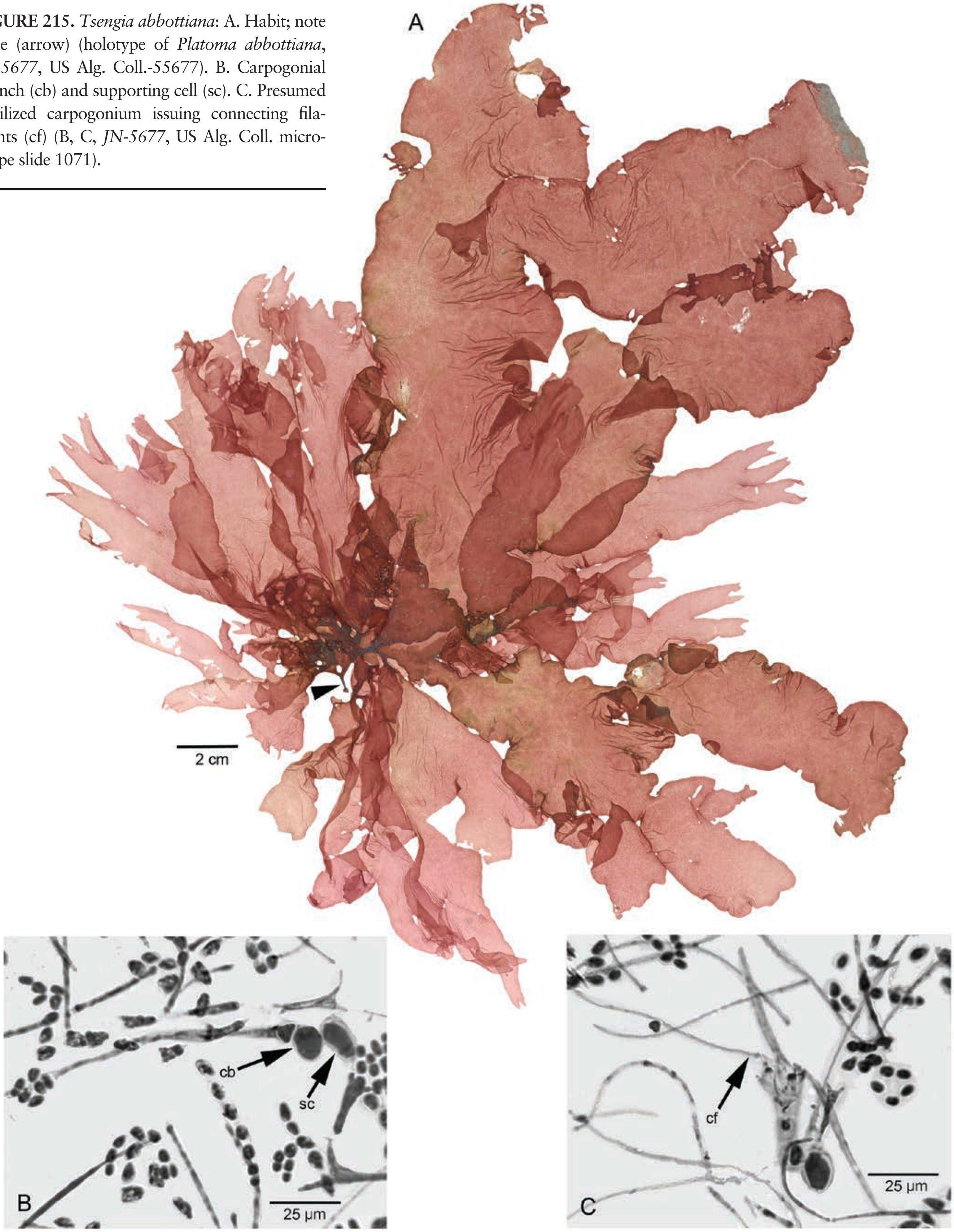
* Contributed by Katina E. Bucher and James N. Norris. K. E. Bucher: Department of Botany, National Museum of Natural History, Smithsonian institution, Washington, D.C. 20013-7012, USA.

FIGURE 215. *Tsengia abbottiana*: A. Habit; note stipe (arrow) (holotype of *Platoma abbottiana*, *JN-5677*, US Alg. Coll.-55677). B. Carpogonial branch (cb) and supporting cell (sc). C. Presumed fertilized carpogonium issuing connecting filaments (cf) (B, C, *JN-5677*, US Alg. Coll. microscope slide 1071).



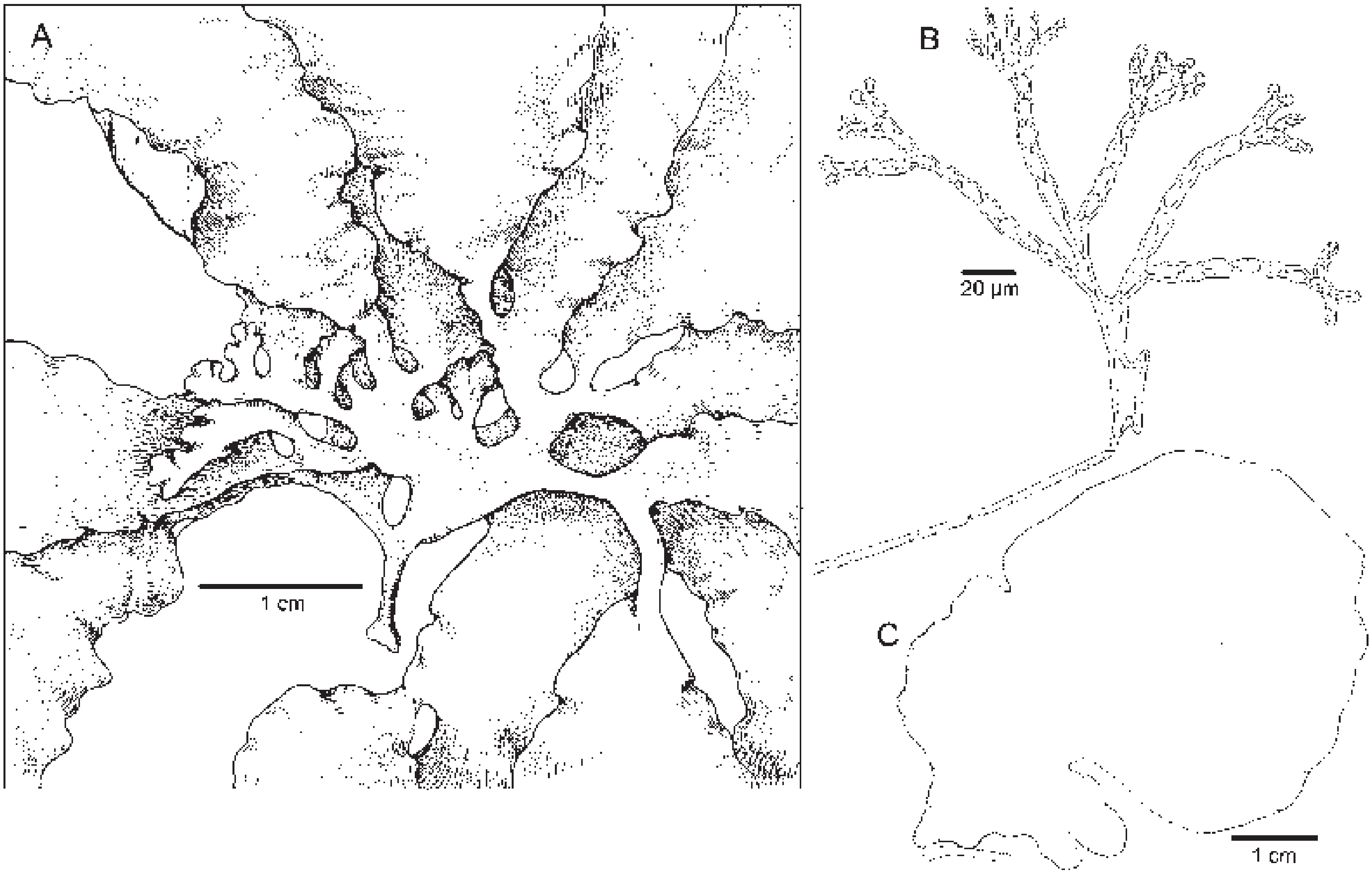


FIGURE 216. A, B. *Tsengia abbottiana*: A. Detail of lower branching developed above stipe. B. Cortical filament (A, B drawn from holotype: *JN-5677*, US Alg. Coll.-55677). C. *Predaea masonii*: Habit of thick gelatinous blade with faint veins (after Dawson, 1961a: pl. 3, fig.1).

filaments, 4.5–15 µm wide and to 56 µm in length, and with some X-shaped cells that issue rhizoidal filaments. Outer medullary filaments bear numerous laterals, which branch outward to form the cortex of dichotomously branched, 5–7 times, cortical fascicles. Inner cortical cells cylindrical, 9–15 µm wide and 16.5–27.0 µm long, decreasing in size toward the surface; cortical surface cells tear shaped, 3–6 µm in diameter (Figure 216B). Gland cells absent.

Gametophytes apparently dioecious. Carpogonial branches 3-celled, with a long, straight trichogyne, borne on a supporting cell (darkly staining with aniline blue) (Figure 215B) on inner dichotomies of cortical fascicles. Connecting filaments arise directly from a fertilized carpogonium (Figure 215C). Auxiliary cells intercalary, usually borne on separate cortical filaments from carpogonial branches, within inner dichotomies of cortical fascicles and indistinguishable from vegetative cells before fusion with a connecting filament, which results in the formation of a single gonimoblast initial by the auxiliary cell, generally opposite the site of fusion. Mature cystocarps spherical to irregular in shape, 130–195 µm in diameter, and immersed in the cortex. Carposporangia are spherical, to 9 µm in diameter. Tetrasporangia and spermatangia unknown.

HABITAT. On rocks; subtidal, down to 20–25 m depths.

DISTRIBUTION. Gulf of California: Isla Mejía and Puerto Refugio, Isla Ángel de la Guarda.

TYPE LOCALITY. 23 m depth; in channel off SE end of Isla Mejía, northwest side of Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura), Gulf of California, Mexico.

REMARKS. The female reproductive features of *Platoma abbottianum* differ from those of the genus *Platoma* Schousboe ex F. Schmitz (1894) as it is currently defined (Masuda and Guiry, 1995a). Species of *Platoma* possess darkly staining “nutritive auxiliary” cells, borne to each side of the supporting cell of the carpogonial branch, and carpogonia may or may not divide (depending on species) after fertilization, and one or both of these derivatives fuse or pit connect with the adjacent nutritive auxiliary cells before sending out connecting filaments to effect diploidization of the "generative" auxiliary cells. *Platoma abbottianum* does not have "nutritive auxiliary" cells associated with its carpogonial branch nor this postfertilization development and, consequently, needs to be transferred to a more appropriate genus.

The female gametophyte of *P. abbottianum* has a close anatomical affinity with two genera, *Tsengia* and *Itonoa* Masuda et Guiry (1995b), that are in two different orders. Both genera lack gland cells and lack darkly staining "nutritive auxiliary" cells on the supporting cell of their carpogonial branch and have connecting filaments issued directly from fertilized carpogonia. A key feature separating *Tsengia* and *Itonoa* is their life history: sporophytes and gametophytes are isomorphic in species of *Tsengia,* whereas those of *Itonoa* are heteromorphic, involving erect gametophytic fronds and a sporophyte that is either a crust or tuft of filaments (Masuda and Guiry, 1995b). However, since the tetrasporophyte of *P. abbottianum* is unknown, female reproductive morphology is used as a primary distinguishing feature. There are differences between the carpogonial branches; those of *Itonoa* contain a greater number of cells and have extraneous lateral branchlets, both sterile and/or fertile (can be compound), borne on it, whereas the carpogonial branch of *P. abbottianum* is three-celled, with a straight trichogyne, and does not have any extraneous cells or filaments attached, more akin to the carpogonial branch of *Tsengia.* Connecting filaments of *P. abbottianum* resemble those of *Itonoa*, in that the filaments branch before reaching the auxiliary cell, with one fork terminating at the auxiliary cell and the other continuing to lengthen, presumably forging ahead to the next auxiliary cell. Although connecting filaments of *Tsengia* do not fork just before auxiliary cells, they fuse laterally with auxiliary cells and then continue on, presumably to diploidize additional auxiliary cells. Vegetative X- shaped cells that occur in the medulla of *Itonoa* and *P. abbottianum* are also known in species of other genera [see Gabriel et al., 2010, *Platoma cyclocolpum* (Montagne) F. Schmitz (1894)], so their presence may not be a good character for generic distinction. Since the tetrasporophyte of *P. abbottianum* is unknown, the species is tentatively assigned to *Tsengia* on the basis of its unadorned three-celled carpogonial branch. Further studies, such as DNA sequence analysis, the discovery of the tetrasporophyte, or life history studies, will enable resolution of its generic placement.

Tsengia abbottiana is apparently rare in occurrence in the Gulf of California, thus far only known off the northern end of Isla Ángel de la Guarda in the central Gulf. It has been also reported in the South Pacific from Moorea, French Polynesia (Payri et al., 2000; N'Yeurt and Payri, 2010, as *Platoma abbottianum*).

NEMASTOMATALES*

Nemastomatales Kylin, 1925:39 [as "Nemastomales"]; Saunders and Kraft, 2002:1257.

Gametophytes are multiaxial in structure, with thalli of various shapes and are usually gelatinous or lubricous in texture. Thalli possess a medulla composed of loosely to densely arranged slender filaments and rhizoids. The cortex is composed of usually pseudodichotomously branched anticlinal cortical filaments and adventitious rhizoidal filaments, and there are no secondary pit connections (except in *Schizymenia apoda* (J. Agardh) J. Agardh, 1851). Gland cells are present in some members and absent in others.

Life histories, where known, are of heteromorphic tetrasporophytes and gametophytes. Tetrasporophytes are minute to expanding fleshy crusts or A*crochaetium*-like filaments and produce zonately divided tetrasporangia. Carpogonial branches are (2–)3(–5) cells long, and one family has additional dark staining "nutritive auxiliary" cells borne on the supporting cell of the carpogonial branch. After fertilization, the carpogonium either directly generates septate, branching, connecting filaments, or in members of one family, divides once, and one or both halves fuse or pit connect to the nutritive auxiliary cells and then produce connecting filaments. Connecting filaments grow to generative auxiliary cells to transfer the diploid nucleus. Generative auxiliary cells are intercalary in cortical filaments, usually located in cortical filaments separate from those bearing the carpogonial branches. Connecting filaments diploidize auxiliary cells by a lateral fusion and continue on or terminate at the auxiliary cell. Gonimoblast issued lateral or outward either from the auxiliary cell or from the connecting filament at its site of fusion with the auxiliary cell. Carposporophytes of one to three gonimolobes of carposporangia usually develop outward toward the thallus surface but develop inwardly in one genus, *Adelophycus* Kraft (in Womersley and Kraft, 1994), from Australia. Cystocarps are compact and with or without an ostiole. Spermatangia are scattered or in patches on cells near the thallus surface (after Saunders and Kraft, 2002.)

The order is represented by both of its families in the northern Gulf of California.

KEY TO THE FAMILIES OF NEMASTOMATALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli soft and gelatinous; supporting cell of carpogonial branch without adjoining darkly staining "nutritive auxiliary" cells; connecting filaments issued directly from fertilized carpogonia . . . . **Nemastomataceae**

1b. Thalli membranous (not gelatinous), may be slippery; supporting cell of carpogonial branch bearing adjoining, darkly staining "nutritive auxiliary" cells; carpogonia may or may not divide after fertilization, and one or both derivatives fuse or pit connect with nutritive auxiliary cell(s) before issuing connecting filaments . . . . **Schizymeniaceae**

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* Contributed by Katina E. Bucher and James N. Norris. K. E. Bucher: Department of Botany, National Museum of Natural History, Smithsonian institution, Washington, D.C. 20013-7012, USA.

NEMASTOMATACEAE

Nemastomataceae F. Schmitz in Engler, 1892:22, *nom. cons*; Schmitz and Hauptfleisch, 1897d:521 (both as 'Nemastomaceae').

Gymnophlaeaceae Kützing, 1843:389, *nom. rej.* [see Silva, 1993b:708].

Gametophytes are erect above a discoid base, soft and flaccid, often gelatinous, and may be either (1) foliose, compressed to flattened, and simple to divided or branched blades or (2) complanate to compressed and entire or lobed or (3) cylindrical and subdichotomously to irregularly branched. All are multiaxial in structure, with a medulla of loosely entangled or sometimes longitudinally aligned filaments and a more compact cortex of subdichotomously branched filaments with progressively smaller cells toward the blade surface. Adventitious rhizoidal filaments may be issued from medullary and cortical filaments. Some medullary filaments with X-shaped cells. Medullary and cortical filament cells are without secondary pit connections, and gland cells are lacking in most members but are present in some others. Millar and Guiry (1989) proposed the use of the term vesicular cells for structures that were earlier called "gland cells" or "secretory cells" as they have no known secretory function.

Life histories are mostly unknown, but heteromorphic phases have been reported. The heteromorphic sporophyte is filamentous or may be crustose. Tetrasporophytes, where known, produce zonately divided tetrasporangia. Monosporangia are reported in at least one species (Millar and Guiry, 1989). In this family, foliose or terete gametophytes produce carpogonial branches and auxiliary cells on separate cortical fascicles (nonprocarpic). The auxiliary cells are intercalary in the cortical filaments. After fertilization, the carpogonia directly issue connecting filaments that grow toward auxiliary cells, where they fuse, transferring the diploid nucleus. The gonimoblast develops outwardly toward the blade surface in most members, with nearly all of its cells forming carposporangia. Cystocarps are embedded within the thallus and consist of groups of carposporangia in various stages of maturity. Spermatangia are cut off from the outer cortical cells.

The Nemastomataceae is represented by one genus in the northern Gulf of California.

Predaea G. De Toni

Predaea G. De Toni, 1936b:[5].

Clarionea Setchell et N. L. Gardner, 1930:174, *nom. illeg.* [non *Clarionea* Lagasca ex A. P. de Candolle, 1812:65].

Algae are blade-like, ovoid, irregularly divided or variously lobed and soft and gelatinous in texture. The thallus is with or without a small stipe above a small discoid holdfast. The broad medulla is composed of loosely arranged slender filaments and rhizoidal filaments embedded in and traversing a matrix of soft clear jelly. The medullary filaments give rise to a short anticlinal layer of loosely arranged cortical fascicles that form the thallus surface. Cortical filaments are dichotomously to trichotomously branched and lack secondary pit connections between cells in adjacent cortical fascicles. Gland cells are present in some species, borne intercalary in cortical filaments.

Heteromorphic sporophytes (not known for all species) are acrochaetioid filaments known only from culture studies (Athanasiadis, 1988; Vergés et al., 2004) or crustose thalli that produce cruciately (Lemus and Ganesan, 1977) or zonately divided tetrasporangia or monosporangia (Millar and Guiry, 1989). Bisporangia (possibly propagules; Guiry and Guiry, 2008–2010) are reported on the outer cortical cells of the gametophyte of one species (Kajimura, 1987b). Gametophytes are monoecious or dioecious, carpogonial branches are (2–)3(–5)-celled and are typically borne on a cell near the basal dichotomy of inner cortical filaments. Auxiliary cells are intercalary and near the base of cortical filaments (separate from carpogonial branches). Modified vegetative cells adjacent to auxiliary cells bear short, simple to branched chains of small nutritive cells (cellules nourricieres) that form clusters near the auxiliary cells. The nutritive cellules near the auxiliary cells and cystocarps are a distinguishing character of this genus and are present before fertilization. One to many septate, branched connecting filaments arise directly from a fertilized carpogonium and grow the distance to diploidize the auxiliary cells. The gonimoblast initial usually originates from the connecting filament near the point where it fuses with the auxiliary cell, or in a few species the gonimoblast initial is issued by the auxiliary cell. Carposporophytes are ovoid to lobed and immersed in the cortex, scattered over the thallus. They lack a pericarp, involucral filaments, or an ostiole. All gonimoblast cells except the gonimoblast initial become carposporangia. Spermatangia are clustered at the apices of cortical filaments and produce subspherical spermatia.

Two species of *Predaea* are reported in the northern Gulf of California.

KEY TO THE GELATINOUS FOLIOSE SPECIES IN THE NORTHERN GULF OF CALIFORNIA: *PREDAEA* (NEMASTOMATACEAE), *PLATOMA* (SCHIZYMENIACEAE), AND *TSENGIA* (TSENGIACEAE)

Note: These Gulf of California species are distinguished from the other Gulf foliose reds by their soft, mucilaginous to gelatinous, and very lubricous texture.

1a. Mucilaginous blades with or without a stipe; cells adjacent to auxiliary cells without short chains of small nutritive cellules 2
1b. Mucilaginous blades without a stipe; cells adjacent to auxiliary cells with short chains of small, nutritive cellules . . . 3

2a. Mucilaginous blades, divided into portions above a distinct short stipe; younger blades somewhat dichotomously divided in upper portion . . . . *Tsengia abbottiana*
2b. Mucilaginous blades, broadly lobed; without a stipe . . . . *Platoma fanii*
3a. Mucilaginous blade with faint, broad, more or less opposite veins from a central vein; gland cells lacking; cortical cell shape linear to oblong . . . . *Predaea masonii*
3b. Mucilaginous blade lacking any evident venation; gland cells present, spherical; cortical cell shape spherical to ovoid . . . . *Predaea japonica*

Predaea japonica T. Yoshida

FIGURE 217

Predaea japonica T. Yoshida, 1980:69, figs. 1–4; Kajimura, 1990:530, figs. 1–17; Yoshida, 1998:761.

Predaea masonii sensu Norris, 1975:332, pl. 15: fig. C; Norris and Bucher, 1976:14, fig. 6c; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:209 [non *Predaea masonii* (Setchell et N. L. Gardner) G. De Toni, 1936b:[5].

Algae erect, compressed, gelatinous, deeply divided foliose blades (usually of 3–5 broadly rounded lobes), up to 23 cm in height, 15 cm wide; without a stipe. Cortical filaments of moniliform cells that become progressively smaller toward the surface; dichotomously branched, 3–5 times, cortex up to 100 µm thick; occasional unbranched rhizoidal filaments issued from cortical filaments. Outermost surface cells very small, about 2.7 µm in diameter. Gland cells spherical, 10–15(–22) µm in diameter, prominent, intercalary in cortical filaments, (2–)3–5 cell layers below surface. Medullary cells slender, 3.6–4.0 µm in diameter, of varying lengths, loosely arranged, infrequently branched, within gelatinous matrix.

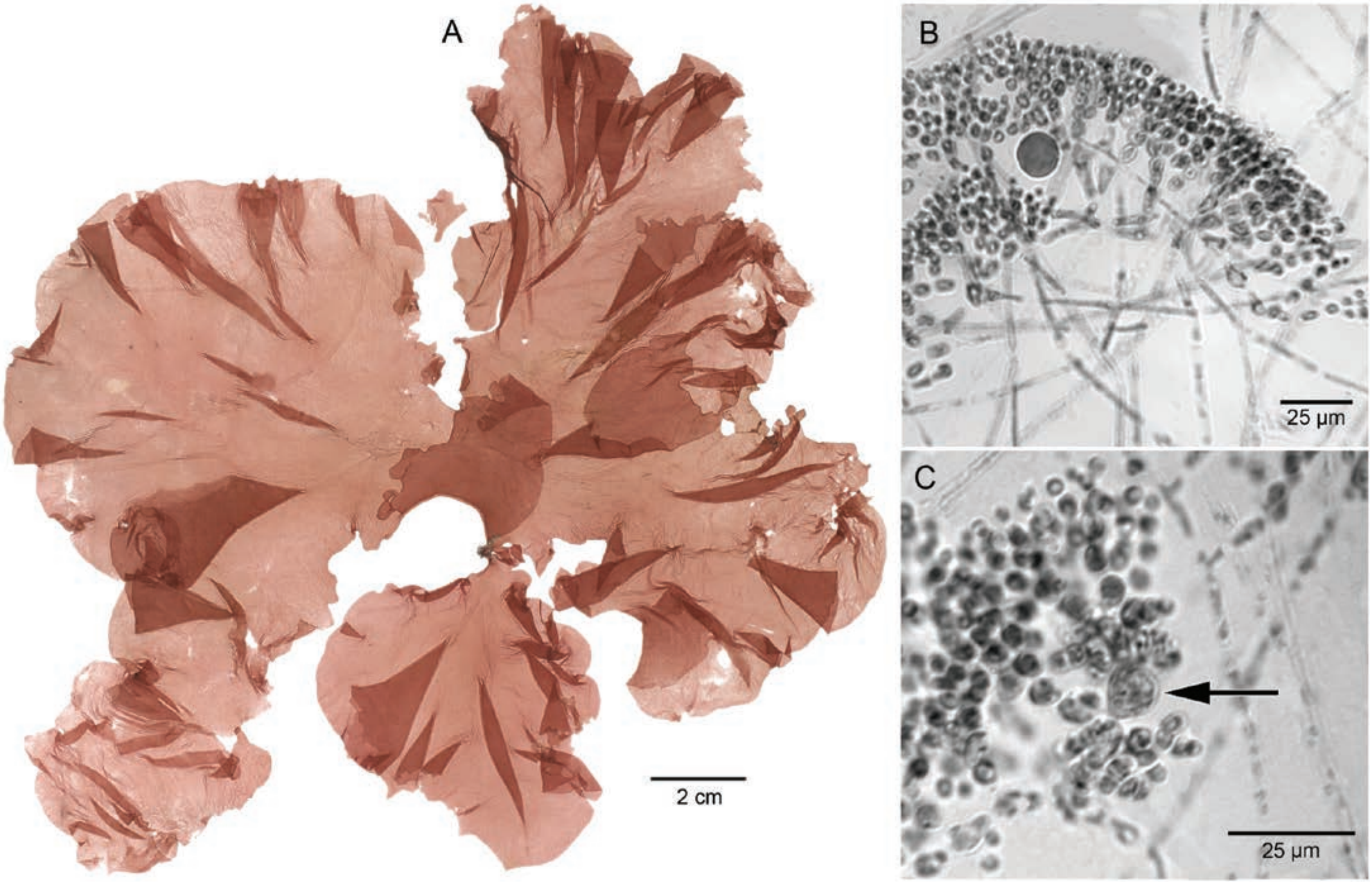

FIGURE 217. *Predaea japonica*: A. Habit (*JN-5300*, US Alg. Coll.-160633). B. Gland cell intercalary in cortical filaments (*JN-5607*, US Alg. Coll. microscope slide-5296). C. Clusters of nutritive cellules borne on cortical cells on both sides of the auxiliary cell (arrow) (*JN-5295*, US Alg. Coll. microscope slide 5298).

Sporophyte not known. Gametophytes monoecious or dioecious. Carpogonial branch 2-celled, borne off innermost cortical cells; shape of cells distinctive, urn-like basal cell, carpogonium with a pit connection to a wide based trichogyne (cf. Yoshida, 1980: fig. 3). Auxiliary cells are usually borne in cortical filaments separate from carpogonial branches and are larger (10 µm in diameter) than adjacent cortical cells. Cells to either side of the auxiliary cell bear several simple to pinnately branched chains of small nutritive cells (subspherical, about 3 µm in diameter). Connecting filaments fuse with a side of an auxiliary cell, resulting in a bulge; this bulge then cuts off the gonimoblast initial that develops the carposporophyte. Spermatangial thalli have not been found in the Gulf of California (as described for *P. japonica* from Japan: spermatangia occur on ends of cortical filaments and can also arise on rhizoidal filaments that upturn into the cortex, a distinctive feature of this species; Kajimura, 1990).

Habitat. Rare; subtidal, down to 20 m depths.

Distribution. Gulf of California: Isla Ángel de la Guarda; Isla Estanque; Islas de Los Gemelos, Bahía de Los Ángeles. Western Pacific: Japan.

Type Locality. Mitsuse, near Cape Nomo, Nagasaki Prefecture, Kyūshū, Japan.

Remarks. *Predaea japonica* differs from *P. masonii* in having gland cells, a thinner cortex (up to 100 µm thick within the gelatinous matrix), and in lacking any evident venation in the blade.

Predaea masonii **(Setchell et N. L. Gardner) G. De Toni**

FIGURE 216C

Clarionea masonii Setchell et N. L. Gardner, 1930:174, pl. 9: figs. 34–38; Serviere-Zaragoza et al., 2007:9.

Predaea masonii (Setchell et N. L. Gardner) G. De Toni, 1936b:[5]; Dawson, 1954a:335, pl. 2: figs. 1–6; 1961a:196, pl. 3: figs. 1–6; 1961b:427; Dawson and Neushul, 1966:177; Kraft and Abbott, 1971:200; Abbott and Hollenberg, 1976:481, fig. 427; Stewart and Stewart, 1984:144; Bula-Meyer, 1992:61, 64; González-González et al., 1996:259; Serviere-Zaragoza et al., 2007:11.

Blade-like thallus, complanate, mucilaginous, pale red, up to 15 cm tall and to 9 cm wide; without an evident stipe, attached below by a small, more or less discoid holdfast. Blades irregularly ovate, slightly lobed, often with a faint indication of broad, pinnate to seemingly opposite veins from a central axial vein; up to 8 mm thick (sometimes more) below and 1–3 mm thick in upper portions. Medulla of elongated branching filaments, 2.5–4.0 µm in diameter, traversing a clear, gelatinous matrix. Cortical filaments about 300 µm in length, branched, of linear to oblong-elliptical cells, about 4 µm in diameter by 8–16 µm long; cells become progressively smaller outward, to 2.0 µm in diameter, toward thallus surface.

Tetrasporangial thalli unknown. Carpogonial branch 2-celled. Auxiliary cells intercalary in inner cortical filaments, small-celled nutritive cellules on cells adjacent to auxiliary cells. Carposporangia roundish to irregular, carposporangial mass to 200 µm in diameter. Spermatangial thalli not seen in Gulf material.

Habitat. On rocks; subtidal, 4–30 m depths.

Distribution. Gulf of California: Isla Carmén (east of Loreto); Canal de San Lorenzo (off southern end of Isla Espíritu Santo). Eastern Pacific: Anacapa Island and Santa Catalina Island (California Channel Islands); Isla Guadalupe (off Baja California); Isla Clarión (Islas Revillagigedo).

Type Locality. Growing on a crustose coralline; Isla Clarión (Islas Revillagigedo), west of Colima, Pacific Mexico.

Remarks. The generitype *Predaea masonii* was described from Pacific Mexico. It is apparently rare in the Gulf of California, only known in the southern Gulf from a few specimens (Dawson, 1961a). New collections as well as those earlier-reported specimens need to be studied in order to evaluate the taxonomic status and phylogenetics of *P. masonii* in the Gulf of California.

Dawson (1961a:198) found that a specimen identified as "*Platoma tenuis*" (*W. R. Taylor*, 10 April 1939; AHFH-2996, now UC) was not *Platoma tenue* M. Howe et W. R. Taylor (1931; now *Predaea tenuis* (M. Howe et W. R. Taylor) Bula-Meyer in Gabriel et al. (2010) but was referable to *Predaea,* probably *P. masonii*. CONANP (2002) list "*Predaea masonii*" without comment from Bahía de Loreto; these specimens should be reexamined and may belong here or possibly be *P. japonica*. *Predaea masonii* has also been reported in the Atlantic from the Canary Islands (Haroun et al., 2002), Ghana (Lawson and John, 1987), and North Carolina and in the Caribbean (Schneider and Searles, 1991). Differences between Pacific Mexico *Predaea masonii*, the Atlanic *P. tenuis* (Howe et W. R. Taylor) Bula-Meyer (in Gabriel et al., 2010; Bula-Meyer, 1992), and *P. japonica* suggest these records should also be comparatively studied.

SCHIZYMENIACEAE

Schizymenieae F. Schmitz et Hauptfleisch, 1897f:522.

Schizymeniaceae (F. Schmitz et Hauptfleisch) Masuda et Guiry, 1995b:66.

Gametophytes are erect, with simple (unbranched) blades or branched blade-like thalli. In texture they may be either soft and gelatinous or slippery, membranous, and firm. Most genera are noncalcified, but one, *Titanophora,* is calcified. Internally, the medulla is composed of loosely arranged, entangled filaments, which are usually periclinally directed. The cortex is more compact, formed by anticlinal fascicles of branched cortical filaments; secondary pit connections between cells of adjacent cortical filaments are absent (with the exception of *Schizymenia apoda,* which has some secondary pit-connections linking inner cortical cells (Gabriel et al., 2011). Gland cells are found in many species.

Life histories are triphasic, involving an alternation of heteromorphic sporophytes and gametophytes. In *Schizymenia*, the crustose, noncalcified sporophyte, often referred to as the *Haematocelis*-phase, produces terminal, zonately divided tetrasporangia (Ardré, 1980; DeCew et al., 1992). In other genera the life history is not completely understood. Crustose sporophytes are also reported in *Platoma* (Masuda and Guiry, 1995a; Huisman, 1999), and Gabriel et al. (2010) indicated there are morphologically different crustose tetrasporangial stages [note: for alternative interpretation see Zuccarello and West, 2010].

Gametangial thalli may be monoecious or dioecious. Carpogonial branches are borne on the inner cells of cortical filaments, and generative auxiliary cells are borne in separate cortical filaments. Carpogonial branches are three-celled, with adjoining cortical cells on either side of the supporting cell modified to nutritive or subsidiary auxiliary cells that also stain densely with aniline blue. Upon fertilization, the carpogonium divides and fuses or develops secondary pit connections with one or more of the nutritive auxiliary cells borne on the supporting cell before issuing few to many secondary connecting filaments that grow to reach and transfer the diploid zygote nucleus to the generative auxiliary cells. Generative auxiliary cells produce a gonimoblast that develops outward and forms a compact carposporophyte. The mature cystocarp is loosely surrounded by elongated cortical cells (rudimentary involucres) and releases carposporangia through a surface pore. Spermatangia develop in pairs on outer cortical cells, forming superficial patches.

REMARKS. At least one genus of the family, *Schizymenia,* has been shown to contain natural products with antiviral activity (Nakashima et al., 1987; Bourgougnon et al., 1996).

Two of the five genera presently included in the Schizymeniaceae are reported to occur in the northern Gulf of California.

KEY TO THE GENERA OF SCHIZYMENIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades lobed or divided; flaccid, soft, and gelatinous; medulla of loosely aggregated slender filaments; gland cells absent or intercalary in some cortical filaments . . . . *Platoma*

1b. Blades entire or divided; membranous, firm in texture, sometimes more or less "leather-like"; medulla of relatively dense slender filaments; large gland cells terminal on some cortical filaments . . . . *Schizymenia*

Platoma Schousboe ex F. Schmitz

Platoma Schousboe ex F. Schmitz, 1894:627.

Gametophytes are erect or decumbent, soft, smooth, compressed gelatinous blades that may be foliose and lobed or divided or irregularly subdichotomously branched. They are attached to the substratum by a small, crustose holdfast. Blade margins are entire and may be ruffled or undulate or sometimes have marginal proliferations. Thalli are composed of filaments embedded within a gelatinous matrix. Medullary filaments are slender, septate, and loosely entwined, some X-shaped cells occur in some species. Cortical filaments are relatively more compact, with fascicles of branching anticlinal filaments composed of pigmented, progressively smaller cells outward. Gland cells are intercalary in some cortical filaments or absent.

A diploid, sporophytic crustose phase has been reported in life history studies (Gabriel et al., 2010). Culture studies have shown (1) carpospores that develop directly into erect, branched filaments, (2) carpospores that initially develop monostromatic crusts or multilayered pseudodiscs of loosely aggregated filaments, from which erect filamentous thalli were produced, and (3) direct development of carpospores to an apparently permanent, multistromatic crustose thallus with monostromatic margins (Gabriel et al., 2010). Gametophytes are monoecious or dioecious. The carpogonial branch is three-celled, borne on a cortical filament cell, with its supporting cell developing "nutritive auxiliary" cells before fertilization in some species or after fertilization in others. There are two kinds of auxiliary cells: "generative" auxiliary cells that are intercalary in a cortical filament and spatially separate from the carpogonial branches, and "nutritive" auxiliary cells that are distal on the supporting cell of the carpogonial branch. Post-fertilization, the carpogonium (may or may not divide depending on species) fuses with one or both nutritive auxiliary cells and then issues connecting filaments that grow to the generative auxiliary cells in separate cortical filaments. Developing carposporophytes produce gonimolobes, which, when mature, consist almost entirely of carposporangia. Several contiguous cortical cells elongate to arch around the carposporophyte. Cystocarps are immersed and scattered over the thallus, with carpospores released through an obscure ostiole (carpostome) or a gap in the cortex. Spermatangia develop in groups on the surface of cortical cells.

REMARKS. The conservation of the name *Platoma* as being neuter gender (Athanasiadis, 2000; Compère, 2003), rather than feminine (Norris and Bucher, 1976), was approved (McNeill et al., 2006). Therefore, the spelling of species names, where necessary, is correctable.

There is currently one species described as a *Platoma* in the Gulf of California (see also "Key to the Gelatinous Foliose Species in the Northern Gulf of California" following *Predaea*).

Platoma? *fanii* E. Y. Dawson

Platoma fanii E. Y. Dawson, 1961a:197, pl. 5, pl. 6: figs. 1–6; 1961b:427; González-González et al., 1996:248.

Sarcodiotheca linearis sensu Guiry and Guiry, 2008–2010 [non *Sarcodiotheca linearis* Setchell et N. L. Gardner, 1937:80].

Algae erect, foliose, complanate, very gelatinous, pale rose; up to 8 cm tall by 14 cm wide and 800–1200 µm thick, irregularly lobed and partially divided. Medulla of sparse, little-branched, interwoven filaments, cells of medullary filaments 47–58 µm long by 4.5–12.0 µm in diameter. Cortex about 150–200 µm thick, of pigmented, dichotomously branched cortical filaments; cells of inner cortical filaments, 23–28 µm long by 7–11 µm in diameter; cortical cells becoming smaller outward; ultimate cells ovoid to elliptical, 3–4 µm diameter.

Tetrasporangia not known. Carpogonial branch borne on cortical filaments, three-celled, with a long, often coiled, trichogyne; connecting filaments, branched, septate, 4–5 μm in diameter. Auxiliary cells modified from intercalary cells of inner cortical region, 16–19 μm long by 11–16 μm in diameter. The gonimoblast develops from a diploidized auxiliary cell, often opposite the fusion site with the incoming connecting filament. The carposporophyte is initially broadly ovoid, sometimes later becoming slightly lobed, and usually with a "pedicel" (presumably the auxiliary cell and gonimoblast initial). Spermatangial thalli unknown.

Habitat. Growing on rock; subtidal, depths of 9–37 m (Dawson, 1961a).

Distribution. Gulf of California: Isla San Esteban.

Type Locality. Isla San Esteban (Islas de la Cintura), Gulf of California, Mexico.

Remarks. An endemic species from the northern Gulf, *Platoma fanii* is still only known from the type material of two specimens. Species of *Platoma* have two kinds of auxiliary cells: auxiliary cells intercalary in cortical filaments and "nutritive auxiliary" cells borne distally on the supporting cell of the carpogonial branch. The described characteristics of the carpogonial branch of *P. fanii* with its lack of "nutritive auxiliary" cells suggest *P. fanii* does not belong in the genus *Platoma,* and may belong in *Tsengia* K.-C. Fan et Y.-P. Fan (1962) or *Itonoa* Masuda et Guiry (1995b). It is uncertain if gametophytes and sporophytes of *P. fanii* are heteromorphic (*Itonoa*) or isomorphic (*Tsengia*). Although the internal anatomy and some reproductive characters of *P. fanii* (Dawson, 1961a, pl. 6: figs. 1–6) are similar to *Tsengia abbottiana,* the external morphology of *P. fanii* differs in that it has no stipe, lacks branching, and is broadly lobed. Recognizing its generic placement is problematic; for now, this species is reluctantly left in *Platoma*, until additional Gulf specimens are discovered for the morphological, developmental, and molecular analyses needed to elucidate its taxomomic status.

Another eastern Pacific specimen identified as "*Platoma fanii*" was recently reported in Pacific Panama (Littler and Littler, 2010; Fernández-García et al., 2011). Examination of liquid-preserved portions of short erect blades (*M. & D. Littler-69030*, liquid-preserved; US Alg. Coll.) revealed tetrasporangia, about 6 μm in diameter. The tetrasporangial parent cell is a cortical cell borne toward the end of the cortical filament. Although this suggests the Pacific Panama material is probably a species of *Tsengia*, without female gametophytes its identification remains uncertain.

Schizymenia J. Agardh

Schizymenia J. Agardh, 1851:158.

Gametophytes are erect, with one or more flattened, membranous foliose blades, generally firm in texture, above an inconspicuous cylindrical stipe, which attaches to the substrate by a small discoid holdfast. Blades are ovoid to lanceolate and may be entire or divided. Thalli are multiaxial in structure, with a medulla composed of colorless, interwoven filaments. The cortex is composed of anticlinal fascicles of subdichotomously branched filaments whose cells become progressively smaller toward the surface. Gland cells are interspersed in the cortex, located terminally on cortical filaments, often conspicuous and numerous.

Life histories are triphasic but are not known in all species. Where known, the tetrasporophytes and gametophytes are heteromorphic. Culture studies of the generitype, *S. dubyi* (Chauvin ex Duby) J. Agardh (1851), by Ardré (1980) showed germinating carpospores to develop *Haematocelis*-like tetrasporangial crusts. Tetrasporangia are zonately to occasionally irregularly divided and are embedded in the cortex, scattered over the thallus surface. Gametophytes can be monoecious or dioecious. Carpogonial branches are three-celled, with the "nutritive auxiliary" cells (also darkly staining) adjoining the support cell. After fertilization, the carpogonium divides and fuses or pit-connects with one or more nutritive auxiliary cells that issue connecting filaments. The diploid nucleus is transferred by the connecting filaments to generative auxiliary cells; nearly all cells of the gonimoblasts become carposporangia. The cortical cells pit-connected to the generative auxiliary cells elongate and develop into a loose involucre around the carposporophyte. Cystocarps are globose, with a distinct carpostome, and develop in the cortex and protrude into the medulla. Spermatangia are cut off from outer cortical cells.

Remarks. Two species, *Schizymenia johnstonii* and *S. violacea*, originally described from the Gulf of California by Setchell and Gardner (1924) were later considered to be a single species by Dawson (1944a) as *S. violacea*. Subsequently, Dawson (1961a) recognized *S. violacea* to be a member of the genus *Grateloupia*, as *G. violacea* (Setchell et N. L. Gardner) E. Y. Dawson.

Crustose *Haematocelis* are known to be sporophytes in life histories of some *Schizymenia* species (Guiry and Guiry, 2013). *Haematocelis zonalis* E. Y. Dawson et Neushul (1966:176) was described from Anacapa Island (California Channel Islands) and Bahía Agua Verde (Baja California Sur) in the southern Gulf, but culture and genetic studies are needed to see if it is involved in the life history of Gulf *Schizymenia*.

Currently, there is one species of *Schizymenia* reported in the northern Gulf of California.

***Schizymenia pacifica* (Kylin) Kylin**

FIGURE 218

Turnerella pacifica Kylin, 1925:21, fig. 10a–e; Kylin, 1930:38, figs. 25, 26.

Schizymenia pacifica (Kylin) Kylin, 1932:10; Kylin, 1941:17; Smith, 1944:258, pl. 60: fig. 4, pl. 61: fig. 1; Dawson, 1961a:199, pl. 3: fig. 7, pl. 7; 1961b:427; Abbott, 1967b:162, figs. 1–3; Abbott and North, 1972:76; Norris, 1973:11; Abbott and Hollenberg, 1976:481, fig. 426; Silva, 1979:321; Pacheco-Ruíz and Aguilar-Rosas, 1984:73, 77; Ramírez and Rojas, 1988:22, figs. 5, 6, 27-29; Scagel et al., 1989:258; Stewart, 1991:99; Ramírez and Santelices, 1991:277; González-González et al., 1996:269; Pacheco-Ruíz and Zertuche-González, 2002:468; Spalding et al., 2003:277; Pacheco-Ruíz et al., 2008:210.

Sarcophyllis californica sensu Setchell and Gardner, 1903:354 [non *Sarcophyllis californica* J. Agardh, 1876:263, which is *Dilsea californica* (J. Agardh) Kuntze, 1891:892].

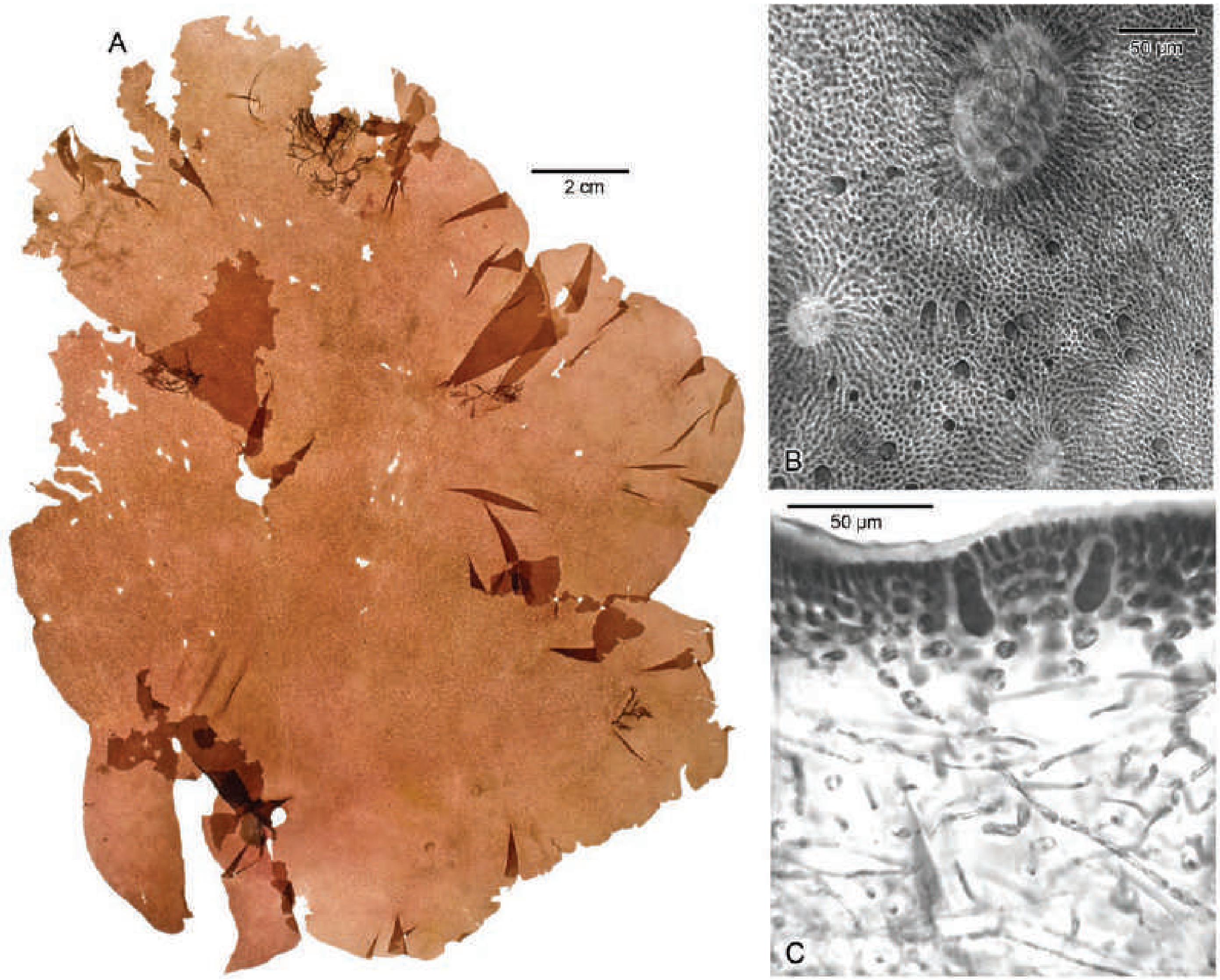

FIGURE 218. *Schizymenia pacifica:* A. Habit (female gametophyte) (*JN-5759*, US Alg. Coll.-160898). B. Surface view showing gland cells in cortex and several carpostomes of cystocarps, the largest with carposporangia visible within (*JN-5747c*, US Alg. Coll. microscope slide 4524). C. Portion of transection showing elongate gland cells terminating cortical filaments (*JN-5747*, US Alg. Coll. microscope slide 4526).

Algae of 1 to several foliose blades, dull brownish red in color; up to 30 cm tall and (4–)12–20 cm wide, 250–500 µm thick; ovate to broadly lanceolate (usually longer than wide; occasionally broader than long), sometimes falcate; undivided, or sometimes divided or deeply split; margins mostly slightly undulate, or sometimes irregular; blades either above a short stipe, 1.0–2.0 mm long, or expanding directly from a small discoid holdfast. Medulla of entangled, slender, branched filaments about 7–11 µm in diameter; mostly periclinal and fewer anticlinal, outward tending to be mostly anticlinal. Cortex compact, of anticlinal fascicles of short branched filaments of 6–8(–15) cells; inner cortex of highly granular cells, 8–10 µm in diameter, becoming progressively smaller toward surface; outer cortex of 4–5 pigmented cells, terminal cortical cells may be slightly elongated. Darkly staining gland cells terminal on some cortical filaments, elongate, ovoid to pyriform, 20–40(–60) µm in length, 10–20 µm in diameter.

Sporangial thalli not seen in Gulf material. Cystocarps about 150–210 µm in diameter; scattered, slightly bulging over the blade surface; embedded within thallus, of several gonimolobes; carposporangia 30–45 µm long, 15–20 µm in diameter; with carpostome at thallus surface to discharge carpospores. Spermatangia about 4–5 µm in diameter; superficial, covering upper portions of blade; spermatia about 2 µm in diameter.

HABITAT. On rocks, sometimes sand-covered rocks; mid intertidal to shallow subtidal, down to 5(–10) m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda (Islas de la Cintura); Bahía Willard (northwest of Bahía San Luis Gonzága); Bahía de Las Ánimas. Eastern Pacific: Aleutian Islands, Alaska to Isla Magdalena (northwestern side of Bahía Magdalena), Baja California Sur; central Chile.

LECTOTYPE LOCALITY. On pilings of dock; Friday Harbor, San Juan Island, San Juan Islands, San Juan County, Washington, USA.

REMARKS. *Schizymenia pacifica* is known in the Gulf of California from only a few collections. It can be distinguished from the other Gulf foliose reds by its brown-reddish color and somewhat "leathery" texture in the field and by the presence of ovoid to long-elliptical gland cells in its cortex. Dawson (1961a) suggested a drift fragment found at Bahía Agua Dulce, Isla Tiburón, might also be *S. pacifica*.

PLOCAMIALES

Plocamiales G. W. Saunders et Kraft, 1994:1260.

Algae of this order are uniaxial and may be autotrophic or parasitic.

Gametophytes and tetrasporophytes are isomorphic. Tetrasporangia are zonately divided and borne in stichidia. Female reproductive structures are procarpic, with a three-celled carpogonial branch borne on an intercalary cortical supporting cell. After presumed fertilization, the carpogonium fuses with the supporting cell, and the supporting cell then additionally functions as the auxiliary cell. A single outwardly directed gonimoblast initial is issued by the auxiliary cell and develops several gonimolobes, most cells of which (except for basal cells) differentiate into carposporangia. A carposporophyte nutritive system is developed by the modification of cortical cells that are pit-connected to the auxiliary cell, but there is no fusion between these cells and the developing carposporophyte.

One family of the Plocamiales, the Plocamiaceae, occurs in the Gulf of California.

PLOCAMIACEAE

Plocamiaceae Kützing, 1843:442, 449.

The family consists of only two genera: *Plocamium* J. V. Lamouroux and *Plocamiocolax* Setchell. *Plocamium* is an erect, pigmented, free-living macroalga of various shades of red that has a firm thallus of compressed to flattened axes that branch from the margins, often in a zigzag manner as growth is ramisympodial and pectinate from axes margins. Species of *Plocamium* are uniaxial in structure, with each central axial filament cell surrounded by four periaxial cells (most evident only in transections of the upper portions of the thallus, becoming obscure below) that produce the pseudoparenchymatous anatomy. Carposporophytes have nonostiolate pericarps. The other genus, *Plocamiocolax* is an adelphoparasite on its host *Plocamium*. Species of *Plocamiocolax* form whitish (lacking chlorophyll and phycobilin pigments), small globose to pulvinate clusters (usually less than 5 mm). Carposporophytes have ostiolate pericarps (Kugrens and Delivopoulos, 1986).

The Plocamiaceae is represented by one genus in the northern Gulf of California.

***Plocamium* J. V. Lamouroux**

Plocamium J. V. Lamouroux, 1813:137.

Algae are erect, with several compressed to flattened axes that are repeatedly pectinately branched in a unilateral alternating series of 2 or more lateral branches. Several axes often form a clump of fronds that is attached to the substrate by a haptera-like holdfast or prostrate terete branches with discoid holdfasts. Primary branching is ramisympodial, with a regular pattern of pairs or series of three or more laterals (depending on species), distichously arranged along alternating sides of axes margins. The most distal branch of each lateral series may continue to grow and repeats the branching pattern that is characteristic for the species, whereas the lowermost branch of the series usually remains undivided. However, in at least one species, adventitious branchlets occur in addition to the basic determinate branching pattern. Margins are entire or serrate, and in certain species branchlets may be recurved. Thalli are uniaxial in structure, with each axial filament cell bearing four pericentral cells (first two are lateral, and the other two are transverse). The pericentral cells in turn produce the pseudoparenchymatous medulla of successively smaller cells outward that form a compact cortex.

Tetrasporangia are zonately divided, within simple or branched stichidia that are either derived from the conversion of ultimate branchlets or are adventitious laterals that form distinct clusters in axils of branches. Sexual thalli are dioecious. In female gametophytes, the carpogonial branch is three-celled, with the supporting cell functioning as the auxiliary cell (after fusion with the fertilized carpogonium). Cystocarps have a lobed gonimoblast that is surrounded by a nonostiolate pericarp formed by cortical cell divisions. Most gonimoblast cells develop into carposporangia. Cystocarps are either scattered on axes margins, sessile, on a terete pedicel, or in axils of branchlets. Spermatangia develop from parent cells and cover the ultimate branchlet surfaces or are on special spermatangial branchlets that form tufts in axils of branchlets.

REMARKS. *Plocamium* is a diverse genus of more than 45 currently recognized species (Wynne, 2002; Saunders and Lehmkuhl, 2005) distributed primarily in temperate to subtropical waters. The most widely reported species of *Plocamium*, *P. cartilagineum* (Linnaeus) Dixon (1967), has generally been accepted with a broad species concept, showing much morphological variability and being worldwide in distribution. More recently, molecular sequence data of northeastern Atlantic "*P. cartilagineum*" (Saunders and Lehmkuhl, 2005) showed specimens within the broadly defined species included an assemblage of cryptic or unrecognized species. Among this assemblage they distinguished four taxa: *P. cartilagineum* sensu stricto, *P. subtile* Kützing (1866), and two new species: *P. nanum* G. W. Saunders et Lehmkuhl (2005) and *Plocamium maggsiae* G. W. Saunders et Lehmkuhl (2005). Cremades et al. (2011: 129, figs. 1–10) clarified the types of *Plocamium cartilagineum* and found *P. subtile* Kützing (1866) to be conspecific (Cremades et al., 2011: 131, figs.11–15). They also recognized two others, *P. lyngbyanum* Kützing (1843) (Cremades et al., 2011: 134, figs. 29–51, 59) and *P. raphelisianum* P. J. L. Dangeard (1949; see also Cremades Ugarte et al., 2007), as being distinct from *P. cartilagineum*.

Natural product chemistry has been studied in some specimens of *Plocamium* (Faulkner, 1977; Fenical, 1983). Although all "*Plocamium cartilagineum*" tested contained a mixture of halogenated monoterpenes, there were also some differences in the natural products of the California specimens versus those analyzed from elsewhere. For example, North Atlantic specimens from the British coast of the English Channel (Faulkner, 1977:6) contained three compounds that were analogues of the compounds found in Pacific Coast (USA) specimens and one major new component that was not found in Pacific material (Stallard and Faulkner, 1974). Furthermore, there were differences between populations of "*P. cartilagineum*" in Santa Cruz (northern California) and La Jolla (southern California) (Faulkner, 1977). Together these studies revealed that the taxonomy of *Plocamium* in the eastern Pacific needs to be critically studied.

Many of the Pacific and Australasia specimens referred to a broadly defined "*P. cartilagineum*" may represent morphologically similar but different entities, some of which may be undescribed species (Saunders and Lehmkuhl, 2005). One species of *Plocamium* is known in the Gulf of California. It is recognized as being distinct from those of the Pacific Coasts of California and Baja California and herein is described as new.

Plocamium katinae J. N. Norris, *sp. nov.*

FIGURE 219

Plocamium coccineum sensu Dawson, 1966a:23; González-González et al., 1996:250 [in part; Gulf of California references only; non *Plocamium coccineum* Lyngbye, 1819:39].

Plocamium cartilagineum sensu Norris, 1985d:213; González-González et al., 1996:250 [in part; Gulf of California references only]; Mateo-Cid et al., 2006:52, 56 [non *Plocamium cartilagineum* (Linnaeus) Dixon, 1967:58; basionym: *Fucus cartilagineus* Linnaeus, 1753:1161].

Latin Diagnosis. Thalli erectis ramosis molliter in unicum planum, saepe ramosis in uno piano ad rubeum, plerumque minus quam 5 cm alt; vel aliqua compressa axes tenues plerumque ad 500 µm latae (quibusdam 750 µm), saepe ramosi axes margine, discoidea appensa pronus implicuit holdfast ramis secundis stolonifera develop attachments, main prima sympodiales axium ramosa, secundarium et ramosa subquent in plus minusve regularibus exemplum, rami marginalis producta series (2–)3–4(–5) ramos marginibus lateribus alternatalternis ramis lateribus ad 3–4 ordinibus, ramorum singulorum ordinum gradatim ad apices latus, imo ramosa manet ramulus, distal sublime in ramulis successive plures palmites series, distal maxime lateralis ramus saepe series indeterminata aucta iterum ramosis alternis regularem normam; ramuli ultimi determinata, recta vel leviter recurvata, acuta, apicibus attenuata. Stichidia tetrasporangial plerumque simplices et ramosa flendo turgiduli similem ramulus ultima (one apicem divisum visurus pars sterilis) 310–510 µm in longitudine 120–150 µm latus, non stichidia dense aggregatae in axillis sed lateralibus margin tollitur in superiorem partem ramulis vel terminales ramulus, plerumque breviter stipitati, 30–60 µm longa. Tetrasporangiis 35–45 µm longus de 20 µm diametro (forsan immatura, ut illi observanda nondum distincte zonate) duo ferri versus bene definitae stichidia. Thalli cystocarpic et spermatangial ignotum.

Algae erect, delicate (not cartilaginous), richly branched in 1 plane, bright red in color, mostly less than 5(–7) cm in height; of 1 or more compressed, slender axes, mostly to 500 µm wide (some to 750 µm), repeatedly branched from opposite margins of axes, up to 3–4 orders; attached by discoid holdfast and entangled lowermost branches that develop secondary stoloniferous attachments. Main axes compressed, with primary branching ramisympodial; secondary and subsequent branching in a more or less regular pattern; marginal branches produced in a series of (2–)3–4(–5) branches to alternating sides. Lowermost branchlet of the lateral series (being the previous apex of the ramisympodial growing axis) remains unbranched and narrows to a tip; margins are smooth. The more distal branchlets of a lateral series are progressively more developed; the most distal branch of the lateral series often indeterminate and growing to repeat the regular alternate branching pattern. Ultimate branchlets determinate, straight or occasionally slightly recurved, tapered to acute apices.

Tetrasporangial stichidia extend in a series along the margins of branches, being derived from conversion of branchlets. Presumably only young tetrasporangial stichidia were observed as tetrasporangia were not yet zonately divided. Most stichidia were simple, resembling a slightly swollen ultimate branchlet; a few were apically bifurcated (see Figure 219C), 310–510 µm in length by 120–150 µm in width; stichidia usually on a short stalk, 30–60 µm long. Tetrasporangia 35–45 µm long, about 20 µm in diameter (probably immature); aligned in two offset rows. Cystocarpic and spermatangial thalli unknown.

Habitat. On rocks, tidal platforms, and sides of tide pools and in crevices and drainage channels of shaded habitats; mid to low intertidal and shallow subtidal, down to 6 m depth.

Distribution. Gulf of California: Puerto Peñasco; Puerto Lobos to El Desemboque (*Haxöl Iihom* in the language of the Seri); Cabeza Ballena.

Type Locality. Mid intertidal; Cumpleaños Tide Pool on tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Gulf of California, Mexico.

Holotype. *JN-3632A* (US Alg. Type Coll.-160510), 24 November 1972, Coll. J. N. Norris and K. E. Bucher; isotype (US Alg. Type Coll.-160511).

Paratypes. Sonora, Puerto Peñasco: Playa Las Conchas (Playa Estación) tidal platform, *EYD-27484* (US Alg.

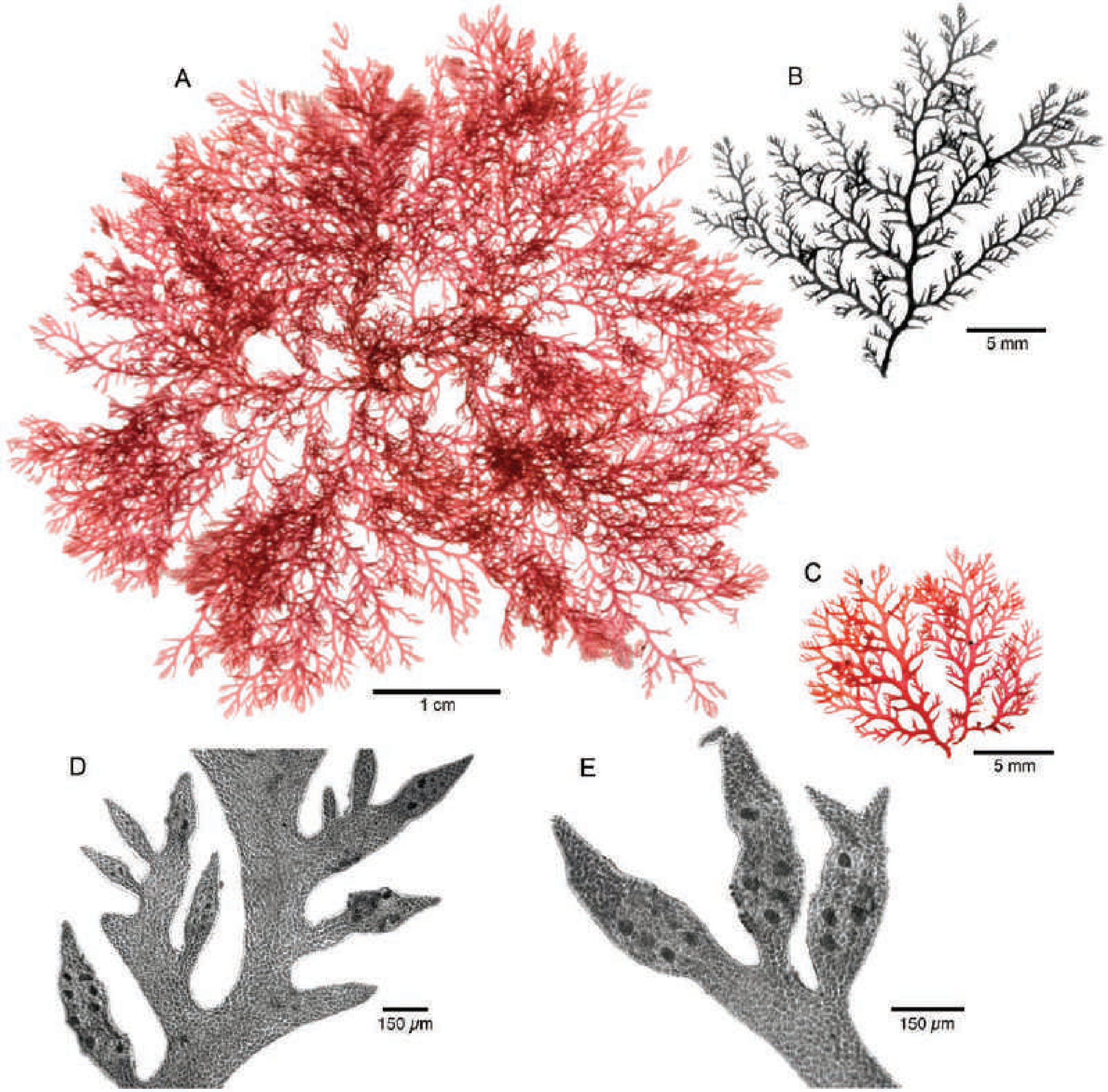

FIGURE 219. *Plocamium katinae* J. N. Norris, *sp. nov.*: A. Holotype, habit (*JN-3632a*, US Alg. Coll.-160510). B, C. Upper portion of branches showing axis with regular alternating series of 3–4 lateral branchlets (B, *JN-4163*, US Alg. Coll.-217348; C, *JN-3897*, US Alg. Coll.-160514). D. Branch axis with tetrasporangial branchlets (*JN-5916*, US Alg. Coll. microscope slide 8682). E. Tetrasporangial branchlets (*JN-5916*, US Alg. Coll. microscope slide 8683).

Coll.-40818), Coll. A. E. Dennis, 29 June 1965; *JN-2948* (US Alg. Coll.-160507), 29 April 1972, Coll. J. N. Norris; *JN-3150* (US Alg. Coll.-160508 and -160509), Coll. J. N. Norris and K. E. Bucher, 11 July 1972. Sonora: Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación): *JN-3656* (US Alg. Coll.-160512), Coll. J. N. Norris and K. E. Bucher, 25 November 1972; *JN-3897* (US Alg. Coll.-160514), 15 April 1973, Coll. J. N. Norris and K. E. Bucher; *JN-4163* (US Alg. Coll.-217348), 1 June 1973, Coll. J. N. Norris and W. Fenical; *JN-4652* (US Alg. Coll.-160158), 4 July 1973, Coll. J. N. Norris, K. E. Bucher, and E. Johansen. Sonora, Punta Pelícano, northwest of Puerto Peñasco: *EYD-27277* (US Alg. Coll.-40854), 6 April 1966, Coll. E. Y. Dawson; *MM/DSL-s.n.* (US Alg. Coll.-163917), Coll. M. M. Littler and D. S. Littler, 5 March 1973; *JN-5884* (US Alg. Coll.-160529), 21 June 1974, Coll. J. N. Norris; *JN-5072* (US Alg. Coll.-160523), Coll. N. McKibbin, 14 February 1974. Sonora, Puerto Lobos: *JN-5916* (tetrasporic), off north side of point, on rock outcropping, about 6 m depth, 17 February 1973, Coll. J. N. Norris and K. E. Bucher. Baja California Sur: *JN-4119* (US Alg. Coll.-160515), Cabeza Ballena (vicinity of the exposed wreck of the Japanese ship, *Inari Maru No. 10*), 3 m depth, 2 January 1973, Coll. J. N. Norris, K. E. Bucher, and H. Sleeper.

ETYMOLOGY. The species is named for Katina Elizabeth Bucher (National Museum of Natural History, Smithsonian Institution) in recognition of her contributions to our knowledge of the northern Gulf's marine algae. It is with Katy that I have shared many adventures in pursuit of our seaweed interests, traveling through the desert and beaches and diving offshore on the reefs of Sonora, Baja California, and Baja California Sur and the islands (Islas de la Cintura) of the Gulf of California.

REMARKS. *Plocamium katinae,* although apparently not a common species in the northern Gulf, is distinctive. Its bright red, compressed axes, with a regular branching pattern in one plane, make it easily recognizable among the Gulf's algae. One specimen with undivided tetrasporangia was collected in February, although the rest of our specimens collected from November to February (once in July) were nonreproductive. Reproduction was previously unknown in Gulf of California specimens (Dawson, 1966a, as "*P. coccineum*").

The Gulf of California *P. katinae* is distinct from the California and Pacific Baja California *Plocamium pacificum* Kylin (1925; G. M. Smith, 1944; =*P. cartilagineum* subsp. *pacificum* P. C. Silva, 1979; =*P. coccineum* var. *pacificum* (Kylin) E. Y. Dawson, 1961a). The Pacific Coast of North America *Plocamium pacificum* (often identified as "*P. cartilagineum*," e.g., Abbott and Hollenberg, 1976) is a more robust, cartilaginous species and usually is much larger (up to 25 cm tall), with axis widths of 1.0–1.5 mm. The Gulf of California *Plocamium katinae* is more delicate, smaller and more compact overall, consistently shorter in height (usually less than 5 cm tall), and thinner in axial width, mostly 500 µm (occasionally to 750 µm) wide, and more finely branched, in an alternating series of (2–)3–4(–5). The one tetrasporophyte of *P. katinae* discovered had a limited number of immature tetrasporangial stichidia; they were mostly simple, in the position of branchlets in a lateral series, and none were found in clusters in the axils of branches. In *P.pacificum*, the stichidia are mostly compound.

Uncertain Record:
***Plocamium violaceum* Farlow**

Plocamium violaceum Farlow, 1877:240; Mendoza-González and Mateo-Cid, 1986:424; González-González et al., 1996:251 [in part, Gulf of California reports only].

REMARKS. Described from central California, *Plocamium violaceum* is reported from Alaska to Pacific Baja California (Abbott and Hollenberg, 1976; Pacheco-Ruíz and Aguilar-Rosas, 1984; Scagel et al., 1989), and Pacific Panama (Fernández-García et al., 2011) and Chile (Ramírez and Santelices, 1991). Specimens referred to "*P. violaceum* Farlow" by Mendoza-González and Mateo-Cid (1986) from Puerto Peñasco should be reexamined to verify its occurrence in the northern Gulf of California.

Excluded Species:
***Plocamium pacificum* Kylin**

Plocamium pacificum sensu Dawson, 1945d:48 [in part; only Gulf of California specimens]; González-González et al., 1996:251 [in part; only Gulf of California references; non *Plocamium pacificum* Kylin, 1925:42].

Plocamium coccineum var. *pacificum* sensu Dawson, 1961a:220 [in part; only Gulf of California specimens]; 1961b:428 [in part; only Gulf of California references]; González-González et al., 1996:250 [in part; only Gulf of California references; non *Plocamium coccineum* var. *pacificum* (Kylin) E. Y. Dawson, 1961a:220].

Plocamium cartilagineum sensu González-González et al., 1996:250 [in part; Gulf of California references only; non *Plocamium cartilagineum* (Linnaeus) Dixon, 1967:58; basionym: *Fucus cartilagineus* Linnaeus, 1753:1161].

REMARKS. Examination of northern Gulf of California specimens identified as "*Plocamium pacificum*" (US Alg. Coll.) has shown them to be the new species *P. katinae,* and the presence of *P. pacificum* in the northern Gulf is doubtful. Currently, *P. pacificum* is known on the Pacific coasts of North America from Alaska to Isla Magdalena, Baja California Sur (Smith, 1944, as *P. pacificum*; Dawson, 1961a, as *P. coccineum* var. *pacificum*; Silva, 1979, as *P. cartilagineum* subsp. *pacificum*; Scagel et al., 1989, as *P. cartilagineum*; Withall and Saunders, 2007, as *P. pacificum*), and Isla Clarión (Islas Revillagigedo) (Taylor, 1945, as *P. pacificum*), in Central America from Pacific Panama (Littler and Littler, 2010; Fernández-García et al., 2011, both as *P. cartilagineum* subsp. *pacificum*), and in South America from the Galápagos Islands (Taylor, 1945, as *P. pacificum*).

SEBDENIALES

Sebdeniales Withall et G. W. Saunders, 2007:388.

Growth is multiaxial in members of this order, and thalli have a filamentous medulla surrounded by a pseudoparenchymatous cortex.

Life histories include isomorphic tetrasporophytes and gametophytes. Tetrasporangia are cruciately to irregularly divided.

Carpogonia and auxiliary cells develop in separate branch systems (nonprocarpic) and are not positioned in specialized ampullae. After diploidization, auxiliary cells produce a single gonimoblast initial that develops thallus outward.

The Sebdeniales is currently a monotypic order, with its single family, the Sebdeniaceae, occurring in the northern Gulf of California.

SEBDENIACEAE

Sebdeniaceae Kylin, 1932:12.

Algae are erect or repent, terete to compressed, branched to foliose, and soft to firm in texture. Growth is multiaxial. The cortex is composed of layers of round to elongate cells, which become progressively smaller toward the thallus surface. Centrally, the medulla is composed of parallel to entangled filaments that grade outward to stellate or ganglioid cells that connect to inner cortical cells.

Tetrasporophytes and gametophytes are isomorphic. Tetrasporangia are cruciately to irregularly cruciately divided (sometimes appearing zonate), produced laterally from outer cortical cells, and are scattered throughout the cortex or in nemathecia depending on the genus. Gametophytes are monoecious or dioecious. Female reproductive structures are nonprocarpic and lack ampullar structures for carpogonial branches or auxiliary cell branches. Carpogonial branches are three- to four-celled and borne laterally on or in unmodified cortical filaments separate from those bearing intercalary auxiliary cells. After fertilization, carpogonia of most species produce a number of connecting filaments that radiate out and fuse with auxiliary cells. A gonimoblast initial is issued directly from an auxiliary cell and develops toward the thallus surface to form the carposporophyte. The auxiliary fusion cell remains at the base of the developing carposporophyte. Some species have rudimentary pericarps. Compact lobes of carposporangia develop from all but the innermost gonimoblast cells. Cystocarps are embedded in the thallus, only slightly protuberant, and scattered or aggregated throughout the thallus. Spermatangia are hyaline, pyriform to subglobose, produced from outer cortical cells, and form superficial sori.

REMARKS. Since the family was recognized on the basis of *Sebdenia*, two other genera have been described, *Crassitegula* C. W. Schneider, C. E. Lane et G. W. Saunders (2006) and *Lesleigha* Kraft et G. W. Saunders (2011). Kraft and Saunders (2011) also documented the existence of additional taxa, noting a higher diversity is likely to be found in this order, as well as additional species richness within *Sebdenia*.

The Sebdeniaceae is represented by one genus, *Sebdenia,* in the northern Gulf of California.

Sebdenia (J. Agardh) Berthold

Halymenia sect. *Sebdenia* J. Agardh, 1876:134.

Sebdenia (J. Agardh) Berthold, 1882a:530; Berthold, 1884:21; Hansen, 1989:54–59.

Algae erect, terete and tubular to flattened and blade-like, the various morphologies arising above a small stipe that is attached by a small discoid or crustose holdfast. Cortex pseudoparenchymatous, of few to many layers of cells, cells becoming progressively smaller from inner to outer cortex; outermost cortical cells pigmented and slightly elongate. Medulla of loosely arranged, mostly longitudinal filaments (arms or rays), which radiate outward from stellate or ganglioid cells and connect to other filament cells; ganglioid cells with shorter filaments radiating outward. Dark staining “gland cells” (“conjunctor cells” of Gavio et al., 2005; “ray primordial” of Kraft and Saunders, 2011) are borne occasionally on some cells of the inner cortex and medulla in some species.

Tetrasporangia are scattered in the outer cortex. Carpogonial branches are 3–4 celled and develop on inner cortical cells, separate from auxiliary cells, in otherwise unmodified cortical filaments. Fertilized carpogonia of most species directly produce connecting filaments that radiate out and fuse with auxiliary cells. Connecting filaments may terminate at the base of the auxiliary cell or may continue to grow and effect diploidizations of additional auxiliary cells (Hansen, 1989). Auxiliary cell often surrounded by nutritive cells. Cystocarps are embedded and protuberant as the chamber with the developing carposporophyte uplifts the thallus surface. Depending on the species, cystocarps are with or without an ostiole, some with a rudimentary ostiole (Hansen, 1989).

There is one species of *Sebdenia* currently recognized in the Gulf of California.

Sebdenia flabellata (J. Agardh) P. G. Parkinson

FIGURE 220

Isymenia flabellata J. Agardh, 1899:62, 66.

Sebdenia flabellata (J. Agardh) P. G. Parkinson, 1980:12; Schneider and Wynne, 1991:473, fig. 1 (lectotype); Yoshida, 1998:796, fig. 3-71 C; Xia and Zhang, 1999:115, fig. 67, pl. 7: fig. 6; Pacheco-Ruíz et al., 2008:210; Hernández-Kantún et al., 2009:249, tbl. 1; Fernández-García et al., 2011:64; Acleto O. and Zúñiga A., 2011:109, figs. 41–48.

Halymenia agardhii De Toni, 1905:1542 [new name; to avoid creating a homonym of *Halymenia flabellata* F. Schmitz, 1895:140]; Okamura, 1930:21, pl. 266: figs. 1–3; 1936:534; Taylor, 1945:205; Dawson, 1954c:268, pl. 11: fig. 54; Dawson et al., 1960a:20; Dawson, 1961b:423; Mateo-Cid and Mendoza-González, 1992:21; Serviere-Zaragoza et al., 1993a:483; Pacheco-Ruíz and Zertuche-González, 2002:467.

Sebdenia agardhii (De Toni) Codomier, 1972:747.

Halymenia polydactyla Børgesen, 1932a:122, fig. 10, pl. IV; Yamada, 1938b:126, pl. 28.

Sebdenia polydactyla (Børgesen) M. S. Balakrishnan, 1961a:89; 1961b:212, figs. 28–41, pl. 6: figs. 1, 2; Norris and Bucher, 1976:14, figs. 11a–c, 12a–c; Acleto O., 1980:11, figs. 14, 25–29; Hansen, 1989:58; Ramírez and Santelices, 1991:292; González-González et al., 1996:270; Pacheco-Ruíz et al., 2008:210.

Algae are subcylindrical to slightly compressed (more or less oval in transection), dichotomously branched in 1 plane, up to 21 cm tall, rose red to dark purple-red in color, elastic and tough in texture, with a smooth lubricous surface and attached below by a discoid holdfast. Branches are mostly 0.5–1.1 cm wide, occasionally 1.6(–2.3) cm broad below the branch forks,

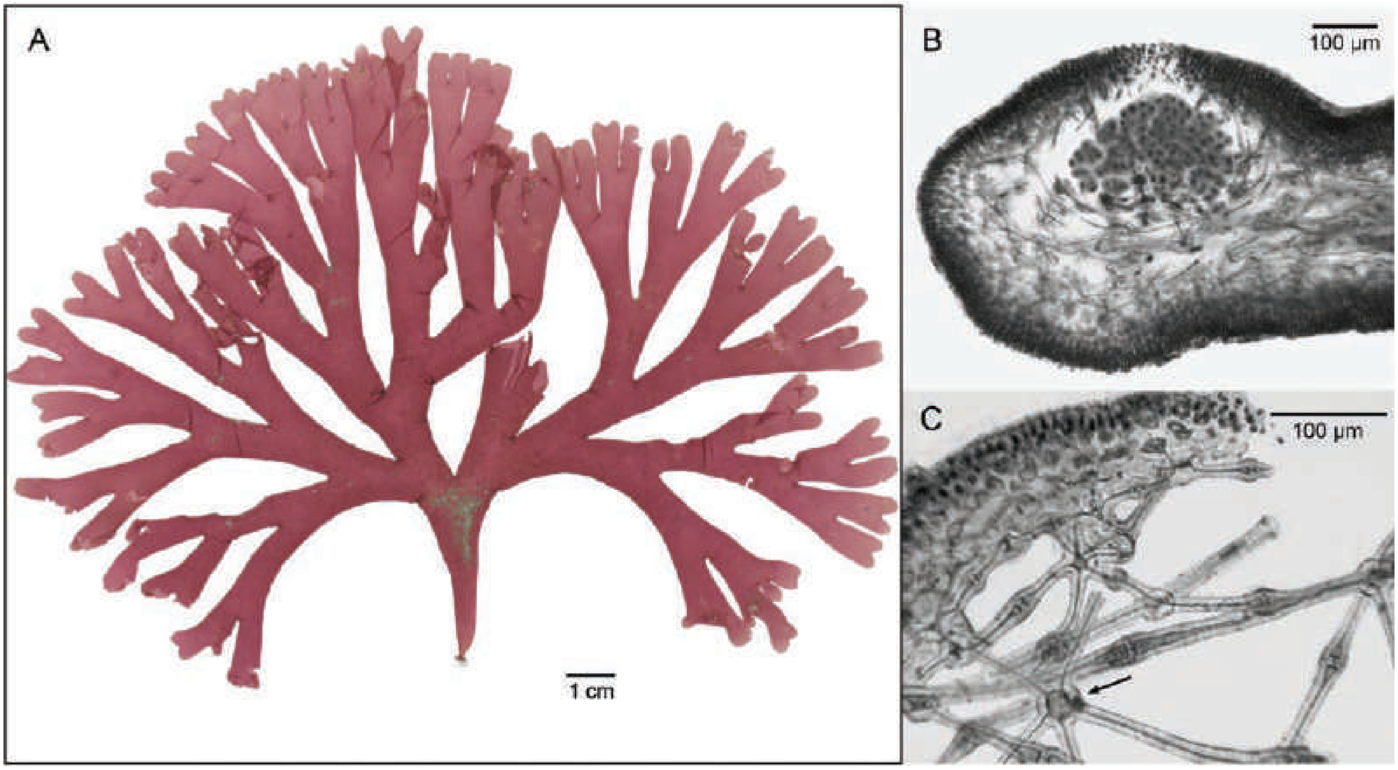

FIGURE 220. *Sebdenia flabellata*: A. Habit (*JN-5490*, US Alg. Coll.-217352). B. Transection of cystocarp showing basal fusion cell (*JN-4430*, US Alg. Coll. microscope slide 4503). C. Transection through cortical and medullary layers showing pigmented gland cell (arrow) on a large stellate cell of the inner medulla (*JN-3398*, US Alg. Coll. microscope slide 4501).

with blunt or broadly rounded apices. Small marginal proliferations are rarely present. Medulla composed of numerous stellate cells, each with a number of long, thin filaments (rays or arms) radiating outward. Stellate cells are dense in the outer medulla, markedly ganglioid, with centers 12–23 μm in diameter, and radiating, short filaments (to 30 μm long). In the inner medulla, the stellate cells are more loosely arranged and larger, with centers 18–40 μm in diameter, and narrow, straight radiating filaments 130–180(–300) μm long. Pigmented "gland-like" cells (ray primordia, conjunctor cells), about 10–30 μm long, are occasional on the stellate cells and filiform medullary filaments. Cortex pseudoparenchymatous and narrower, 4–5(–7) cells thick. Outer cortex is of small pigmented cells, 3–6 μm in diameter, 3.0–12.5 μm long, that grade into the larger and more loosely arranged unpigmented inner cells, 20–30 μm in diameter.

Tetrasporangia cruciately divided, spherical to vertically elongate, 13–18 μm in diameter, 20–31 μm long, scattered in the outer cortex. Gametophytes dioecious. Cystocarps 180–310 μm in diameter, scattered over middle portions of thallus. Cystocarps embedded, bulging out the cortex above and forming an arched wall of vertical rows of 5–7 cortical cells. The developing carposporophyte has a dense base, an irregularly shaped auxiliary fusion cell, and nutritive cells, and the stellate cells of the outer medulla appear to stretch around the developing carposporophyte, creating a rudimentary pericarp.

HABITAT. On rocks; shallow subtidal, 3–23 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Caleta Santa María (north of Santa Rosalía); Nayarit to Jalisco; Isla María Magdalena (Islas Marías; =Islas Tres Marías). Eastern Pacific: Isla Asunción, Baja California Sur; Panama; Peru. Western Pacific: Japan; China.

TYPE LOCALITY. Guadeloupe, French West Indies, Lesser Antilles, Caribbean Sea.

REMARKS. Although most have followed Børgesen (1932a) in recognizing the similarity of the western Atlantic *Sebdenia flabellata* (type locality: Guadeloupe, Caribbean Sea) and Indian Ocean *S. polydactyla* (type locality: Port Okha, Gujarat, India), Silva et al. (1996a) noted that their being conspecific needs to be tested by studying their respective type specimens. The Gulf of California specimens tentatively referred to *S. flabellata* should also be critically compared with the type materials to elucidate their relationships. The sulfated polysaccharides from the Indian Ocean *Sebdenia flabellata* exhibited antiviral activity (Ghosh et al., 2009, as "*S. polydactyla*"). It would be interesting to investigate those of the northern Gulf *S. flabellata* to test if they too exhibit similar properties.

RHODYMENIALES

Rhodymeniales F. Schmitz in Engler, 1892:19.

Algae are cylindrical to foliose and tubular, compressed, or flattened and simple or branched. Most are erect, although some may be low growing or prostrate or partly erect and partly prostrate. Thalli are multiaxial in construction and can be solid or hollow or with solid axes and hollow branches. In those that are solid throughout or partially solid, the medulla is pseudoparenchymatous, composed of large cells (never filamentous). The cortex is composed of small cells. In those that are hollow, the inner cortical cells are lined with a limited number of longitudinal filaments that border the mucilage-filled cavity.

Tetrasporophytes produce regular or irregular cruciately or tetrahedrally divided tetrasporangia or produce polysporangia within the cortex that are either scattered over the surface or in nemathecial sori in some members. Gametophytes are dioecious or monoecious. Carpogonial branches are either three- or four-celled. The auxiliary cell is the terminal cell of two cells borne on the supporting cell of the carpogonial branch. After fertilization, gonimoblast filaments are produced outward from an auxiliary cell, with most of the cells developing into carposporangia. Spermatangia develop from outer cortical cells to form various-sized sori.

Four families of the Rhodymeniales are represented in the northern Gulf of California.

KEY TO THE FAMILIES OF RHODYMENIALES IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli solid throughout; medulla pseudoparenchymatous; cystocarps with well-developed and persistent *tela arachnoidea* . . . . **Faucheaceae**

1b. Thalli may be solid or hollow throughout or partly solid and partly hollow; cystocarps with *tela arachnoidea*–like filaments or lacking them 2

2a. Thalli may be solid centrally with pseudoparenchymatous medullary cells (filaments absent) or with solid stipe and centrally hollow, nonseptate branches without longitudinal filaments bordering the hollow cavity; tetrasporangia cruciately (or decussately) divided; cystocarps lacking *tela arachnoidea* . . . . **Rhodymeniaceae**

2b. Thalli with centrally hollow branches divided into segments by septa; bordering the hollow cavity are longitudinal filaments lining inner cortical cells; tetrasporangia tetrahedrally (rarely cruciately) divided; cystocarps with or without spiderweb-like filaments (=*tela arachnoidea*) 3

3a. Branches divided at consistent (regular) intervals into segments by septa (diaphragms) of a single cell layer; carpogonial branches 4-celled; some *tela arachnoidea*–like filaments in cystocarpic cavity; tetrasporangia scattered in cortex . . . . **Champiaceae**

3b. Branches divided into irregularly (variably) sized segments by septa of multiple cell layers or irregular filamentous plugs; carpogonial branches 3-celled; *tela arachnoidea* filaments absent from cystocarpic cavity; tetrasporangia terminal on cortical cells in small sunken sori formed by invagination of the cortex . . . . **Lomentariaceae**

CHAMPIACEAE

Champiaceae Kützing, 1843:438; Saunders et al., 1999:35.

Algae are cylindrical to compressed, regularly segmented fronds that are hollow and filled with a dilute mucilage. The primary axes and stipitate region may also be hollow or may be solid in some members. Branch cavities are divided into segments that are separated by monostromatic transverse septa (diaphragms) (except *Dictyothamnion*) and lined by multiple longitudinal filaments bearing secretory cells. Cortex of one to a few (four) cell layers. Thalli multiaxial in structure, with a group of apical cells at their tips.

Sporophytes produce tetrahedrally divided tetrasporangia, developed from cortical cells, scattered in the cortex of branches, and/or polysporangia are produced in some species of *Gastroclonium*. Gametophytes dioecious or monoecious. Female gametophytes are procarpic; carpogonial branches are four-celled, with the auxiliary cell fusing with other cells after fertilization. The gonimoblast is globular, with most of its cells becoming carposporangia; hemispherical, with carposporangia borne directly on the fusion cell; or radiating, with only its terminal cells producing carposporangia. The fusion cell is usually small and compact, with outlines of its component cells remaining discernible; however, in some members, the fusion cell is comparatively massive, and outlines of constituent cells are obscured. Cystocarps are large, subspherical, and protruding. Spermatangia are developed in superficial sori over outer cortical cells of branches.

Two genera of the Champiaceae are represented in the northern Gulf of California.

KEY TO THE GENERA OF CHAMPIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Fronds with solid, terete, simple to branched stipe and primary axes and hollow, cylindrical to compressed, segmented branches; pericarp without *tela arachnoidea*–like filaments surrounding carposporophyte . . . . ***Gastroclonium***

1b. Fronds without solid stipe or axes; hollow throughout, cylindrical to compressed, segmented axes and branches; pericarp with *tela arachnoidea*–like filaments surrounding carposporophyte . . . . ***Champia***

Champia Desvaux

Champia Desvaux, 1809:245.

Algae may be entirely erect, prostrate, or partly prostrate and erect and composed of terete, compressed, or flattened axes, depending on the species. Thalli are segmented and alternately or sometimes oppositely or irregularly branched. Growth is multiaxial, from a group of apical cells, and the thallus is attached by a discoid holdfast. Thalli are divided into hollow segments filled with a dilute mucilage, separated by septa (diaphragms) one cell layer thick at regular intervals and may or may not be constricted at the septa. The hollow cavities are bordered by a limited number of longitudinal filaments that bear secretory cells (gland cells), and connect with cells of the septa. The cortex is thin, 1–2(–3) cells thick, with an inner layer of large cells and an outer incomplete layer of small cells.

Tetrasporangia are tetrahedrally divided, often numerous, and scattered over upper portions of branches, transformed from cortical cells and protruding inward toward the hollow cavity. Two types of sporangial development have been reported: intercalary on cortical cells (Irvine and Guiry, 1983) and from a single division of a terminal cortical cell to produce a tetrasporangium (Ballantine and Lozada-Troche, 2008). Gametangial thalli are dioecious. Procarps develop in cortical layers and consist of a four-celled carpogonial branch and a single two-celled auxiliary cell branch. After fertilization, the gonimoblast develops outward from a fusion cell, and terminal cells of the gonimoblast produce carposporangia. Cystocarps have a well-developed pericarp and an ostiole. The pericarp has a filamentous inner lining, with inner cells that become stellate and spiderweb-like (resembling *tela arachnoidea*). Cystocarps are scattered and conspicuously protrude from their bearing branch. Spermatangia develop in superficial sori on branches, with spermatia borne subterminal on elongated parent cells issued from cortical cells.

REMARKS. Species of *Champia* are widely reported in warm-temperate to tropical seas. Spore germination and frond development was reported by Boillot (1961). A triphasic life history was described for *C. parvula* by Steele and Thursby (1983), who also suggested that with its ease of maintenance in culture and relatively short life history (completed in six weeks), it could be used as a bioassay organism. It has also been used for studies on the genetics of red algae (Kehoe and van der Meer, 1990). The two different methods of tetrasporangia development are problematic, and its implication for possible generic separation needs to be further investigated (Ballantine and Lozada-Troche, 2008).

Of the three species in the Gulf of California, two were described from the northern Gulf, and a third, *C. parvula,* is reportedly widespread in distribution.

KEY TO THE SPECIES OF *CHAMPIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Fronds cylindrical; of open, loose, segmented branches; mostly 1.0 mm or more in diameter (0.5–2.5 mm) .... ***C.* cf. *parvula***

1b. Fronds compressed; of somewhat open to dense, segmented branches; mostly less than 1.0 mm wide (0.6–0.9 mm in width) 2

2a. Fronds erect; of somewhat open, distichously branched, strongly compressed branches; segments 600–1100 µm wide by 200–350 µm high in transection .... ***C. disticha***

2b. Fronds low growing (mostly repent or only partially erect); compact, dense mats of entangled, overlapping, slightly compressed branches (oval in transection); multifariously branched; segments about 900 µm wide by 500 µm high in transection .... ***C. caespitosa***

Champia caespitosa E. Y. Dawson

FIGURE 221B

Champia caespitosa E. Y. Dawson, 1944a:311, pl. 46: figs. 3, 4; 1950d:341 [in part; not including *Champia parvula*]; Levring, 1960:59; Dawson, 1963a:468 [in part; only *C. caespitosa* specimens]; Ramírez and Santelices, 1991:294; González-González et al., 1996:190.

Algae forming low-growing, dense mats of repent to partially erect, entangled and often rhizoidally adjoined, overlapping branches, up to 2 cm tall. Thalli subterete in younger portions and slightly compressed in older portions, regularly constricted, hollow segments divided by septa 1 cell layer thick; segments oval in transection about 700–900 µm wide by 450–500 µm high; branching multifarious; branches attached to other branches by numerous accessory holdfasts and to the substratum or other algae by several irregular, rhizoidal discs formed by elongation and division of surface cells. Branches originate primarily from internodal segments and possibly at septal nodes as well (Dawson, 1944a: pl. 46: fig. 3). Outer cortex a layer of elongated cortical cells, interspersed with smaller irregularly shaped cells; inner side of cortical cells occasionally with secretory cells and lined with longitudinal filaments bearing secretory cells.

Reproductive sporophytes and gametophytes not known.

HABITAT. On rocky shore; epiphytic on other algae, such as *Amphiroa*, *Digenea,* and *Centroceras*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda, and Isla Estanque (Islas de la Cintura). Eastern Pacific: Chile.

TYPE LOCALITY. Isla Estanque (Pond Island), off southeast end of Isla Ángel de la Guarda, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. *Champia caespitosa* is separated from Gulf *C. parvula* by their habit morphology (Dawson, 1944a). Fronds of *C. caespitosa* are repent, composed of compressed branches (oval in transection; Dawson, 1944a, pl. 46: fig. 4) that form compact,

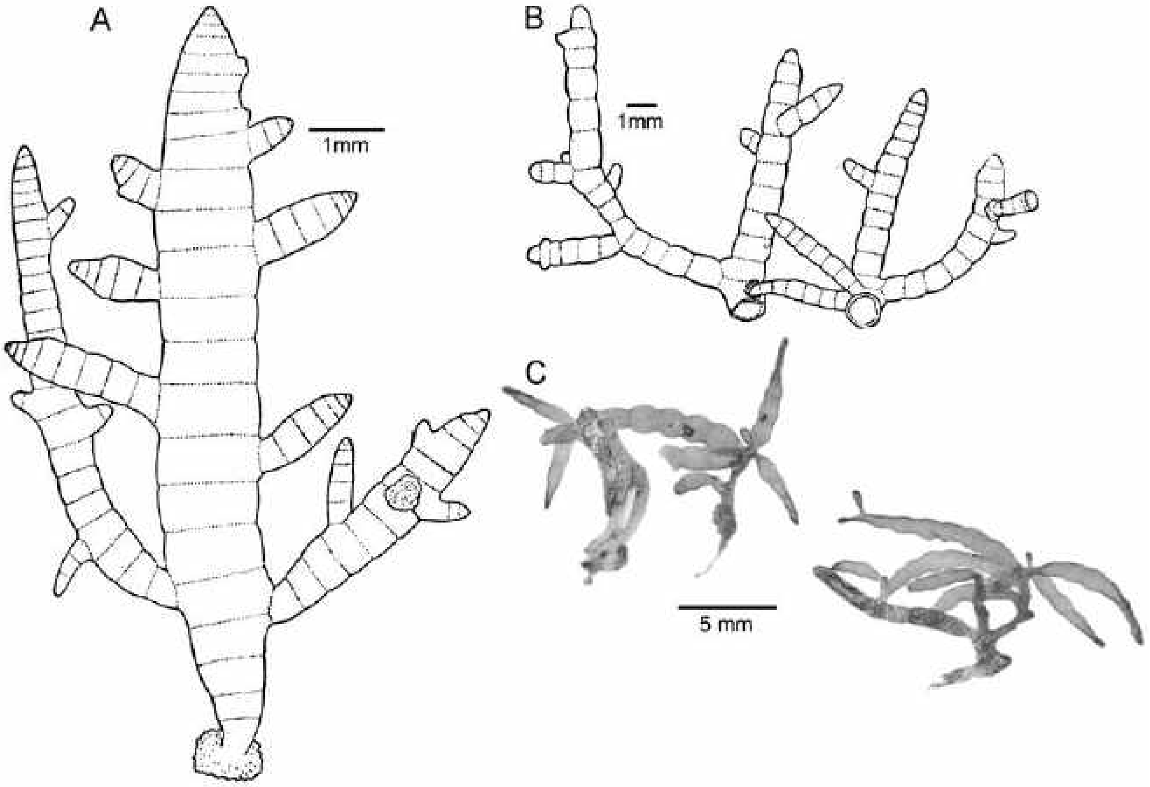

FIGURE 221. Species of *Champia* and *Gastroclonium*. A. *Champia disticha*: Holotype (after Dawson, 1944a: pl. 46: fig. 5). B. *Champia caespitosa*: Holotype (after Dawson, 1944a: pl. 46: fig. 3). C. *Gastroclonium compressum*: Habit (*JN-5234*, US Alg. Coll.-158972).

low-growing, dense mats, with fronds that abundantly produce rhizoidal attachment structures that make it rigid. In contrast, Gulf *C. parvula* is terete throughout, more erect, and composed of more open, looser, less rigid branches. Later, Dawson (1963a) considered *Champia caespitosa* to be a synonym of a broadly defined *C. parvula*; however, others still recognized it as distinct (e.g., Ramírez and Santelices, 1991). The taxonomic status of the two described northern Gulf of California species, *C. caespitosa* and *C. disticha,* needs to be reinvestigated. A comparative systematic study using molecular markers of type locality material of these Gulf species and type locality material of *C. parvula* would help determine if species separation is supported.

Champia disticha E. Y. Dawson

FIGURE 221A

Champia disticha E. Y. Dawson, 1944a:310, pl. 46: fig. 5; 1950d:341 [in part; not including *Champia parvula*]; 1963a:468 [in part; only *C. disticha* specimens]; González-González et al., 1996:190.

Small epiphytes 5–15 mm tall; of strongly compressed, hollow, regularly segmented axes and branches; in transection, 600–1100 µm wide and about 350 µm tall; distichously branched; short branches little constricted at base, with acute apices; branch segments much shorter than wide and slightly constricted at septa; attached below by a small rhizoidal holdfast, and sometimes secondarily by rhizoidal attachments from branches. Branches apparently developed at both septal nodes of segments and between the septa (internodes) (Dawson, 1944a: pl. 46: fig. 5). Cortex a single layer of small, slightly elongate, angular cells; inner side of cortical cells lined with longitudinal filaments that bear secretory cells toward the hollow cavity.

Reproductive structures unknown.

HABITAT. Epiphytic on various algae, including *Laurencia*, *Corallina*, and *Amphiroa*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Isla San Esteban (Islas de la Cintura).

TYPE LOCALITY. Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. Dawson (1944a) characterized *Champia disticha,* a little-known species, by its small size, strongly compressed branches, and distichous branching. In species of *Champia* the origin of the branches is a character considered unique to the species (Ballantine and Lozada-Troche, 2008; Lozada-Troche and Ballantine, 2010). Since the illustration of Dawson (1944a: pl. 46: fig. 5) shows branches developed at the septal nodes of segments and from the internodes between the septa, the manner of branch formation in *C. disticha* needs to be re-examined. *Champia disticha* somewhat resembles another flattened species, *C. vieillardii* Kützing (1866). Although similar in width to *C. disticha* (0.6–1.0 mm), *C. vieillardii* (0.7–1.5 mm) is not constricted at the septa, and it branches alternately to irregularly in more than one plane. Dawson (1963a) later considered *C. disticha* to be conspecific with a broadly defined *C. parvula*, but others have continued to recognize it (e.g., Silva et al., 1987). These two differ in that *C. parvula* is terete and usually radially alternately branched, and *C. disticha* is flattened and distichously branched. (See also Remarks for *Champia caespitosa*.)

***Champia* cf. *parvula* (C. Agardh) Harvey**

FIGURE 222

Chondria parvula C. Agardh, 1824:207; Lozada-Troche and Ballantine, 2010:140, fig. 18 [type specimen].

Champia parvula (C. Agardh) Harvey, 1853:76; Setchell and Gardner, 1930:153; Dawson, 1944a:310; Taylor, 1945:256; Dawson, 1950d:337, 341 [in part]; 1957c:20; 1959a:28; Levring, 1960:58; Dawson, 1961b:437; 1963a:468 [in part; excluding *C. caespitosa* and *C. disticha*], pl. 93; Huerta-Múzquiz and Tirado-Lizárraga, 1970:129; Chávez-Barrear, 1972b:269; Norris, 1973:15; Huerta-Múzquiz and Garza-Barrientos, 1975:9; Abbott and Hollenberg, 1976:565, fig. 511; Y.-P. Lee, 1978:140, figs. 60–68, pl. IV: figs. D–F; Schnetter and Bula-Meyer, 1982:145, pl. 24: figs. B,C; Tseng, 1983:122, pl. 64: fig. 2; Irvine and Guiry, 1983:78; Mendoza-González and Mateo-Cid, 1986:425; Santelices and Abbott, 1987:9; Sánchez-Rodríguez et al., 1989:44; Dreckmann et al., 1990:32, pl. 5: fig. 1; Ramírez and Santelices, 1991:294; Serviere-Zaragoza et al., 1993a:483; Stout and Dreckmann, 1993:15; Mateo-Cid et al., 1993:47; Mendoza-González et al., 1994:107; González-González et al., 1996:306; Anaya-Reyna and Riosmena-Rodríguez, 1996:864, tbl. 1; Riosmena-Rodríguez et al., 1998:28; Xia and Zhang, 1999:149, fig. 87; Mateo-Cid et al., 2000:66; L. Aguilar-Rosas et al., 2000:131; Cruz-Ayala et al., 2001:191; CONANP, 2002:141; L. Aguilar-Rosas et al., 2002:234; Pacheco-Ruíz and Zertuche-González, 2002:468; López et al., 2004:11; Riosmena-Rodríguez et al., 2005a:33; Mateo-Cid et al., 2006:56; Serviere-Zaragoza et al., 2007:9; Pacheco-Ruíz et al., 2008:210; Lozada-Troche and Ballantine, 2010:139 [as "*C.* cf. *parvula*"], figs. 1–6, tbl. 3; Fernández-García et al., 2011:61.

Algae erect and spreading, forming soft clumps; up to 1.0(–3.0) cm tall in the Gulf; cylindrical, of segmented hollow axes and branches. Hollow portions separated by transverse, monostromatic septa, constricted at the septal regions. Axes 1.0–2.5 mm in diameter; branches 0.5–1.5 mm in diameter, narrowing toward rounded apices. Branches originating at septal nodes of segments, axes irregularly alternately branched, radially arranged. Thalli attached basally to substratum and may be secondarily attached by prostrate axes and branches in contact with substratum, host alga, or sea grass. Cortical layer 1–2(–3) cells thick, a mixed pattern of large cells (up to about 30–40 µm in diameter by 60–80 µm long) and frequent small spherical cells (to 10 µm in diameter) interspersed. Secretory cells simple, rounded, borne along multiple longitudinal filaments bordering the hollow cavities.

Tetrasporangia ovoid, 50–60 µm long, tetrahedrally divided, scattered in cortex, projecting inward.. Cystocarps sessile, protruding, conspicuous, 800–1000 µm in diameter, with an ostiole. Carposporangia clavate-obconical (up to 50 µm in diameter distally and up to 140 µm in length; e.g., Dawson, 1963a: pl. 93, fig. D). Spermatangia not seen in Gulf material.

HABITAT. On rocks or epiphytic on other algae; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Tornillal (Gulfo de Santa Clara) to San José del Cabo. Eastern Pacific: California Channel Islands to La Jolla (southern California); Baja California to Guerrero; Isla Socorro, Isla Clarión, and Isla San Benedicto (Islas Revillagigedo); El Salvador; Costa Rica; Isla Gorgona, Colombia; Ecuador; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands (Abbott, 1999). Western Pacific: China (Tseng, 1983; Xia and Zhang, 1999); Japan (I. K. Lee, 1978; Yoshida, 1998); Korea (Y.-P. Lee, 2008).

TYPE LOCALITY. "Ad Gades" (Agardh, 1824:207); Cádiz, Iberian Peninsula, southwestern Spain.

REMARKS. The Gulf of California specimens that have been identified as "*Champia parvula*" need to be reinvestigated as the worldwide, broadly defined species concept of *C. parvula* appears to represent a complex of several species rather than a single entity. Molecular systematic studies will help elucidate if there is one or more species.

***Gastroclonium* Kützing**

Gastroclonium Kützing, 1843:441, *nom. cons.*
Coeloseira Hollenberg, 1941[1940]:871.

Algae consisting of an erect, solid, terete stipe and erect or arching branches that arise from stoloniferous or discoid holdfasts. Branches are terete or compressed and either short and vesicle-like or long and divided into segments by transverse septa, with segments hollow and filled with a watery mucilage. Branching can be dichotomous, lateral, or irregular. Thalli multiaxial in structure, with grouped apical cells at apices. Branches composed of an outer incomplete layer of small cortical cells and an inner cortex of larger cells that are lined with parallel longitudinal filaments bearing inwardly directed secretory cells. Longitudinal filaments connect with the monostromatic septa separating the segments.

Reproductive structures are produced only on branches. Life history, where known, is triphasic (*Polysiphonia*-type; West and Hommersand, 1982). Polysporangia usually of 8–16 polyspores, or tetrahedrally divided tetrasporangia are scattered in distal branches (Guiry, 1990b). Gametangial thalli are dioecious. Female gametophytes are procarpic, with a 4-celled carpogonial branch that has two 2-celled auxiliary cell branches. The gonimoblast develops outward and produces large, wedge-shaped carposporangia directly from a large fusion cell. Cystocarps are scattered, protrude from the branch surface, and have a thick pericarp that lacks an ostiole and is without *tela arachnoidea* filaments. Spermatangia are developed in superficial sori

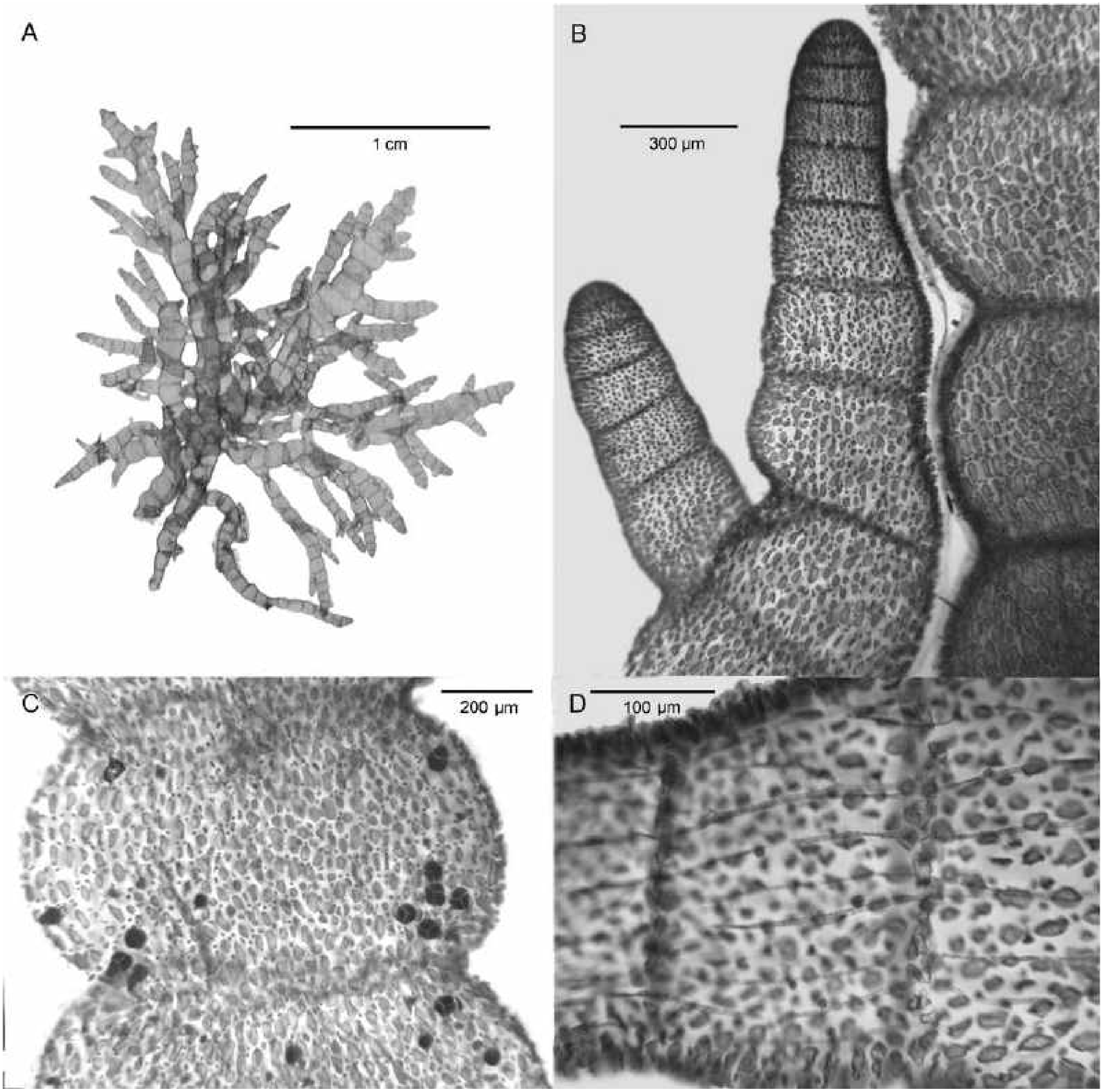

FIGURE 222. *Champia* cf. *parvula*: A. Habit, showing branching pattern and segments at consistent intervals (*JN-5311*, US Alg. Coll.-158921). B. Branch originating from septal region and intermixed cortical pattern of larger cells cutting off small cells. C. Surface view of tetrasporangia scattered in cortex. D. Several segments with focus on the longitudinal filaments connecting with monostromatic septa cell layer (note orientation of this figure is perpendicular to the previous figures; B–D, *JN-4001*, US Alg. Coll. microscope slide 4583).

on the distal branches; spermatia terminal on elongated parent cells borne on branched filaments produced from the cortical cells.

Remarks. The solid, terete stipe and branched axes of *Gastroclonium* are the primary characters that differentiate it from the similar genera *Chylocladia* Greville in W. J. Hooker (1833) and *Champia*, both of which lack solid stipes or solid axes. Species of *Gastroclonium* occur in the North and South Atlantic, the Pacific Coast of North America, Gulf of California, Japan, China, and India.

Three species of *Gastroclonium* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *GASTROCLONIUM* IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli 3–8 cm tall; branches more or less terete; cystocarps large, about 500 μm in diameter . . . . ***G. pacificum***
1b. Thalli smaller, usually less than 3 cm tall; branches terete to compressed; cystocarps smaller, less than 350 μm in diameter 2
2a. Branches compressed; branch walls mostly 1 cell layer thick . . . . ***G. compressum***
2b. Branches terete; branch walls of 2–3 cell layers . . . . ***G. parvum***

Gastroclonium compressum (Hollenberg) C. F. Chang et B.-M. Xia

FIGURE 221C

Coeloseira compressa Hollenberg, 1941:874, figs. 7c,d, 13–17; Smith, 1944:304, pl. 76: fig. 2; Dawson et al., 1960a:24; Dawson, 1961b:438; 1963a:469, pl. 95: figs. 3, 4, 7; Abbott and Hollenberg, 1976:566, fig. 512; Devinny, 1978:359; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; R. Aguilar-Rosas et al., 1990:125; R. Aguilar-Rosas and Aguilar-Rosas, 1994:523; González-González et al., 1996:192; Riosmena-Rodríguez et al., 2005a:33.

Gastroclonium compressum (Hollenberg) C. F. Chang et B.-M. Xia, 1978:209, 213; Ramírez and Santelices, 1991:295; Stewart, 1991:121; Hughey et al., 1996:432.

Algae erect, spreading, low growing, mostly 1–2(–3) cm tall in the Gulf; primary axes cylindrical, solid, short, up to 7 mm long; branches slightly compressed, up to 1 mm wide, appearing somewhat horizontal to axis, recurving toward substratum; attached by stoloniferous base; and where downward-curving branch apices contact substratum, a new thallus may develop at contact point. Hollow tubular branches divided by septa into regular segments, constricted at septa; branches simple or with a few short branchlets on side away from substratum. Outer cortex a continuous single cell layer, with an incomplete layer of slender, longitudinal filaments connecting to outer cells and bearing secretory cells.

Polysporangia globose, divided into 12–16 polyspores; scattered in upper portion of branches. Cystocarps scattered, protruding beyond surface of branches, 300–350 μm in diameter; without an ostiole. Spermatangia unknown in Gulf of California specimens.

Habitat. On rocks or tidal platform or sometimes epiphytic or entangled with other algae; mid intertidal to shallow subtidal, down to 2 m depths.

Distribution. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco, to Isla Estanque (Islas de la Cintura). Eastern Pacific: Pacific Grove (central California) to Bahía de Ballenas (Baja California Sur); Islas Todos Santos (off Ensenada), Baja California; Chile.

Type Locality. Corona del Mar, Orange County, southern California, USA.

Remarks. Intertidal specimens of *Gastroclonium compressum* from Puerto Peñasco (*JN-5129, JN-5234*) and the south end of Isla Estanque (*JN-5599*) establish its presence in the northern Gulf of California. Northern Gulf *G. compressum* occurs in the intertidal to shallow subtidal, whereas in Pacific Mexico, it has been collected from 19 m depths in a large kelp bed off Islotes Chester, in the vicinity of Punta Eugenia ("San Eugenio"), Baja California Sur (Dawson, 1963a). Some Pacific Mexico *Gastroclonium compressum* are similar to *G. cylindricum* Santelices, I. A. Abbott et M. E. Ramírez (1989). Endemic to central Chile, it differs primarily in having cylindrical branches throughout and branch walls of 2–4 cell layers.

Gastroclonium pacificum (E. Y. Dawson) C .F. Chang et B.-M. Xia

FIGURE 223

Coeloseira pacifica E. Y. Dawson, 1950a:343, fig. 2; 1961b:438; 1963a:469, pl. 94: figs. 1, 2; 1966a:25; González-González et al., 1996:192.

Gastroclonium pacificum (E. Y. Dawson) C. F. Chang et B.-M. Xia, 1978:209; Yoshida, 1998:835, fig. 3-76E; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:56; Pacheco-Ruíz et al., 2008:210.

Gastroclonium clavatum sensu Dawson, 1944a:312 [non *Gastroclonium clavatum* (Roth) Ardissone, 1883:322].

Gastroclonium ovale sensu Okamura, 1907:74, pl. 17: figs. 1–10; 1936:688, fig. 2 [non *Gastroclonium ovale* (Hudson) Kützing, 1843:441, which is now *Gastroclonium ovatum* (Hudson) Papenfuss, 1944b:344; basionym: *Fucus ovatus* Hudson, 1762:468].

Algae erect, 3–8(–12) cm tall; 1 or more partially erect, arching, simple to multibranched, solid, cylindrical axes develop from stoloniferous basal branches and produce septate, tubular, hollow branches, 1–2 mm in diameter; branches often with secondary branches. Branch walls of 2–3 cell layers; outermost cortical cells slightly anticlinally elongate.

Polysporangia scattered in outer wall of branches. Cystocarps protruding, basally somewhat constricted; about 500 μm

FIGURE 223. *Gastroclonium pacificum*: Habit (*EYD-1808*, US Alg. Coll.-207564).

in diameter, without an ostiole; carpospores 100 µm long, 20–50 µm in diameter. Spermatangia in a superficial layer over the upper portions of branches.

Habitat. On sand flats and on rocks and in crevices and tide pools; mid to low intertidal.

Distribution. Gulf of California: Bahía La Choya (Bahía Cholla) and Playa Tucson, Puerto Peñasco, to Bahía Bocochibampo, Sonora. Western Pacific: Japan.

Type Locality. Bahía Bocochibampo, near Guaymas, Sonora, Gulf of California, Mexico.

Remarks. Within the Gulf of California, *Gastroclonium pacificum* is possibly restricted in distribution to the northern Gulf. A single polysporic specimen that apparently lacked a solid axis from Punta Los Frailes (Baja California Sur) was also tentatively referred to *G. pacificum* (Dawson, 1963a, as "*Coeloseria pacifica*"); therefore, its southern Gulf distribution needs to be confirmed. It is also reported in Japan.

***Gastroclonium parvum* (Hollenberg) C. F. Chang et B.-M. Xia**

Coeloseira parva Hollenberg, 1941:871, figs. 7a,b, 8–12; Dawson, 1961b:438; 1963a:470, pl. 86: fig. 4, pl. 95: fig. 6; Abbott and Hollenberg, 1976:566, fig. 513; L. Aguilar-Rosas, 1981:94; Pacheco-Ruíz and Aguilar-Rosas, 1984:73; Stewart and Stewart, 1984:144; L. Aguilar-Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1986:425; Sánchez-Rodríguez et al., 1989:44; González-González et al., 1996:192.

Gastroclonium parvum (Hollenberg) C. F. Chang et B.-M. Xia, 1978:209; Stewart, 1991:121; Ramírez and Santelices, 1991:296; Mateo-Cid and Mendoza-González, 1994b:40; L. Aguilar-Rosas et al., 2000:131.

Algae of 1 or more erect individuals or in clumps, 2.0–3.0 cm tall, or forming dense mats (to 10 cm wide); erect, branched axes above unbranched or divided solid stipes (up to 1.0 mm in diameter) developed from a small discoid holdfast or from basal stoloniferous branches. Branching multifariously, branches terete, tubular; constricted septate branches, 1.0–1.5 mm in diameter, simple to repeatedly branched; branch walls of 2–3 cell layers; outermost cells 20–25 µm in diameter; inner cells 120–145 µm long, 60–70 µm in diameter, lined with few longitudinal filaments bearing secretory cells (gland cells).

Polysporangia 80–120 µm in diameter, divided into 12–16 polyspores, scattered in walls of septate branches. Cystocarps prominent, subglobose, mostly 280–300 µm in diameter, without an ostiole; developed on septate branches. Spermatangia unknown.

Habitat. On rocks, sometimes among algal turf; mid to low intertidal, probably also shallow subtidal.

Distribution. Gulf of California: Puertecitos; Roca Rojo, Bahía Kino. Eastern Pacific: Pacific Grove (central California); Redondo Beach, southern California to Playa Los Cerritos (south of Todos Santos), Baja California Sur; Isla Guadalupe; Isla Cedros; Chile.

Type Locality. Intertidal rocks; Redondo Beach, Los Angeles County, southern California, USA.

FAUCHEACEAE

Faucheaceae I. M. Strachan, G. W. Saunders et Kraft in Saunders et al., 1999:36 [non Gloiocladiaceae Harvey, 1836:160, as "Gloiocladeae," which is based on *Gloiosiphonia* Carmichael in Berkeley, 1833:45, and not on *Gloiocladia*].

Algae are constructed with an assortment of different anatomical structures. Internally, some have a solid, pseudoparenchymatous medulla, whereas in other members the medulla is hollow. The cortex may be either thin and of small cells or thicker, with numerous cells in anticlinal rows.

Tetrasporangia are cruciately to irregularly divided and borne terminally or laterally. Gametophytes are monoecious or dioecious. Female gametophytes are procarpic; carpogonial branches are three-celled. Gonimoblasts are globular, composed of several gonimolobes, with most of their cells developing into carposporangia. The fusion cell is narrow. Well-developed *tela arachnoidea* (network of slender stellate cells that look like spiderwebs) filaments surround the carposporophyte.

Two genera of the Faucheaceae are represented in the northern Gulf of California.

KEY TO THE GENERA OF FAUCHEACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Thalli not mucilaginous; dichotomous branches remaining free (not anastomosing) . . . . ***Gloiocladia***

1b. Thalli mucilaginous; abundantly dichotomously to subdichotomously branched; branches anastomosing . . . . ***Gloioderma***

Gloiocladia J. Agardh

Gloiocladia J. Agardh, 1842:87; J. Agardh, 1851:246; Rodríguez-Prieto et al., 2007:156.

Fauchea Montagne et Bory de Saint-Vincent in Montagne, 1846b:64; Kylin, 1956:330.

Algae are erect or prostrate, terete, compressed, or flattened, variously branched fronds that are attached to the substratum by a discoid holdfast and secondarily by marginal haptera. Branching is usually radially or complanately branched, but some are subdichotomously or pinnately branched. The Gulf of California species are mostly repeatedly, dichotomously branched (not always clear). Thalli are multiaxial in construction and solid. The medulla is composed of large, colorless cells (elongated in longitudinal section), and smaller secondary medullary cells may be present. Rhizoidal filaments that are issued from inner cortical or outer medullary cells may be present in the medulla, usually in the basal portions of the thallus. The inner subcortex is of smaller, ovoid to angular cells that are interconnected by numerous secondary pit connections. The outer cortical filaments arise from the subcortex, composed of simple or pseudodichotomously branched anticlinal rows of small cells that are without lateral secondary pit connections.

Tetrasporangia are ovoid, oblong, or fusiform, cruciately, decussately cruciate, or irregularly divided, and scattered or either within slightly elevated nemathecial sori or in distinctly raised nemathecia. Gametophytes are monoecious or dioecious. Female gametophytes are procarpic, with a three-celled carpogonial branch that either lacks or has a lateral sterile cell on the first cell of the carpogonial branch, borne on a supporting cell, which also bears a two-celled auxiliary cell branch (auxiliary parent cell and an auxiliary cell). After fertilization, the carpogonial branch cells fuse and connect to the auxiliary cell, which divides transversely to form a primary gonimoblast cell. A fusion cell is formed by the coalescence of the auxiliary and auxiliary parent cell and the fused cells of the carpogonial branch and the surrounding cells; the supporting cell may also sometimes participate in the fusion process. Only the supporting cell of the fusion cell remains discernible; other cells forming the fusion cell become unrecognizable as the structure matures. The gonimoblast is produced from the distal end of the primary gonimoblast cell, above a spherical mass of nutritive cells, and generates elongated lobes of ovoid carposporangia that are surrounded by *tela arachnoidea* (a network of persistent spiderweb-like filaments) in the cystocarp. Cystocarps are protruding, globose, and ostiolate, with surfaces that may be smooth (without ornamentation) or, in some species, coronate and either sessile or borne substipitate along the margins or scattered over the thallus surface. Spermatangia cut off singly or in pairs from spermatangial parent cells that arise from outer cortical cells, forming superficial sori (after Rodríguez-Prieto et al., 2007).

Remarks. Species of *Gloiocladia* occur mostly in warm-temperate to tropical seas, although a few are known in cold-temperate waters. Ballantine and Norris (1989) noted that the species cannot be distinguished by only using the characters of thallus shape and branching.

The closely related genera *Gloiocladia* and *Fauchea* had been separated on morphological characters (e.g., Irvine and Guiry, 1980; Norris, 1991). The respective type species for these two genera—*Gloiocladia furcata* (C. Agardh) J. Agardh, 1842 [basionym: *Chondria furcata* C. Agardh, 1827)] and *Fauchea repens* (C. Agardh) Montagne et Bory de Saint-Vincent in Montagne, 1846b [basionym: *Sphaerococcus repens* C. Agardh, 1823, which is now *Gloiocladia repens* (C. Agardh) Sánchez et Rodríguez-Prieto]—were shown to be congeneric by Rodríguez-Prieto et al. (2007). Because *Gloiocladia* is the oldest validly published name, other species referred to "*Fauchea*" will require generic reassessment and molecular confirmation.

Three species of *Gloiocladia* are known in the Gulf of California; all of them are currently considered to be endemic species.

KEY TO THE SPECIES OF *GLOIOCLADIA* IN THE GULF OF CALIFORNIA

1a. Thalli forming dense clumps of short, congested, often overlapping branches; branches 3–5 mm wide . . . . . . *G. mollis*
1b. Thalli openly branched (not in dense clumps); branches narrower, mostly 2–3 mm wide 2
2a. Branches mostly 2.0–2.5 mm wide; branching generally 3–5 times at intervals of 1–2 cm; cystocarps distinctly coronate, with horn-like projections up to 1 mm long . . . . *G. hoshawii*
2b. Branches mostly 2.0–4.0 mm wide; branching generally 4–11 times at intervals of (1)2–4 cm; cystocarps with smooth surface (not ornamented) . . . . *G. sefferi*

Gloiocladia hoshawii (E. Y. Dawson) J. N. Norris, *comb. nov.*

FIGURE 224

Fauchea hoshawii E. Y. Dawson, 1966b:64, fig. 5 [type specimen]; González-González et al., 1996:201; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:210.

Algae erect, up to 5 cm tall; fronds lubricous, of narrow, strap-like dichotomous branches, 2.0–2.5 mm wide; 3–4(–7) times divided, mostly at intervals of (0.5–)1–2 cm; upper branches narrower, ultimate branches 1 mm wide below bifurcate apices; branch angles wider in lower portions, narrowing in upper portions; attachment structures not known. Transection about 300 µm thick, medulla pseudoparenchymatous and compact, of large hyaline ovoid cells; cortex of anticlinal rows of small cells.

Tetrasporangia ovoid, cruciately divided, small, 24–35 µm long, (10–)12–15 µm in diameter; among modified cortical filaments (slightly longer as cortical cells become more elongate), creating a slightly elevated nemathecial sori borne on one side of a branch (Figure 224C). Cystocarps borne along margins; about 750 µm in diameter; distinctly coronate, with 3–5 straight or curved horn-like projections up to 1 mm or more in length; *tela arachnoidea* surround carposporophyte. Spermatangia not known.

Habitat. On rocks; subtidal, down to at least 21 m depths.

Distribution. Gulf of California: Islas de Los Gemelos (Islas Los Hermanitos), off Bahía de Los Ángeles; Isla San Pedro Nolasco.

Type Locality. Isla San Pedro Nolasco, off Guaymas, Sonora, Gulf of California, Mexico.

Remarks. A northern Gulf of California endemic, *Gloiocladia hoshawii* is easily recognized from the other Gulf species of *Gloiocladia* by its distinctly ornamented, coronate cystocarps. Tetrasporophytes are reported for the first time from subtidal collections from Islas de Los Gemelos (*JN-3008*, US Alg. Coll.-159134). This species was named for Robert W. Hoshaw (University of Arizona), phycologist, teacher, and mentor, who supported and encouraged studies of the Gulf of California marine algae.

Gloiocladia mollis (M. Howe) J. N. Norris, *comb. nov.*

FIGURE 225

Fauchea mollis M. Howe, 1911:507, pl. 32, pl. 33: fig. 6; Dawson, 1944a:304; 1961b:435; 1963a:440, pl. 78: fig. 2; González-González et al., 1996:201.

Algae low growing, forming a dense clump, 6–9 cm wide; of dichotomous branches developed centrally and growing radially outward, more or less overlapping; outer portions of branches becoming erect, short and polychotomous, with segments 3–5 mm wide; outermost segments very short, rounded lobes, 1.5–2.0 mm wide. Branches 165–350 µm thick; medulla pseudoparenchymatous of 2–3 layers of large cells, 75–275 µm in diameter.

Tetrasporangial thalli (apparently immature) with cortex of 4–5 cell layers; small cortical cells 5–9 µm in diameter. Gametangial thalli of type (apparently immature; queried by Dawson, 1963a) with cortex of 2 layers of small cells, 5–9 µm tall and 5–9 µm in diameter (after Dawson, 1963a).

Habitat. On rocks; subtidal, dredged at 10–40 m depths.

Distribution. Gulf of California: Isla San Esteban; La Paz.

Type Locality. "Apparently dredged, vicinity of La Paz," Baja California Sur, Gulf of California, Mexico (Dawson, 1963a:441).

Remarks. Dawson (1963a, as "*Fauchea mollis*") noted the structure of the Isla San Esteban *Gloiocladia mollis* was very close to his understanding of the genus *Fauchea* (cf. Kylin, 1931). The finding of mature gametangial thalli, as well as tetrasporangial thalli, is needed to confirm the generic placement of this Gulf species and its relationship to Pacific coast *Gloiocladia laciniata* (J. Agardh) Sánchez et Rodriguez-Prieto (Rodriguez-Prieto et al., 2007; basionym: *Fauchea laciniata* J. Agardh, 1885).

Gloiocladia sefferi (M. Howe) J. N. Norris, *comb. nov.*

FIGURE 226

Fauchea sefferi M. Howe, 1911:506, fig. 31; Dawson, 1944a:304; 1961b:455; 1963a:441, pl. 78: fig. 1; 1966b:64; González-González et al., 1996:201; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:210.

Algae erect, up to 12 cm tall; of narrow, strap-like dichotomous to subdichotomous branches of similar width throughout, (1–)2–4 mm wide, more or less divaricately branched 4–11 times, mostly at (1–)2–4 cm intervals, with smooth margins; ultimate segments abruptly tapering to blunt to semiacute apices; attached by small, irregularly discoid holdfast. Transection 150–400 µm thick; medulla of 4–6 irregular rows of pseudoparenchymatous cells, 70–100 µm in diameter; abrupt transition to subcortex of 1–2 layers of small, pigmented cells, wider than tall, about 10 µm wide; outer cortex of anticlinal rows of 4–8, pigmented cortical cells, 3–8 µm in diameter.

Tetrasporangial thalli unknown. Cystocarps relatively sparse on margins; sessile, subspherical, 600–700 µm in diameter, noncoronate (lack ornamentation); *tela arachnoidea* surround the carposporophyte. Spermatangial thalli unknown.

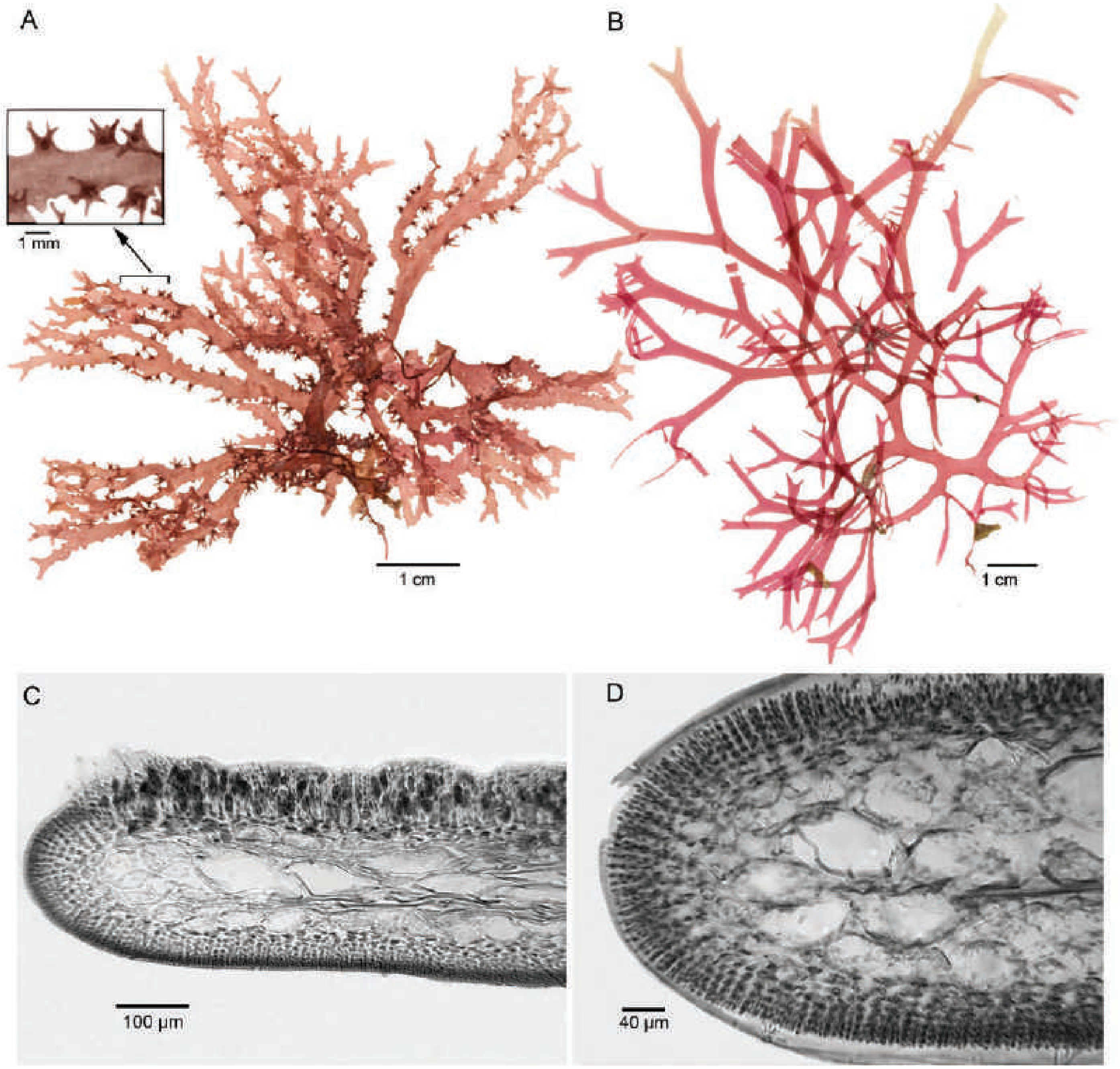

FIGURE 224. *Gloiocladia hoshawii*: A. Thallus with marginal cystocarps that are adorned with straight or curved coronate "horns." Inset: Detail of coronate horns on cystocarps (holotype: *R. Hoshaw & E. Y. Dawson, s.n.*, US Alg. Coll.-40926). B. Habit of tetrasporangial thallus (*JN-3008*, US Alg. Coll.-159134). C. Transection of branch with tetrasporangial sori in modified cortex. D. Transection of branch (C, D, *JN-3008*, US Alg. Coll. microscope slides 4595 and 4596).

Habitat. On rocks; subtidal, 8–14 m (also dredged to 40 m depths).

Distribution. Gulf of California: Isla Estanque (off southeast end of Isla Ángel de la Guarda), Isla San Esteban and Isla San Lorenzo (Islas de la Cintura); Isla Coronado (Isla Smith), off Bahía de Los Ángeles; Puerto Escondido to La Paz.

Type Locality. "Apparently dredged, vicinity of La Paz," Baja California Sur, Gulf of California, Mexico (Dawson, 1963a:441).

Remarks. Specimens from the subtidal off the north end of Isla Coronado (*JN-4336*, US Alg. Coll.-159135) have the prominent, smooth (nonornamented) cystocarps, with a small

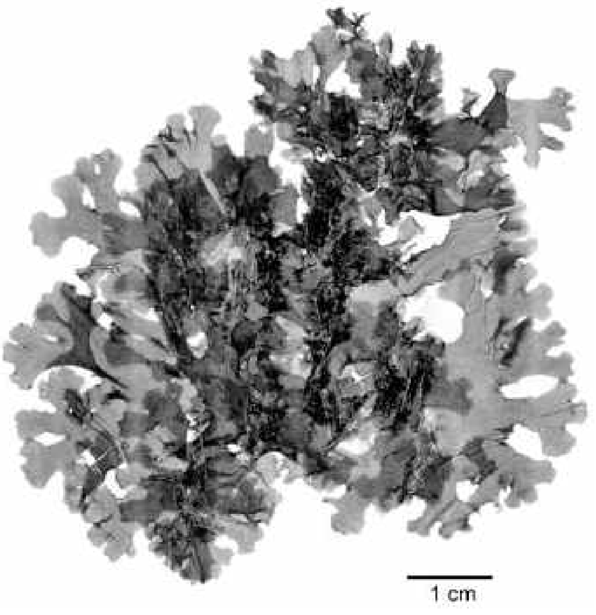

FIGURE 225. *Gloiocladia mollis*: Habit (*EYD-21579*, US Alg. Coll.-51351).

ostiole, characteristic of *Gloiocladia sefferi* (US Alg. Coll. microscope slide 4233).

Gloioderma J. Agardh

Gloioderma J. Agardh, 1851:243.
Estebania Setchell et N. L. Gardner, 1924:783.

Thalli in the Gulf of California are of compressed, highly lubricous, strap-like fronds with branching that either remains dichotomous or becomes subdichotomous; the uppermost portions are dichotomously branched. Branches fuse where they are in contact with each other frequently anastomosing with small to large openings. Medulla is initially of 1–2(–3) layers of large, thick-walled ovoid cells; subsequently, thin, medullary filaments begin growing and branch, becoming intertwined and densely filling the central medulla. Cells of the outer medulla grade into an inner cortex of one to two layers of smaller ovoid cells. The outer cortex is formed by anticlinal rows of little cells.

Tetrasporangia are cruciately divided and scattered over the thallus surface (not in sori). Cystocarps and spermatangia remain unknown (genus description modified from Setchell and Gardner, 1924).

REMARKS. Norris (1991) and others (e.g., Womersley, 1996; Sánchez and Rodríguez-Prieto, 2005) considered *Gloioderma* (generitype: *Gloioderma australe* J. Agardh, 1851:243; type locality: Western Australia) to be congeneric with *Gloiocladia* (generitype: *Gloiocladia furcata* (C. Agardh) J. Agardh, 1842; type locality: Trieste, Italy). Nevertheless, on the basis of morphological and molecular analyses, Rodríguez-Prieto et al.

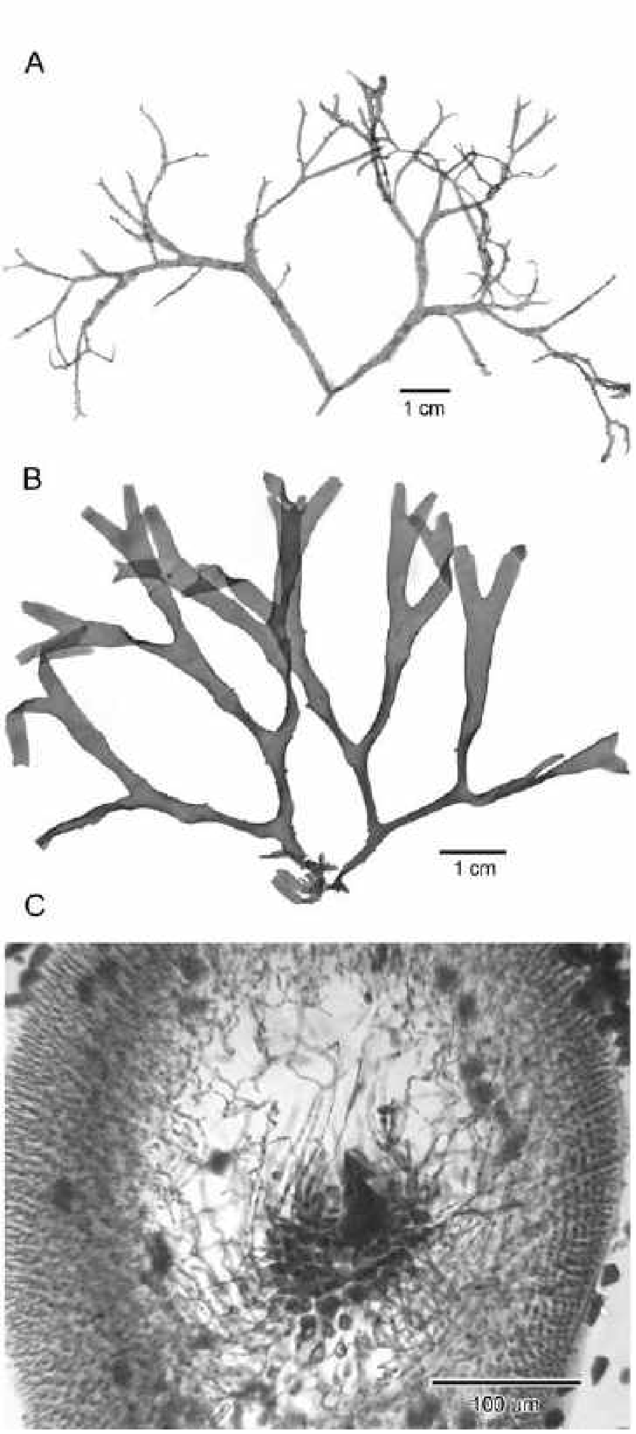

FIGURE 226. *Gloiocladia sefferi*: A. Habit, narrow branched axes; note cystocarps protruding along margins (*JN-4336*, US Alg. Coll.-159135). B. Habit, wide axes with unornamented cystocarps borne along margins (*EYD-21558*, US Alg. Coll.-7202). C. A cystocarp in transection showing nutritive cells below the fusion cell and "*tela arachnoidea*" (spiderweb-like filaments) that surround the carposporophyte (note slide preparation has squashed the carposporangia out) (*JN-4336*, US Alg. Coll. microscope slide 4233).

(2007) and Dalen and Saunders (2007) concluded that *Gloioderma* should be reinstated.

For now, the Gulf of California species is considered to belong to *Gloioderma*, until the generic status of Gulf *G. conjuncta* can be further investigated with the finding of carposporangial and spermatangial thalli and with new anatomical and molecular data. If the Gulf *G. conjuncta* proves to be a distinct genus, then the name *Estebania* Setchell et N. L. Gardner (1924) would be available for consideration.

There is one species of *Gloioderma* represented in the northern Gulf of California.

Gloioderma conjuncta (Setchell et N. L. Gardner) E. Y. Dawson

FIGURE 227

Estebania conjuncta Setchell et N. L. Gardner, 1924:783, pl. 25: figs. 35, 36, pls. 85, 86; Dawson, 1944a:281.

Gloioderma conjuncta (Setchell et N. L. Gardner) E. Y. Dawson, 1959a:26; 1961b:435; 1963a:442, pl. 79; 1966a:27; Norris, 1973:14; González-González et al., 1996:212; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:52; Pacheco-Ruíz et al., 2008:210.

Gloiocladia conjuncta (Setchell et N. L. Gardner) R. E. Norris, 1991:592.

Algae erect, of flattened, branched, strap-like fronds, mostly 4–5(–8) mm wide, up to 70 cm in length; divaricately dichotomously branched (easily seen in upper [distal] growing portions); extensively branched and developing into distinctive anastomosing fronds with open spaces between branches formed by coalescing of developing branches; initially, openings less than 0.5 mm in diameter, becoming much larger, up to 2(–5) cm in diameter as branches grow, anatomoses often becoming torn open; thallus firm with a slippery mucilaginous texture, iridescent light greenish rose or yellowish to coral-red (drying reddish orange to brick brown); usually entangled, attachment not fully understood or apparently attached where branches contact host alga. Medulla initially (young developing thalli) of 1–2 layers of large, thick-walled, ovoid cells, up to 200 µm in diameter; later, central medulla develops intertwined, branched medullary filaments, 3–4 µm in diameter; thin filaments becoming dense; medullary filaments surrounded by 2(–3) layers of large, ovoid medullary cells that grade into outer medulla; inner cortex of (1–)2–3 layers of small, thin-walled cells; outer cortex of anticlinal rows of 4–7 subspherical cells, each 4–6 µm in diameter.

Asexual reproduction by fragmentation; drifting portions becoming entangled with other algae. Tetrasporangia cruciately divided; developed in inner cortical layers; scattered over both thallus surfaces. Gametangial thalli unknown.

HABITAT. Usually epiphytic or entangled with other algae; sometimes free floating or also apparently occasionally on rocks; shallow subtidal, down to 40 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla San Pedro Mártir; Puerto Refugio, Isla Ángel de la Guarda and Isla San Esteban (Islas de la Cintura) to Bahía Agua Verde; Isla de Tortuga, about 24.1 km (15 miles) northeast of Isla San Marcos (Baja California Sur).

TYPE LOCALITY. Isla San Esteban, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. The Gulf endemic *Gloioderma conjuncta,* with its slippery texture, extensively branched, distinctive anastomosing fronds with open spaces (holes) formed by the coalescing of developing branches, is unique among the Gulf of California algae.

LOMENTARIACEAE

Lomentariaceae J. Agardh, 1876:606, 630, *nom. cons.*; Saunders et al., 1999:35.

Chondrosiphonaceae Kützing, 1843:438, *nom. rej.*

Algae are soft and flaccid, semicartilaginous to rigid, and oppositely, alternately, or irregularly branched; axes and branches are terete to compressed; thalli are entirely solid or partially to mostly hollow, with polystromatic partitions (septa) dividing the hollow space. Thalli are multiaxial in structure, with a cortex of one to several cell layers; the medulla is either compact to loosely aggregated and solid throughout, of larger, elongated cells, or is hollow with pseudoparenchymatous septa, and a network of loosely arranged, narrow, longitudinal filaments peripherally lining the hollow central cavities.

Life histories, where known, involve isomorphic sporophytes and gametophytes. Tetrasporangia are tetrahedrally (or infrequently cruciately) divided, borne terminal on cortical cells, developed within sori associated with sterile filaments, in depressions or cavities in branches or branchlets or in swollen branch apices. Gametophytes are dioecious. Carpogonial branches are three-celled, borne on a supporting cell that also bears one to two two-celled auxiliary cell branches (procarpic). The gonimoblast develops from the basal fusion cell. Nearly all of the gonimoblast cells become carposporangia. Cystocarps, with a cortical pericarp and ostiole, protrude above the thallus surface and are scattered over the branches. Spermatangia are developed from initials that are cut off from outer cortical cells in inconspicuous sori on thallus surface or in swollen branch apices.

Two genera of the Lomentariaceae occur in the northern Gulf of California.

KEY TO GENERA OF THE LOMENTARIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Axes and branches wiry, stiff, terete, less than 1 mm in diameter; internally solid, with a medulla of loose to compact, longitudinal filaments . . . . *Ceratodictyon*

1b. Axes and branches flaccid to semicartilaginous, terete to compressed, most greater than 1 mm in diameter; internally with hollow portions separated by polystromatic partitions (multiple cell layers) . . . . *Lomentaria*

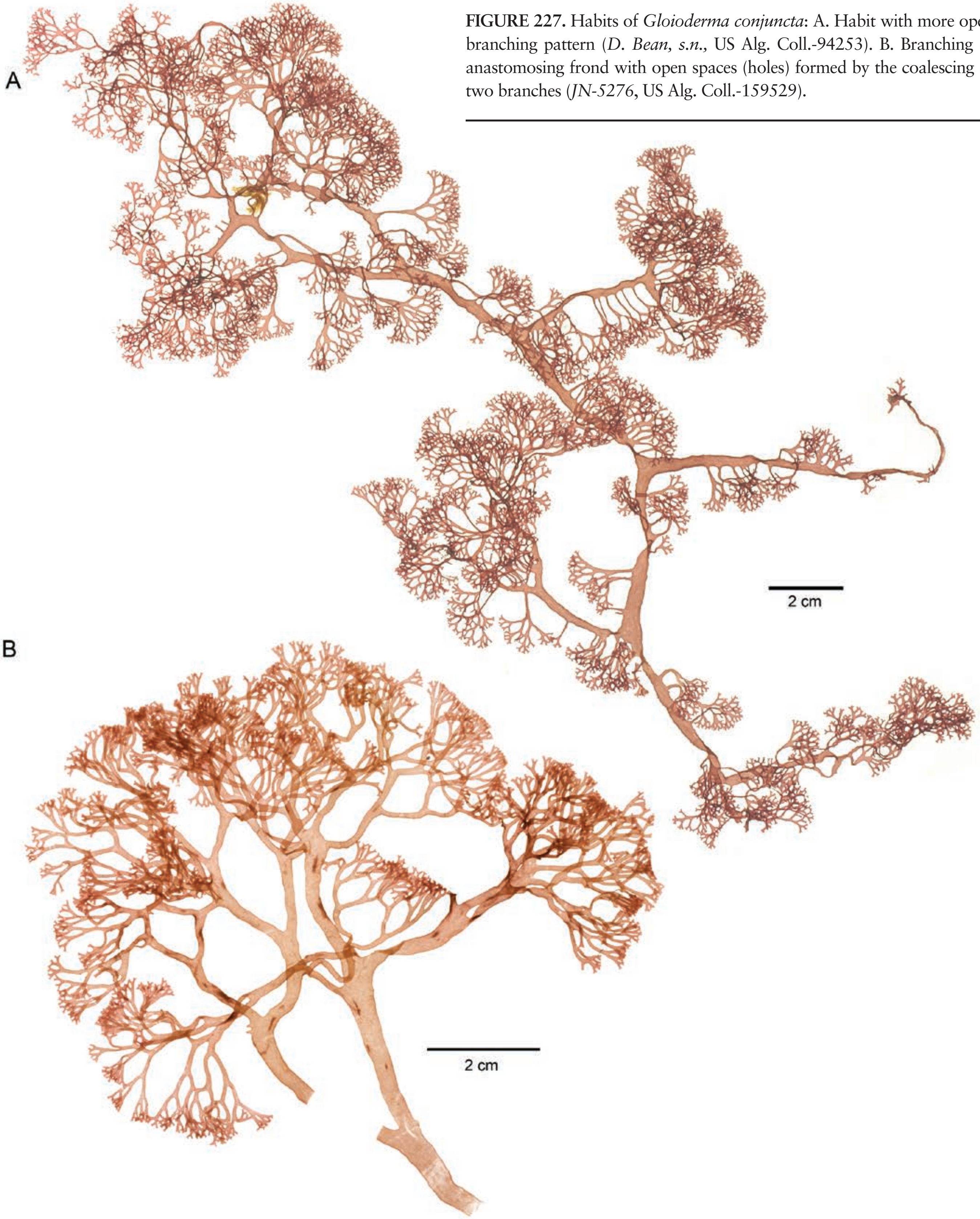

FIGURE 227. Habits of *Gloioderma conjuncta*: A. Habit with more open branching pattern (*D. Bean, s.n.*, US Alg. Coll.-94253). B. Branching of anastomosing frond with open spaces (holes) formed by the coalescing of two branches (*JN-5276*, US Alg. Coll.-159529).

Ceratodictyon Zanardini

Ceratodictyon Zanardini, 1878:36.
Gelidiopsis F. Schmitz, 1895:148.

Algae are erect, composed of thin, terete, or subcylindrical (sometimes to compressed) cartilaginous axes that are subdichotomously to irregularly branched, with rounded apices, and arise from prostrate stoloniferous branch systems. Axes and branches are often entangled, sometimes anastomosing (in a few species), and often form clumps or are mat-like. Thalli are multiaxial in construction, with a medulla composed of slender, elongated filaments that become larger and increasingly elongate toward the center (seen in longitudinal section). The cortex has one to several layers of smaller cuboidal or rectilinear cortical cells.

Reproductive structures are on swollen terminal branches. Tetrasporangia are regularly or irregularly cruciately divided, within terminal nemathecia that completely encircle the terete unbranched fertile axes. Tetrasporangia initials are formed terminally in a lateral position. Gametangial thalli are dioecious. Procarpic; carpogonial branches are three-celled, borne on a slightly enlarged supporting cell with a two-celled auxiliary cell branch. After presumed fertilization, the initial division of the zygote is oblique or nearly longitudinal. The gonimoblast develops outward from a fusion cell that remains as a large columnar structure within the cystocarp. Carposporangia are borne in short terminal chains on gonimoblast filaments, most develop synchronously in a single gonimolobe, and *tela arachnoidea* are absent. Cystocarps have an ostiole and are mostly in groups on the branches, each conspicuously protruding outward. Spermatangia develop from spermatangial initials that are produced from cortical cells.

Remarks. Some of the species are free-living, others grow symbiotically within sponges. In describing the genus, *Gelidiopsis,* Schmitz (1895a) recognized its similarities to *Ceratodictyon* Zanardini (1878). Although much later Norris (1987b) would consider *Gelidiopsis* to be congeneric with *Ceratodictyon*, Price and Kraft (1991) suggested that the two should be retained as separate genera. More recent molecular systematic studies of Le Gall et al. (2008) included some species of *Ceratodictyon* and provided support to Norris' (1987b) merging of the two genera.

Ceratodictyon (as *Gelidiopsis*) has an interesting history of familial placement. Primarily on the basis of its usual lack of reproduction and habit resemblance to *Gelidium,* some placed it as *Gelidiopsis* in the Gelidiaceae (e.g., Dawson, 1953a; Taylor, 1960). Kylin (1956) placed the genus in the Gigartinales. Subsequently, Dawson (1961a) and, later, Norris (1987b), after studying the generitype, *Gelidiopsis variabilis*, considered the genus in the Gracilariaceae, whereas Price and Scott (1992) placed it in the Rhodymeniaceae. The molecular systematic studies of Saunders et al. (1999) showed the now congeneric *Ceratodictyon* and *Gelidiopsis* should be placed in the Lomentariaceae.

Two species of *Ceratodictyon* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *CERATODICTYON* IN THE NORTHERN GULF OF CALIFORNIA

1a.	Thalli short, up to 6 cm tall; with narrow branches, 250–400 µm in diameter	***C. tenuis***
1b.	Thalli taller, up to 20 cm tall; branches wider, 500–850 µm in diameter	***C. variabile***

Ceratodictyon tenuis (Setchell et N. L. Gardner) J. N. Norris, *comb. nov.*

Gelidiopsis tenuis Setchell et N. L. Gardner, 1924:749, pl. 22: fig. 2; Dawson, 1944a:264, pl. 70: fig. 1; 1949c:246; 1953a:85; 1957c:16; 1959a:20; 1961a:201, pl. 9: fig.1; 1961b:429; Huerta-Múzquiz and Tirado-Lizárraga, 1970:128; Chávez-Barrear, 1972b:268; Huerta-Múzquiz and Garza-Barrientos, 1975:9; Huerta-Múzquiz and Mendoza-González, 1985:50; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:483; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:48; Mendoza-González et al., 1994:107; González-González et al., 1996:204; Cruz-Ayala et al., 2001:191; CONANP, 2002:139; López et al., 2004:11; Serviere-Zaragoza et al., 2007:10; Benecker, 2009:CD-Rom p. 64.

Gelidiopsis variabilis sensu Fernández-García et al., 2011:62 [non *Gelidiopsis variabilis* (Greville ex J. Agardh) Schmitz, 1895:148].

Algae up to 6 cm tall, of erect, terete to compressed axes and branches, 250–400 µm in diameter; subdichotomously to irregularly branched, usually at 2–10 mm intervals; apices rounded; thallus base of loosely entangled, horizontal stoloniferous axes, up to 500 µm in diameter, attached at various points by small discs. Medulla a central core of narrow elongated cells, 8–9 µm in diameter, 90–135 µm long; outward surrounded by wider and shorter medullary cells, up to 30 µm in diameter; merging into a cortex of 2–3 layers; outermost cortical layer of small cells, mostly about 8 µm in diameter.

Reproduction not known in the Gulf of California.

Habitat. On rocks or loosely aggregated rock and sand or on crustose corallines; intertidal, also dredged down to 40 m depths (Dawson, 1953a).

Distribution. Gulf of California: Guaymas to San José del Cabo; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Isla Socorro and Isla Clarión (Islas Revillagigedo); Jalisco to Oaxaca; El Salvador; Costa Rica; Nicaragua; Panama.

Type Locality. Santa Rosalía, Baja California Sur, Gulf of California, Mexico.

Remarks. *Ceratodictyon tenuis* is similar in habit to *C. variabile* but smaller in overall size, including the diameter of its branches (Dawson, 1953a). Comparisons of reproductive structures, once they are found in Gulf specimens, are needed, as well as molecular analyses of Gulf *C. tenuis* and Gulf *C.variabile,* to help elucidate their taxonomic status and relationship to type locality *C. variabile*.

Ceratodictyon variabile (Greville ex J. Agardh) R. E. Norris
FIGURE 228

Gelidium variabile Greville ex J. Agardh, 1851:468; Kützing, 1869:9, pl. 23: figs. c,d.

Ceratodictyon variabile (Greville ex J. Agardh) R. E. Norris, 1987a:243, figs. 1–9; Le Gall et al., 2008:1567.

Gelidiopsis variabilis (Greville ex J. Agardh) Schmitz, 1895:148; Feldmann, 1931:156, fig. 2B; Dawson, 1944a:225, pl. 70: fig. 1; 1953a:86; 1960b:38; 1961a:201, pl. 9: fig.2; 1961b:429; 1966a:21; Santelices and Abbott, 1987:9; Norris, 1985d:212; Sánchez-Rodríguez et al., 1989:44; Ramírez and Santelices, 1991:273; Mateo-Cid and Mendoza-González, 1992:20; Mendoza-González and Mateo-Cid, 1992:19; Serviere-Zaragoza et al., 1993a:483; Mendoza-González et al., 1994:107; González-González et al., 1996:204; Abbott, 1999:222, fig. 61C,D; Mateo-Cid et al., 2000:65; L. Aguilar-Rosas et al., 2000:131; Mateo-Cid et al., 2006:56; Y.-P. Lee, 2008:415, figs. A–C.

Acrocarpus gracilis Kützing, 1849:761.

Gelidiopsis gracilis (Kützing) Feldmann, 1931:157; Yoshida, 1998:853.

Algae erect, up to 20 cm tall; of wiry, stiff, terete to sometimes slightly compressed axes, 500–850 μm in diameter; subdichotomously, irregularly alternately, or more or less oppositely branched; axes arising from loosely entangled, stoloniferous basal axes that attach by small discs. Medulla solid, of closely packed cells; central cells 10–15 μm in diameter, 150–280 μm

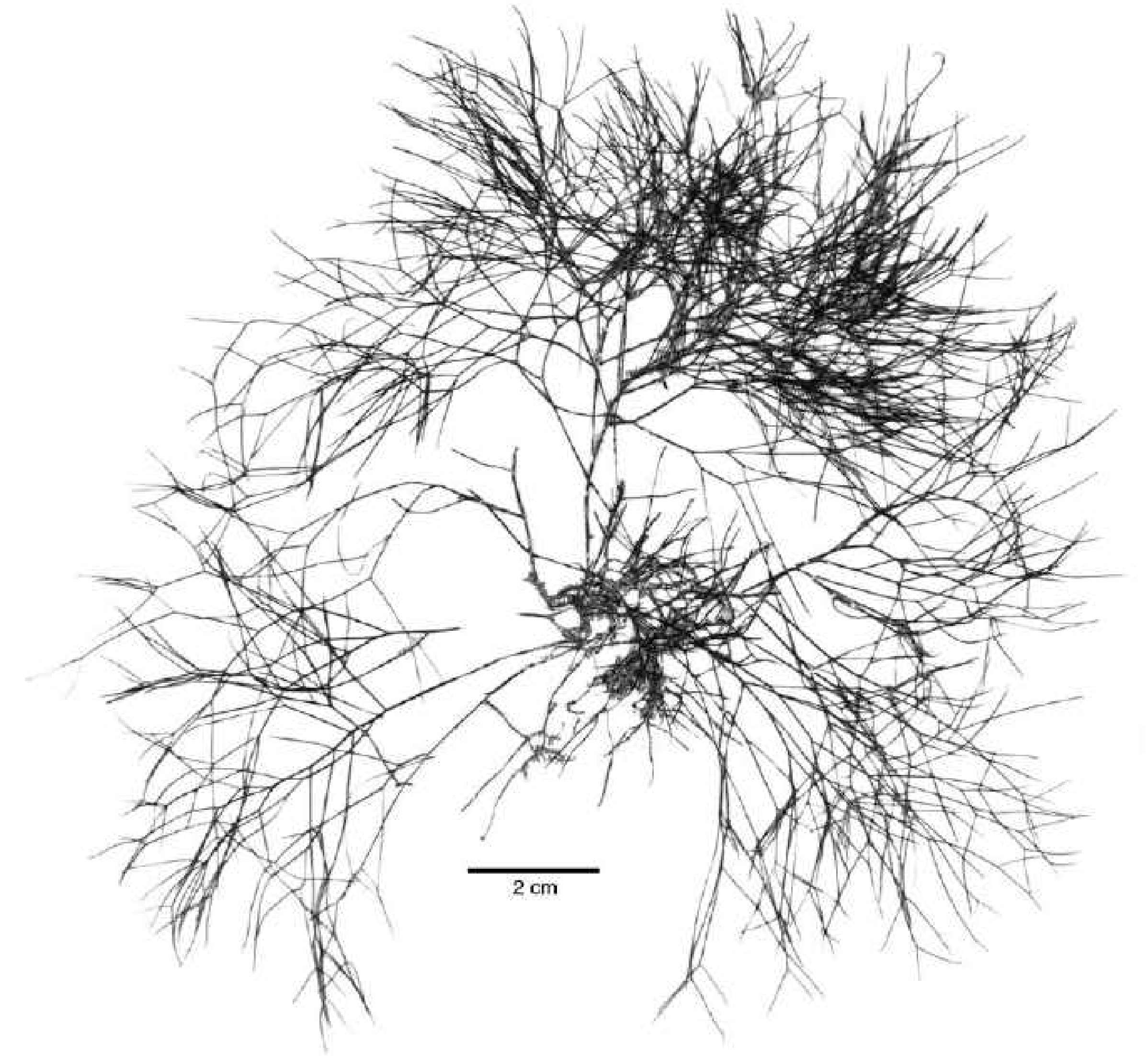

FIGURE 228. *Ceratodictyon variabile*: Habit, from a clump of rigid, wiry thalli (*JN-6087*, US Alg. Coll.-159333).

long (in longitudinal section); becoming slightly wider outward, with medullary cells 15–20 µm in diameter and shorter, 45–80 µm long. Cortex of 2–3 layers of squarish cells, up to 8.0 µm in diameter; outermost cells, slightly flattened.

Tetrasporangial and gametangial thalli unknown in the Gulf of California. Tetrasporangia as reported elsewhere: with cruciately arranged spores, among slender filaments; in wide, swollen arrowhead-shaped sori borne terminal on tetrasporangial branchlets (after Abbott, 1999). Carpogonial branches (Norris, 1987a) and cystocarps have been reported elsewhere (see Price and Kraft, 1991).

HABITAT. On rocks and tidal platforms; mid intertidal to shallow subtidal, down to 1.5 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena; Mazatlán, Sinaloa to Nayarit. Eastern Pacific: Bahía Magdalena, Baja California Sur; Jalisco to Colima; Rapa Nui (Easter Island; Isla de Pascua). Central Pacific: Hawaiian Islands. Western Pacific: Japan; Korea; Vietnam.

TYPE LOCALITY. Madras (now Chennai), Tamil Nadu, southeastern India.

REMARKS. Northern Gulf specimens appear to be in agreement with *Ceratodictyon variabile* but should be tested and compared to type locality materials of *G. variabile,* the smaller Gulf of California *C. tenuis*, and to the generitype *C. spongiosum* (Zanardini, 1878) from Indonesia (Silva et al., 1996a). Specimens of "*G. variabilis*" from Isla San Pedro Nolasco were noted by Dawson (1959a:20) to have "compressed branches and axes and occasional opposite branches" and should be reexamined.

Lomentaria Lyngbye

Lomentaria Lyngbye, 1819:101.

Algae are usually erect, but some may be repent or partly prostrate, composed of terete to compressed axes that are variously branched; branches are hollow with solid septa, and branch tips are rounded. Multiaxial in construction, thalli have a cortex of one to three cell layers and medulla of three to six cell layers, with hollow cavities lined with a network of longitudinal elongated medullary cells. Medullary cells become compacted into transverse polystromatic partitions (septa) at various intervals. Some species have multilayered septa that separate the hollow space into segments (sometimes constricted); other species have septa that only occur at branch bases. Secretory cells are borne on the medullary filaments, on the inward side facing the mucilage filled cavity.

Life histories, where known, include isomorphic tetrasporophytes and gametophytes. Tetrasporangia are tetrahedrally divided, borne within sunken sori formed by depressions as the cortex infolds, and cut off thallus inward from small cells lining the depressions. Gametophytes are typically dioecious but are monoecious in a few species. Carpogonial branches are three-celled, with one or two (one of which is nonfunctional) auxiliary cell branches composed of two cells. Gonimoblast filaments develop outward from a columnar fusion cell, with most of their cells forming carposporangia. Cystocarps are scattered and protrude above the thallus surface, with a three- to six-cell-thick pericarp (derived from the outer cortex), with a prominent pore and weakly developed *tela arachnoidea* internally. Spermatangia are in superficial sori, borne terminally on parent cells that are derived from outer cortical cells.

REMARKS. Although the genus *Lomentaria* is widely reported, it is more common in distribution in subtropical to temperate seas and less so in the tropics and polar regions. Guiry (in Irvine and Guiry, 1983) has suggested the compressed to flattened species of *Lomentaria* with nonconstricted segments should be placed into a separate genus, *Chondrothamnion* Kützing (1843), thus restricting *Lomentaria* to the species with constricted segments. Many of the species are poorly understood, and the phylogenetic relationship between species of *Lomentaria*, *Coelothrix* Børgesen (1920), *Binghamia* J. Agardh (1894), and *Binghamiopsis* I. K. Lee, J. A. West et Hommersand (1988) needs comparative morphological and molecular testing and elucidation (Guiry and Guiry, 2009).

Two species of *Lomentaria* are recorded in the northern Gulf of California.

KEY TO THE SPECIES OF *LOMENTARIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Semicartilaginous; terete branches 1.0–2.0 mm in diameter, sometimes slightly constricted at more or less regular intervals into fusiform segments; variously branched; thallus wall 120–160 µm thick in transection from surface to hollow cavity; tetrasporangia surrounded by filamentous network within sunken sori . . . . *L. catenata*

1b. Flaccid, gelatinous; terete to compressed branches, mostly 0.8–1.0 mm (occasionally to 1.3 mm) wide, slightly constricted only at branch bases; branching mostly opposite; thallus wall thinner in transection, 75–120 µm thick from cortex to hollow cavity; network of filamentous cells not well developed in sunken tetrasporangial sori . . . . *L. hakodatensis*

Lomentaria catenata Harvey

FIGURES 229

Lomentaria catenata Harvey, 1857:331; Harvey, 1860:331; Okamura, 1902:75, 103, pl. 26; Dawson, 1944a:308, pl. 74: fig. 1; 1953c:3; 1954e:340; 1959b:16; 1960c:97; 1961b:437; 1963a:465, pl. 92: figs. 1–10; Norris, 1973:15; Huerta-Múzquiz, 1978:337; I. K. Lee, 1978:124, figs. 53–59, pl. 5: figs. D–F; Norris, 1985d:213; Masuda et al., 1995:196, fig. 20; González-González et al., 1996:242; Yoshida, 1998:837, fig. 3-76H–J; Xia and Zhang, 1999:153, fig. 89; L. Aguilar-Rosas et al., 2000:131; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:56; Y.-P. Lee, 2008:416, figs. A–E; Pacheco-Ruíz et al., 2008:210.

Corallopsis excavata Setchell et N. L. Gardner, 1924:756, pls. 23: figs. 24, 25, 44b, 48.

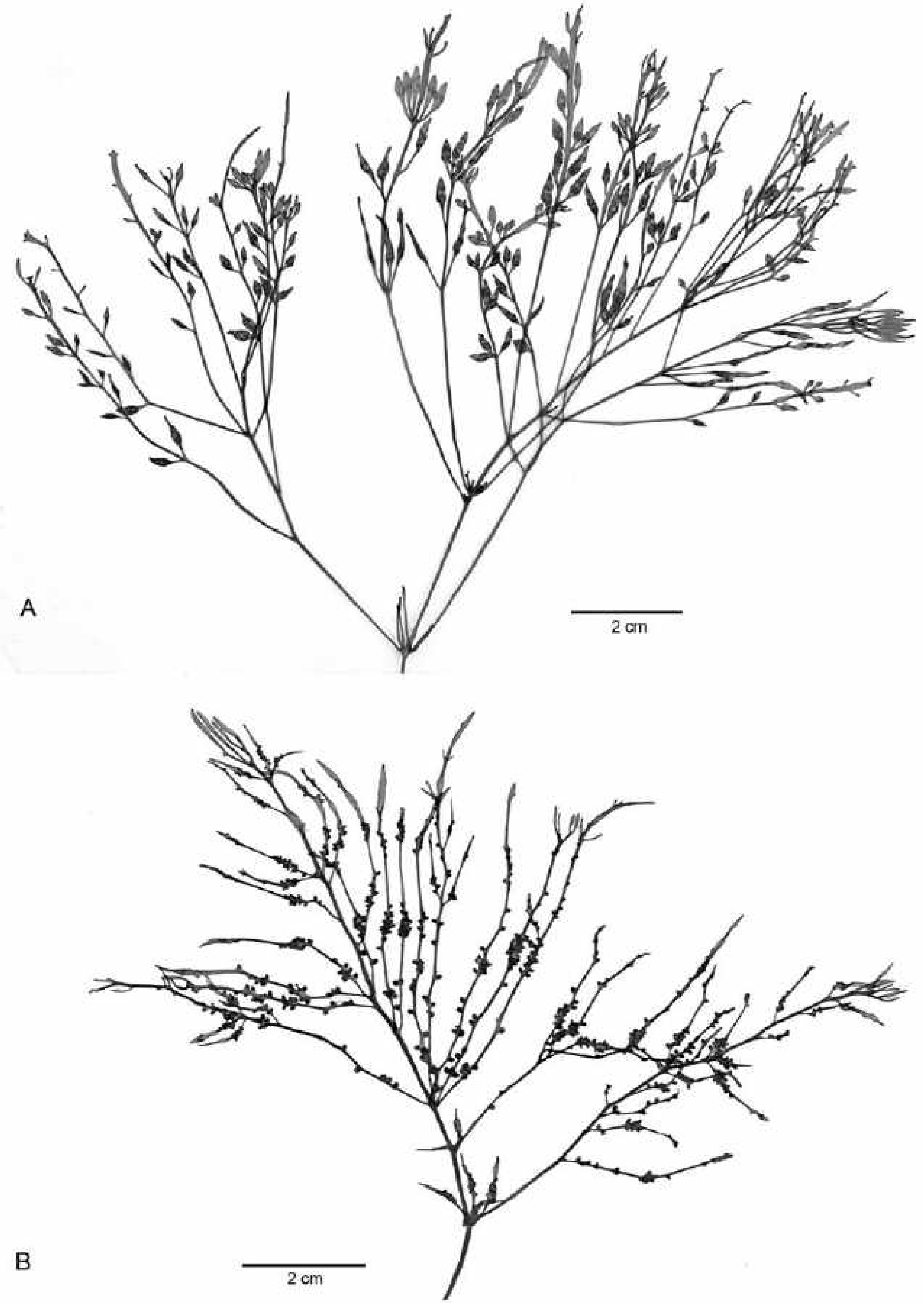

FIGURE 229. *Lomentaria catenata*: A. Habit of tetrasporophyte, note characteristic swollen branchlets with sunken tetrasporangial sori (*JN-5899*, US Alg. Coll.-160462). B. Female gametophyte with protruding cystocarps (*JN-5899*, US Alg. Coll.-160463).

Taylorophycus laxa sensu Norris, 1973:11, pl. 4; Pacheco-Ruíz et al., 2008:209 [non *Taylorophycus laxa* (W. R. Taylor) E. Y. Dawson, 1961a:224].

Algae mostly 8–14 cm tall, dark red, of few to many erect, semicartilaginous, terete axes; multifariously branched, up to 3–5 orders, opposite, whorled or alternate; axes 1–2 mm in diameter, occasionally laterally fused; branches sometimes constricted at regular intervals forming fusiform segments, 0.7–1.0 mm in diameter, 2.5–7.0 mm long; attached by a discoid holdfast that produces horizontally growing stolons that attach by small discs at irregular intervals. Cortex and medulla in transection 120–160 µm thick, surrounding a central hollow, mucilage-filled cavity. Cortex of 1(–2) layers; outermost cortical layer of anticlinally elongated pigmented cells. Medulla of 4–6 rows of cells, 20–30 µm wide, 80–200 µm long; with a loose network of filaments lining the innermost medullary cells, bearing single or small groups of secretory cells, facing inward toward central hollow cavity. Branch constrictions solid, pseudoparenchymatous.

Tetrasporangia tetrahedrally divided, subspherical to oblong, up to 90 µm long, up to 60 µm in diameter, surrounded by a filamentous network; in sori submerged within depressions of the cortex of swollen branchlets; sori become open cavities, sometimes merging. Cystocarps spherical to urn shaped, 750–900 µm in diameter, ostiolate; prominently elevated above branch surface; carposporangia 95–120 µm in diameter. Spermatangia not observed in Gulf specimens; as reported elsewhere: on bladder-like spermatangial branchlets. Spermatangia 1–2 terminal and subterminal on parent cell; spermatia elongated, 4.6 µm long, 3.2 µm in diameter (after I. K. Lee, 1978).

HABITAT. On rocks; low intertidal to shallow subtidal, down to 6 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to El Coloradito; Isla San Jorge to Guaymas; Isla de Tortuga (NE of Isla San Marcos) to Isla San Esteban; Bahía de Loreto. Eastern Pacific: Punta Santa Rosaliita (“Punta Santa Rosalía”), Baja California to Isla Magdalena (Bahía Magdalena), Baja California Sur; Isla Cedros. Western Pacific: China; Korea; Japan.

TYPE LOCALITY. Shimoda (near southern end of Izu Peninsula), Shizuoka Prefecture, Japan (Harvey, 1860; Dawson, 1959b).

REMARKS. *Lomentaria catenata* is a perennial species in Japan (I. K. Lee, 1978). In the northern Gulf *L. catenata* attains its largest sizes in summer and is apparently absent by fall (Dawson, 1963a). Though of similar dimensions, *L. catenata* is more rigid, generally darker red, and has constricted segments, whereas *L. hakodatensis* is flaccid, lighter and more purple in color, and has constrictions only at the base of the branches.

Lomentaria hakodatensis Yendo

FIGURE 230

Lomentaria hakodatensis Yendo, 1920:6; Dawson, 1944a:308, pl. 75: fig. 2; 1950d:341; 1951:56; 1953c:3; 1960a:48; 1960c:97; Dawson et al., 1960b:24; Dawson, 1961b:437; 1962c:278 ; 1963a:466, pl. 86: fig. 2; pl. 95: figs. 1, 2; Dawson and Neushul, 1966:180; Abbott and North, 1972:76; Abbott and Hollenberg, 1976:569, fig. 516; I. K. Lee, 1978:108, figs. 42–52, pl. 5: figs. A–C; I. K. Lee and West, 1980:419; Tseng, 1983:122, pl. 64: fig. 4; Stewart and Stewart, 1984:144; Hawkes and Scagel, 1986:332; Scagel et al., 1989:206; Stewart, 1991:122; Serviere-Zaragoza et al., 1993a:484; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:48; González-González et al., 1996:242; Yoshida, 1998:837, fig. 3–77E; Abbott, 1999:224, fig. 62A–D; Xia and Zhang, 1999:156, fig. 90, pl. 9: fig. 2; Mateo-Cid et al., 2000:66 [with query]; Abbott et al., 2002:310; Y.-P. Lee, 2008:418, figs. A–C; Pacheco-Ruíz et al., 2008:210; Bernecker, 2009:CD-Rom p. 64; Fernández-García et al., 2011:62.

Lomentaria sinensis M. Howe, 1924:139, pl. 1: fig. 1; Tseng and Li, 1935:221; Okamura, 1936:684.

Hooperia baileyana sensu Setchell et N. L. Gardner, 1930:153 [non *Hooperia baileyana* J. Agardh, 1896:89, which is now *Lomentaria baileyana* (Harvey) Farlow, 1876:698].

Algae erect, mostly 3–9 cm tall, reddish purple to greenish-purple, often forming bushy clumps, of flaccid, gelatinous, terete to compressed axes and branches, narrow (0.5–)0.8–1.3 mm in diameter, branching opposite, sometimes somewhat whorled or irregularly alternate, to 3–5 orders; prostrate basal portion of entangled stoloniferous axes, 0.7–1.3 mm in diameter, attached to each other and to substratum by numerous discs. Branches slightly to barely constricted at base (most evident at base of ultimate

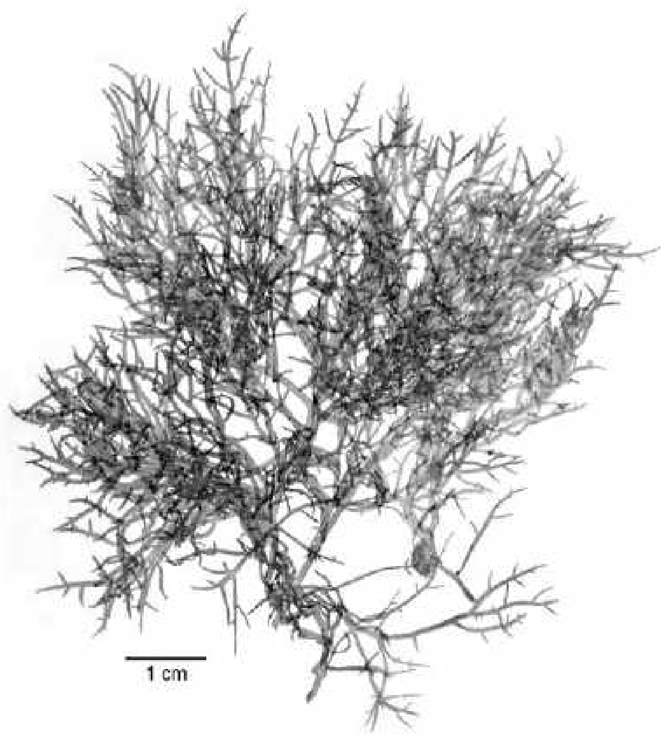

FIGURE 230. *Lomentaria hakodatensis*: Habit (*EYD-10896*, US Alg. Coll.-12228).

branchlets), gradually tapering upward to apex; branches may be laterally adjoined at various contacts. Thallus wall 75–125 µm thick in transection; transverse septa composed of 3–4 irregularly arranged cell rows. Cortex of 1(–2) cell layer; cortical cells oblong to elliptical, 17–24 µm long, 10–15(–19) µm in diameter. Medulla of 3–4 cell layers; cells more or less isodiametrical, up to 50–60 µm in diameter, inward becoming wider than tall; hollow cavity lined with a few slender elongated filaments, these bearing occasional gland cells, single or in aggregations.

Tetrasporangia tetrahedrally divided, subspherical, 90–110 µm long, 95–125 µm in diameter; borne in swollen fusiform branchlets within cavities (100–400 µm wide) in the cortex; filamentous cells among the tetrasporangia are poorly developed. Carpogonial branch 3-celled. Gonimoblast and auxiliary cells form a fusion cell, trunk-like column in shape. Cystocarps sessile, 700–1000 µm in diameter, with 1(–2) ostiole; scattered in upper portions of branches; carpospores 90–100 µm in diameter. Spermatangium terminal, 1 on parent cell; in superficial sori on somewhat swollen branches (in surface view appearing more or less reticulate, or circular in arrangement about basal cell); spermatia 4.5 µm long, 2.9 µm in diameter (reproduction after I. K. Lee, 1978).

Habitat. On rocks and sometimes other algae; low intertidal to subtidal, down to 20 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Bahía Empalme (south of Guaymas); Bahía Concepción to Cabo Pulmo; Nayarit to Jalisco. Eastern Pacific: southern British Columbia to Oregon; Anacapa Island (California Channel Islands) to La Jolla, California; Isla Guadalupe and Islas San Benito (off Baja California); Bahía San Quintín (Baja California) to Punta Lobos (near Todos Santos, Baja California Sur); Colima to Guerrero; Costa Rica. Central Pacific: Hawaiian Islands. Western Pacific: China; Korea; Japan; Vietnam.

Type Locality. Seven localities: "Hakodate, Otaru, insulam Rishiri, prov. Hidaka, prov. Inaba, prov. Bōshū, prov. Owari" (Yendo, 1920:6). Lectotype locality: Hakodate, Hokkaidō Pref. (Oshima subpref.), Hokkaidō, Japan (I. K. Lee, 1978).

Remarks. A Japanese species, *Lomentaria hakodatensis* was first reported in the Gulf of California by Dawson (1944a). Hawkes and Scagel (1986) suggested that *L. hakodatensis* from Vancouver Island to Washington state may have been introduced with oysters imported from Japan. It apparently has also been similarly introduced in northern France (Cabioch and Magne, 1987), Spain (Bárbara and Cremades, 1996), Italy (Curiel et al., 2006), California (Miller, 2004), Russia, Hawaii (Abbott, 1999), and Australia (Millar and Kraft, 1993; Miller et al., 2011). It can be invasive: since being recorded in Humboldt Bay, northern California, it has increased in abundance (Miller et al., 2011). While *L. hakodatensis* is not presently a problem in the northern Gulf of California, it should be monitored.

Culture studies of *Lomentaria hakodatensis,* an annual western Pacific species (I. K. Lee, 1978), from Korea (I. K. Lee and West, 1980) showed a triphasic life history of isomorphic tetrasporophytes and gametophytes.

RHODYMENIACEAE

Rhodymeniaceae Harvey, 1849a:75, 120; Saunders et al., 1999:35.

Algae are erect; axes and branches are terete to flat, strap-like to foliose, and some genera have hollow, mucilage-filled vesicles. Thalli may be alternately, pinnately, palmately, dichotomously to polychotomously, or irregularly branched. Multiaxial in construction, species may be solid or partially solid and partially hollow. Anatomically, they lack longitudinal medullary filaments. The medulla may be pseudoparenchymatous, composed of compact large cells; in others the medulla may become hollow or partially solid and hollow. The cortex is composed of (1–)2–4(–6) cell layers, with cells often in anticlinal rows. Secretory cells (gland cells) occur in some members and can be solitary or in groups.

Gametophytes and tetrasporophytes are isomorphic. Tetrasporangia are usually cruciately divided, intercalary (or rarely terminal) on cortical filaments. The gametophytes of most members are dioecious, while some have monoecious gametophytes. Carpogonial branches are four-celled or rarely (two) three-celled. Auxiliary cell filaments of two or three cells develop before fertilization and are borne on the supporting cell of the carpogonial branch (procarpic). Auxiliary cells usually do not fuse with other cells. Cystocarps are generally compact, more or less globose, partly immersed, and prominently protruding and scattered over the thallus surface, with a pericarp that either has or lacks an ostiole. Most of the gonimoblast cells become carposporangia, and the fusion cell is elongate (fusing cells still discernible), and *tela arachnoidea* are absent. Spermatangia are cut off from initials formed from the outer cortical cells and are superficial and scattered over the outer cortex or in sori.

The family is represented by three of its genera in the northern Gulf of California.

KEY TO THE GENERA OF RHODYMENIACEAE IN THE NORTHERN GULF OF CALIFORNIA

1a. Algae with vesicle-like laterals that are internally hollow and filled with watery mucilage, above a solid, narrow stipe or a solid stipe and solid axes 2
1b. Algae without hollow, mucilage-filled vesicular laterals, internally with a solid pseudoparenchymatous medulla throughout . . . . ***Rhodymenia***
2a. Axes terete, solid, simple to branched, above a solid stipe, that bear hollow (mucilage filled) spherical to pyriform, sometimes elongated or saccate, unbranched vesicular laterals . . . . ***Botryocladia***
2b. Axes and branches of hollow (mucilage filled), elongated, saccate vesicles that bear similar hollow, lobed vesicles, borne above a usually short, solid stipe . . . . ***Irvinea***

Botryocladia (J. Agardh) Kylin

Chrysymenia sect. *Botryocladia* J. Agardh, 1851:214, *nom. cons.*
Botryocladia (J. Agardh) Kylin, 1931:17.
Botryocladia (J. Agardh) Harvey, 1853:249, *nom. rej.*

Algae are erect, deep pink, dark rosy-reds to orange-brown in color, composed of solid, terete, branched or unbranched axes bearing inflated, hollow, mucilage-filled, vesicle-like laterals; above a discoid or rhizomatous holdfast. Solid axes are internally compact, of large, nearly colorless, medullary cells that grade into a cortex of small, pigmented cells. The vesicle-like laterals are variously shaped; spherical, ovoid, pyriform, or saccate. At the interior of the vesicles is a hollow cavity (without a filamentous medulla) filled with a watery mucilage. Vesicle walls have a cortex of 2–3(–6) layers of small cells over a layer(s) of relatively larger rounded medullary cells bordering the hollow interior. The outermost cortical layer of the vesicles may be continuous or discontinuous. If the cortex is incomplete, it appears net-like in surface view, with the small pigmented cells arranged in open rosettes (circular arrangement) around and above the medullary cells. However, in some species the vesicle cortical layer is net-like and incomplete initially, but later cortical cells fill in the open areas, resulting in a complete cortical layer at maturity. The medulla is one to three cell layers; inner medullary cells are oblong to polygonal and bear secretory cells ("gland" cells) singly or in groups, that project into the mucilage-filled cavity. Secretory cells may be sessile on unmodified medullary cells or borne on special initials.

Asexual reproduction has been reported in all the rhizomatous species. Life histories are presumed to be triphasic, with isomorphic tetrasporophytes and gametophytes. Tetrasporangia are regularly or irregularly cruciately divided, formed in an intercalary position in the cortical layers, and scattered over the vesicles. Gametangial thalli are dioecious or monoecious. The carpogonial branch is four-celled. Most gonimoblast cells become carposporangia, developed in two to three lobes inside a thick pericarp. Cystocarps are ostiolate, without ornamentation, and scattered over the vesicles; they are immersed within or protruding above the vesicle surface (cortex thickens over cystocarp) and inward into the medulla. Spermatangia are in superficial sori, scattered over the vesicle surface; spermatia are terminal on elongated initials developed from cortical cells.

REMARKS. Species of *Botryocladia* are easily recognized in the field by their distinctive, mucilage-filled, vesicle-like (often "grape-like" in appearance) laterals borne on solid, terete stalks and branches. These characters separate *Botryocladia* from the completely saccate or vesiculate thalli of *Chrysymenia* J. Agardh (1842), which lack a solid stipe. The lack of branching in the vesicles of most *Botryocladia* species is the primary field character used to distinguish the genus from the recently described *Irvinea* Guiry (in Saunders et al., 1999) that has vesiculate branches that further develop vesicular branches (compound). The function of the "gland cells" in this genus was found to be secretory (Young, 1978), and they are now generally referred to as secretory cells.

The Pacific Mexico species, *Botryocladia adhaerens* E. Y. Dawson (1963a:449, pl. 82: figs. 1–3), described from Rocas Alijos off Pacific Baja California Sur, is composed of elongated vesicles, with the primary vesicle issuing one or more secondary vesicles, thus exhibiting some of the morphological characteristics of *Irvinea*. However, with vesicles that have an "essentially continuous outer layer" (Dawson, 1963a), *B. adhaerens* cannot be transferred to *Irvinea* until additional reproductive or morphological features can be found and molecular data can be acquired to elucidate its generic status. Another similar species, *Botryocladia chiajeana* (Meneghini) Kylin (1931, basionym: *Chrysymenia chiajeana* Meneghini, 1844b; see also Afonso-Carrillo et al., 2006), is also recorded from Rocas Alijos (Silva et al., 1996b).

The oligosaccharides, compounds derived from sulfated polysacchardies, of western Atlantic *Botryocladia occidentalis* (Børgesen) Kylin (1931) have been shown to have anticoagulant activity (Farias et al., 2000; Pereira et al., 2005; Jiao et al., 2011) and anti-venom activity (Toyama et al., 2010). The biological activities of chemical compounds of northern Gulf of California species of *Botryocladia* have not yet been investigated.

There are three species of *Botryocladia* in the northern Gulf of California.

KEY TO THE SPECIES OF *BOTRYOCLADIA* AND *IRVINEA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Vesicles bearing secondary vesicles (compound); vesicles large, elongate; thalli with a short, solid stipe . . . . **Irvinea hancockii**
1b. Vesicles not bearing additional vesicles (simple); vesicles spherical, globose, ovoid, or pyriform; vesicles borne on solid, terete, branched axes above the stipe 2
2a. Outermost cortical layer of vesicles not continuous, appearing net-like, arranged in open rosettes over inner cells . . . . . **Botryocladia guaymasensis**
2b. Outermost cortical layer continuous over vesicle surface 3
3a. Vesicles subspherical, numerous, densely set along entire length of axes; less than 4 mm in diameter and up to 6 mm in length . . . . **Botryocladia uvarioides**
3b. Vesicles mostly longer than wide; larger than 4 mm in diameter and longer, up to 17 mm in length . . . . **Botryocladia datilensis**

Botryocladia datilensis **(E. Y. Dawson) J. N. Norris, *comb. nov.***

FIGURE 231

Botryocladia pseudodichotoma var. *datilensis* E. Y. Dawson, 1944a:305, pl. 45: fig. 7, pl. 73: fig. 1 [type specimens]; 1961b:436; González-González et al., 1996:178.

Botryocladia uvarioides sensu Dawson, 1963a[in part; only specimens of *B. pseudodichotoma* var. *datilensis*]:454, pl. 82: only fig. 4 [non *Botryocladia uvarioides* E. Y. Dawson, 1944a:306].

Algae erect, 3–8 cm tall; composed of solid, terete branched axes that bear subspherical to elongate, unbranched vesicles, mostly 5–17 mm long, 4–6 mm in diameter, each above a very short pedicel, about 0.5 mm long; thalli attached by a small discoid holdfast. Vesicles with a complete outermost cortical layer of small, pigmented cells, continuous over larger inner cells. Secretory cells 30–35 μm long; mostly borne in groups of 5–6 on innermost medullary cells facing inward toward cavity.

Reproduction not described (although a tetrasporophyte was reported by Dawson, 1944a:305).

HABITAT. On rocks, in crevices, and in tide pools; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Tiburón; Isla Turner; Guaymas.

TYPE LOCALITY. Isla Turner (El Datil; Turners Island), off southeast end of Isla Tiburón, Islas de la Cintura, Gulf of California, Mexico.

REMARKS. Although Dawson (1963a:455, as *B. pseudodichotoma* var. *datilensis*) seemed less certain of its taxonomic separation from *B. uvarioides, B. datilensis* is recognized as distinct from the other known Gulf of California species of *Botryocladia* and the California *B. pseudodichotoma* (Farlow) Kylin (1931).

Botryocladia guaymasensis **E. Y. Dawson**

FIGURE 232

Botryocladia guaymasensis E. Y. Dawson, 1963a:451, pl. 82: fig. 11, pl. 84 [holotype]; González-González et al., 1996:178.

Algae erect, up to 15 cm tall, attached below by a relatively small discoid holdfast. A solid, terete, irregularly branched main axis bears numerous, ovoid, unbranched elongate vesicles, mostly 4–12(–14) mm long and 2–5 mm in diameter (at mid vesicle), borne on short pedicels, 0.5–1.0 mm long. Vesicle walls composed of an inner layer of thin-walled, elliptical medullary cells, 50–150 μm wide, that bear secretory cells, 15–25 μm long, extending into the cavity. Outermost cortical layer of vesicles discontinuous

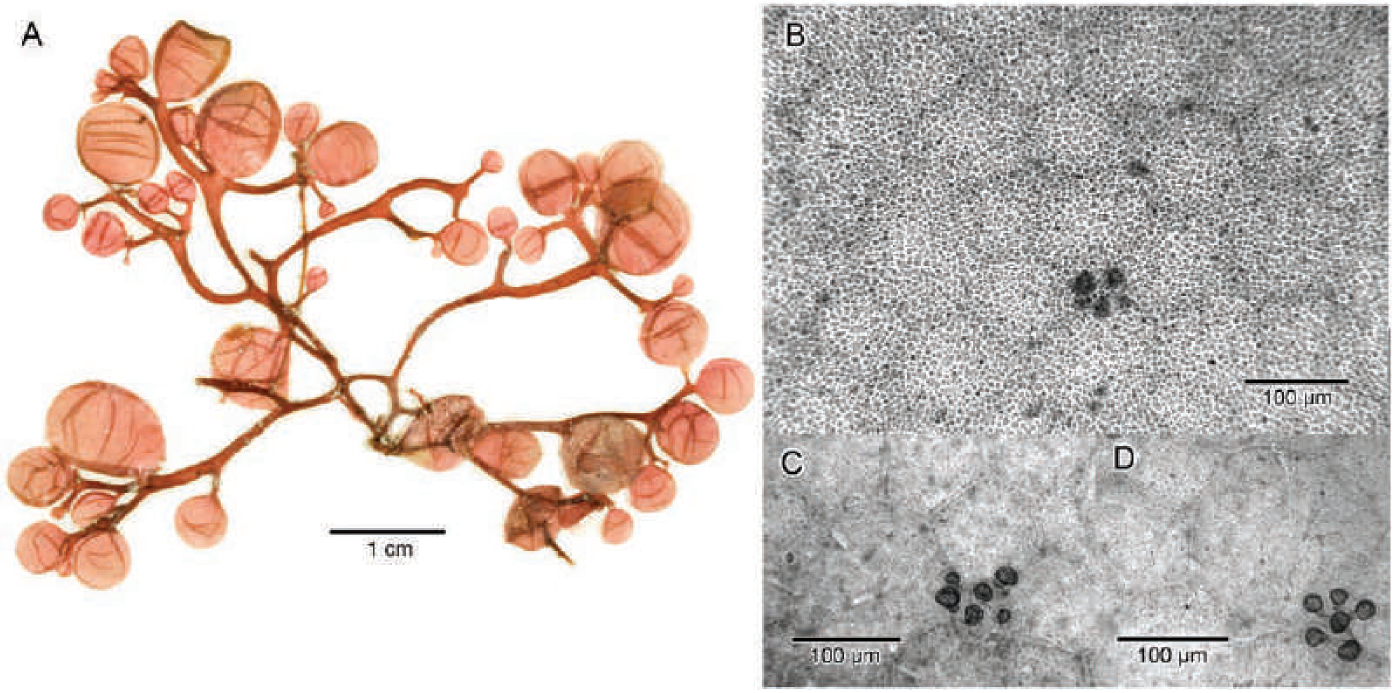

FIGURE 231. *Botryocladia datilensis*: A. Habit (*JN-2993*, US Alg. Coll.-158661). B. Surface view of portion of vesicle showing continuous outer cortical layer, underlying polygonal pattern of larger medullary cells, and one group of secretory cells. C, D. Groups of secretory cells (darkly stained) on cells of the inner wall of vesicles (B–D, *JN-4429*, US Alg. Coll. microscope slide 4589).

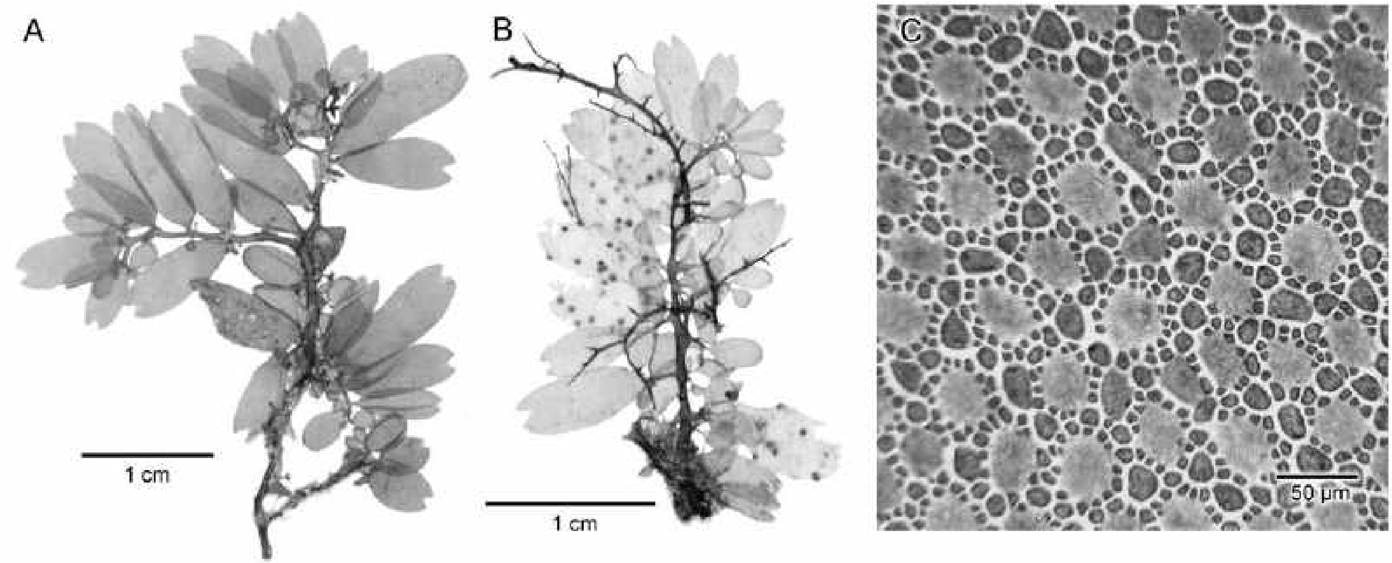

FIGURE 232. *Botryocladia guaymasensis*: A. Habit (*JN-6083b*, US Alg. Coll.-158697). B. Habit, cystocarpic specimen (*JN-5858*, US Alg. Coll.-158696). C. Surface view of vesicle wall showing the incomplete outer cortical layer that forms a network of rosettes around the inner cells (*JN-4847*, US Alg. Coll. microscope slide 4588).

(in surface view); small surface cells, 6–10 µm in diameter, and an underlying secondary layer of larger, pigmented cells (subcortical cells), 20–25 µm in diameter, together form a network of open rosettes over medullary cells (Figure 232C). Secretory cells sessile, usually sparse to few, either solitary or in groups of 2–6.

Tetrasporangia ovoid, 25–30 µm long; scattered in cortex over distal portions of vesicles. Cystocarps about 500 µm in diameter; protruding from and scattered over vesicle walls. Spermatangia not known.

HABITAT. On rocks; low intertidal to shallow subtidal, down to 15 m depths.

DISTRIBUTION. Gulf of California: Playa Las Conchas (Playa Estación), Puerto Peñasco to Punta Robinson (vicinity of Puerto Libertad); Bahía San Carlos to Guaymas.

TYPE LOCALITY. Bahía San Francisco, within east shore of Bahía San Carlos (about 11 km [~7 mi] northwest of Guaymas), Sonora, Gulf of California, Mexico.

Botryocladia uvarioides E. Y. Dawson

FIGURE 233

Botryocladia uvarioides E. Y. Dawson, 1944a:306, pl. 45: figs. 8–10, pl. 75: fig.1 [type specimen]; 1959a:28, fig. 8; 1961b:436; 1963a:454 [in part; excluding specimens of *B. pseudodichotoma* var. *datilensis*], pl. 82: figs. 9, 10, pl. 83: fig. 3; 1966a:25; Norris, 1973:14, pl. 5; Huerta-Múzquiz, 1978:338; Mateo-Cid and Mendoza-González, 1992:21; Mendoza-González and Mateo-Cid, 1992:20; Serviere-Zaragoza et al., 1993a:483; Mateo-Cid and Mendoza-González, 1994b:40; Mendoza-González et al., 1994:108; González-González et al., 1996:179, fig. 21; Mateo-Cid et al., 2000:65; Cruz-Ayala et al., 2001:191; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:468; Mateo-Cid et al., 2006:56; Pacheco-Ruíz et al., 2008:210.

Botryocladia pseudodichotoma sensu Taylor, 1945:255 [in part; non *Botryocladia pseudodichotoma* (Farlow) Kylin, 1931:18; basionym: *Chrysymenia pseudodichotoma* Farlow, 1889:1].

Algae erect, up to 22 cm tall, with solid axes and branches, up to about 1 mm in diameter, above a solid stipe, dividing into axes that branch irregularly up to 5 orders; dense, with numerous, subspherical mucilage-filled vesicles, closely set along entire solid axes and branches. Subspherical vesicles 2–4(–6) mm in diameter; each on a short pedicel; vesicle wall of 3 cell layers with hollow, mucilage-filled cavity. Outermost cortical layer of vesicles with small cells, 4–6 µm in diameter, continuous over vesicle surface; subcortical cells 12–18 µm in diameter; innermost cells larger, 50–90 µm in diameter. Secretory cells relatively rare to infrequent, sessile, either solitary, 10–12 µm in diameter, mostly 1(–2) (if 2, not close together) on an inner cell (Figure 233B), or still sparse but occasionally in groups of 3–5 (Figure 233B), with a slender attachment between them; borne on inward-facing surface of innermost medullary cells.

Tetrasporangia 20–25 µm in diameter, scattered over the vesicles. Gametangial thalli not seen.

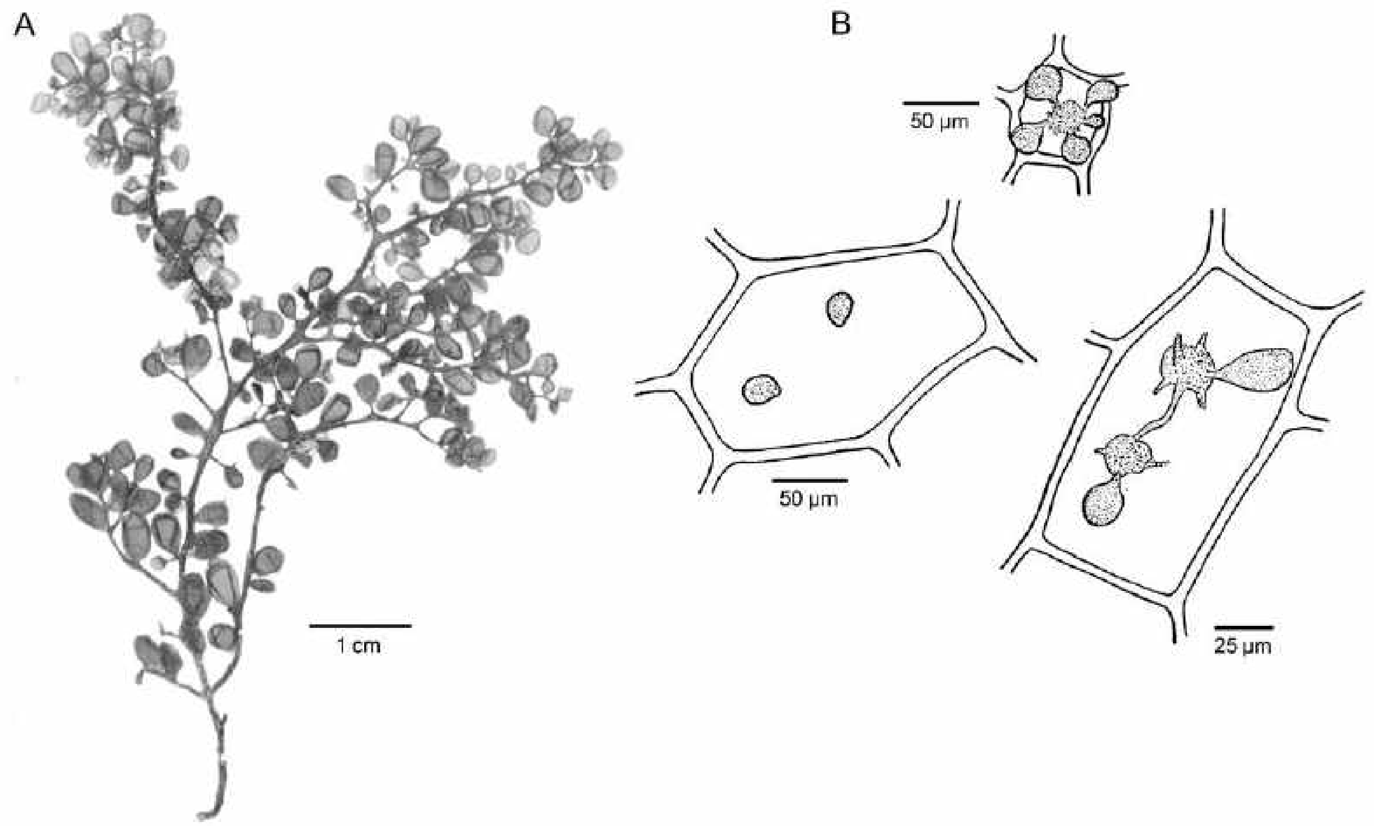

FIGURE 233. *Botryocladia uvarioides*: A. Habit (*JN-3145*, US Alg. Coll.-217353). B. Secretory cells on inner medullary cells facing into the hollow cavity (drawn from syntypes after Dawson, 1944a: pl. 45: figs. 8–10).

Habitat. On rocks, in crevices, and in tide pools; mid intertidal to subtidal; also dredged from 40 m depth (Dawson, 1944a).

Distribution. Gulf of California: Puerto Peñasco to San José del Cabo; Mazatlán, Sinaloa to Jalisco; Isla María Magdalena, Islas Marías (Islas Tres Marías). Eastern Pacific: Playa Los Cerritos (south of Todos Santos), Baja California Sur.

Type Locality. San José del Cabo, Baja California Sur, southern entrance to Gulf of California, Mexico.

Uncertain Record:
***Botryocladia pseudodichotoma* (Farlow) Kylin**

Botryocladia pseudodichotoma (Farlow) Kylin, 1931:18; Mendoza-González and Mateo-Cid, 1986:424.

Remarks. Specimens reported as "*Botryocladia pseudodichotoma*" from Isla Tiburón and estero Punta Perla (Mendoza-González and Mateo-Cid, 1986) need to be reexamined to verify the presence of this species in the northern Gulf.

Irvinea Guiry in G. W. Saunders, I. M. Strachan et Kraft

Irvinea Guiry in G. W. Saunders, I. M. Strachan et Kraft, 1999:36.

Algae are erect, consisting of solid, terete, branched stipes that bear elongated, cylindrical or saccate vesicles that branch or bear secondary vesicles that are formed sympodially and are irregularly arranged. Thalli are attached below by a branched stoloniferous holdfast that coalesces to form a discoid structure and may issue additional erect axes. Thalli are multiaxial in construction; with a cortex of two to three layers of small cells that initially form a discontinuous layer over the medullary cells, arranged in open rosettes. The medulla is composed of 1–2 layers of larger rounded cells. Vesicles appear hollow and are filled with a mucilage that is likely produced by the secretory cells. Secretory cells are singular or in groups of two to six, borne on special support structures (unique, rotund, bearing cells sensu Dawson and Neushul, 1966, or "special initial" sensu Guiry and Guiry, 2009) that develop on the inner faces of the medullary cells lining the cavity.

Life histories, where known, involve isomorphic tetrasporophytes and gametophytes. Tetrasporangia are cruciately divided, developed in an intercalary position from cortical cells within irregularly shaped sori on the vesicles. Gametophytes are dioecious. Four-celled carpogonial branches are borne on inner-cortical supporting cells that also bear a two-celled auxiliary cell branch. The carposporophyte develops outwardly from a basal fusion cell and forms two to three developing lobes of carposporangia in different stages of maturity; a few slender, elongate cells, perhaps with a nutritive function, persist in the mature ostiolate cystocarp. Cystocarps, with a thick pericarp, protrude from and are scattered over vesicles. Spermatangia in sori cover most of a vesicle, cut off from elongate initials formed from cortical cells.

Remarks. Molecular systematic studies revealed that *Botryocladia ardreana* J. Brodie et Guiry (1988) and some other species referred to *Botryocladia* belong in a segregate genus, *Irvinea* (generitype: *I. ardreana* (J. Brodie et Guiry) Guiry in Saunders et al., 1999; Wilkes et al., 2006). Morphological characters used to separate *Irvinea* from related genera (Guiry in Saunders et al., 1999; Wilkes et al., 2006; Guiry and Guiry, 2009) include strongly protruding cystocarps and vesicles with an incomplete outer cortex (i.e., arrangement of cortical cells in rosettes, at least initially) in combination with the formation of secretory cells on special initials (bearing cells). However, because of features that overlap with some species of *Botryocladia*, it is difficult to distinguish *Irvinea* solely on morphological characters (e.g., Schneider and Lane, 2000, 2008), and Afonso-Carrillo et al. (2006) concluded *Irvinea* was only separable on molecular evidence. Schneider and Lane (2008) suggested that a characteristic for *Irvinea* might be its vesicle with branched or secondary vesicles of indeterminate growth, whereas the few species of *Botryocladia* with branched vesicles have determinate growth.

Currently, there is one species of *Irvinea* known in the northern Gulf of California. (See "Key to the Species of *Botryocladia* and *Irvinea*.")

Irvinea hancockii (E. Y. Dawson) R. Wilkes, L. McIvor et Guiry

FIGURE 234

Botryocladia hancockii E. Y. Dawson, 1944a:305, pl. 45: figs. 2–5; 1961b:436; 1963a:452, pl. 82: figs. 6–8, 12; Dawson and Neushul, 1966:180, pl. 43: figs. 1–3; Norris and Bucher, 1976:18, fig. 6b; Abbott and Hollenberg, 1976:551, fig. 495; González-González et al., 1996:178; CONANP, 2002:141; Pacheco-Ruíz and Zertuche-González, 2002:468; Pacheco-Ruíz et al., 2008:210.

Irvinea hancockii (E. Y. Dawson) R. Wilkes, L. McIvor et Guiry, 2006:488.

Algae erect, 3–15 cm tall; thalli composed of hollow, broad, elongated primary main axis that bears radially arranged lobed to elongated saccate vesicles, 4–6 mm in diameter, with few to many elongated secondary vesicles, that in turn may further produce more lobed protuberances or elongated saccate vesicles. Primary elongate vesicle borne above a short, solid, branched, terete stipe, about 1.0–1.5 mm in diameter; attached below by a small discoid holdfast. Vesicle wall of 3 cell layers, outermost cortical layer is discontinuous, appearing net-like in surface view, with small cells arranged in open rosettes over inner cells. Secretory cells occasional, borne from a distinctive rotund bearing cell ("special initial" sensu Guiry and Guiry, 2009) issued from large cells of the inner medulla bordering the cavity. Secretory cells pyriform to subspherical, either single or in groups of 2–6.

Tetrasporophytes unknown. Cystocarps hemispherical, protruding, about 300 μm tall and 600 μm in diameter, with an ostiole, 50 μm in diameter. Spermatangia not known.

Habitat. On rocks; subtidal, 8–19 m depths; also dredged from 20–40 m depths (Dawson, 1944a).

Distribution. Gulf of California: Isla Mejía (northwest side of Puerto Refugio, Isla Ángel de la Guarda) to Isla Estanque; Bahía Agua Verde to Punta Los Frailes. Eastern Pacific: Anacapa Island (California Channel Islands) to Bahía Sebastián Vizcaíno (Baja California Sur).

Type Locality. Bahía Agua Verde, Baja California Sur, Gulf of California, Mexico.

Remarks. *Irvinea hancockii* can be recognized in the Gulf primarily by its short solid stipe and very elongated, more or less tubular, saccate axes and branches. These characters separate *I. hancockii* in the field from the Gulf species of *Botryocladia*, which have subspherical to pyriform vesicles on solid, slender, terete axes and branches.

Rhodymenia Greville

Rhodymenia Greville, 1830: xlviii, 84, pl. 12 [as "*Rhodomenia*"]; Sparling, 1957:353.

Rhodymenia (Greville) Montagne, 1841:151.

Epymenia Kützing, 1849:787; Womersley, 1996:69; Saunders et al., 1999:37.

Algae are erect or partially prostrate, composed of flattened, semicartilaginous, ligulate to foliose fronds that may be simple but are usually dichotomously, palmately, or irregularly branched. Fronds are attached to substratum by a basal disc or stolons. Blades sometimes have marginal, surface, or apical proliferations, and some are perforated (not known in Gulf species). Many species are sessile (without a terete stipe); some have a short to long, simple or branched stipe above a discoid holdfast, and others arise and spread from terete stoloniferous basal branches that are secondarily attached by small discs. Growth in some species is monopodial and in others is ramisympodial. Thalli are multiaxial in structure, with a pseudoparenchymatous medulla, composed of a few to many layers of large, nearly colorless, isodiametric cells. The cortex is thin, of two to five layers of progressively smaller cells, the outermost of which is pigmented and axially elongated.

Life histories are incompletely known but are presumed to be isomorphic. Tetrasporangia are cruciately divided, developed in an intercalary position within the unmodified cortex, and either (1) scattered over the blade, (2) in subapical sori, or (3) formed in special proliferations. Gametangial thalli are dioecious. Carpogonial branches (three-)four-celled, borne on a large, multinucleate supporting cell that also bears a two-celled

FIGURE 234. *Irvinea hancockii*: Habit of a cystocarpic thallus; note short, solid, terete stipe from which the large elongate, cylindrical vesicles of the main axis arise and elongate vesicle branches from axial vesicles (*JN-5600*, US Alg. Coll.-217355).

auxiliary cell branch (procarpic). The gonimoblast develops outward, often creating two to three compact gonimolobes, with almost all cells becoming carposporangia; *tela arachnoidea* (network of spiderweb-like filaments between the gonimoblast and pericarp) are absent. Cystocarps with a basal fusion cell and a thick ostiolate pericarp, they are hemispherical, large, and protruding, and they occur scattered over the upper portion of blades. Spermatangia are cut off from outer cortical cells and occur in small subapical sori or in larger irregular patches, scattered over blades.

Remarks. *Rhodymenia* species occur worldwide and are know from low intertidal to depths of 100 m (Guiry and Guiry, 2009).

There are four species of *Rhodymenia* known in the northern Gulf of California. One additional species, *Rhodymenia californica* Kylin (1931), has been reported in the southern Gulf from Punta Arena (Mateo-Cid et al., 2000) and in Pacific Mexico (Pacheco-Ruíz and Aguilar-Rosas, 1984; R. Aguilar-Rosas et al., 1990; Dreckmann et al., 1990; Serviere-Zaragoza et al., 1993a; Mateo-Cid and Mendoza-González, 1994b; Riosmena-Rodríguez et al., 2005b).

KEY TO THE SPECIES OF *RHODYMENIA* IN THE NORTHERN GULF OF CALIFORNIA

1a. Blades above a distinct terete stipe 2
1b. Blades sessile, arising directly from holdfast (lacking a stipe) 3
2a. Blade segments less than 3 mm wide (0.7–2.5 mm) . . . . ***R. dawsonii***
2b. Blade segments wider than 4 mm (4–7 mm) . . . . ***R. hancockii***
3a. Blades markedly divaricately, dichotomously to irregularly branched; segments 2–3 mm wide . . . . ***R. divaricata***
3b. Blades dichotomously branched at narrow angles; segments 3.5–4 mm wide . . . . ***R. huertae***

Rhodymenia dawsonii W. R. Taylor

FIGURE 235A,B

Rhodymenia dawsonii W. R. Taylor, 1945:251, pl. 84: fig. 2; Dawson et al., 1960b:24; Dawson, 1961b:436; 1963a:459, pl. 88; Mendoza-González and Mateo-Cid, 1985:32; González-González et al., 1996:266.

Rhodymenia arborescens sensu Dawson et al., 1960a:76 [in part]; Dawson et al., 1960b:22 [in part]; Pacheco-Ruíz et al., 2008:210 [non *Rhodymenia arborescens* E. Y. Dawson, 1941b:149].

Rhodymenia hancockii sensu Dawson, 1959a:28, fig. 9A [non *Rhodymenia hancockii* E. Y. Dawson, 1941b:146].

Fronds dull to bright red in color, up to 12 cm tall, attached by a subconical, discoid holdfast; with a cylindrical stipe, 0.8–1.2 mm in diameter, 2–5 cm long; upper end of stipe becoming compressed into dichotomously branched blade; repeatedly dichotomously branched, mostly branching at intervals of 5–12 mm; blade segments (branches) very narrow, 1.5–2.5 mm wide in lower to mid blade, 0.7–1.0 mm wide in upper portions; with subacute apices. Initial stipe of primary axes may successively produce secondary stipitate axes from its upper portion. Segments of mid thallus 170–370 μm thick; medulla of 3–7 layers of large colorless cells, 30–70 μm in diameter, grading through 3–5 layers of smaller cortical cells; outermost cortical cells anticlinally elongate, up to 6–7 μm in diameter.

Tetrasporangia ellipsoidal, 30 μm long; within small nemathecial sori, bordered by narrow sterile margin, on both sides of upper branch segments. Cystocarps prominent, primarily along margins in upper portions of thallus; subspherical, about 750 μm in height and width, rostrate. Spermatangial thalli unknown.

Habitat. Subtidal; down to 16 m depths.

Distribution. Gulf of California: Isla San Pedro Nolasco; Bahía Agua Verde to Isla Cholla (off Isla Carmén); Isla San Francisco. Eastern Pacific: Arrecife de Sacramento (south-southeast of Isla San Gerónimo, Baja California) to Isla Magdalena (Baja California Sur).

Type Locality. Dredged; off Cabo San Lázaro, about 5.6 km (~3.5 miles) north of Punta Hughes, Baja California Sur, Pacific Mexico.

Rhodymenia divaricata E. Y. Dawson

FIGURE 235C

Rhodymenia divaricata E. Y. Dawson, 1941b:141, pl. 23: fig. 31; 1944a:307; Taylor, 1945:251; Dawson, 1961b:436; 1963a:460, pl. 89: fig. 2; Norris, 1985d:214; González-González et al., 1996:267; CONANP, 2002:141; Pacheco-Ruíz et al., 2008:210.

Fronds 3–5 cm tall; blades expanded directly above attachment (lacking a distinct stipe); irregularly dichotomously branched at 3–12 mm intervals, strongly divaricate; blade

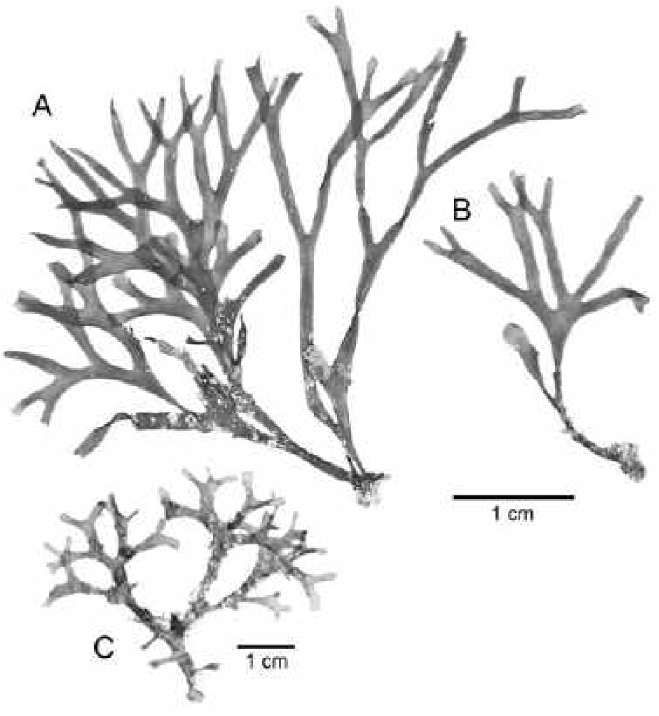

FIGURE 235. Species of *Rhodymenia*. A, B. *Rhodymenia dawsonii*: Habits (*EYD-18658*, US Alg. Coll.-13019).C. *Rhodymenia divaricata*: Holotype (*EYD-53-40*; AHFH-1, now UC).

segments 2–3 mm wide, 200–300 µm thick; apices broadly rounded (lobe-like). Medulla of 5 layers of large cells, largest about 50 µm in diameter; outer medulla grading in size into cortex of 1–2 layers of smaller cells, 8–10 µm in diameter.

Reproductive structures unknown.

HABITAT. On rocks and mud bottom; subtidal, 3–10 m depths; dredged from 8–28 m depths.

DISTRIBUTION. Gulf of California: Isla Mejía (northwest side of Puerto Refugio, Isla Ángel de la Guarda) to Canal de San Lorenzo (off southern end of Isla Espíritu Santo). Eastern Pacific: Galápagos Islands.

TYPE LOCALITY. On mud bottom, dredged from about 3.6–5.5 m (2–3 fathoms), Bahía Guaymas, Sonora, Gulf of California, Mexico.

REMARKS. *Rhodymenia divaricata,* described from the Gulf of California, has also been reported in the eastern United States from North Carolina to Florida (Schneider and Searles, 1991). However, Dawes and Mathieson (2008) suggested most or all of these western Atlantic records may be *Gracilaria galetensis* Gurgel, Fredericq et J. Norris (2004).

Rhodymenia hancockii E. Y. Dawson

FIGURE 236

Rhodymenia hancockii E. Y. Dawson, 1941b:146, pl. 20: fig. 20; pl. 26: fig. 38 [type specimen]; 1944a:307; 1961b:436; 1963b:461, pl. 89: fig. 1; 1966a:25; 1966b:64, fig. 4A; Abbott and Hollenberg, 1976:557, fig. 502; Norris, 1985d:214; Ramírez and Santelices, 1991:303; González-González et al., 1996:267; Pacheco-Ruíz and Zertuche-González, 2002:468.

Dendrymenia hancockii (E. Y. Dawson) Santelices, 1989:340, 342, pl. MM: fig. 9.

Fronds dark red, firm in texture, up to 8 cm tall; blades usually dichotomously to subdichotomously divided, of segments 4.0–7.0(–10) mm wide, 150–400 µm thick, with broadly rounded apices; dichotomous-flabellate blade abruptly expanded at right to acute angles from a stout, thick, terete, sympodially branched stipe; basal attachment structure incompletely known. Medulla of several layers of large, somewhat irregular, roundish to oval cells, becoming progressively smaller into outer medulla of 1–2 cells and grading into cortical layer of 1–3 small cells.

Reproductive structures unknown.

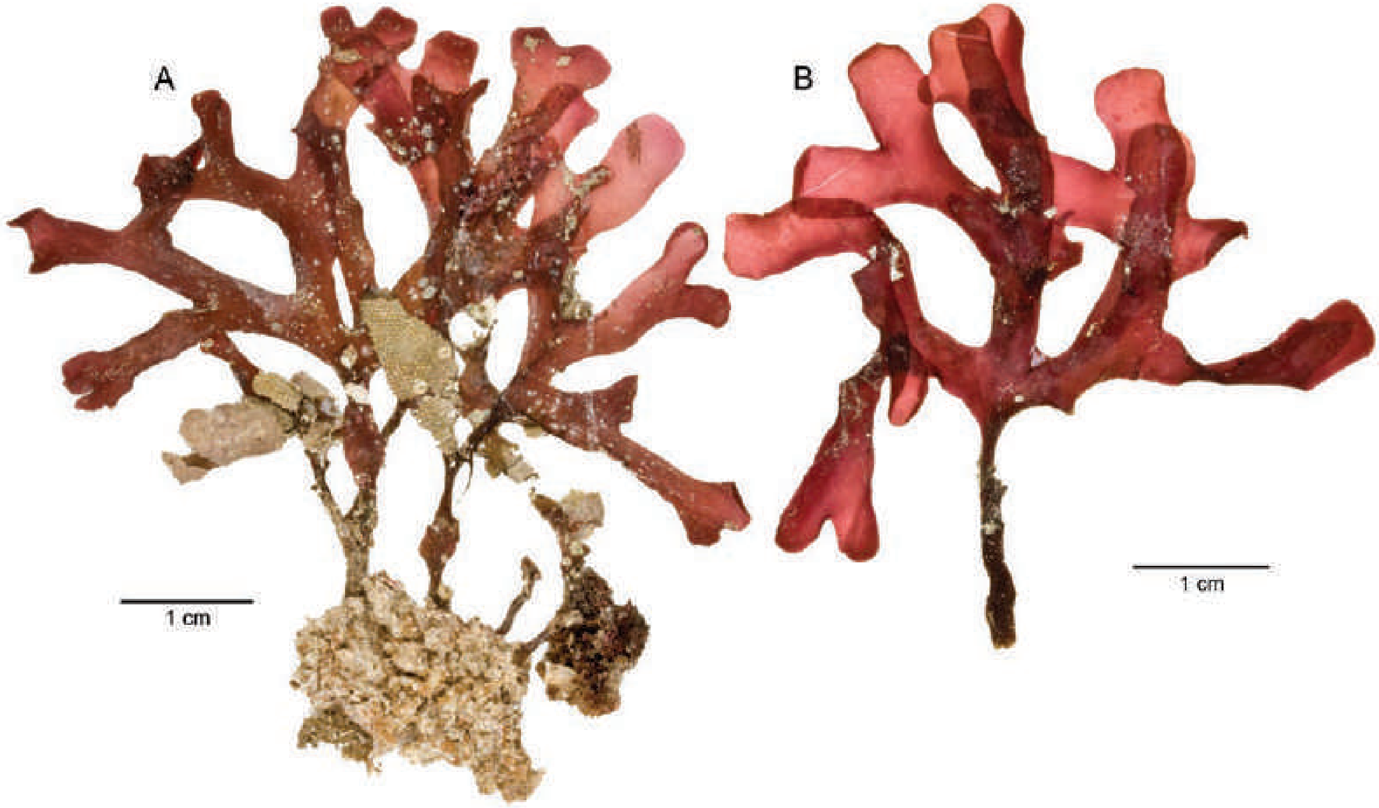

FIGURE 236. *Rhodymenia hancockii*: A, B. Habit variations (A, *JN-2938*, US Alg. Coll.-160805; B, *JN-4875*, US Alg. Coll.-160814).

Habitat. On shell-hash bottom and probably other hard substrata; subtidal, down to 10 m depths or more; also dredged from about 38 m depth.

Distribution. Gulf of California: Puerto Peñasco to Isla Ángel de la Guarda. Eastern Pacific: southern California; Chile.

Type Locality. On shell bottom, dredged from 38.4 m (21 fathoms); west side of Puerto Refugio, Isla Ángel de la Guarda, Islas de la Cintura, Gulf of California, Mexico.

Remarks. Dawson (1941b:46; 1963a:461) noted “lowest basal parts unknown” in the type specimen of the Gulf of California *Rhodymenia hancockii*. However the photograph of the type (Dawson, 1941b: pl. 26: fig. 38 [center specimen]; 1963a: pl. 89: fig. 1) suggests attachment may be a basal, prostrate, stoloniferous axis. Dawson (1966b:64) noted his Puerto Peñasco specimens referred to “*R. hancockii*” had a “sympodial branched rather short stipe” with a “woody cone without any stolons.” Thus, more collections of each of these different forms of *R. hancockii* are needed for further study and elucidation of their basal attachments to clarify the species.

Rhodymenia huertae* J. N. Norris, *nom. nov.

Rhodymenia rosea E. Y. Dawson, 1941b:141, *nom. illeg*., pl. 23: figs. 32, 33; 1944a:307; 1961b:437; 1963a:463 [with generic query]; González-González et al., 1996:267; Pacheco-Ruíz et al., 2008:210 [non *Rhodymenia rosea* Harvey, 1855:554, which is now *Leptosomia rosea* (Harvey) Womersley, 1996:103].

Fronds bright rose, arising directly from a simple holdfast (without a terete stipe), up to 7 cm tall; branching primarily dichotomous, branching at intervals of 1–2 cm; blade segments (2–) 3.5–4 mm wide, about 100 µm thick, with rounded apices; margins entire in upper portions and sparsely denticulate in lower portions; proliferous bladelets produced from denticulations along margins; bladelets narrow at base and remaining simple or often dichotomously branched. Medulla of 1–2 layers of large, thin-walled cells, 50–80 µm in diameter; medulla to cortex sharply delimited; outer cortex a single layer of small, flattened, thin-walled, pigmented cells, 5–9 µm in diameter; cortical cells angular in surface view.

Reproduction unknown.

Habitat. Subtidal; dredged from 12–22 m depths.

Distribution. Gulf of California: Isla Ángel de la Guarda; Isla Tiburón.

Type Locality. Isla Mejía, northwest side of Puerto Refugio, Isla Ángel de la Guarda, Islas de la Cintura, Gulf of California, Mexico.

Remarks. *Rhodymenia huertae* is given as the new name for *R. rosea* E. Y. Dawson (1941b), which is a later homonym of *R. rosea* Harvey (1855). It is named for the late Laura Huerta-Múzquiz (Professor, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional, Mexico D. F.) in recognition of her contributions to our knowledge of the marine algae of Mexico, including Baja California and the Gulf of California (Calderón de Rzedowski and Rzedowski-Rotter, 2000). It was my pleasure to have interacted with her during her visits to the Smithsonian National Museum of Natural History.

Dawson (1963b, as ?*Rhodymenia rosea*), noted some *R. huertae* superficially resembled some small forms of *Gracilaria tepocensis* (E. Y. Dawson) E. Y. Dawson (1962a; see also Norris, 1985c), which was originally described as *Rhodymenia tepocensis* E. Y. Dawson (1941b). When reproductive material of Gulf *Rhodymenia huertae* is found, its generic placement can be further elucidated and molecularly tested.

Acknowledgments

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Appendix 1: New Names, Taxa, Combinations, and Typification

RHODOPHYTA

New Genus
Tacanoosca J. N. Norris, P. W. Gabrielson et D. P. Cheney (Solieriaceae, Gigartinales)

New Section
Neosiphonia sect. *Multisiphonia,* J. N. Norris (Rhodomelaceae, Ceramiales)

New Species
Chondracanthus zertuchei J. N. Norris et Fredericq (Gigartinaceae, Gigartinales)
Gracilariopsis animasensis Gurgel et J. N. Norris (Gracilariaceae, Gracilariales)
Laurencia aguilar-rosasorum J. N. Norris (Rhodomelaceae, Ceramiales)
Laurencia fenicalii J. N. Norris (Rhodomelaceae, Ceramiales)
Laurencia iriei J. N. Norris et Fenical (Rhodomelaceae, Ceramiales)
Palisada pedrochei J. N. Norris (Rhodomelaceae, Ceramiales)
Plocamium katinae J. N. Norris (Plocamiaceae, Plocamiales)
Polysiphonia hollenbergii J. N. Norris (Rhodomeaceae, Ceramiales)

New Name
Rhodymenia huertae J. N. Norris (Rhodymeniaceae, Rhodymeniales)

New Combinations
Acrochaetium seriaspora (E. Y. Dawson) J. N. Norris (Acrochaetiaceae, Acrochaetiales)
Ahnfeltiopsis hancockii (E. Y. Dawson) J. N. Norris et Fredericq (Phyllophoraceae, Gigartinales)

Botryocladia datilensis (E. Y. Dawson) J. N. Norris (Rhodymeniaceae, Rhodymeniales)
Ceratodicyton tenuis (Setchell et N. L. Gardner) J. N. Norris (Lomentariaceae, Rhodymeniales)
Colaconema hancockii (E. Y. Dawson) J. N. Norris (Colaconemataceae, Colaconematales)
Colaconema punctatum (E. Y. Dawson) J. N. Norris (Colaconemataceae, Colaconematales)
Colaconema scinaiae (E. Y. Dawson) J. N. Norris (Colaconemataceae, Colaconematales)
Colaconema sinicola (E. Y. Dawson) J. N. Norris (Colaconemataceae, Colaconematales)
Colaconema variabile (K. M. Drew) J. N. Norris (Colaconemataceae, Colaconematales)
Dasya pedicellata subsp. *stanfordiana* (Farlow) J. N. Norris et Bucher (Dasyaceae, Ceramiales)
Dasya pedicellata subsp. *stanfordiana* var. *nudicaulis* (E. Y. Dawson) J. N. Norris et Bucher (Dasyaceae, Ceramiales)
Gloiocladia hoshawii (E. Y. Dawson) J. N. Norris (Faucheaceae, Rhodymeniales)
Gloiocladia mollis (M. Howe) J. N. Norris (Faucheaceae, Rhodymeniales)
Gloiocladia sefferi (M. Howe) J. N. Norris (Faucheaceae, Rhodymeniales)
Haliptilon roseum var. *verticillatum* (E. Y. Dawson) J. N. Norris (Corallinaceae, Corallinales)
Mazzaella digitata (E. Y. Dawson) J. N. Norris et Fredericq (Gigartinaceae, Gigartinales)
Mazzaella diffusa (E. Y. Dawson) J. N. Norris et Fredericq (Gigartinaceae, Gigartinales)
Neosiphonia cheloniae (Hollenberg et J. N. Norris) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia concinna (Hollenberg) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia confusa (Hollenberg) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia eastwoodae (Setchell et N. L. Gardner) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia johnstonii (Setchell et N. L. Gardner) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia masonii (Setchell et N. L. Gardner) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia mexicana (E. Y. Dawson) J. N. Norris (Rhodomelaceae, Ceramiales)
Neosiphonia paniculata (Montagne) J. N. Norris (Rhodomelaceae, Ceramiales)
Osmundea estebaniana (Setchell et N. L. Gardner) J. N. Norris (Rhodomelaceae, Ceramiales)
Palisada paniculata (Kützing) J. N. Norris (Rhodomelaceae, Ceramiales)
Pterocladia sonorense (E. Y. Dawson) J. N. Norris et J. G. Stewart (Pterocladiaceae, Gelidiales)
Tacanoosca uncinata (Setchell et N. L. Gardner) J. N. Norris, P. W. Gabrielson et D. P. Cheney (Solieriaceae, Gigartinales)
Tsengia abbottiana (J. N. Norris et Bucher) J. N. Norris et Bucher (Tsengiaceae, Cryptonemiales)

Typification: Lectotype
Laurencia paniculata Kützing (Rhodomelaceae, Ceramiales)

Appendix 2: Endemic Rhodophyta of the Gulf of California that Occur in the Northern Gulf

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Bangiales: Bangiaceae
Pyropia hollenbergii
Pyropia pendula

Acrochaetiales: Acrochaetiaceae
Acrochaetium seriaspora

Colaconematales: Colaconemataceae
Colaconema hancockii
Colaconema punctatum

Nemaliales: Liagoraceae
Liagora magniinvolucra

Corallinales: Corallinaceae
Heteroderma corallinicola
Heteroderma gibbsii
Lithophyllum diguetii
Lithophyllum margaritae

Ceramiales: Callithamniaceae
Callithamnion bisporum var. *australe*

Ceramiales: Ceramiaceae
Ceramium obesum
Ceramium periconicum
Ceramium sinicola var. *johnstonii*
Gayliella species A
Pterothamnion tepocense

Ceramiales: Dasyaceae
Dasya pedicellata subsp. *stanfordiana* var. *nudicaulis*

Ceramiales: Delesseriaceae
Myriogramme auricularis
Myriogramme divaricata
Phycodrys amplissima
Phycodrys lucasana
Phycodrys simplex
Polyneurella hancockii var. *rhizoidea*

Ceramiales: Rhodomelaceae
Chondria species A
Laurencia aguilar-rosasorum
Laurencia fenicalii
Laurencia iriei
Neosiphonia cheloniae
Osmundea estebaniana
Polysiphonia hollenbergii
Polysiphonia sonorensis

Ceramiales: Wrangeliaceae
Lejolisia hoshawii

Gelidiales: Gelidiaceae
Gelidium decompositum
Gelidium refugiensis
Pterocladia sonorense

Gigartinales: Gigartinaceae
Chondracanthus squarrulosus
Chondracanthus zertuchei
Mazzaella diffusa
Mazzaella digitata

Gigartinales: Kallymeniaceae
Kallymenia baldwini
Kallymenia bleckii
Kallymenia pertusa

Gigartinales: Phyllophoraceae
Gymnogongrus? carnosus

Gigartinales: Solieriaceae
Agardhiella mexicana
Sarcodiotheca dichotoma
Sarcodiotheca taylorii

Gracilariales: Gracilariaceae
Gracilaria ascidiicola
Gracilaria marcialana
Gracilaria pinnata
Gracilaria rubrimembra
Gracilaria spinigera
Gracilaria subsecundata
Gracilaria tepocensis
Gracilaria vivesii

Cryptonemiales: Halymeniaceae
Cryptonemia opuntioides
Cryptonemia veleroae
Grateloupia dactylifera
Grateloupia violacea
Halymenia bifida
Halymenia megaspora
Prionitis abbreviata var. *guaymasensis*

Nemastomatales: Schizymeniaceae
Platoma? fanii

Plocamiales: Plocamiaceae
Plocamium katinae

Rhodymeniales: Champiaceae
Champia disticha

Rhodymeniales: Faucheaceae
Gloiocladia hoshawii
Gloiocladia mollis
Gloiocladia sefferi
Gloioderma conjuncta

Rhodymeniales: Rhodymeniaceae
Botryocladia datilensis
Botryocladia guaymasensis
Rhodymenia huertae

Appendix 3: Rhodophyta Specimens Illustrated: Species Locality Information and Herbarium

Stylonema alsidii (**Figure 9A**)**:** Epiphytic on *Cladophora*, subtidal, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4491b*; US Alg. Coll. microscope slide 4268).

Stylonema cornu-cervi (**Figure 9B**)**:** Epiphytic on *Anotrichium secundum*, rock reef, 1.5–4.6 m depths, off the west side of sand-cobble beach, Punta Robinson (~2.4 km east of Puerto Libertad), Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4836*; US Alg. Coll. microscope slide 4974).

Erythrocladia irregularis (**Figure 10A**)**:** Epizoic on *Sertularia*, 9.1–18.3 m depths, Peavine Pass (between Obstruction Island and Barkley Island), and Shaw Island, San Juan Islands, Washington, Coll. H. Kylin (LD).

Sahlingia subintegra (**Figure 10B**)**:** Epizoic on *Sertularia*, 9.1–18.3 m depths, Peavine Pass (between Obstruction Island and Barkley Island), and Shaw Island, San Juan Islands, Washington, Coll. H. Kylin (LD).

Erythrotrichia biseriata (**Figure 11**)**:** Epiphytic on *Halymenia californica* (*JN-3202a*), Estero de Bahía de Las Ánimas, Baja California, Coll. J. N. Norris (*JN-3203c*, US Alg. Coll. microscope slide 4251).

Erythrotrichia biseriata (**Figure 12A–C**)**:** Hatidyō Island, Japan (Type: BLIH 1829c, Herbarium of the Biological Laboratory, Imperial Palace, Tokyo).

Erythrotrichia carnea* f. *tenuis (**Figure 12D, E**)**:** Type locality uncertain, several syntype localities listed by Tanaka (1944).

Erythrotrichia parksii* var. *minor (**Figure 13**)**:** Epiphytic on *Colpomenia tuberculata*, 9 m depth, rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5037*, US Alg. Coll. microscope slide 4276).

Erythrotrichia tetraseriata **(Figure 14):** Epiphytic on *Chondria decipiens*, Municipal Wharf, Monterey, California, Coll. H. Kylin (type of *Erythrotrichia californica* Kylin: LD).

Porphyrostromium boryanum **(Figure 15A, B):** On *Gelidium corneum*, Fort des Anglais, Algeria, Coll. J. B. G. M. Bory de Saint-Vincent (type of *Porphyra boryana* Montagne, 1846b, Montagne Herbarium in PC; after Ardré, 1970: pl. 4: figs. 10, 11).

Porphyrostromium ciliare **(Figure 15C):** Punta Baja, Pacific Baja California, Coll. E. Y. Dawson (*EYD-1255*, AHFH, now UC).

Bangia enteromorphoides **(Figure 16):** 2.4–6 m depths, entangled with *Asparagopsis*, Punta la Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3030b*, US Alg. Coll. microscope slide 8696).

***Bangia vermicularis*?** **(Figure 17):** Pebble Beach, Monterey, California (GMS).

Pyropia thuretii **(Figure 18A):** Intertidal, Punta Diggs, south of San Felipe, Baja California, Coll. L. Carpelan (*EYD-12546*, US Alg. Coll.-41997).

Pyropia pendula **(Figure 18B):** Northeast side of cove, Isla San Pedro Nolasco, Coll. N. P. Yensen (*JN-5194a*, US Alg. Coll.-160625).

Pyropia thuretii **(Figure 18C, D):** Northeast side of cove, Isla San Pedro Nolasco, Coll. N. P. Yensen (*JN-5194b*: C, US Alg. Coll.-160627; D, US Alg. Coll. microscope slide 4297).

***Conchocelis*-phase** **(Figure 19):** Laboratory cultures of filaments of *Conchocelis* developed from carpospores of *Pyropia perforata* that were collected from intertidal rocks, Hopkins Marine Station of Stanford University, Pacific Grove, California, Coll. G. J. Hollenberg

Hildenbrandia prototypus **(Figure 20):** Outer, seaward shore of San Quintin Peninsula (opposite Isla San Martín), Baja California, Pacific Mexico, Coll. E. Y. Dawson (*EYD- 8730*, AHFH, now UC).

Acrochaetium secundatum **(Figure 21F):** Bahía Bocochibampo, Sonora, Coll. E. Y. Dawson (*EYD-462a,* AHFH, now UC).

Acrochaetium seriaspora **(Figure 21G–J):** Isla Turner, Coll. E. Y. Dawson (*EYD-736-40,* AHFH, now UC).

Acrochaetium crassipes **(Figure 22):** Epiphytic on *Cladophora*, intertidal rock platform, Playa Hermosa, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4040b,* US Alg. Coll. microscope slide 4254).

Colaconema hancockii **(Figure 23A, B):** Epiphytic on *Gelidium,* Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (*EYD-218a*, type collection, AHFH, now UC).

Colaconema punctatum **(Figure 23G):** Bahía Bocochibampo, Sonora (*EYD-462b* type collection, AHFH, now UC).

Colaconema sinicola **(Figure 23J):** Epiphytic on *Dictyota*, Isla Turner, Coll. E. Y. Dawson (*EYD-739*, type collection, AHFH-17, now UC).

Dichotomaria marginata **(Figure 24A):** On rocks, 4.6–9.0 m depths, Caleta Santa María (north of Santa Rosalía), Baja California Sur, Coll. D. G. Lindquist (*JN-3400a*, US Alg. Coll.-159143).

Dichotomaria marginata **(Figure 24B, C):** Off west side of small cove, 6 m depth, Punta Cirio (south of Puerto Libertad), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4891a*, US Alg. Coll. microscope slide 8707).

Dichotomaria spathulata **(Figure 25A):** Intertidal, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5859*, US Alg. Coll.-159150).

Dichotomaria spathulata **(Figure 25B):** Off west side of small cove, 6 m depth, Punta Cirio (south of Puerto Libertad), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4891b*, US Alg. Coll. microscope slide 8708).

Dichotomaria spathulata **(Figure 25C):** Intertidal rocks fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-2941*, US Alg. Coll. microscope slide 5366).

Galaxaura ramulosa **(Figure 26A):** Rocky intertidal and tide pools, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3563*, US Alg. Coll.-159169).

Galaxaura ramulosa **(Figure 26B):** Rocky intertidal fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. A. E. Dennis (*EYD-27457*, US Alg. Coll.-40824).

Galaxaura ramulosa **(Figure 26C):** Low intertidal rocks in front of Casa Garcia, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3080*, US Alg. Coll.-159167: liquid material in US Alg. Coll. jar 560, vial 5720).

Galaxaura ramulosa **(Figure 26D, E):** 1.5–6.1 m depths, Nueva Guaymas (Bahía de San Carlos), Sonora, Coll. D. Evanson (*JN-4280*, US Alg. Coll. microscope slide 8697).

Galaxaura rugosa **(Figure 27A):** Intertidal rock platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3634*, US Alg. Coll.-159199).

Galaxaura rugosa **(Figure 27B–D):** Low intertidal rocks in front of Casa Garcia, Playa Las Conchas (Playa Estación), Puerto

Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3077*, US Alg. Coll. microscope slide 8698).

Tricleocarpa cylindrica **(Figure 28A):** Rocky intertidal, Cabo Tepoca (SE of Puerto Lobos), Sonora, Coll. J. N. Norris (*JN-5955*, US Alg. Coll.-159165).

Tricleocarpa cylindrica **(Figure 28B):** Intertidal rocks in front of Casa Garcia, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3078*, US Alg. Coll. microscope slide 8699).

Ganonema farinosum **(Figure 29A):** 1.8 m depth, near the reef off south end of Isla San Diego, Coll. E. Y. Dawson (*EYD-18914*, US Alg. Coll.-8101).

Ganonema farinosum **(Figure 29B):** Shallow subtidal, Los Frailes, Baja California Sur, Coll. Valerie Paul (*JN-7173*, US Alg. Coll.-160431).

Liagora ceranoides **(Figure 30):** Drift cast ashore, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3195,* US Alg. Coll.-160430).

Liagora magniinvolucra **(Figure 31A):** In tide pool, Playa Arenosa, vicinity of Puerto Peñasco, Sonora, Coll. R. D. Staker, *s.n.* (US Alg. Coll.-204280).

Liagora magniinvolucra **(Figure 31B, C):** On side of rock in Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4046*, US Alg. Coll. microscope slide 4283).

Scinaia confusa **(Figure 32A):** Intertidal to 9 m depth, NW of the rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5302*, US Alg. Coll.-217350).

Scinaia confusa **(Figure 32B, C):** 9 m depth, on rocks, off rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5024*, US Alg. Coll. microscope slide 4247).

Scinaia johnstoniae **(Figure 33A, B):** 15–22 m depths, dive off east end of Isla Mejia, Isla Ángel de la Guarda, Coll. J. N. Norris, J. Paul, and K. Robertson (*JN-5670*: A, US Alg. Coll.-217351; B, US Alg. Coll.-160916).

Scinaia johnstoniae **(Figure 33C):** Dive to 9 m depth, on rocks, off rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5023*, US Alg. Coll.-160907).

Scinaia johnstoniae **(Figure 34):** 9 m depth, on rocks, off rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5023*, US Alg. Coll. microscope slide 4301).

Scinaia latifrons **(Figure 35):** 9 m depth, on rocks, off rocky point, SE side of Punta Peícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5049*, US Alg. Coll.-160925).

Corallina officinalis* var. *chilensis **(Figure 36A):** Rocky shore, low intertidal, Cabo Colnett, Baja California, Pacific Mexico (*EYD-53*, AHFH, now UC).

Corallina vancouveriensis **(Figure 36B):** Small reef and boulder beach, Rio San Telmo, Baja California, Pacific Mexico, Coll. D. Fork (*EYD-147*, AHFH, now UC).

Corallina pinnatifolia* var. *pinnatifolia **(Figure 37A):** Intertidal rocks east of the village, San Felipe, Baja California, Coll. E. Y. Dawson, H. B. S. Womersley, and M. S. Doty (*EYD-10673*, US Alg. Coll.-6998).

Corallina polysticha **(Figure 37B):** Intertidal rocky shore, ~4.0 km north of South Bluff, Isla Guadalupe, Baja California, Pacific Mexico (holotype: *EYD-8355*, AHFH, now UC).

Corallina pinnatifolia* var. *digitata **(Figure 37C, D):** On tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3687,* US Alg. Coll.).

Corallina pinnatifolia* var. *digitata **(Figure 37E):** On rocks, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4593,* US Alg. Coll.).

Jania adhaerens **(Figure 38A):** Epiphytic on *Sargassum,* mid to low intertidal, tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3632b*, US Alg. Coll.).

Jania adhaerens **(Figure 38B):** Some on *Sargassum* stipes, Playa Arenosa (Sandy Beach and Norse Beach), Puerto Peñasco, Sonora, Coll. H. W. Johansen, E. Johansen, and J. N. Norris (*JN & HWJ-73-7-12*, US Alg. Coll.).

Jania adhaerens **(Figure 39A):** Intertidal, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3529*, US Alg. Coll.).

Jania longiarthra **(Figure 39C):** Near the reef, along south end of island, Isla San Diego, Baja California Sur (*EYD-18920,* US Alg. Coll.-8022).

Jania longiarthra **(Figure 39E):** Among turf algae, in inner Bahía San Gabriél, Isla Espíritu Santo, Baja California Sur, Coll. E. Y. Dawson (holotype: *EYD-7041*, AHFH, now UC).

Jania mexicana **(Figure 39F):** Bahía Petatlán, Guerrero, Pacific Mexico (isotype: *WRTaylor -34-569*, MICH).

Jania huertae **(Figure 40):** Among intertidal turf algae, Bahía Kino, southeast of Isla Pelícanos, Sonora, Coll. Oscar Olguin Q., *s.n.* (holotype: ENCB).

Amphiroa beauvoisii **(Figure 41):** Intertidal, on rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, H. W. Johansen, E. Johansen, and K. E. Bucher (*JN & HWJ-73-7-3*, US Alg. Coll.).

Amphiroa misakiensis (**Figure 42A**): Mid intertidal, on rocks of tidal platform and Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3674*, US Alg. Coll.).

Amphiroa misakiensis (**Figure 42B**): Mid intertidal on rocks of tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3684*, US Alg. Coll.).

Amphiroa misakiensis (**Figure 42C**): Mid intertidal rock platform and tide pools, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5102*, US Alg. Coll.).

Amphiroa valonioides (**Figure 43A**): Mid intertidal, on tidal platform, west of Casa Garcia, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3146b*, US Alg. Coll.).

Amphiroa valonioides (**Figure 43B**): On rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, H. W. Johansen, E. Johansen, and K. E. Bucher (*JN & HWJ-73-7-4,* US Alg. Coll.).

Amphiroa valonioides (**Figure 43C**): Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. H. W. Johansen, E. Johansen, and J. N. Norris (*JN & HWJ-73-7-33,* US Alg. Coll.).

Amphiroa vanbosseae (**Figure 44A**): Rocky shore, Punta Colorado, near Guaymas, Sonora, Coll. E. Y. Dawson (type of *Amphiroa subcylindrica*: *EYD-555*, AHFH-4277, now UC).

Amphiroa vanbosseae (**Figure 44B**): On low intertidal rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, H. W. Johansen, E. Johansen, and K. E. Bucher (*JN & HWJ-73-7-1,* US Alg. Coll.).

Amphiroa vanbosseae (**Figure 44C**): 2.4–6 m depths, Punta la Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3050*, US Alg. Coll.).

Litholepis sonorensis (**Figure 45A**): Canal de San Lorenzo, between southern end of Isla Espíritu Santo and Punta San Lorenzo on east coast of Baja California (NE of La Paz), Baja California Sur, Coll. E. Y. Dawson (holotype: *EYD-592-40*, AHFH, now UC).

Heteroderma corallinicola (**Figure 45B**): On *Corallina* in intertidal pools in the cove north of Cabo Arco, Guaymas, Sonora (holotype: *Drouet & Richards-3328a*, AHFH, now UC).

Lithophyllum diguetii (**Figure 46**): Dredged, Canal de San Lorenzo, channel between southern end of Isla Espíritu Santo and Punta San Lorenzo on east coast of Baja California (northeast of La Paz), Baja California Sur, Coll. E. Y. Dawson (A, C–G, *EYD-591-40*, AHFH, now UC; B, isotype: *L. Diguet-1894*, UC).

Lithophyllum hancockii (**Figure 47**): Shallow lagoon, Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, Coll. E. Y. Dawson (holotype *EYD-619a-40*, AHFH-22, now UC).

Lithophyllum imitans (**Figure 48A**): On rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, H. W. Johansen, E. Johansen, and K. E. Bucher (*JN & HWJ-73-7-11a*, US Alg. Coll.).

Lithophyllum imitans (**Figure 48B**): Intertidal rock platform, Playa Hermosa (~0.8 km west of Playa Hermosa Hotel), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4025*, US Alg. Coll.).

Lithophyllum margaritae (**Figure 48C**): Canal de San Lorenzo (channel between the southern end of Isla Espíritu Santo and northern peninsula from Punta Coyote to Punta San Lorenzo, near entrance to Báhia de La Paz), Baja California Sur, coll. E. Y. Dawson (*EYD-6942*, AHFH, now UC).

Lithophyllum pallescens (**Figure 49A**): Dredged 12–22 m depths, on sand–rhodolith bottom, Canal de Mejia (between southern end of Isla Mejia and northern end of Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (*EYD-278-40*, AHFH, now UC).

Lithophyllum pallescens (**Figure 49B**): Dredged 38.4 m depth, on shell bottom, west side of Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (*EYD-250-40*, AHFH, now UC).

Lithophyllum pallescens (**Figure 49C**): On hermit crab shell, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3586*, US Alg. Coll.).

Lithophyllum pallescens (**Figure 49D**): On sand bottom with some coralline clumps, shallow lagoon, 1.5–2.4 m depths, Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, Coll. E. Y. Dawson (*EYD-572-40*, AHFH, now UC).

Lithophyllum pallescens (**Figure 49E**): In tide pool, Playa Hermosa, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3503*, US Alg. Coll.).

Lithophyllum proboscideum (**Figure 50A**): Growing on intertidal rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3825*, US Alg. Coll.).

Lithophyllum proboscideum (**Figure 50B**): Intertidal rock platform and tide pools, Playa Hermosa (~0.8 km west of Playa Hermosa Hotel), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3471*, US Alg. Coll.).

Titanoderma dispar (**Figure 51**): Irregularly shaped crusts epiphytic on *Gelidium*, some completely surrounding host branches, intertidal rocks in front of Japanese shipwreck, Cabeza Ballena, Coll. J. N. Norris and K. E. Bucher (*JN-4112*, US Alg. Coll.).

Hydrolithon farinosum (**Figure 52**): Intertidal, epiphytic on *Padina*, tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3169,* US Alg. Coll.).

Heteroderma gibbsii (**Figure 53**): Epiphytic on *Padina,* on "rough" cobbles, intertidal rocky shore south side of bay, Ensenada Bocochibampo, Sonora, Coll. E. Y. Dawson (*EYD-457*, AHFH, now UC).

Heteroderma gibbsii **(Figure 54A):** Epiphytic on *Padina,* Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. H. W. Johansen, E. Johansen, and J. N. Norris (*JN & HWJ-73-7-22c,* US Alg. Coll.).

Heteroderma gibbsii **(Figure 54B):** Thin crusts epiphytic on *Padina,* Playa Arenosa (Sandy Beach, Norse Beach), vicinity of Puerto Peñasco, Sonora, Coll. H. W. Johansen, E. Johansen, and J. N. Norris (*JN & HWJ-73-7-15*, US Alg. Coll.).

Heteroderma subtilissimum **(Figure 55):** On *Cladophoropsis*, south end of Isla Guadalupe, Pacific Mexico (*EYD-8191*, AHFH, now UC).

Spongites decipiens **(Figure 56A):** Intertidal, Punta Prieta, outer Bahía Topolobampo, Sinaloa, Coll. E. Y. Dawson (*EYD-10967*, AHFH, now UC).

Spongites decipiens **(Figure 56B):** High intertidal in tide pool, growing on small rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and R. W. Hoshaw (*JN-3829*, US Alg. Coll.).

Spongites decipiens **(Figure 56C):** Intertidal platform, Playa Arenosa (Norse Beach; Sandy Beach), Coll. J. N. Norris, Y. Lipkin, and S. Lipkin (*JN-3932*, US Alg. Coll.).

Spongites decipiens **(Figure 56D):** Intertidal rock platform and tide pools, Playa Hermosa (~0.8 km west of Playa Hermosa Hotel), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3504*).

Neogoniolithon trichotomum **(Figure 57A):** Vicinity of La Paz, Baja California Sur (isotype: *L. Diguet-1894*, UC).

Neogoniolithon trichotomum **(Figure 57B):** Bahía San Gabriel, Isla Espíritu Santo, Baja California Sur, Coll. E. Y. Dawson (*EYD-619-40*, AHFH, now UC).

Neogoniolithon trichotomum **(Figure 57C):** Reef and tidal flat, near entrance to Bahía San Carlos, north side of Ensenada de San Francisco, vicinity of Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-1972*, AHFH, now UC).

Neogoniolithon trichotomum **(Figure 57D):** Rocky shore and tidal benches, west side of Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (*EYD-226-40*, AHFH, now UC).

Porolithon sonorense **(Figure 58A, B):** Rocky shore and tidal benches, west side of Puerto Refugio, Isla Ángel de la Guarda (type collection, *EYD-226a-40,* AHFH-25, now UC).

Porolithon sonorense **(Figure 58C):** Intertidal on rock, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and M. M. Littler (*JN-3775*, US Alg. Coll.).

Porolithon sonorense **(Figure 58D):** Isla Partida, near Isla Espíritu Santo, Baja California (EYD-984, AHFH now UC).

Lithothamnion australe **(Figure 59A):** Dredged in 3.6–5.5 m depths, Bahía Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-61-40,* AHFH, now UC).

Lithothamnion australe **(Figure 59B, C):** Dredged in 10–24 m depths, Canal de San Lorenzo, between Punta San Lorenzo on Gulf coast of Baja California and southern end of Isla Espíritu Santo, Baja California Sur, Coll. E. Y. Dawson (*EYD-593a,* AHFH, now UC).

Lithothamnion microsporum **(Figure 60A):** Rock sides and ledges, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3532,* US Alg. Coll.).

Lithothamnion microsporum **(Figure 60B):** Playa Tucson, north side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3462,* US Alg. Coll.).

Mesophyllum crassiusculum **(Figure 61A):** Dredging 12–14.6 m, South Coronado Island, Islas Coronado, Baja California, Pacific Mexico, Coll. E. Y. Dawson (*EYD-4277*, AHFH, now UC).

Mesophyllum crassiusculum **(Figure 61B, C):** Isla Concha, Laguna de Ojo de Liebra (Scammon's Lagoon), Baja California Sur, Pacific Mexico, Coll. K. Kenyon and W. Williams (*EYD-2636,* AHFH, now UC).

Ahnfeltia svensonii **(Figure 62):** Isla Cholla, off north end of Isla Carmen, Baja California Sur, Coll. E. Y. Dawson (cruise of M/V *Stella Polaris*) (*EYD-18747*, US Alg. Coll.-6444).

Asparagopsis taxiformis **(Figure 63A):** 7.6,–9 m depths, attached to rocks, west side of large rock, Rocas Consag, upper Gulf of California, Coll. D. G. Lindquist (*JN-3113*, US Alg. Coll.-158607).

Asparagopsis taxiformis **(Figure 63B):** Rock reef, off sand-cobble beach, 1.5–4.6 m depths, west side of Punta Robinson, ~2.4 km east of Puerto Libertad, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4822*, US Alg. Coll. microscope slide 4975).

Falkenbergia hillebrandii*-phase of *Asparagopsis **(Figure 64A):** 7.6–18 m depths, rocky substrate, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (*JN-4438*, US Alg. Coll. microscope slide 4292).

Falkenbergia hillebrandii*-phase of *Asparagopsis **(Figure 64B, C):** Dive to 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4758*, US Alg. Coll. microscope slide 4295).

Bonnemaisonia hamifera **(Figure 65A, C):** 1–7.6 m depths, Punta la Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5438*, US Alg. Coll.-158653).

Bonnemaisonia hamifera **(Figure 65B, D):** 15 m depth, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-2989*, US Alg. Coll. microscope slide 4277).

Callithamnion bisporum* var. *australe **(Figure 66):** Dredged 5.5–9 m depths, Puerto Escondido, Baja California Sur, Coll. E. Y. Dawson (isotype: *EYD-7190*, US Alg. Coll. microscope slide 333).

Crouania attenuata **(Figure 67):** Epiphytic on *Amphiroa,* near rock reef, 1.5–4.6 m depths, west side of Punta Robinson, ~2.4 km east of Puerto Libertad, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4842*, US Alg. Coll. microscope slide 4705).

Crouanophycus mcnabbii **(Figure 68):** Epiphytic on *Dictyota crenulata,* 4.6–9 m depths, Caleta Santa María Cove, 9.7 km north of Puerto Santa Rosalía, Baja California Sur, Coll. D. G. Lindquist (sta. DGL 720811-1) (*JN-3406*, US Alg. Coll. microscope slide 4717).

Antithamnion decipiens **(Figure 69A):** Epiphytic on *Sargassum* stipe, dive to 6 m depth off west side of small cove, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4921*, US Alg. Coll. microscope slide 4750).
Antithamnion decipiens **(Figure 69B):** Epiphytic on *Dictyopteris*, dive 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris (*JN-4146*, US Alg. Coll. microscope slide 4719).

Antithamnion defectum **(Figure 70A):** Dive 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4758b*, entangled with *Falkenbergia*-stage of *Asparagopsis,* US Alg. Coll. microscope slide 4295).
Antithamnion defectum **(Figure 70B):** Dive 10.6–30 m depths, Islas de Los Gemelos, Bahía de los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4757*, US Alg. Coll. microscope slide 4731).

Antithamnion kylinii **(Figure 71A, B, D):** On carapace of female *Chelonia* (black sea turtle), 9 m depth, vicinity of Campo Ona, Canal de Infiernillo, Sonora, Coll. R. S. Felger, E. Moser, Guadalupe Méndez (harpooned turtle, Seri) (*JN-4780*: A, US Alg. Coll. microscope slide 4741; B, US Alg. Coll. microscope slide 4736; D, US Alg. Coll. microscope slide 4735).
Antithamnion kylinii **(Figure 71C):** 13.7 m depth, attached to sea shells on muddy bottom, Canal de Infiernillo, midway between Isla Tiburón and west of Campo Viboras, Sonora, Coll. G. L. Kooyman and E. Sinnett (*JN-4735*, US Alg. Coll. microscope slide 4729).

Antithamnionella breviramosa **(Figure 72A):** Epiphytic on *Gelidium,* dive 7.6–18 m depths, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (*JN-4435*, US Alg. Coll. microscope slide 4727).
Antithamnionella breviramosa **(Figure 72B):** Epiphytic on *Lomentaria,* dive to 6 m depth, off small cove, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4908*, US Alg. Coll. microscope slide 4751).
Antithamnionella breviramosa **(Figure 72C):** Dive to 9 m depth, rocky point inside SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5064b*, US Alg. Coll. microscope slide 4840).
Antithamnionella breviramosa **(Figure 72D, E):** Epizoic on a bryozoan, rocky point inside SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5042*, US Alg. Coll. microscope slide 4757).
Antithamnionella breviramosa **(Figure 72F):** Hand dredge 9.1–22.8 m, Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (California Department of Fish and Game; M/V *Alaska* expedition) (*EYD-26126,* US Alg. Coll. microscope slide 788).

Antithamnionella* cf. *spirographidis **(Figure 73):** On carapace of female *Chelonia* (black sea turtle), 9 m depth, vicinity of Campo Ona, Canal de Infiernillo, Sonora, Coll. R. S. Felger, E. Moser, and Guadalupe Méndez (Seri) (*JN-4769*, US Alg. Coll. microscope slide 4734).

Centroceras gasparrinii **(Figure 74A):** 1.5–6 m depths, Nueva Guaymas, Bahía de San Carlos, Sonora, Coll. D. Evanson (*JN-4285,* US Alg. Coll. microscope slide 4792).
Centroceras gasparrinii **(Figure 74B–D):** Dive 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and K. E. Bucher (B, *JN-4131a*, US Alg. Coll. microscope slide 4784; C, *JN-4131b*, US Alg. Coll. microscope slide 8700; D, *JN-4131e*, US Alg. Coll. microscope slide 4759).

Ceramium aduncum **(Figure 75A):** Dive to 9 m depth, off rocky point, inside of SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5060*, US Alg. Coll. microscope slide 8701).
Ceramium aduncum **(Figure 75B):** Rocky intertidal, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3098*, US Alg. Coll. microscope slide 8690).

Ceramium affine* var. *peninsularis **(Figure 76):** Intertidal rocky platform, Playa Hermosa (~0.8 km west of Playa Hermosa

Hotel), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4002*, US Alg. Coll. microscope slide 8702).

Ceramium caudatum (**Figure 77A**): Epiphytic on *Padina,* dive to 6 m depth, off small cove, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4904b*, US Alg. Coll. microscope slide 5256).
Ceramium caudatum (**Figure 77B**): Epiphytic on *Prionitis*, dive 3–15 m depths, off north end of island, Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4400*, US Alg. Coll. microscope slide 8709).
Ceramium caudatum (**Figure 77C**): Epiphytic on *Dictyota,* 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris, K. E. Bucher, and H. Sleeper (*JN-4138b*, US Alg. Coll. microscope slide 5223).
Ceramium caudatum (**Figure 77D**): Epiphytic on *Sargassum sinicola*, Puertecitos, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3289*, US Alg. Coll. microscope slide 5211).

Ceramium aduncum (**Figure 78A**): Epiphytic on *Sargassum,* low intertidal, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3191*, US Alg. Coll. microscope slide 4763).
Ceramium clarionense (**Figure 78B**): Epiphytic on *Codium simulans,* Isla Clarión, Islas Revillagigedo, Pacific Mexico, Coll. H. L. Mason (*Mason-75*, holotype; UC).
Ceramium caudatum (**Figure 78C**): Epiphytic on *Dictyota*, 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris, K. E. Bucher and H. Sleeper (*JN-4138b*, US Alg. Coll. microscope slide 5223).

Ceramium equisetoides (**Figure 79A–C**): Entangled with *Callithamnion*, intertidal, tidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3178e*, US Alg. Coll. microscope slide 4666).
Ceramium hamatispinum (**Figure 79D–G**): Entangled with *Gayliella* and *Polysiphonia,* intertidal, inner shallow lagoon of Bahía San Carlos, north of Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-11019b,* US Alg. Coll. microscope slide 492).

Ceramium horridulum (**Figure 80**): Dive to 9 m depth, off "rock window" on northwest shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5310*: A, US Alg. Coll.-217345; B, US Alg. Coll. microscope slide 8703).

Ceramium howellii (**Figure 81A–C**): 0.9–7.6 m depths, Punta la Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5464b*, US Alg. Coll. microscope slide 5271).
Ceramium howellii (**Figure 81D**): Dredged 45–55 m depths, off Sandstone Point, Isla Guadalupe, off Baja California, Pacific Mexico, Coll. E. Y. Dawson (*EYD-8425*, US Alg. Coll. microscope slide 479).

Ceramium interruptum (**Figure 82A**): Epiphytic on *Gelidiopsis,* intertidal, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4201*, US Alg. Coll. microscope slide 4788).
Ceramium interruptum (**Figure 82B–D**): Epiphytic on *Prionitis*, dive 3–15 m depth, off north end of island, Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4404*, US Alg. Coll. microscope slide 4794).

Ceramium mazatlanense (**Figure 83**): Intertidal rocky shelf, Ensenada de San Francisco, near Puerto San Carlos, Sonora, Coll. E. Y. Dawson (*EYD-11031*, US Alg. Coll. microscope slide 512).

Ceramium obesum (**Figure 84A**): Intertidal rocky shore, Bahía Agua Dulce, north end of Isla Tiburón, Islas de la Cintura (holotype: *EYD-964*, AHFH, now UC).
Ceramium serpens (**Figure 84B**): Epiphytic of *Laurencia*, La Paz, Baja California Sur (*Marchant-67c*, CAS, now UC).

Ceramium paniculatum (**Figure 85A, C–F**): Rock sides and ledges, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4396*, US Alg. Coll. microscope slide 8704).
Ceramium paniculatum (**Figure 85B**): Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4539*, US Alg. Coll. microscope slide 4258).

Ceramium periconicum (**Figure 86A**): Dredged, Bahía San Lucas, Baja California Sur, Coll. E. Y. Dawson (*EYD-6851a*, US Alg. Coll. microscope slide 557).
Ceramium periconicum (**Figure 86B, C**): Epiphytic on *Gelidium,* 7.6–18 m depths, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (*JN-4436*, US Alg. Coll. microscope slide 8705).

Ceramium procumbens (**Figure 87**): Epiphytic on *Dichotomaria spathulata*, dive off small cove, to 6 m depth, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4897*, US Alg. Coll. microscope slide 8706).

Ceramium sinicola (**Figure 88**): Epiphytic on *Laurencia iriei*, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4584*, US Alg. Coll. microscope slide 4798).

Corallophila bella (**Figure 89C**): Cast ashore, Guaymas, Sonora (type: *Marchant-85*, CAS, now UC).

Gayliella fimbriata (**Figure 90**): Epiphytic on *Padina*, dive intertidal to 9 m depth, off rocky point inside SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N.

Norris, K. E. Bucher, and D. Moore (*JN-5062*, US Alg. Coll. microscope slide 5263).

Gayliella **species A (Figure 91A):** Epiphytic on *Sargassum,* dive 3.0–15 m depths, off north end of island, Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4406*, US Alg. Coll. microscope slide 5233).

Gayliella **species A (Figure 91B):** Epiphytic on *Dichotomaria spathulata*, 1.5–4.6 m depths, rock reef, west side of Punta Robinson (~2.5 km east of Puerto Libertad), Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4834*, US Alg. Coll. microscope slide 5250).

Gayliella **species A (Figure 91C, D):** Dive 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris, K. Bucher, and H. Sleeper (*JN-4139*, US Alg. Coll. microscope slide 5225).

Gayliella recticortica **(Figure 92):** Tide pools, rocky shore on south side of bay, Ensenada Bocochibampo, Sonora, Coll. E. Y. Dawson (*EYD-46-501*, AHFH, now UC).

Gayliella taylorii **(Figure 93):** Intertidal rock shelf with tide pools, Ensenada de San Francisco, between Bahía San Carlos and Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-1962*: A, US Alg. Coll. microscope slide 441; B, US Alg. Coll. microscope slide 440).

Pterothamnion pectinatum **(Figure 95A, C):** Epiphytic on *Sebdenia flabellata,* 0.9–10.6 m depths, south end of Isla Estanque, Coll. J. N. Norris and K. E. Bucher (*JN-5512,* US Alg. Coll. microscope slide 4706).

Pterothamnion pectinatum **(Figure 95B, D):** Epiphytic or entangled with *Sporochnus neushulii*, 23 m depth, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5263*: B, US Alg. Coll. microscope slide 4711; D, US Alg. Coll. microscope slide 4710).

Dasya pedicellata **subsp.** ***stanfordiana*** **(Figure 96A):** Dive to 13.7 m depth, attached to seashells on muddy bottom; Canal de Infiernillo, midway between Isla Tiburón and west of Camp Viboras, Sonora, Coll. G. L. Kooyman and E. Sinnett (*JN-4731*, US Alg. Coll.-159017).

Dasya pedicellata **subsp.** ***stanfordiana*** **(Figure 96B, C, E):** Dive to 13.7 m depth, attached to seashells on muddy bottom; Canal de Infiernillo, midway between Isla Tiburón and west of Camp Viboras, Sonora, Coll. G.L. Kooyman and E. Sinnett (*JN-4724*: B, US Alg. Coll.-159015; C, E. US Alg. Coll. microscope slide 4855).

Dasya pedicellata **subsp.** ***stanfordiana*** **(Figure 96D):** Epiphytic on other algae, beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5165*, US Alg. Coll. microscope slide 4852).

Dasya pedicellata **subsp.** ***stanfordiana*** **var.** ***nudicaulis*** **(Figure 97):** Dive 15–21 m depths, off rocky shoreline, west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Islas de la Cintura, Coll. J. N. Norris (*JN-5800*, US Alg. Coll.-159009).

Dasya sinicola **var.** ***californica*** **(Figure 98A):** Intertidal reef, ~30 m south of "La Jolla Beach Club," south side of La Jolla bay, La Jolla, California, Coll. E. Y. Dawson (drawn from topotype specimen: *EYD-303,* AHFH, now UC).

Dasya spinigera **(Figure 98B, C):** On sand bottom, dredged 20 m depth, Bahía San Lucas, Baja California Sur, Coll. E. Y. Dawson (*EYD-6845a*, AHFH, now UC).

Dasya sinicola **var.** ***sinicola*** **(Figure 98D):** Rocky intertidal shore, south side of bay, Ensenada Bocochibampo, near Guaymas, Sonora (*EYD-468*, AHFH, now UC).

Dasya sinicola **var.** ***californica*** **(Figure 99A):** Intertidal rock platform, Playa Hermosa, (west side of Playa Hermosa Hotel), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3696*, US Alg. Coll.-159037).

Dasya sinicola **var.** ***sinicola*** **(Figure 99B, C):** Hand dredge 9.1–22.8 m, Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, off Baja California, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (California Department of Fish and Game; M/V *Alaska* expedition) (*EYD-26119*, US Alg. Coll. microscope slide 792).

Heterosiphonia crispella **var.** ***laxa*** **(Figure 100A, B, D):** Epiphytic on *Padina*, west side of small cove, dive to 6 m depth, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4898*, US Alg. Coll. microscope slide 4889).

Heterosiphonia crispella **var.** ***laxa*** **(Figure 100C, E):** 1.5–4.6 m depths, ~0.8 km [~0.5 mile] south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris, K. E. Bucher, and H. Sleeper (C, *JN-4155*, US Alg. Coll. microscope slide 4883; E,.*JN-4155*, US Alg. Coll. microscope slide 4884).

Heterosiphonia erecta **(Figure 101A):** Dive to 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4746*, US Alg. Coll.-160012).

Heterosiphonia erecta **(Figure 101B):** Epiphytic on *Botryocladia,* dive 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4750*, US Alg. Coll. microscope slide 4879).

Heterosiphonia erecta **(Figure 101C, D):** 3.0–15 m depths, dive off north end of island, Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4417*: C, US Alg. Coll. microscope slide 4885; D, US Alg. Coll. microscope slide 4886).

Apoglossum gregarium **(Figure 102):** On a hydroid dredged from 8–16 m, Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, Coll. E. Y. Dawson (type of *Hypoglossum gregarium* E. Y. Dawson) (*EYD-26123*, US Alg. Coll. microscope slide 791).

Branchioglossum bipinnatifidum **(Figure 103A, B):** 9 m depth, off rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (A, *JN-5036*, US Alg. Coll.-217354; B, US Alg. Coll. microscope slide 4615).

Branchioglossum bipinnatifidum **(Figure 103C):** Rock sides and ledges, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4309*, US Alg. Coll. microscope slide 4619).

Branchioglossum bipinnatifidum **(Figure 103D):** Intertidal rock platform, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. Bucher (*JN-3987*, US Alg. Coll. microscope slide 4625).

Branchioglossum undulatum **(Figure 104):** Epiphytic on *Sargassum* stipe, 6 m depth, west side of small cove, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4920*, US Alg. Coll. microscope slide 4617).

Caloglossa apomeiotica **(Figure 105A):** Mangaratiba City, Rio de Janeiro (state), Brazil, Coll. C. F. D. Gurgel (=D. M. Krayesky-73) (US Alg. Coll.).

Caloglossa apomeiotica **(Figure 105B, C):** Isla Perico, Balboa, Pacific Panama, Coll. B. S. Wysor (=D. M. Krayesky-64) (US Alg. Coll.).

Erythroglossum californicum **(Figure 106):** Drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6578a*, US Alg. Coll.-217358).

Grinnellia lanceolata **(Figure 107A, C, D):** Dredged from 12–16 m, off Isla Salsipuedes (Islas de San Lorenzo), Coll. E. Y. Dawson (type of *Apoglossum punctatum*: *EYD-26143*, US Alg. Coll. microscope slide 779).

Grinnellia lanceolata **(Figure 107B):** Dredged to 50 m, off Punta Gorda, Baja California, Pacific Mexico, Coll. E. Y. Dawson (holotype of *Grinnellia lanceolata*: *EYD-626-40*, AHFH now UC).

Hypoglossum attenuatum* var. *abyssicola **(Figure 108A):** About 13.7 m depth, muddy bottom, attached to seashells, Canal de Infiernillo midway between Isla Tiburón and west of Campo Viboras, Sonora, Coll. G. L. Kooyman and E. Sinnett (*JN-4722*, US Alg. Coll.-160075).

Hypoglossum attenuatum* var. *abyssicola **(Figure 108B):** Hand dredge 18.3–30.5 m depths, Isla San Lorenzo (Isla San Lorenzo del Sur), Islas de San Lorenzo, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (*EYD-26163*, US Alg. Coll. microscope slide 774).

Hypoglossum attenuatum* var. *abyssicola **(Figure 108C):** Entangled with *Sorella pinnata*, beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5156a*, US Alg. Coll. microscope slide 4609).

Hypoglossum attenuatum* var. *abyssicola **(Figure 108D, E):** D. Hand dredge 9.1–22.8 m depths, Isla Las Ánimas (Islas San Lorenzo del Norte), Islas de San Lorenzo, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (*EYD-26117* (♂, ♀), US Alg. Coll. microscope slide 793).

Myriogramme divaricata **(Figure 109A):** 0.9–10.6 m depths, dive off the south end of Isla Estanque, Islas de la Cintura, Coll. J. N. Norris and K. E. Bucher (*JN-5583a*, US Alg. Coll.-217360).

Myriogramme auricularis **(Figure 109B, C):** Dredged from 19–30 m, Isla San Lorenzo del Sur, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (holotype: *EYD-26167*, US Alg. Coll. microscope slide 771).

***Myriogramme* sp. (Figure 109D):** Dive to 6 m depth, off west side of small cove, Punta Cirio, south of Puerto Libertad, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4901*, US Alg. Coll. microscope slide 5289).

Phycodrys amplissima **(Figure 110A):** Cast ashore, beach in front of Seri village, Desemboque de San Ignacio, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6578b*, US Alg. Coll.-217347).

Phycodrys amplissima **(Figure 110B):** Dredged from depth of 9.0–36 m, Isla San Esteban, Coll. L. Pinkas, E. Smith, and D. Miller (California Department of Fish and Game; M/V *Alaska* expedition) (isotype: *EYD-21580*, US Alg. Coll. microscope slide 635).

Phycodrys simplex **(Figure 111):** Dredged in 22–44 m, Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (holotype: *EYD-183-40*, AHFH, now UC).

Polyneurella hancockii **(Figure 112):** Dive to 13.7 m depth, attached to seashells, muddy bottom; Canal de Infiernillo, midway between Isla Tiburón and west of Camp Viboras, Sonora, Coll. G. L. Kooyman and E. Sinnett (A, *JN-4720*, US Alg. Coll.-217356; B, *JN-4727*, US Alg. Coll.-217357; C, *JN-4725*, US Alg. Coll. microscope slide 5283; D, *JN-4720*, US Alg. Coll. microscope slide 5285).

Schizoseris pygmaea **(Figure 113A, B):** On intertidal rocks, Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3823*: A, US Alg. Coll. microscope slide 5282; B, US Alg. Coll.-160889).

***Schizoseris pygmaea* (Figure 113C):** Mid to low intertidal rock platform and tide pools, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3902*, US Alg. Coll. microscope slide 5286).

***Sorella pinnata* (Figure 114A–C):** Dive to 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4749*, US Alg. Coll. microscope slide 4642).

***Sorella pinnata* (Figure 114D):** Beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5154*, US Alg. Coll. microscope slide 4643).

***Sorella pinnata* (Figure 114E):** 7.6–9.0 m depths, attached to rocks, west side of large rock, Rocas Consag, Coll. D.G. Lindquist (*JN-3131*, US Alg. Coll. microscope slide 4645).

***Taenioma perpusillum* (Figure 115):** On intertidal rocks, near inner wharf of inner bay, Topolobampo, Sinaloa, Coll. E. Y. Dawson (A,C, *EYD-10891*, US Alg. Coll. microscope slide 569; B, *EYD-10908*, US Alg. Coll. microscope slide 570).

***Platysiphonia decumbens* (Figure 116A):** Intertidal to 9 m depth, NW of rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5324b*, US Alg. Coll. microscope slide 5290).

***Platysiphonia decumbens* (Figure 116B, C):** Hand dredged 9.1–22.8 m depths, Isla Las Ánimas (Islas San Lorenzo del Norte), Islas de San Lorenzo, Coll. E. Y. Dawson, R. Banks, E. Wilson, and J. Sloan (*EYD-26116*, US Alg. Coll. microscope slide 794).

***Chondria acrorhizophora* (Figure 117A):** Eureka, near La Paz, Baja California Sur (isotype: *D.R. Marchant-44*, US Alg. Coll.-56205).

***Chondria acrorhizophora* (Figure 117B):** Drift, Desemboque de San Ignacio, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6577*, US Alg. Coll.-158967).

***Digenea simplex* (Figure 119):** Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and L. Gleye (both *JN-4204*: A, US Alg. Coll.-159105; B, US Alg. Coll.-159104).

***Herposiphonia littoralis* (Figure 120):** Epiphytic on *Padina,* beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5153*, US Alg. Coll. microscope slide 4946).

***Herposiphonia plumula var. plumula* (Figure 121):** Epiphytic on *Sargassum sinicola* var. *camouii*, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4301*, US Alg. Coll. microscope slide 4913).

***Herposiphonia plumula* var. *parva* (Figure 122):** Lady's Harbor, Santa Cruz Island, California Channel Islands, Coll. G. J. Hollenberg (holotype: *GJH-1337*, US Alg. Coll.-61192; US Alg. Coll. microscope slides 3440–3446).

***Herposiphonia spinosa* (Figure 123A):** Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4390*, US Alg. Coll. microscope slide 4912).

***Herposiphonia spinosa* (Figure 123B):** Intertidal platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3175*, US Alg. Coll. microscope slide 4907).

***Laurencia aguilar-rosasorum* (Figure 124A):** Rocky intertidal platform and tide pools, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4369*, US Alg. Coll.-217740).

***Laurencia fenicalii* (Figure 124B):** On rocks, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4515*, US Alg. Coll.-217741).

***Laurencia iriei* (Figure 124C):** On rocks, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4519*, US Alg. Coll.-217742).

***Laurencia johnstonii* (Figure 124D):** On rocks and tidal platform, Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-4068*, US Alg. Coll.-160140).

***Osmundea estebaniana* (Figure 125A):** Intertidal to 6 m depth, Isla Mejia, off north end of Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5832*, US Alg. Coll.-160119).

***Osmundea estebaniana* (Figure 125B):** 9–23 m dive, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris, J. Paul, and K. Robertson (*JN-5273*, US Alg. Coll.-160111).

***Osmundea sinicola* (Figure 125C):** Cast ashore, Bahía San Carlos, Sonora, Coll. Dana Bean, *s.n.* (US Alg. Coll.-30106).

***Palisada paniculata* (Figure 126B, C):** Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and R. W. Hoshaw (*JN-5006,* US Alg. Coll.-160223).

***Palisada pedrochei* (Figure 126D):** Intertidal rock platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (holotype: *JN-5879*, US Alg. Coll.-160250).

***Neosiphonia cheloniae* (Figure 127):** Epizoic on dorsal surface of head and flippers of a living female black sea turtle, Canal de Infiernillo, vicinity of Campo Ona, Sonora (opposite the east coast of Isla Tiburón), Coll. R. S. Felger, E. W. Moser, and E. Méndez (*JN-4765.5*, US Alg. Coll. microscope slide 5046).

Neosiphonia concinna **(Figure 128A):** On other intertidal algae, near Scripps Institution of Oceanography, La Jolla, California, Coll. G.J. Hollenberg (holotype: *GJH-2015*, US Alg. Coll.-61210, US Alg. Coll. microscope slide 1225).

Neosiphonia confusa **(Figure 128B):** Corona del Mar, California, Coll. G. J. Hollenberg (topotype: *GJH-1383*, US Alg. Coll.-64866).

Neosiphonia johnstonii* var. *johnstonii **(Figure 128C):** Puerto Libertad, Sonora, Coll. E. Y. Dawson (*EYD-670*, AHFH, now UC).

Neosiphonia eastwoodae **(Figure 128D):** Epiphytic on various algae, False Bay (now Mission Bay), San Diego, California (isotype: *Polysiphonia snyderae* Kylin, 1941; Collins et al., 1899: Fasciculus 13, No. 638, US Alg. Coll-64991).

Neosiphonia masonii **(Figure 128E):** North side of reef, off southwest end of Isla Guadalupe, Pacific Baja California (*EYD-4073,* AHFH, now UC).

Neosiphonia masonii **(Figure 128F):** Off Islote Zapato, Isla Guadalupe (*EYD-19277,* AHFH, now UC).

Neosiphonia flaccidissima **(Figure 129A):** 1.5–6 m depths, Nueva Guaymas, Sonora, Coll. D. Evanson (*JN-4267*, US Alg. Coll. microscope slide 5029).

Neosiphonia flaccidissima **(Figure 129B, C):** Epiphytic on *Padina,* 1.5–6 m depths, Nueva Guaymas, Sonora, Coll. D. Evanson (*JN-4270*, US Alg. Coll. microscope slide 5031).

Neosiphonia savatieri **(Figure 130A):** Intertidal platform and Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-4195*, US Alg. Coll. microscope slide 5027).

Neosiphonia savatieri **(Figure 130B):** 1.5–6 m depths, Nueva Guaymas, Sonora, Coll. D. Evanson (*JN-4266*, US Alg. Coll. microscope slide 5030).

Neosiphonia confusa **(Figure 131A):** Epizoic on sand dollar *Encope grandis,* in sand tidal channels, Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco, Sonora (*JN-5577*, US Alg. Coll. microscope slide 5052).

Neosiphonia confusa **(Figure 131B):** On NASA buoy, anchored off Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3835*, US Alg. Coll. microscope slide 5000).

Neosiphonia simplex **(Figure 131C):** Mid intertidal rock platform and tide pools, from laboratory to Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5098b*, US Alg. Coll. microscope slide 4996).

Neosiphonia simplex **(Figure 131D):** 9 m depth, off rocky point, SE side of Punta Pelicano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5038*, US Alg. Coll. microscope slide 4994).

Neosiphonia mexicana **(Figure 132A):** A. Bahía Sulphur, Isla Clarión, Islas Revillagigedo, Pacific Mexico, Coll. J. T. Howell (paratype: *JTH-238a*, AHFH, now UC).

Neosiphonia mexicana **(Figure 132B–D):** On rocks with other minute algae, low intertidal, Isla Estanque (Pond Island), off southeastern end of Isla Ángel de la Guarda, Coll. E. Y. Dawson (holotype: *EYD-430-40*, AHFH-62, now UC).

Neosiphonia paniculata **(Figure 132E):** Esquimalt, near inner harbor of Victoria, Vancouver Island, British Columbia, and Juan de Fuca Strait (between Vancouver Island and Olympic Peninsula, Washington).

Polysiphonia sonorensis **(Figure 132F):** Drift, southeastern shore of Bahía Empalme, Sonora, Coll. F. Drouet and D. Richards (*Drouet & Richards-3426a*: holotype F; isotype: US Alg. Coll.-66807, microscope slides 1237–1239).

Neosiphonia paniculata **(Figure 133):** Epiphytic on *Encope grandis* (sand dollar), sand-mud flats, Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco, Sonora, Coll. J. Kudenov and J. N. Norris (*JN-4552*, US Alg. Coll.-160578).

Polysiphonia hollenbergii **(Figure 134):** 7.6 m depth, Isla La Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and G. Boehlert (holotype: *JN-2998b,* US Alg. Coll. microscope slide 5004).

Polysiphonia pacifica* var. *delicatula **(Figure 135):** Epiphytic on *Gelidium johnstonii,* 3.3 m depth, rock reef, Cabo Lobos, vicinity of Puerto Libertad, Coll. J. N. Norris and K. E. Bucher (*JN-4848a*, US Alg. Coll. microscope slide 4260).

Polysiphonia scopulorum* var. *villum **(Figure 136A):** Mid intertidal, tidal platform and Cumpleaños Tide Pool, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5098a*, US Alg. Coll. microscope slide 4995).

Polysiphonia scopulorum* var. *villum **(Figure 136B):** Intertidal, tidal platform fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3744*, US Alg. Coll. microscope slide 5025).

Pterosiphonia dendroidea **(Figure 137A):** Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper, and W. Baines (*JN-4742*, US Alg. Coll. microscope slide 4899).

Pterosiphonia californica **(Figure 137B):** 9 m depth, off rocky point, SE side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-5021*, US Alg. Coll. microscope slide 4900).

Pterosiphoniella williamsii **(Figure 138A–C):** Dive 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and K. E. Bucher (*JN-4126*, US Alg. Coll. microscope slide 4914).

Pterosiphoniella williamsii **(Figure 138D):** Intertidal rocks, in front of wrecked Japanese ship, Inari Maru 10, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and K. E. Bucher (*JN-4103*, US Alg. Coll. microscope slide 4915).

Amplisiphonia*? *pacifica **(Figure 139):** Epiphytic on *Palisada paniculata,* north side of Puerto Calamajue, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-4682*, US Alg. Coll. microscope slide 4984).

Veleroa subulata **(Figure 140):** On hydroid, dredged 22 m depth, Bahía Tepoca, Sonora, Coll. E. Y. Dawson (holotype: *EYD-381d-40,* AHFH-63, now UC).

Spyridia* cf. *filamentosa **(Figure 141A):** Intertidal rocks fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3140*, US Alg. Coll.-160963).

Spyridia* cf. *filamentosa **(Figure 141B):** Mudflats, Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-4060*, US Alg. Coll.-160981).

Spyridia* cf. *filamentosa **(Figure 141C, D):** Epiphytic, intertidal, in front of Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-4075*, US Alg. Coll. microscope slide 4836).

Spyridia* cf. *filamentosa **(Figure 141E, F):** Intertidal, tidal platform, Playa Hermosa (~0.4 km west of Playa Hermosa Hotel), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4019*, US Alg. Coll. microscope slide 4834).

Anotrichium furcellatum **(Figure 142):** Growing on shell, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4487*, US Alg. Coll. microscope slide 4969).

Anotrichium secundum **(Figure 143A):** Beach drift, Desemboque de San Ignacio, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5187*, US Alg. Coll. microscope slide 4952).

Anotrichium secundum **(Figure 143B):** Epizoic on sponge, intertidal, Playa Hermosa (~0.4 km west of Playa Hermosa Hotel), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4032*, US Alg. Coll. microscope slide 4961).

Griffithsia pacifica **(Figure 144A):** Epiphytic on *Gelidium*, beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5159*, US Alg. Coll. microscope slide 4980).

Griffithsia pacifica **(Figure 144B):** Beach drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5148*, US Alg. Coll. microscope slide 4955).

Lejolisia hoshawii **(Figure 145):** Epiphytic on *Sargassum* in the drift, Playa Hermosa, Puerto Peñasco, Sonora, Coll. A. E. Dennis (type illustrations *EYD-27530*, US Alg. Coll. microscope slide 989).

Tiffaniella saccorhiza **(Figure 146A, B):** Bahía de Los Ángeles, Baja California, Coll. E. Y. Dawson (*EYD-46-1330*, US Alg. Coll. microscope slide 917).

Pleonosporium globliferum **(Figure 147A, C):** Dive 1.5–4.6 m depths, ~0.8 km south of shipwreck, Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and K. E. Bucher (*JN-4147,* US Alg. Coll. microscope slide 4682).

Pleonosporium globliferum **(Figure 147B):** Epiphytic on *Dictyopteris undulata*, Punta Los Frailes, Baja California Sur, Coll. V. Paul (*JN-7175a,* US Alg. Coll. microscope slide 4673).

Pleonosporium mexicanum **(Figure 148):** Lowermost intertidal on small reef, 3 km north of Belmar Hotel, Playa de Olas Atlas, vicinity of Mazatlán, Sinaloa (holotype: *EYD-3610,* US Alg. Coll. microscope slide 398).

Pleonosporium vancouverianum **(Figure 149):** Dive 10.6–30 m depths, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris (*JN-4745,* US Alg. Coll. microscope slides 4690, 4689).

Gelidium crinale **(Figure 150F):** Intertidal, Punta Estrella, ~3.2 km south of San Felipe, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3310*, US Alg. Coll.-159270).

Gelidium crinale **(Figure 150G):** Intertidal, on tidal platforms, Playa Hermosa, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3483*, US Alg. Coll.-159274).

Gelidium decompositum **(Figure 151):** Rocky intertidal, Puerto Calamajue, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-4611a*, US Alg. Coll.-159296).

Gelidium johnstonii **(Figure 152A):** 3.0–7.6 m depths, dive off SE end of Isla San Esteban, Islas de la Cintura, Coll. J. N. Norris and K. E. Bucher (*JN-5539*, US Alg. Coll.-159337).

Gelidium johnstonii **(Figure 152B):** Low intertidal, tidal platform fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3796*, US Alg. Coll.-159339).

Gelidium mcnabbianum **(Figure 153A, B):** Rocky shore, fronting Laboratorio de Biología Marina, Playa Las Conchas

(Playa Estación), Puerto Peñasco, Coll. E. Y. Dawson (*EYD-27340*, US Alg. Coll.-40743).

Gelidium pusillum **(Figure 153C):** On tidal platform, Playa Hermosa, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3482,* US Alg. Coll.-159272).

Pterocladia sonorense **(Figure 156):** On intertidal rocks, tidal platform fronting Laboratorio de Biología Marina, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. E. Y. Dawson (*EYD-27304*, US Alg. Coll.-40860).

Pterocladiella capillacea **(Figure 157):** Rocky intertidal, north side of Puerto Calamajue, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-4611b,* US Alg. Coll.-159295).

Hypnea cervicornis **(Figure 158):** Rocky reef Playa Tucson, Bahía La Choya (Bahía Cholla) on bay side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. E. Y. Dawson (*EYD-27213*, US Alg. Coll.-40586).

Dicranema rosaliae **(Figure 159A):** Intertidal rocks near inner wharf of the inner bay, Topolobampo, Sinaloa, Coll. E. Y. Dawson (*EYD-10897*, US Alg. Coll.-7173).

Dicranema rosaliae **(Figure 159C):** Tidal platform in sand-covered areas, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3263,* US Alg. Coll. microscope slide 4534).

Dudresnaya colombiana **(Figure 160A, C):** 1–10 m depths, south end of Isla Estanque, Coll. J. N. Norris and K. E. Bucher (*JN-5480*: A, US Alg. Coll.-8760; C, US Alg. Coll. microscope slide 3769).

Dudresnaya colombiana **(Figure 160B):** 15–23 m depths, east end of Isla Mejia, Isla Ángel de la Guarda, Coll. J. N. Norris, J. Paul, and K. Robertson (*JN-5680*, US Alg. Coll. microscope slide 3767).

Chondracanthus acicularis **(Figure 161):** Rocky reef, Playa Tucson, on Bahía La Choya (Bahía Cholla) side of Punta Pelícano, vicinity of Puerto Peñasco, Sonora, Coll. E. Y. Dawson (*EYD-27263*, US Alg. Coll.-40576).

Chondracanthus squarrulosus **(Figure 162A, B):** Intertidal platform, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and J. Kudenov (*JN-3690*: A, US Alg. Coll.-159405; B, US Alg. Coll.-159404).

Chondracanthus squarrulosus **(Figure 162C):** 3.3 m depth, Puertecitos, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3298*, US Alg. Coll.-159444).

Chondracanthus squarrulosus **(Figure 162D):** Punta La Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-3026*, US Alg. Coll.-159478).

Chondracanthus squarrulosus **(Figure 162E):** In sandy pockets among rocks, 3.3 m depth, La Mona, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris (*JN-2982*, US Alg. Coll.-159475).

Chondracanthus tepidus **(Figure 163):** Dive 1.0–7.6 m depths, Punta La Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5451*, US Alg. Coll.-159488).

Chondracanthus zertuchei **(Figure 164):** Intertidal, Bahía San Francisquito, Baja California, Coll. J. N. Norris (holotype: *JN-3227*, US Alg. Coll.-159436).

Mazzaella diffusa **(Figure 165):** Dive 15–24 m depths, Isla La Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. H. Hommersand, M. Yoshizaki, and G. Boehlert (*JN-2999*: A, US Alg. Coll.-160802; B, US Alg. Coll. microscope slide 5340).

Mazzaella digitata **(Figure 166):** Cobble shore at mouth of two small estuaries on north side of island, Isla Rasa (Islas de la Cintura), Coll. E. Y. Dawson (*EYD-1045*: A, US Alg. Coll.-12964; B, US Alg. Coll. microscope slide 893).

Mazzaella hancockii **(Figure 167):** Dive 3–7.6 m depths, southeast side of Isla San Esteban, Coll. J. N. Norris (*JN-5563*; US Alg. Coll.-160803).

Kallymenia baldwinii **(Figure 168A):** Attached to rock, about 20 m depth, Bahía Santa Inez, Bahía Concepción, Baja California Sur, Coll. W. Baldwin (holotype: *EYD-25819*; US Alg. Coll.-40928).

Kallymenia bleckii **(Figure 168B):** 15 m depth, off Punta Púlpito (~12.5 km north of Punta San Basilio), Baja California Sur, Coll. John Bleck (holotype: *EYD-25919*; US Alg. Coll.-40927).

Kallymenia pertusa **(Figure 169):** Dive 15–23 m depths, off east end of Isla Mejía, northern end of Isla Ángel de la Guarda, Coll. J. N. Norris, J. Paul, and K. Robertson (*JN-5667,* US Alg. Coll.-217346).

Pugetia mexicana **(Figure 170A):** Dive 15–22 m depths, off east end of Isla Mejía, northern end of Isla Ángel de la Guarda, Coll. J. N. Norris, J. Paul, and K. Robertson (*JN-5668,* US Alg. Coll.-217349).

Pugetia mexicana **(Figure 170B):** Dive off small islet, 4.6–26 m depths, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5362,* US Alg. Coll.-160774).

Ahnfeltiopsis hancockii **(Figure 171A):** Intertidal rocky shore and cobble beach, Punta San Felipe (near San Felipe), Baja California, Coll. E. Y. Dawson (*EYD-405,* US Alg. Coll.-208111).

Ahnfeltiopsis hancockii **(Figure 171B):** Bahía San Francisquito, Baja California, Coll. J. N. Norris (*JN-3228,* US Alg. Coll.-159896).

Ahnfeltiopsis serenei **(Figure 172):** Isla San Benedicto, Islas Revillagigedo, Pacific Mexico (*EYD-12058,* AHFH, now UC).

Gymnogongrus johnstonii **(Figure 173A):** Intertidal to 7.6 m depth, off northeast end of island, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-6205*, US Alg. Coll.-159912).

Gymnogongrus johnstonii **(Figure 173B):** Intertidal, rocky shoreline, northeast end of island, Puerto Refugio, Isla Ángel de la Guarda, Coll. K. E. Bucher (*JN-5736*, US Alg. Coll.-159906).

Petroglossum parvum **(Figure 174):** 13–18 m depths, off Isla Salsipuedes (Islas de San Lorenzo), Islas de la Cintura, Coll. E. Y. Dawson (*EYD-26138*: A, B, US Alg. Coll.-78080; C, D, US Alg. Coll. microscope slide 783).

Sarcodiotheca dichotoma **(Figure 175A, B):** Dive to 18 m depth, rocky bottom, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. L. Sleeper (*JN-4432,* US Alg. Coll.-160847).

Sarcodiotheca dichotoma **(Figure 175C):** Drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6554,* US Alg. Coll.-160887).

Sarcodiotheca furcata **(Figure 176):** Dive to 9 m depth, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5328,* US Alg. Coll.-160855).

Sarcodiotheca furcata **(Figure 177A):** Dive off small islet, 4.6–26 m depths, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5349*, US Alg. Coll.-160859).

Sarcodiotheca furcata **(Figure 177B):** Dive 15–22 m depths, off west side of rocky shoreline of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5798,* US Alg. Coll.-160864).

Sarcodiotheca gaudichaudii **(Figure 178A, B):** 1–7.6 m depths, Punta la Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (A, *JN-5439a*, US Alg. Coll.-160874; B, *JN-5439b* (♂), US Alg. Coll.-160875).

Sarcodiotheca gaudichaudii **(Figure 178C):** Drift, Desemboque de San Ignacio, Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6555,* US Alg. Coll.-160877).

Sarcodiotheca taylorii **(Figure 179):** Dive 7.6–18 m depths, rocky substrate, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. L. Sleeper (*JN-4460*: A, US Alg. Coll.-160878; B, US Alg. Coll.-160879).

Tacanoosca uncinata **(Figure 180A, D):** Beach drift at high tide, Punta Colorado, near Guaymas, Sonora, Coll. E. Y. Dawson (A, *EYD-1800* (♂), US Alg. Coll.-7181; D, *EYD-1800* (♀), US Alg. Coll.-7181).

Tacanoosca uncinata **(Figure 180B):** On rock, 6 m depth, Punta Willard, Bahía San Luís Gonzaga, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5415*, US Alg. Coll.-210494).

Tacanoosca uncinata **(Figure 180C):** 3.0–4.6 m depths, Bahia San Francisquito, Baja California, Coll. J. N. Norris (*JN-238*, US Alg. Coll.-89992).

Weeksia coccinea **(Figure 181A):** Drift, Desemboque de San Ignacio (Seri village), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Coon (*JN-6546*, US Alg. Coll.-159943).

Weeksia templetonii **(Figure 182):** Dive 3–15 m depths, north end of Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4349*, US Alg. Coll.-159945).

Cruoriella fissurata **(Figure 183):** On intertidal rocks, Cabeza Ballena, Baja California Sur (holotype: *EYD-6830a*; AHFH, now UC).

Cruoriella mexicana **(Figure 184A):** Growing on shells, 13–15 m depths, off South Coronado Island, Islas Los Coronados, Baja California, Pacific Mexico (holotype: *EYD-4283c*, *Cruoriopsis mexicana*; AHFH, now UC).

Cruoriella mexicana **(Figure 184B):** Growing on the articulate coralline *Bossiella,* dredged at the type locality (off Isla Coronado Sur, Islas Los Coronados, off northern Baja California) along with the type (paratype: *EYD-4280*, AHFH, now UC).

Metapeyssonnelia mexicana **(Figure 185):** Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. G. J. Hollenberg (*GJH-67-54*, US Alg. Coll. microscope slide 3109).

Peyssonnelia mexicana **(Figure 186A):** Binners Cove, Isla Socorro, Islas Revillagigedo, Pacific Mexico, Coll. E. Y. Dawson (*EYD-12137,* US Alg. Coll.-12357).

Peyssonnelia mexicana **(Figure 186B–D):** Dredged from 9–22 m, Isla Las Ánimas (Isla San Lorenzo del Norte), Islas de San Lorenzo, Coll. E. Y. Dawson (B, *EYD-26098*, US Alg. Coll. microscope slide 800; C, D, *EYD-26099,* US Alg. Coll. microscope slide 799).

Peyssonnelia orientalis **(Figure 187A, B):** Northeast side of cove, Isla San Pedro Nolasco, Coll. N. P. Yensen (*NPY 740320-3*, =*JN-5214*, US Alg. Coll. microscope slide 4564).

Peyssonnelia orientalis **(Figure 187C):** Punta Palmilla, Baja California Sur, Coll. E. Y. Dawson (*EYD-3245*, AHFH, now UC).

Gracilaria ascidiicola **(Figure 188):** 3.6–7.3 m depths, innermost bay, Puerto Escondido, Baja California Sur, Coll. E. Y. Dawson (*EYD-7149*: A, US Alg. Coll.-5690; B, isotype: US Alg. Coll.-41708).

Gracilaria crispata **(Figure 189A):** Intertidal rock platform with sand areas, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-3258,* US Alg. Coll.-159559).

Gracilaria crispata **(Figure 189B):** Intertidal rock platform, Playa Las Conchas (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5866,* US Alg. Coll.-159568).

Gracilaria crispata **(Figure 190A–D):** On cobbles, rocky intertidal shore on south side of bay, Bahía Bocochibampo, Sonora (*EYD-1713* (♀), AHFH, now UC).

Gracilaria rubrimembra **(Figure 190E–G):** Intertidal, on flat, igneous reef with tide pools, south side of bay (near entrance to Puerto San Carlos), Ensenada de San Francisco, Sonora (E, holotype: *EYD-1918* (♀), AHFH-4522, now UC; F, G, isotypes: *EYD-1918*, AHFH, now UC.

Gracilaria veleroae **(Figure 190H):** Netted in fish seine, shallow water of innermost bay (locally known as “Bahía Santa Lucia”) near center of town, Acapulco, Guerrero, Pacific Mexico (*EYD-3916* (♂), AHFH, now UC).

Gracilaria pachydermatica **(Figure 191A):** Growing on granite rock, mid to low intertidal tide pools, Punta Pelícano, Sonora, Coll. J. N. Norris (*JN-3953*, US Alg. Coll.-159595).

Gracilaria pachydermatica **(Figure 191B):** On upper intertidal rocks, Isla Tortuga (northeast of Puerto Santa Rosalía), off Baja California Sur, Coll. I. M. Johnston (*I.M.Johnston-122,* holotype: CAS-1355, now UC).

Gracilaria pachydermatica **(Figure 191C):** Intertidal, rocky shore, south side of bay Ensenada de San Francisco, near Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-1822* (♂), AHFH, now UC).

Gracilaria pachydermatica **(Figure 191D):** Bahía Carrizal, near Cabo Arco (vicinity of Guaymas), Sonora, Coll. E. Y. Dawson (*EYD-1682* (♀), AHFH, now UC).

Gracilaria pachydermatica **(Figure 191E):** On flat igneous reef with tide pools, south side of bay, Ensenada de San Francisco (near entrance to Puerto San Carlos), Sonora, Coll. E. Y. Dawson (*EYD-1909*, AHFH, now UC).

Gracilaria pinnata **(Figure 192):** 6–9 m depths, northwest of rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5334*, US Alg. Coll.-159632).

Gracilaria ramisecunda **(Figure 193):** Type collection (♀, ♂, and tetrasporophyte), in low intertidal tide pools on granitic reef, Cabeza Ballena (headland ~8 km east of Cabo San Lucas), Baja California Sur, Coll. E. Y. Dawson (holotype: *EYD-3314*, AHFH-12870, now UC).

Gracilaria rubrimembra **(Figure 194):** 6 m depth, Punta La Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris and G. Boehlert (*JN-3032*: A, US Alg. Coll.-159638; B, US Alg. Coll.-159637).

Gracilaria spinigera **(Figure 195):** Drift along shore Ensenada de San Francisco, near Bahía San Carlos, Sonora, Coll. E. Y. Dawson (*EYD-10986,* US Alg. Coll.-7536).

Gracilaria spinigera **(Figure 196A):** Ensenada de San Francisco (between Bahía San Carlos and Guaymas), Sonora, Coll. E. Y. Dawson (*EYD-574-40*, AHFH, now UC).

Gracilaria spinigera **(Figure 196B, D, E):** Near Guaymas (*EYD-1659*, AHFH, now UC).

Gracilaria spinigera **(Figure 196C):** From type collection, Ensenada de San Francisco (between Bahía San Carlos and Guaymas), Sonora, Coll. E. Y. Dawson (holotype: *EYD-1903* (♂); AHFH-4949, now UC).

Gracilaria subsecundata **(Figure 197A, B):** Sand-mud tidal flats, 1.8–3.0 m depths on rock reef, Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4990*, US Alg. Coll.-159647).

Gracilaria veleroae **(Figure 197C):** Dredged 4.0–30 m, off Isla Tiburón, near Isla Turner, Coll. E. Y. Dawson (holotype: *EYD-141a-40*, AHFH-37, now UC).

Gracilaria tepocensis **(Figure 198A):** 4.5–9.5 m depths, dive off small islet, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5356*, US Alg. Coll.-156380).

Gracilaria turgida **(Figure 198B):** In shallow tidal channels near mouth of mangrove estuary, Estero de Bahía de Las Ánimas, Coll. J. N. Norris (*JN-3212*, US Alg. Coll.-159687).

Gracilaria vivesii **(Figure 199A):** Dive 9.0–23 m depths, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5252*, US Alg. Coll.-159675).

Gracilaria vivesii **(Figure 199B):** Dive 15–23 m depths, north of Punta La Gringa, Bahía de Los Ángeles, Baja California, Coll. F. Aguilar (*JN-2966*, US Alg. Coll.-159659).

Gracilaria vivesii **(Figure 199C):** Intertidal to 7.6 m depth, Puerto Refugio, shore on NE end of Isla Ángel de la Guarda, Islas de la Cintura, Coll. J. N. Norris and K. E. Bucher (*JN-6198,* US Alg. Coll.-159683).

Gracilariopsis animasensis, sp. nov. **(Figure 200A):** About 0.3 m depth, in shallow tidal channel near mouth of mangrove estuary, Estero de Bahía de Las Ánimas, Coll. J. N. Norris and K. E. Bucher (holotype: *JN-3215*, US Alg. Coll.-89276).

Gracilariopsis animasensis, sp. nov. **(Figure 200B–D):** Ensenada San Francisco (between Bahía San Carlos and Guaymas), Sonora (B, *EYD-1814*, AD-A6283; C, AD microscope slide 21062; D, AD microscope slide 21061).

Gracilariopsis animasensis, sp. nov. **(Figure 201):** Lake Butler, Robe, South Australia, Coll. H. B. S. Womersley (A, B, AD-A64282c; C, AD-A63430, AD microscope slide 14314).

Gracilariopsis animasensis, sp. nov. **(Figure 202):** Lake Butler, Robe, South Australia, Coll. H. B. S. Womersley (A, AD-A63430, AD microscope slide 14316; B, C, AD-A63430, microscope slide 14317; D, AD-A63430, microscope slide 14320; E, AD-A63430, microscope slide 14319).

Cryptonemia angustata **(Figure 203):** Subtidal, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4500*, US Alg. Coll.-158994).

Cryptonemia guaymasensis **(Figure 204A, B):** Rocky shore fronting Laboratorio de Biología Marina, Playa Las Conches (Playa Estación), Punta Peñasco, Sonora, Coll. A. E. Dennis (*EYD-27492*, US Alg. Coll.-40772).

Cryptonemia opuntioides **(Figure 204C):** Dredged 12–16 m depths, off Isla Salsipuedes (Islas de San Lorenzo), Islas de la Cintura, Baja California (holotype: *EYD-26126*, US Alg. Coll. microscope slide 786).

Cryptonemia obovata **(Figure 205A):** About 13.7 m depth, muddy bottom, attached to seashells, Canal de Infiernillo, midway between Isla Tiburón and west of Campo Viboras, Sonora, Coll. G. L. Kooyman and E. Senate (*JN-4729,* US Alg. Coll.-158996).

Cryptonemia obovata **(Figure 205B):** Dredged 9–36 m depths, Isla San Esteban, Coll. L. Pinkas, E. Smith, and D. Miller (California Department of Fish and Game; M/V *Alaska* expedition) (*EYD-21577*, US Alg. Coll.-7069).

Grateloupia catenata **(Figure 206):** Puerto Lobos, Sonora, Coll. J. N. Norris and M. Helvey (*JN-6058*: A, US Alg. Coll.-159869; B, US Alg. Coll. microscope slide 8684).

Grateloupia hancockii **(Figure 207A):** Intertidal, south end of Isla Estanque, Coll. J. N. Norris and K. E. Bucher (*JN-5597*, US Alg. Coll.-159781).

Grateloupia hancockii **(Figure 207B):** On rocks in mud-sand flats, Bahía La Choya (Bahía Cholla), vicinity of Puerto Peñasco, Sonora, Coll. R. B. Searles (*JN-5894*, US Alg. Coll.-159782).

Grateloupia howei **(Figure 208A):** 4.6 m depth, southeast side of Isla San Esteban, Coll. K. E. Bucher (*JN-5519*, US Alg. Coll.-159785).

Grateloupia howei **(Figure 208B):** Low intertidal, rock outcropping cobblestone beach, NW side of Punta Robinson (Cabo Lobos), Puerto Libertad, Sonora, Coll. J. N. Norris (*JN-5920*. US Alg. Coll.-159790).

Grateloupia prolongata **(Figure 209A):** Beach drift, Desemboque de San Ignacio, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5167*, US Alg. Coll.-159794).

Grateloupia prolongata **(Figure 209B):** Off sand islet, 4.5–10.6 m depths, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5351*, US Alg. Coll.-159796).

Grateloupia prolongata **(Figure 209C):** Dive to 4.6–6 m depths, rock outcropping, north side of point, Punta Lobos (vicinity of Puerto Lobos), Sonora, Coll. J. N. Norris (*JN-5898*, US Alg. Coll.-159804).

Grateloupia versicolor **(Figure 210):** 3.0–7.6 m depths, off southeast side of Isla San Esteban, Coll. J. N. Norris (*JN-5720*, US Alg. Coll.-159814).

Grateloupia violacea **(Figure 211):** 2.4–6 m depths, Punta La Gringa, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. H. Hommersand, M. Yoshizaki, and G. Boehlert (A, *JN-3053*, US Alg. Coll.-159831; B, *JN-3053-III*, US Alg. Coll. microscope slide 4332; C, *JN-3053-IX*, US Alg. Coll. microscope slide 4521).

Halymenia actinophysa **(Figure 212A):** Beach drift, Desemboque de San Ignacio, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5137,* US Alg. Coll.-159936).

Halymenia actinophysa **(Figure 212B–D):** Subtidal, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4501c*, US Alg. Coll. microscope slide 4399).

Halymenia megaspora **(Figure 213):** Dredged 7.3–18.2 m [4–10 fathoms], from bottom of free-living rhodoliths (species of *Lithothamnion*), about mid channel, Canal de San Lorenzo, between Isla Espíritu Santo and Gulf coast of Baja California Sur, Coll. E. Y. Dawson (*EYD-6904A*; paratype: US Alg. Coll.-206130).

Prionitis abbreviata var. abbreviata **(Figure 214A):** 3–5 m depths, dive off Campo Dolar, Cabo Tepopa, Sonora, Coll. J. N. Norris, D. P. Cheney, and C. J. Dawes (*JN-7059*, US Alg. Coll.-160707).

Prionitis acroidalea **(Figure 214B):** Lower littoral, rocky reef at Bahía Agua Dulce, Isla Tiburón, Coll. E. Y. Dawson (*EYD-961,* US Alg. Coll.-12842).

Prionitis abbreviata **var.** ***guaymasensis*** **(Figure 214C):** Rocky shore in front of Laboratorio de Biología Marina, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. E. Y. Dawson (*EYD-27341,* US Alg. Coll.-40742).

Prionitis abbreviata **var.** ***guaymasensis*** **(Figure 214D):** Mid intertidal, Cumpleaños Tide Pool, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. K. E. Bucher (*JN-4051,* US Alg. Coll.-160679).

Tsengia abbottiana **(Figure 215):** 15–23 m depths, on rock-shell bottom, dive off southeast end of Isla Mejía, in narrow channel between Isla Mejía and Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5677*: A, holotype: US Alg. Coll.-55677; B, C, squash preparation of type, US Alg. Coll. microscope slide 1071).

Predaea japonica (**Figure 217A**): 9 m depth, off NW side of the rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5300*; US Alg. Coll.-160633).

Predaea japonica (**Figure 217B**): Subtidal, Isla Estanque, Coll. J. N. Norris and K. Bucher, *s.n.* (US Alg. Coll. microscope slide 5296).

Predaea japonica (**Figure 217C**): Dive 23 m depth, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5295*, US Alg. Coll. microscope slide 5298).

Schizymenia pacifica (**Figure 218A**): Intertidal, NE side, rocky shoreline, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5759*, US Alg. Coll.-160898).

Schizymenia pacifica (**Figure 218B, C**): Intertidal, rocky shoreline, northeast end of Puerto Refugio, Isla Ángel de la Guarda, Coll. K. Bucher (B, *JN-5747c*, US Alg. Coll. microscope slide 4524; C, *JN-5747*, US Alg. Coll. microscope slide 4526).

Plocamium katinae, sp. nov. (**Figure 219A**): Intertidal rock platform and Cumpleaños Tide Pool, Playa Las Conches (Playa Estación), Puerto Peñasco, Coll. J. N. Norris and K. E. Bucher (holotype: *JN-3632*a, US Alg. Coll.-160510).

Plocamium katinae, sp. nov. (**Figure 219B**): Intertidal rock platform and Cumpleaños Tide Pool, Playa Las Conches (Playa Estación), Puerto Peñasco, Coll. J. N. Norris and W. Fenical (*JN-4163,* US Alg. Coll.-217348).

Plocamium katinae, sp. nov. (**Figure 219C**): 4.6–6.0 m depths, off north side of point, Punta Lobos (vicinity of Puerto Lobos), Sonora, Coll. J. N. Norris (*JN-5916,* US Alg. Coll.-160531; left specimen, US Alg. Coll. microscope slide 8682, and right specimen, US Alg. Coll. microscope slide 8683).

Plocamium katinae, sp. nov. (**Figure 219D, E**): Dive 4.5–6 m depths, Punta Lobos, north side of point, Coll. J. N. Norris (*JN-5916,* US Alg. Coll. microscope slides 8682, 8683).

Sebdenia flabellata (**Figure 220A**): 10.1 m depth, dive off the south end of Isla Estanque, Islas de la Cintura, Coll. J. N. Norris and K. E. Bucher (*JN-5490*; US Alg. Coll.-217352).

Sebdenia flabellata (**Figure 220B**): 7.6–18 m depth, rocky substrate, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (*JN-4430*, US Alg. Coll. microscope slide 4503).

Sebdenia flabellata (**Figure 220C**): On rocks, 9 m depth, Caleta Santa María (north of Santa Rosalía), Baja California Sur, Coll. D. G. Lindquist (sta. no. DGL-720811-1) (*JN-3398*, US Alg. Coll. microscope slide 4501).

Champia disticha (**Figure 221A**): Epiphytic on *Laurencia*, mid intertidal, Isla San Esteban, Coll. E. Y. Dawson (holotype: *EYD-441*; AHFH-51, now UC).

Champia caespitosa (**Figure 221B**): Epiphytic on articulated coralline, mid intertidal, Isla Estanque (holotype: *EYD-407-*40; AHFH-52, now UC).

Gastroclonium compressum (**Figure 221C**): Intertidal rock platform, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-5234*, US Alg. Coll.-158972).

Champia* cf. *parvula (**Figure 222A**): Intertidal to 9 m depth, dive NW of the rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5311*, US Alg. Coll.-158921).

Champia* cf. *parvula (**Figure 222B–D**): Intertidal rock platform, Playa Hermosa, (~0.4 km west of Playa Hermosa Hotel), vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4001*, US Alg. Coll. microscope slide 4583).

Gastroclonium pacificum (**Figure 223**): Rocky reefs with large tide pools, Ensenada de San Francisco, near Guaymas, Sonora, Coll. E. Y. Dawson (*EYD-1808,* US Alg. Coll.-207564).

Gloiocladia hoshawii (**Figure 224A**): 15 m depth, Isla San Pedro Nolasco, near Guaymas, Sonora, Coll. R. W. Hoshaw and E. Y. Dawson, *s.n.* (holotype: US Alg. Coll.-40926).

Gloiocladia hoshawii (**Figure 224B–D**): 21 m depth, Islas de Los Gemelos, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris (*JN-3008*: B, US Alg. Coll.-159134; C, US Alg. Coll. microscope slide 4595; D, US Alg. Coll. microscope slide 4596).

Gloiocladia mollis (**Figure 225**): 9–36 m depths, Isla San Esteban, Coll. L. Pinkas, E. Smith, and D. Miller (California Department of Fish and Game; M/V *Alaska* expedition) (*EYD-21579*, US Alg. Coll.-51351).

Gloiocladia sefferi (**Figure 226A, C**): Dive 3–15 m depths, off north end of Isla Coronado, Bahía de Los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (*JN-4336*: A, US Alg. Coll.-159135; C, US Alg. Coll. microscope slide 4233).

Gloiocladia sefferi (**Figure 226B**): 9–36 m depths, Isla San Esteban, Coll. L. Pinkas, E. Smith, and D. Miller (California Department of Fish and Game; M/V *Alaska* expedition) (*EYD-21558,* US Alg. Coll.-7202).

Gloioderma conjuncta (**Figure 227A**): Bahía San Carlos, Sonora, Coll. D. E. Bean, *s.n.* (US Alg. Coll.-94253).

Gloioderma conjuncta (**Figure 227B**): Dive 10 m depth, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (*JN-5276,* US Alg. Coll.-159529).

Ceratodictyon variabile (**Figure 228**): Rocky intertidal (near transect line), Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-6087,* US Alg. Coll.-159333).

Lomentaria catenata (**Figure 229**): On rocks, dive to 4.6–6 m depths, north side of point, Punta Lobos (vicinity of Puerto

Lobos), Sonora, Coll. J. N. Norris (*JN-5899*: A, US Alg. Coll.-160463; B, US Alg. Coll.-160462).

Lomentaria hakodatensis **(Figure 230):** On rocks, inner bay, Bahía de Topolobampo, Sinaloa, Coll. E. Y. Dawson (*EYD-10896,* US Alg. Coll.-12228).

Botryocladia datilensis **(Figure 231A):** 15–24 m depths, rocky substrate, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Yoshizaki, G. Boehlert, and M. H. Hommersand (*JN-2993,* US Alg. Coll.-158661).

Botryocladia datilensis **(Figure 231B–D):** 7.6–24 m depths, rocky substrate, Isla la Ventana, Bahía de Los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (*JN-4429,* US Alg. Coll. microscope slide 4589).

Botryocladia guaymasensis **(Figure 232A):** Rocky intertidal and Cumpleaños Tide Pool, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-6083b*, US Alg. Coll.-158697).

Botryocladia guaymasensis **(Figure 232B):** Rocky intertidal, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-5858,* US Alg. Coll.-158696).

Botryocladia guaymasensis **(Figure 232C):** Rocky reef, off west side of sand-cobble beach, 1.5–4.6 m depths, Punta Robinson (~2.4 km east of Puerto Libertad), Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4847,* US Alg. Coll. microscope slide 4588).

Botryocladia uvarioides **(Figure 233A):** Mid intertidal rocks, west of Casa Garcia, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris and K. Bucher (*JN-3145,* US Alg. Coll.-217353).

Botryocladia uvarioides **(Figure 233B):** Dredged 40 m depth, off San Jose del Cabo, Baja California Sur, Coll. J. T. Howell (syntypes: *JTH-727* and *JTH-598*; CAS, now UC; and AHFH-49, now UC).

Irvinea hancockii **(Figure 234):** 10.6 m depth, south end of Isla Estanque, Coll. J. N. Norris and K. E. Bucher (*JN-5600,* US Alg. Coll.-217355).

Rhodymenia dawsonii **(Figure 235A, B):** 0.3–1.8 m depths, Isla Cholla, off Isla Carmen, Coll. E. Y. Dawson (*EYD-18658,* US Alg. Coll.-13019).

Rhodymenia divaricata **(Figure 235C):** On mud bottom, dredged from about 3.6–5.5 m, Bahía Guaymas, Sonora, Coll. E. Y. Dawson (holotype: *EYD-53-40*; AHFH-1, now UC).

Rhodymenia hancockii **(Figure 236A):** Intertidal rocks to 1.8 m depth, in front of Laboratorio de Biología Marina, Playa Las Conches (Playa Estación), Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-2938*, US Alg. Coll.-160805).

Rhodymenia hancockii **(Figure 236B):** 6 m depth, off west side of small cove Punta Cirio (south of Puerto Libertad), Sonora, Coll. J. N. Norris, K. E. Bucher, and D. Moore (*JN-4875,* US Alg. Coll.-160814).

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Index of Scientific Names

Names of all taxa of marine red algae recognized in the northern Gulf of California are shown in **bold type**. All other taxa listed (non-bold) are either synonyms, have distribution that does not include the northern Gulf, or are otherwise discussed or mentioned in the text. Higher taxa (e.g., orders and families) are in SMALL CAPITAL LETTERS. Genera and species are in *italics*.

Page numbers in **bold type** refer to the start of the taxa descriptions. Numbers in *italic type* refer to pages with figures of the named taxa. All other page numbers refer to basionyms or synonyms or to discussion or mention of the taxa elsewhere in the text.

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