TAXONOMY OF ECONOMIC SEAWEEDS With reference to some Pacific species Volume IV

Isabella A. Abbott, Editor



A Publication of the California Sea Grant College



Rosemary Amidei Communications Coordinator

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Results of an international workshop sponsored by the California Sea Grant College in cooperation with the Pacific Sea Grant College Programs of Alaska, Hawaii, Oregon, and Washington and hosted by Hokkaido University, Sapporo, Japan, July 1991.



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Preface

James J. Sullivan Director, California Sea Grant College

California Sea Grant first sponsored an international conference on the taxonomy of economically important seaweeds of the Pacific in 1984.

The meeting was hosted by the University of Guam and arose out of an observation made to me by Roy Tsuda of that university. His point was that there would not be appreciable progress in seaweed aquaculture or marine natural products chemistry in the Pacific until the taxonomy of commercially interesting species was better understood.

California Sea Grant funded the first meeting in cooperation with the other Pacific Sea Grant programs with the aim of meeting a particular need and with no notion of initiating a continuing series of meetings. In retrospect, this was naive given the enormous ignorance that prevails about warm-water Pacific algae. We subsequently received so much positive feedback from the worldwide scientific community concerning the great need for this work that the Guam meeting evolved into a recurring series of meetings, held in 1986, 1989, 1991, and, most recently, in Honolulu, Hawaii in July 1993. As Dr. Abbott indicates in this volume, the progress made at these workshops has been substantial, and we are pleased to have played a role in bringing together an international community of prestigious systematists to address this important problem.

Introduction

Isabella A. Abbott, Workshop Convener and Editor

Looking back over the past four workshops, I find that each offered something new.

The first workshop on some of the economically important algae of the Pacific (and to a lesser extent, the Western Atlantic) was sponsored by the California Sea Grant College in cooperation with the other Pacific Sea Grant College Programs and hosted by the University of Guam in 1984. This, of course, was our prototype meeting, and we were all gratified to find out how enthusiastically 14 participants representing five nations would share their systematics problems and knowledge with others equally interested. These first participants demonstrated that a workshop divided into four or five groups of specialists had many pluses in its favor over a symposium or seminar format. But at the time we dared not dream that this single workshop would evolve into a series, held on average every second year at some new location in the Pacific Rim.

But continue it did, and in the second workshop, held at the Institute of Oceanology in Qingdao, China, in 1986, a Laurencia group of specialists was added to existing groups on Sargassum, Gracilaria and Polycavernosa, Gelidium and Pterocladia, and Eucheuma. At this workshop, Laurencia species from Hawaii, of which there are many, were studied along with those of China, which had previously been surveyed. (By contrast, Japanese species are well studied). Dr. Karla McDermid used photographs to illustrate on Hawaiian species the features applied by Yuzuru Saito to Japanese and Australian species. The photographs that McDermid used to illustrate projecting cell walls along the radius of the cell, lenticular thickening, and secondary pit connections in the outer cortical cells did indeed look more "real" than did the excellent drawings of Saito. After all, photography presents a kind of reality that is more in keeping with modern ways of communicating scientific information. But photography does not substitute for the knowledge gained from the painstaking microscopic examinations necessary before illustrations of species can be made. In addition, we still need to know, for example, whether lenticular thickenings, present in any given species, occur

throughout the length of a branch or anywhere in the plant (preliminary observations lead me to doubt that lenticular thickenings are present in some species that are characterized as having them). Coupled with this *Laurencia* study was a paper by Zablackis and McDermid, evaluating the characteristics of an agar found in a species from Hawaii, and since named *Laurencia crustiformans* McDermid. No other researcher has elected to study *Laurencia* from an economic perspective.

The third workshop, held at the Scripps Institution of Oceanography in La Jolla, California, included two notable papers on using statistical methods to handle variations shown by populations of *Sargassum*. Much of the research reported in those papers was done while Dr. John Kilar held a postdoctoral position in Florida. Although he has subsequently gone into other research, some of his perspectives are being adopted by other *Sargassum* students, and could well be applied to other taxa that show great variation (for example, *Gelidium* and *Gracilaria*). However, those who consider biometric methods useful in critically evaluating taxa may not be near large populations of these red algae. It is clear to me that a shift of some kind must be made beyond morphology in the "big," variable—and therefore troublesome—species complexes. Now that the ground has been cleared for some areas of the world, the next approaches will probably encompass population analysis and perhaps molecular techniques, as well as other helpful tools to supplement morphological studies.

The fourth workshop, the results of which appear in this volume, introduced several new participants. Dr. Tadahide Noro from Kagoshima University, who had been in Australia looking at *Sargassum* species (both living and herbarium examples) has made observations in this volume that are different from those made before. With him, I have submitted a paper on some few specimens of *Sargassum* from Tahiti and New Caledonia in order to encourage those who live in "outlying" regions to collect specimens that they or others can work on.

Another new researcher in the fourth workshop, was Dr. Michio Masuda, who did a masterful overview and synopsis of the Oriental species of the Phyllophoraceae, placing the systematics in a framework that includes life-history studies in culture. He kindly included Zhang Junfu and Xia Bangmei as authors of the paper he prepared. The Chinese records are few; indeed, it was I who called their attention to the presence of phyllophoraceous algae when I visited Qingdao for six weeks in 1987. Unless many new records are made in this group, it does not look as though more papers will be written on these algae, although they produce highly useful iota carrageenan, which is sometimes in very short supply commercially.

We were also able to expand our geographical horizons to include representatives from Thailand (Dr. K. Lewmanomont), Malaysia (Dr. Siew-Moi Phang), and Korea (Dr. Hae Bok Lee). In this volume, Lewmanomont and Phang have contributed papers on *Gracilaria*, and Hae Bok Lee has written about *Gelidium*.

With the addition of these new researchers, Sea Grant is able to share the knowledge gained at these valuable workshops with an even larger Pacific community. The help and information exchange provided by colleagues to those

whose first interests were not Western-oriented taxonomy continue to go on, to everyone's satisfaction. The friendships made and mutual respect achieved remain perhaps the best results of these truly international meetings.

To be able to use the Okamura and Hokkaido University herbaria and to obtain books that most of us have seen only in photocopy form at best was a thrill for all of us who participated in the fourth workshop. It made us understand the seriousness that the Japanese accord to phycology, and the strong direction provided by having continuous professors of botany (phycology), with all that implies in terms of facilities, publications, and widespread interest and support. Okamura's herbarium is as important to Japanese (and Chinese) phycologists as is the Agardh herbarium to most Western algal workers. But in the same building, younger scholars are learning new techniques for studying algae. I trust that they will remember the old ways as well, and will always appreciate their rich heritage.

Acknowledgments

It is not easy to lead a conference in which the participants speak a variety of languages and have different customs and habits. But some of the arrangements at Hokkaido University were Westernized, which made it easy for those of us visiting from the West to feel comfortable instantly. We stayed in the Western-style Clark *Kaikan* (inn), named after Dr. Clark, one of the early Americans who influenced the layout of the city, including streets running at right angles to each other. He also introduced cows and cheese making to Hokkaido. But it was Japanese inspiration that placed a "fast food" cafeteria within steps of the Faculty of Science. This made it possible to have a different lunch each day, most of it familiar look-ing!

I am pleased to acknowledge the thoughtful planning and warm hospitality shown by Professor Tadao Yoshida and his entire staff and by other Japanese colleagues who were asked to help in hosting this conference. We greatly appreciated their kindnesses, large and small, and their willingness to let us intrude in their busy lives.

Even though I had been to Sapporo many times before (next to Kyoto, my favorite Japanese stop), I found the city and its surroundings much changed. But the Faculty of Science was the same as ever, and therefore comfortable. Partaking of the tea or coffee and cookies that were almost always available provided an opportunity to sit and visit with colleagues and to meet scientists sent by the various environmental firms that helped to support the workshop. Shy at first because of their halting English (though they graciously ignored the fact that we knew *no* Japanese), they became our good friends nevertheless.

The three Japanese parties held in our honor showed a side of Japan few tourists see: The first night we had first-class Japanese food at a lovely old inn; the second, an overly generous "Genghis Khan barbecue"; and the third, a final reception providing food that few ever see or taste, and all so artistically done.

The highlight of that final evening was meeting some of the "alumni" of the Faculty of Science. How wonderful it was for me to see Dr. Yositeru Nakamura after 20 years. I found him much the same, down to his beret. Dr. Yoshio

Hasegawa was also there with his welcoming smile. So too was Dr. Shoji Kawashima, with his brand-new book on Laminariales, which he had promised Yamada-sensei he would write, and here it was. Something to celebrate, indeed. It was kind of the alumni to contribute to this last reception and banquet, and we owe them a vote of thanks.

A personal thank you is due to Dr. James Sullivan, director of California Sea Grant, for showing encouragement and interest to all participants. We will never make him a phycologist, but he has become one of the best marketing advocates for small workshops where people really work—and thoroughly enjoy themselves nonetheless. Were it not for his foresight, we could not have held four workshops and published four volumes on the information we have gathered—events that have made us the envy of many phycologists. Our overseas friends were impressed that the director of a program would come and stay at the workshop for days; they are used to seeing someone in his position open a meeting, and then disappear. We all thank you, Jim.

On behalf of the participants, I also thank the Sea Grant directors of Alaska, Washington, Oregon, and Hawaii for funds to help defray the transportation costs of some participants.

It is a particular pleasure to thank Rosemary Amidei, Communications Coordinator of the California Sea Grant College, and her staff for making this series such a high-quality product. I get all the credit, but they deserve at least half of it.

Isabella A. Abbott

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Notes

About Chinese Names

In accordance with the national change made in China in 1987, Chinese names are listed with surname first, *no comma*, and given name last. A good example of old style and new style is Chang, C. F. (old) vs. Zhang Junfu (new).

Listing Species Names

In accordance with the "Berlin Code" (1988), reference to *place* of publication follows author name(s) for nomenclature of species, basionyms, synonyms, types, and so forth and is *not* listed in the Literature Cited sections (references). On the other hand, if the species and author(s) are listed in the text, this citation is listed in Literature Cited. An example is as follows:

Sargassum ilicifolium (Turner) C. Agardh, Sp. algarum, p. 11, 1820.

Basionym: Fucus ilicifolius Turner, Fuci ..., vol. 1, p. 113, pl. 51, 1808.

The order is species name, author name, *place of publication* (i.e., name of either book or journal), volume number, page number(s) (optional for books and mandatory for journals), plate or figure number(s) (optional), and date. These rules will be adhered to in the next volume also.

In this volume, all references to volumes (1–3) from the first three workshops in this volume are listed in nomenclature setups and in Literature Cited as

"Tax. Econ. Seaweeds 1 (or 2, 3)," followed by page and figure numbers, instead of giving the whole citation including editor, place of publication, and so forth. The entire citations are given here for reference.

Taxonomy of economic seaweeds: with reference to some Pacific and Caribbean species, vol. 1. I.A. Abbott and J.N. Norris, editors. [i-ii] + iii-xv + 1-167, 1985. California Sea Grant College, University of California, La Jolla, Calif. Report No. T-CSGCP-011.

Taxonomy of economic seaweeds: with reference to some Pacific and Caribbean species, vol. 2. I.A. Abbott, editor. [i–ii] + iii–xv, + 1–265, 1988. California Sea Grant College, University of California, La Jolla, Calif. Report No. T-CSGCP-018.

Taxonomy of economic seaweeds: with reference to some Pacific and Western Atlantic species, vol. 3. I.A. Abbott, editor. [i–ii] + iii–xiv + 1–241, 1992. California Sea Grant College, University of California, La Jolla, Calif. Report No. T-CSGCP-023.

INTRODUCTION

Isabella A. Abbott

The first two volumes of this series (Tax. Econ. Seaweeds 1 and 2) established the most common species of *Sargassum* subgenus *Sargassum* and subgenus *Bactrophycus* in the Chinese, Japanese, and Hawaiian coastal waters; and the third volume (Tax. Econ. Seaweeds 3) published in 1992 introduced Korean species and a large number of species from the Philippines, many of them as new species. In addition, in the paper by Kilar, Hanisak and Yoshida, a few common Caribbean species were treated quantitatively on a population basis. That paper by Kilar et al. should be a model for all phycologists, not just *Sargassum* students—a model that we might work toward after we have painstakingly described and evaluated specimens and species on an alpha-taxonomic level. The success of this quantitative approach, even when we have not "finished" any one given geographical area, indicates that we can think about starting to apply biometrics, experimental hybridization, culture work, molecular techniques, and so forth to some of the species around us.

In this section, the new Philippine species of *Sargassum*, described in English in the previous volume (and illustrated) are validated with Latin diagnoses. These 12 new species are added to the 50 or so "known" species in the large Philippine archipelago.

Two contributions in this volume address those species with furcately branching leaves, or compressed primary branches. The first, by Ajisaka, Noro, Trono, Chiang, and Yoshida, treats the characteristics of the species statistically, thus continuing some of the earlier perspectives. The second paper, by Noro, Ajisaka, and Yoshida, places five species in the synonymy of other species, all common or widespread taxa. This indicates that by whatever means, a gradual understanding of the limits of the common *Sargassum* species is being reached. Inasmuch as some of these species are "old" (e.g., species of C. Agardh, who was among the first to distinguish species within this group), perhaps examination of "younger" species will show that the younger species had been named one or more times previously.

I must note the passing of the almost ceremonial deference to the studies of Yukio Yamada, who almost single-handedly trained a generation of Japanese phycologists. He was one of the most progressive systematists I have ever had the pleasure to work with, and I believe he would strongly encourage the younger phycologists to rigorously and critically examine materials, and place his species in synonymy if they felt it appropriate.

Paul Silva, in a review of volume 3 (Tax. Econ. Seaweeds 3) in *Plant Science Bulletin* (Autumn, 1992) praised the new techniques that are being applied to *Sargassum* taxonomy. He also wrote (in a portion omitted by the editor of the *Bulletin*), "Part of the heavy baggage that *Sargassum* taxonomists must carry was provided by Grunow, who segregated minor variants in the herbarium as varieties and forms, thus creating trinomials and quadrinomials whose application is anyone's guess, being divorced from any meaningful biological context." I echo these sentiments strongly. I think that one of the most important contributions a student of *Sargassum* can make is to "straighten out" Grunow's taxonomy, by making a careful examination of the specimens on which he based his opinions.

In the fourth paper included in the section on *Sargassum*, Noro and Abbott tentatively report on some species from New Caledonia and Tahiti, and indicate that the published comments on the Tahitian material by Grunow and Setchell are in need of reevaluation. As editor of this volume, I think that it is important to publish this paper in order to encourage biologists (not just phycologists) to make materials available to students of this genus. Inasmuch as New Caledonia, Tahiti, and Fiji have phycologists in residence, we solicit their interest and cooperation.

NEW SPECIES OF SARGASSUM FROM THE PHILIPPINES

Gavino C. Trono, Jr.

Abstract

Twelve new species of Sargassum are described from the Philippines. These are Sargassum dotyi, S. samarense, S. velasquezii, S. yamadae, S. balingasayense, S. yoshidae, S. abbottiae, S. sullivanii, S. bataanense, S. currimaoense, S. umezakii, and S. ohnoi.

Introduction

Twenty-eight species of Philippine Sargassum were described, illustrated, and published by me in Volume 3 (Tax. Econ. Seaweeds 3) of this series of taxonomy publications.

Of these, 13 were not assigned specific epithets because although they were thought to be new species, I had not yet compared them with other species. The materials of these taxa were taken to the Department of Botany, Faculty of Science, Hokkaido University, at Sapporo, Japan during the fourth taxonomy workshop in July 1991 for further examination. Consultations with colleagues and comparisons with *Sargassum* subgenus *Sargassum* materials deposited in the Yamada Herbarium showed that 12 of the 13 taxa are distinctly different from materials of other distantly related taxa. These 12 taxa are now being published as new species of *Sargassum*.

This paper publishes Latin descriptions to validate species recognized as new and previously listed as *Sargassum* species 1–12. References for these species are found in the third volume of this Sea Grant series and are listed specifically in the following pages.

All holotype materials are deposited in the Gregorio T. Velasquez Phycological Herbarium at the Marine Science Institute, College of Science, University of the Philippines at Quezon City (PUH).

Validation Of The Species

Sargassum dotyi Trono, sp. nov.

S. sp. No. 1. Trono, Tax. Econ. Seaweeds, vol. 3, p. 66, figs. 46–48, 98, 1992.

Hapteron conicum; caulis brevissimus; rami teretes usque compressi. Folia obovata ad lineari-lanceolata; margo foliorum integer usque subtiliter dentatus. Natantia fusiformia, costata vel anguste alata, stipite tereti vel complanato. Receptaculum cyma vel racemus; ramus receptaculi tereti-torulosus.

Holotype: T6613, collected by A. Cortez from Honduras, Puerto Galera, Oriental Mindoro, Philippines, on May 25, 1973.

Etymology: This species is named in honor of my mentor, Professor Maxwell

S. Doty of the University of Hawaii, Honolulu.

Sargassum samarense Trono, sp. nov.

S. sp. No. 2. Trono, Tax. Econ. Seaweeds, vol. 3, p. 69, figs. 49–52, 99, 1992. Hapteron discoideum; caulis teres; rami primarii leviter compressi. Folia oblongo-ovato-lanceolata; margo foliorum irregulariter serratus. Natantia ellipticooblonga, plerumque immutata ad phylocystas. Receptaculum cyma usque panicula triquetrum; alae receptaculi foliaceae, tortae, grosse serratae, phylocystis subtentae.

Holotype: T18501, collected by H. R. Montes and E. Colina from reef in Borangan, Eastern Samar, December 28, 1987.

Other Materials Examined: T18504 collected from Maydolong, Eastern Samar by H. R. Montes and E. Colina, January 29, 1988; T18505 collected by H. R. Montes from the same place, March 30, 1988.

Etymology: The species is named for its type locality.

Sargassum velasquezii Trono, sp. nov.

S. sp. No. 3. Trono, Tax. Econ. Seaweeds, vol. 3, pp. 69–72, figs. 53–55, 100, 1992.

Ramus primarius teres haptero rhizoidei. Folia oblongo-elliptica ad lanceolata; margo foliorum dentatus; cryptostomata leviter elevata. Natantia obovata dentata vel alata; stipes natantium teres usque compressus. Receptaculum cyma; ramus receptaculi teres usque compressus usque leviter triguetrus in extremitate distali.

Holotype: T12087, collected by G. T. Velasquez from San Isidro, Puerto Galera, Oriental Mindoro, April 28, 1953.

Etymology: The species is named in honor of the late Professor Gregorio T. Velasquez of the University of the Philippines at Quezon City, who first introduced me to the science of phycology.

Sargassum yamadae Trono, sp. nov.

S. sp. No. 4. Trono. Tax. Econ. Seaweeds, vol. 3, pp. 73–74, figs. 56–59, 117, 1992.

Hapteron scutatum; basis primariorum ramorum compressa. Folia linearioblonga ad lanceolata; basis foliorum asymmetrica; margo distalis foliorum ramis fertilibus serratus. Cryptostomata numerosa, elevata. Natantia oblongo-ovata, muricata. Planta dioecia; receptaculum masculinum racemoso-paniculatum. Ramus compressus apice, dentatus. Receptaculum femineum panicula densa; ramus receptaculi brevis, compressus et apice tortus, dentatus.

Holotype: T237, collected by Ang Put, Jr., from Barrio Pangil, Currimao, Ilocos Norte, May 1983.

Etymology: This species is named in honor of the late Professor Y. Yamada of the University of Hokkaido, Sapporo, Japan. Professor Yamada contributed important studies on western Pacific species of *Sargassum*.

Sargassum balingasayense Trono, sp. nov.

S. sp. No. 5. Trono, Tax. Econ. Seaweeds, vol. 3, p. 74, figs. 60–64, 101, 1992.

Hapteron scutatum; caulis verrucosus; ramus primarius apice compressus cryptostomatibus elevatis. Folia lineari-lanceolata; basis asymmetrica, dentata; margo serrati-dentatus; costa percurrens; cryptostomata elevata; vesiculae sphaericae muricatae propter cryptostomata; planta dioecia; receptaculum cyma vel racemus; ramus femineus brevis, compressus usque triquetrus, dentatus; ramus masculinus teres.

Holotype: T18502, collected by G. C. Trono, Jr., from Barrio Balingasay, Bolinao, Pangasinan, January 1983.

Etymology: This species is named for its type locality.

Sargassum yoshidae Trono, sp. nov.

S. sp. No. 6. Trono, Tax. Econ. Seaweeds, vol. 3, p. 7477, figs. 65–67, 102, 1992.

Hapteron discoideum; caulis angustatus; rami muricati. Folia coriaceo-elliptica usque oblongo-oblanceolata; verticaliter affixa; basis asymmetrica, dentata et latus eius adaxiale expansum; margo serratus; cryptostomata leviter elevata; vesiculae paucae, sphaericae alatae vel folio coronario; receptaculum cyma; ramus receptaculi teres.

Holotype: T12198, collected by G. T. Velasquez from Cabugao Bay, Virac, Catanduanes, February 22, 1962.

Etymology: This species is named for Professor Tadao Yoshida of the Department of Botany, Faculty of Science, Hokkaido University, Sapporo, Japan. Dr. Yoshida's interest in *Sargassum* species is important for the progress of studies on the genus.

Sargassum abbottiae Trono, sp. nov.

S. sp. No. 7. Trono, Tax. Econ. Seaweeds, vol. 3, p. 77, figs. 6870, 103, 1992. Hapteron discoideum; caulis brevissimus; omnes rami maxime muricati. Folia glaucescentia, verticaliter affixa, oblonga ad elliptica. Basis maxime asymmetrica, grosse dentata et latus eius expanso-alatum; margo integer usque undulatus interdum dentibus parvis. Cryptostomata pauca, parva, sphaerica vel costata; receptaculum cyma; rami receptaculorum compressi dimidio distali; dentati, torti usque triquetri margine dentato.

Holotype: T14853, collected by A. Albano and A. Gutierrez from Pulong Bakaw, Calatagan, Batangas. November 11, 1978. Other materials (T12202 and T12683) were collected from Tiwi Beach, Albay, February 5, 1962 by G. T. Velasquez.

Etymology: This species is named for Professor Isabella A. Abbott of the Department of Botany, University of Hawaii, Honolulu Hawaii, and convener/editor of the taxonomy workshops since their inception.

Sargassum sullivanii Trono, sp. nov.

S. sp. No. 8. Trono, Tax. Econ. Seaweeds, vol. 3, p. 77–78, figs. 71–74, 104, 1992.

Hapteron scutatum; caulis brevis; primarii et rami secundarii compressi; folia lineari-lanceolata; margo grosse serrati-dentatus; cryptostoma elevata; vesiculae paucae, ellipticae, simplices vel alatae; stipes vesicularum compressus, longior quam vesicula; planta dioecia; receptaculum cyma; ramus masculinus teres; ramus femineus compressus, dente magno tortus.

Holotype: T18503 (male) and isotype T18504, collected by G. C. Trono, Jr., from Palawig, Zambales, Philippines, May 27, 1985.

Etymology: This species is named after Dr. James J. Sullivan, director of the California Sea Grant College, University of California, La Jolla, California. Without his strong support and interest, the taxonomy workshops would not have been held.

Sargassum bataanense Trono, sp. nov.

S. sp. No. 9. Trono, Tax. Econ. Seaweeds, vol. 3, p. 80, figs. 75–79, 105, 1992.

Hapteron discoideo-conicum; primarii rami teretes, leviter basi muricati; folia maxime glaucescentia, tenuia lineari-oblonga usque lanceolata; margo integer; cryptostomata parva; vesiculae oblongo-ellipticae usque obovatae, aliquae apiculatae; planta dioecia; receptaculum panicula; zygo-carpica; ramus masculinus tereti-torulosus; ramus femineus compressus vel trigonus apice spinis.

Holotype: T12195, collected by A. E. Santiago from Pulong Bato, Orion, Bataan, June 13, 1970. Other materials (T12115, T12114, T12126), collected by G. T. Velasquez from Sitio Saay, Limay, and Puting Buhangin, Orion, both in Bataan, August 5, 1968.

Etymology: This species is named for its type locality, Bataan.

Sargassum currimaoense Trono, sp. nov.

S. sp. No. 10. Trono, Tax. Econ. Seaweeds, vol. 3, pp. 80–83, figs. 80–82, 106, 1992.

Hapteron scutatum; caulis brevissimus; rami primarii compressi. Folia linearia lanceolato-oblanceolata; margo integro-undulatus usque irregulariter serratus; cryptostomata distincta; vesiculae paucae elliptico-oblongae, anguste alatae dentis paucis; stipes compressus; receptaculum cyma densa; ramus cuneatus, angustus, compressus apice, latior et triquetrus, grosse dentatus vel dimidio distali lobatus.

Holotype: T18504, collected by G. C. Trono, Jr., from rocky wave-exposed reef at Pangil, Currimao, Ilocos Norte, July 16, 1985.

Etymology: This species is named for Currimao, the type locality.

Sargassum umezakii Trono, sp. nov.

S. sp. No. 11. Trono, Tax. Econ. Seaweeds vol. 3, pp. 83–85, figs. 83–85, 1992.

Hapteron discoideum, lobatum; caulis brevissimus; rami primarii e caule et haptero exorientes; rami superi leviter muricati propter cryptostomata elevata; folia parva oblanceolata; basis foliorum asymmetrica; margo serratus; cryptostomata elevata; rami ad receptacum lineari-filiformes; vesiculae numerosae, muricatae, oblongo-ellipticae; receptaculum racemus; ramus receptaculi teres et torulosus.

Holotype: T12209, collected by G. T. Velasquez from Medio Island, Puerto Galera, Oriente Mindoro, May 1, 1955. Other material (T12174), collected from Medio Island, Puerto Galera, Oriente Mindoro, May 1, 1955, by P. Payawal.

Etymology: This species is named after Professor Isamu Umezaki, recently retired from the Faculty of Tropical Agriculture, Kyoto University, Japan. Dr. Umezaki has conducted many studies on the phenology of Japanese species of *Sargassum*.

Sargassum ohnoi Trono, sp. nov.

S. sp. No. 13. Trono, Tax. Econ. Seaweeds vol. 3, pp. 85, 93, figs. 86–92, 118, 1992.

Ramus primarius compressus apice; rami plani altioris teretes, muricati; folia linearia ad elongata, simplicia aut ramosa basi vel apice, coriacea, horizontaliter affixa; costa percurrens elevata ad latus ventrale; basis spinis acutis; margo serrati-dentatus; cryptostomata parva; vesiculae sphaericae stipite brevi et compresso cum dente vel stipite longo et tereti; receptaculum racemus; ramus receptaculi brevis conicus, verrucosus.

Holotype: T12156, collected by G. T. Velasquez from Big Balatero, Puerto Galera, Oriente Mindoro, May 10, 1947. Other material (T12158), collected from Balete Cove, Puerto Galera, April 21, 1948.

Etymology: This species is named for Dr. Masao Ohno, Kochi University, Japan.

Acknowledgments

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SEVERAL SARGASSUM SPECIES (SUBGENUS SARGASSUM) IN EAST ASIA WITH FURCATELY BRANCHING LEAVES

Tetsuro Ajisaka, Tadahide Noro, Gavino C. Trono, Jr., Young-Meng Chiang, and Tadao Yoshida

Abstract

Sargassum asymmetricum Yamada is concluded to be a synonym of *S. alternato-pinnatum* Yamada from a comparative morphological study of type specimens in the Herbarium, Department of Botany, Faculty of Science, Hokkaido University (SAP), and from their descriptions. It is difficult to distinguish *S. hyugaense* Yamada from *S. salicifolioides* Yamada on the basis of their descriptions, except that *S. hyugaense* has nonspinous main branches and compressed stalks of vesicles. However, (1) a comparative morphological study of type and isotype specimens in SAP, (2) the descriptions and figures of these species given by Yamada, and (3) morphological variations of spinous main branches in the population of *S. salicifolioides* from Kushimoto suggest that these two are identical. The four species of *Sargassum* (subgenus *Sargassum*) with furcately branching leaves first described from Japan, *S. alternato-pinnatum*, *S. salicifolioides*, *S. polyphyllum* Montagne and *S.* sp. from Kushimoto, can be distinguished from one another on the basis of morphological variations.

Introduction

In the previous studies of Yendo (1907) and Yamada (1942, 1944), 13 species in the subgenus *Sargassum* from Japan were reported (Yoshida 1988). Yoshida (1988) expected that this number would be increased by succeeding studies.

In the fourth taxonomy workshop in Sapporo, we concentrated our attention on several *Sargassum* species that have furcately branching leaves, especially species from Japan. *Sargassum alternato-pinnatum* Yamada, *S. asymmetricum* Yamada, and *S. salicifolioides* Yamada were described as species (Yamada 1942, 1944) that have characteristic furcate leaves and muriculate main branches. As morphological characters of *S. asymmetricum* were not easily distinguished from those of *S. alternato-pinnatum*, Yoshida (1988) and Noro and Nanba (1990) suggested that these two species were the same entities. We checked the morphological characters of these species in detail and report the results here.

Yamada (1942, 1944) also described as a new species *S. hyugaense* Yamada, which occasionally has furcately branching leaves and main branches without spines. However, its morphological characters were not easily distinguished from those of *S. salicifolioides* except that *S. hyugaense* lacks spines, and its vesicles have compressed stalks.

In the third taxonomy workshop in San Diego, Kilar et al. (1991) reported two *Sargassum* species that have furcately branching leaves and muriculate main branches. *Sargassum polyporum* Montagne has been described from Macao, China, and *S. polyceratium* Montagne has been described from the Caribbean

Sea and the warm Atlantic Ocean. *Sargassum polyporum* has a wide distribution in the Pacific Ocean; it has been reported from the South-West Islands (Okinawa area) in Japan (Kilar et al. 1991), and from Motupore Island in Papua New Guinea (Ajisaka 1990a, 1990b). In the fourth workshop in Sapporo, we found this species from Green Island (Fig. 1) and Orchid Island (Fig. 2) in Taiwan, from Recip Ricaudy near Noumea in New Caledonia (Figs. 3 and 4), and from Yoron Island (Fig. 5) and Amami Island (Kyushu area) in Japan. In specimens from the Pacific Ocean, we can distinguish *S. polyporum* from *S. polyphyllum* J. Agardh from Hawaii (Magruder 1988). We should also compare these two species' morphological characters with those of the previously mentioned *Sargassum* species.

It is important to study the morphological variations between juvenile and matured stages in each species and the variations found in large populations for every *Sargassum* species concerned. Seasonal analysis is better. We should use statistical analysis to examine the range of variations in the morphological characters. In this chapter, we report the range of variations in the morphological characters of four species: *S. alternato-pinnatum, S. salicifolioides, S. polyporum,* and *S.* sp. from Kushimoto.



Figs. 1–5. Sargassum polyporum Montagne. Fig. 1, Specimen from Green Island, Taiwan, collected by Chiang April 28, 1980. Fig. 2, Specimen from Orchid Island, Taiwan, collected by Chiang May 11, 1971. Figs. 3,4, Specimen from Recip Ricaudy near Noumea, New Caledonia, collected by G. Valet September 1990. Fig. 5, Specimen from Yoron Island, Japan, collected by Yamada May 23, 1954 (SAP 053045).

Materials and Methods

Type specimens of *S. alternato-pinnatum* (Figs. 6 and 7), *S. asymmetricum* (Figs. 8 and 9), *S. salicifolioides* (Figs. 10 and 11), and *S. hyugaense* (Figs. 12 and 13) deposited in the herbarium of the Faculty of Science, Hokkaido University (SAP), were observed for their morphological characters. Japanese (Yamada 1942) and Latin (Yamada 1944) descriptions of these characters, some of which have been reported in English by Yoshida (1988), were compared with each other and then with the descriptions of *S. polyporum* (Kilar et al., 1991) and *S. polyphyllum* (Magruder 1988). Table 1 shows observations and measurements taken from the literature which is cited in the lines to the right of Author on the second line. These observations and measurements should be compared with those in our new descriptions, and summarized in Table 2.

The morphological variations among four species were compared in detail: *S. alternato-pinnatum* (July 11, 1990, leg. T. Ajisaka), *S. salicifolioides* (May 25, 1990, leg. T. Ajisaka), *S. species* (June 28, 1991, leg. T. Ajisaka) from Kushimoto, Wakayama Prefecture, and *S. polyporum*, (June 6, 1989, leg. T. Ajisaka) from Taketomi-jima, South-West Islands, Japan (Table 2). Two hundred leaves were measured to determine the following quantitative characters: type of branching, average number of branches, length, width, and length to width ratio. Some qualitative morphological characters were also determined. One hundred vesicles were measured to determine long and short diameters and length of stalk; qualitative morphological characters were also determined. Twenty receptacles were examined to determine their length, width, branching, and other morphological characters. Their sexualities were confirmed by using cross sections.

Description of the Morphological Variations

Sargassum alternato-pinnatum Yamada, J. Jpn. Bot. 18:559. figs. 28–29, 1942. (Figs. 14,15,22)

Synonym: *S. asymmetricum* Yamada, J. Jpn. Bot. 18:561, figs. 30–31, 1942. Holdfast discoid, up to 1.3 cm in diameter; stem terete, 5.0–7.5 mm long, 2.0– 2.5 mm in diameter, not branched, with smooth and warty surface, giving rise to three to six main branches. Main branches 23–46 cm long, terete at base, 1.5–2.0 mm in diameter, slightly compressed from lower portion, 1.8–2.8 mm to 1.8–2.2 mm wide, sometimes with short or scarce spines on the surface, sometimes with many highly branched spines, giving off spirally arranged secondary branches, laterals more densely muriculate than the main branches. Leaves linear to slender elliptical, one to three times furcate (89%) or simple (11%), averaging 1.42 times in branching; base asymmetrical to cuneate, 4.5–28.0 (mean, 15.9) mm long, 0.8– 5.0 (mean, 2.1) mm wide, 3.8–14.4 (mean, 7.8) in length to width ratio, nearly acute apices, margins dentate with teeth on the lower portion or nearly entire, midrib reaching near apex, cryptostomata disposed in one row on both sides of



Figs. 6–13. Type specimens of *Sargassum* in SAP. Figs. 6,7, *S. alternato-pinnatum* Yamada (SAP 023465), collected from Aburatsu by Nakamura in August 1940. Figs. 8,9, *S. asymmetricum* Yamada (SAP 023456), collected from Bonotsu by Nakamura in August 1940. Figs. 10,11, *S. salicifolioides* Yamada (SAP 023459), collected from Kashiwa-jima by Yamada in May 1924. Figs. 12,13, *S. hyugaense* Yamada (SAP 026469), collected from Aburatsu by Nakamura in August 1940. Scale bar in Fig. 13 = 1 cm.

the midrib or scattered. Vesicles spherical to subspherical, 2.2–5.2 (mean, 4.2) mm in long axis, 2.0–5.2 (mean, 3.8) mm in short axis, usually entire at apex or rarely crowned; stalks terete to slightly compressed, 0.8–4.2 (mean, 2.0) mm long, usually shorter than the vesicles themselves, often provided with short spines near the base.

Androgynous receptacles terete, 4.0–7.0 mm long, up to 1.0 mm in diameter, simple or forked one to two times, warty, provided with a few sharp spines here and there, cymosely to racemosely arranged.

Sargassum polyporum Montagne, Ann. Sci. Nat. Bot., ser. 2, 18:250, 1842. (Figs. 16,17,23).

Holdfast conical to discoid, up to 2.2 cm in diameter; stem terete, 8-30 mm long, and 2.0-4.0 mm in diameter, with warty surface, issuing one to eight main branches. Main branches terete, 10-42 cm long, always with spines, usually with many highly branched spines, giving off spirally arranged secondary branches; secondary branches issued at about 5 mm-intervals, up to 17 cm long, always with spines. Leaves sessile or with short petiole, petiole usually with spines, linear, narrowly spatulate, or narrowly elliptical, flat to spirally twisted, and usually one to seven times branched (35% at base to 61% at upper portion) or simple (39% at base to 65% at upper portion), leaves branching 1.27 times on average, base asymmetrical to cuneate, 2.0-48.6 (mean, 20.0) mm long, 1.6-10.9 (mean, 6.3) mm wide, 1.0-8.0 (mean, 3.2) in length to width ratio, obtuse at apices, margin dentate at the base or nearly entire, strongly undulate or straight in lateral view, midrib distinct, reaching to near apex, cryptostomata distinct, disposed in a single row on both sides of the midrib or scattered over the surface. Vesicles spherical to obovoid, 1.6-6.7 (mean, 4.9) mm in long axis, 1.5-6.2 (mean, 4.4) mm in short axis, always round at apex with no appendage; stalk terete with spines and wings, 1.0-3.4 (mean, 1.7) mm long, often shorter than the vesicles themselves.

Androgynous receptacles terete, up to 4.0 mm long, up to 0.5 mm in diameter, forked two to three times, with warty surface and no spines, cymosely or racemosely arranged.

Sargassum salicifolioides Yamada, J. Jpn. Bot. 18:555, figs. 24-26, 1942. (Figs. 18,19,24)

Synonym: S. hyugaense Yamada, J. Jpn. Bot. 18:378, figs. 7-8. 1942.

Holdfast discoid, 1.0–1.8 cm in diameter; stem terete, 4.0–9.5 mm long and 3.0–4.0 mm in diameter, with a warty surface, issuing two to four main branches. Main branches 52–74 cm long, terete to slightly compressed, 2.0–3.5 mm wide, with short spines, or scarcely spinous to no spines; secondary branches clearly distichously arranged, more strongly muriculate than the main branches. Leaves linear to slender lanceolate, one to two times forked (11%) or simple (89%), averaging 0.22 times in branching, base asymmetrical to cuneate, 6.5–62.0 (mean, 36.5) mm long and 1.8–8.6 (mean, 4.9) mm wide, 2.9–13.7 (mean, 7.5) in length to width ratio, leaf apices nearly acute, margins dentate or entire, midrib



Figs. 14–21. Sargassum specimens with furcately branching leaves in Japan. Figs. 14,15, *S. alternato-pinnatum* Yamada collected from Kushimoto by Ajisaka June 11, 1990. Figs. 16,17, *S. polyporum* Montagne collected from Taketomi-jima by Ajisaka June 9, 1989. Figs. 18,19, *S. salicifolioides* Yamada collected from Kushimoto by Ajisaka June 29, 1990. Figs. 20,21, *S.* sp. collected from Kushimoto by Ajisaka June 29, 1991.



Fig. 22. Sargassum alternato-pinnatum Yamada, collected from Kushimoto by Ajisaka June 11, 1990. a-c, Reproductive organs. d-n, Vesicles. o-y, Leaves.

reaching to near apex, cryptostomata distinct, disposed in one row on each side of the midrib or scattered; vesicles spherical to subspherical, 2.8–7.2 (mean, 5.4) mm in long axis, 2.5–6.2 (mean, 4.7) mm in short axis, always round at apices; stalk terete (77%) to compressed (23%), 1.8–13.0 (mean, 3.1) mm long, shorter than the vesicles themselves (93%) or same length as or longer than the vesicles themselves (7%).

Androgynous receptacles terete or short fusiform, 1.0–3.0 mm long, up to 1.0 mm in diameter, forked one to two times, with warty surface and no spines, cymosely or subracemosely arranged.

Sargassum sp. (from Kushimoto). (Figs. 20,21,25)

Holdfast discoid, up to 1.0 cm in diameter; stem terete, up to 9.0 mm long and up to 3.0 mm in diameter, with a warty surface, issuing up to seven main branches. Main branches 18–23 cm long, terete to quadrangular, up to 2.0 mm wide, with smooth surface and no spines, giving off spirally arranged secondary



Fig. 23. Sargassum polyporum Montagne collected from Taketomi-jima by Ajisaka June 6, 1989. a–c, Reproductive organs. d–o, Vesicles. p–v, Leaves on secondary branches. w–ae, Leaves on main branches.

branches. Leaves linear to slender lanceolate, one to three times forked (28%) or simple (72%), averaging 0.31 times in branching, base asymmetrical to cuneate, 7.0–33.0 (mean, 21.0) mm long and 2.2–8.5 (mean, 5.1) mm wide, 2.2–8.1 (mean, 4.2) in length to width ratio, leaf apices nearly obtuse, margins coarse dentate with large teeth, midrib reaching to near apex, cryptostomata disposed in one row on each side of the midrib or scattered. Vesicles spherical to elliptical, 4.0–6.8 (mean, 5.4) mm in long axis, 2.2–5.2 (mean, 4.6) mm in short axis, apices round (82%), apiculate (8%), or crowned (10%); stalk terete (18%) to compressed or leafy (82%), 2.0–8.5 (mean, 3.8) mm long, shorter than the vesicles themselves (89%) or same length as or longer than the vesicles themselves (11%).

Androgynous receptacles terete, 3.0-5.0 mm long, up to 1.0 mm in diameter,



Fig. 24. *Sargassum salicifolioides* Yamada collected from Kushimoto by Ajisaka May 26, 1990. a-d, Reproductive organs. e-l, Vesicles. m-o, Leaves. p,q, Apical portions of secondary branches show clearly distichously branchings.


Fig. 25. Sargassum sp., collected from Kushimoto by Ajisaka June 29, 1991. a,b, Reproductive organs. c-o, Vesicles. p-w, Leaves.

forked one to two times, warty, provided with sharp spines here and there, cymosely or subracemosely arranged.

Discussion

Morphological features were assessed and compared in six *Sargassum* species that previous descriptions indicated had furcately branching leaves (Table 1). *S. alternato-pinnatum* and *S. asymmetricum* have similar morphological characters. Our examinations of the type specimens deposited in SAP showed that *S. asymmetricum* has very few leaves and vesicles, but many receptacles (Figs. 8 and 9). It seems to be an older, overmature plant of *S. alternato-pinnatum*. We came to the conclusion that *S. asymmetricum* should be treated as a synonym of *S. alternato-pinnatum*, in accordance with the studies of Noro and Nanba (1990).

The morphological characters of S. hyugaense were difficult to distinguish from those of S. salicifolioides except for nonspinous main branches and compressed stalks of the vesicles (Table 1). However, we found main branches with

Graciae	C alternatio-pinnation	C commeteico	C astististist	C burneauco		·
Author	Vomade 1040 1044	Vernado 1040 1044	Variation 1040 1044	o. nyugaense Vomodo 1040-1044	S. polyporum	S. polyphynum
	Yoshida 1988		Vochida 1988	Vehida 1942, 1944 Vehida 1988	kilar at al 1001	u. u. Augului 1940 Mensider 1090
l ocality	Aburatau Jacan	Bonoton Janaa	Verhins issue		Television (Jac. 1991)	May uuti 1200
Characteristics	routated, vapall	adinad, dapai	ירמאוואפר 'קווופ' יאלאמוו	Acutation, capall	накекипт-јита, Јарал	IRWall
Holdfast	Small discold	Small disc	Small contral disc	Small rise	Conicatellacoid	Contrat-discold
Diameter	About 1 cm				the tend amount	
Stem	Terete	Terete	Tanata	Tarata	OP to ≥ dei Terrete	Up to z.o cit: Terrete
l endth	lic to 5 mm	linto 6 mm	interesting the second s	lists tem		
Dismotor						up to a cm
Utameter Main Barrat				About 3 mm		2-5 mm
Maint branch	Angulate to quadrangular	I Brete	Compressed	Compressed	Terete	Terete to slightly
	:		:			compressed
Cength	Up to 50 cm	Up to 37 cm	Up to 45 cm	Up to 50 am	Up to 42 cm	4-70 cm
Diameter	About 2 mm	2-3 mm	2-3 mm	Up to 3 mm	Up to 4 mm	0.5-4 mm
Surface	Short spines	Muriculate	Spinous muriculate	No spines	With spines—highly	With spines-highly
					branchad	branched
Secondary Branches	Spirally	Spirally	Distichously	Atternately	Alternately to spirally	Spirally
Length	Up to 25 cm		Up to 15 cm	. ~	Up to 17 cm	
Interval	1-2 cm	0.5-1 cm	1-2 cm	1.5-2.5 am	Up to 0.9 cm	. 6.
Surface	Densely municulate	Muriculate	Strongly muriculate	No spines	Stronoly muriculate	Strongly municulate
Leaves	Linear to linear-lanceolate	Linear to obtong		Long elliptical to linear	Linear, spatulate to narrowly	Narrowh oblong to
				tancentate	alintical	tancorlete linear
Phylotaxis	~	~	a1	10	1/2 or 1/3	
Branching	Furcate or simple	Furnata or simple	Eurosta or eimola	Borahi furnata	Eurosta or simolo	Eurosto su simula
					Construction of Simple	Protected of Simple One to six times
length	1-3 cm	l la to 2 cm	lin to 6 cm	3-8 cm /middle)		
þ				2-0 5 mm (Invier)		
With	1 5-3 mm	lin to 3 mm	lin to 6 mm	2-2.5 mm (middle)	10 H C	1.8 mm
				Z-B mm (lower)		
I anorth/Width Ratio	•		•	(1 . 1 14 7 . 1	3 E · 1 to 20 · 1
Base	Asymmetrical	Asummatrical	4 extremetrical	Asumotrical	desembled in the second s	
Marrito	Controls with othern teeth	Chambi shoolatek:	Aby manageration Mittadi: antino an track of home			
Mikii yiri	Usingle Will Shaip 1990	Sriarjuy, ousoiately	Nearly thruing of local at Dage		Lientare at pase-wavy or	Lentate to entire—wavy or
	ā	spinuloso-centata			straight	straight
	Contrada	Coursevacure		Acute	Cotuse	(Acute)
	to near apex	:	Percurtant	To near apex	Percurrent to apex	To near apex
Uryprostomata	One row or scattered	Une row or scanered	One row or scattered	One row along midnb	One row or scattered	One or two rows
Vesicles	Subspherical or ovate	Ovate to spherical	Spherical to slightly	Subobovoid to spherical	Spherical to abovoid	Sphericai, ovate, ellipto,
c		•	elangated	•		obovate
		Op to 4.2 mm				1-4 mm
Apex	Smooth, or rarely, sharp tip	Smooth, rarely anstate	Pointed	Smooth	Smooth	Smooth
Appendage	Aosent	2	Absent	Absent	Few spines or dentate wings	Few lateral spines or wings
÷						on lower half
CIBIK	Siightly compressed or,	erete	Terete	Compressed with dentate	Terete	Flat or compressed with
	rarely, namened	Charles as set 1	t	margin		spines or wings
Becontrolog		Shorter or, rarely, longer		Slignity Bhorier	Shorter of same as vesicle	Longer
	Armodyneus terete	Andrugynous terete	Androgymous terete	Androgynous terete	Androgynous terete	Androgynous terete
Lengu		~ <	~ 0	Up to 6 mm	Up to 4 mm	4-10 mm
				~	Up to 0.5 mm	0.8-1.5 mm
Forked	Chen	Crien .	Several times	Offen	Often	Several times
Surrace	Sharp spines	sound spines	No spines	No spines	No spines	Few spines
Arrangement	Cymose to racemose	CVIINOSIG	Cymose to subracemose	Condensed raceme	Hacemose	Clustered

Table 1. A Comparative Study of Six Sargassum Species (Subgenus Sargassum) with Furcately Branching Leaves

scarce spines on the isotype specimens (SAP 026417 and 026418). In the specimens of *S. salicifolioides* from Kushimoto, we found main branches with spines and main branches without spines in the same population. On the other hand, vesicles with little compression were not found in Figure 7 of Yamada (1942). We could not find compressed stalks of vesicles, but terete ones are common on the type specimen of *S. hyugaense* in SAP (Figs. 12 and 13). Though the type specimen (SAP 026469) from Aburatsu, Hyuga, was somewhat larger than that of the type specimen of *S. salicifolioides* (Fig. 10), we can treat both specimens as representing the ranges in variation of the two entities. As the type locality (Aburatsu) of *S. hyugaense* has been altered by harbor construction (Noro, personal communication), it is impossible to check the morphological characters in living materials. The results of our study of herbarium collections suggest that these two species are the same entity.

For four *Sargassum* species (subgenus Sargassum) that have furcately branching leaves, we can fix the range of variation of morphological characters in detail (Table 2). The data in Table 2 were obtained by examining specimens preserved in formalin/seawater rather than dried materials. The materials for each species were collected from large populations in the populations' reproductive seasons.

Using the data in Table 2, we can confirm the morphological differences among four Sargassum species and S. polyphyllum from Hawaii (data from Magruder 1988). S. alternato-pinnatum characteristically has dense spines on main and secondary branches, very small and frequently furcate branching of leaves, round apex and terete stalk with spines on vesicles, and a few spinous receptacles. S. polyporum characteristically has dense spines on main and secondary branches, broader and moderately furcate branching of leaves, round apex and terete stalk with spines or wings on vesicles, and no spines on receptacles. S. salicifolioides characteristically has moderately numerous spines and clearly distichous branching on main and secondary branches; broad and slender, scarcely furcate branching of leaves; round apex and terete or leafy stalk on vesicles; and no spines on receptacles. Sargassum sp. from Kushimoto characteristically has no spines on main and secondary branches, broader and occasionally furcate branching on leaves, round/apiculate/crowned apex and terete or leafy stalk on vesicles, and usually spinous receptacles. Finally, S. polyphyllum from Hawaii characteristically has dense spines on main and secondary branches; broad and slender, moderately furcate branching on leaves; round apex and terete or leafy stalk on vesicles; and no spines, or a few spines on receptacles.

Spacies	S atternatio-ninnatium	S polynorum	S calicitolinidae	S en	S polyophylium
Locality	Kushimoto	Taketomi-iima	Kushimoto	Kushimoto	Hawaii
Collection Date	July 11, 1990	June 6, 1989	May 26, 1990	June 28, 1991	(Magruder
					1988)
Characteristics					
Main Branches					
Spines	Dense	Dense	Moderate	Absent	Dense
Branching	Spiral	Spiral	Spiral	Distichous	Spiral
Leaves					
Branching	Frequently	Moderately	Scarcely	Occasionally	Moderately
Dimension	Small, slender	Broader	Broad, slender	Broader	Broad, slender
Vesicles					-
Apex	Round	Round	Round	Round/crowned	Round
Stark	Terete + spine	Terete and wings	Terete > leafy	Terete < leafy	Terete < leafy
Receptacles		•			•
Spines	A few	Absent	Usually	Absent	Absent/few

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Key to the four Asian Sargassum Species with Furcately Branching Leaves and S. polyphyllum from Hawaii

1.	No spines on main and secondary branches	<i>S.</i> sp.
1.	Spinous processes on main secondary branches	
	2. Terete or leafy stalk on vesicles	
	2. Leafy or terete stalk on vesicles	S. polyphyllum
З.	A few spines on receptacles	alternato-pinnatum
З.	No spines on receptacles	
	4. Moderately branching, broader dimension of leaves, and spirally	y
	branching	S. polyporum
	4. Scarcely branching, broad/slender dimension of leaves, and	
	distichously branching	S. salicifolioides

Literature Cited

- Ajisaka, T. 1990a. On one *Sargassum* sp. (subgenus *Sargassum*, Phaeophyceae) from South-West Islands. Jpn. J. Phycol. 38:97 (in Japanese).
- Ajisaka, T. 1990b. Two species of Sargassum (Fucales, Phaeophyceae), collected from Motupore Island, Papua New Guinea. Kagoshima Univ. Res. Center South Pac. Occ. Pap. 20:29–33.
- Kilar, J. A., Ajisaka, T., Yoshida, T., and Hanisak, M. D. 1991. A comparative study of Sargassum polyporum from the Ryukyu Islands (Japan) and Sargassum polyceratium from the Florida Keys (United States). In: Tax. Econ. Seaweeds 3, pp. 119–132, figs. 1–22.

Magruder, W. H. 1988. *Sargassum* (Phaeophyta, Fucales, Sargassaceae) in the Hawaiian Islands. In: Tax. Econ. Seaweeds 2, pp. 65–87, figs. 1–61.

Noro, T., and Nanba, S. 1990. Taxonomy of *Sargassum asymmetricum* Yamada and *S. alternato-pinnatum* Yamada (Phaeophyceae) from Kyushu. Jpn. J. Phycol. 38:97 (in Japanese).

Yamada, Y. 1942. Notes on *Sargassum* from the southern parts of Japan. I. J. Jpn. Bot. 18:369–381, 503–519, 553–562 (in Japanese).

Yamada, Y. 1944. Diagnoses of new *Sargassums* from Japan. Sci. Pap. Inst. Algol. Res. Fac. Sci. Hokkaido Imp. Univ. 3:1–10.

Yendo, K. 1907. The Fucaceae of Japan. J. Coll. Sci. Tokyo Imp. Univ. 21(12):1-174.

Yoshida, T. 1988. Japanese and Taiwanese species of *Sargassum* subgenus *Sargassum*. In: Tax. Econ. Seaweeds 2, pp. 5–21, figs. 1–18.

SPECIES OF SARGASSUM SUBGENUS SARGASSUM (FUCALES) WITH COMPRESSED PRIMARY BRANCHES

Tadahide Noro, Tetsuro Ajisaka, and Tadao Yoshida

Abstract

The species of *Sargassum* subgenus *Sargassum* that bear compressed primary branches are reviewed. Of a total of 10 known species of this group, five are accepted in this chapter: *S. echinocarpum, S. ligulatum, S. oligocystum, S. swartzii* and *S. wightii*. The species *S. subalatum, S. binderi*, and *S. acutifolium* are placed in the synonymy of the second, third, and fourth of the named species, respectively. The remaining two taxa, *S. berberifolium* and *S. sandei*, do not have compressed primary branches and are removed from this group, the first as a synonym of *S. cristaefolium* C. Agardh and the second as a synonym of *S. ilicifolium* (Turner) C. Agardh.

Introduction

Ten species of *Sargassum* subgenus *Sargassum* with strongly flattened or compressed primary branches are known from several districts in the Indo-Pacific area. All 10 belong to *Sargassum* series *Glomerulatae* (i.e., receptacles highly branched clusters and without sterile axes) of section *Acanthocarpicae* (i.e., receptacles not zygocarpic, usually with spines) (J. Agardh 1889, Grunow 1915, Abbott et al. 1988). Depending on the compressed nature of the main branches, this group is easily distinguished from other members of subgenus *Sargassum*. The 10 species are *S. acutifolium* Greville, *S. berberifolium* J. Agardh, *S. binderi* Sonder *ex* J. Agardh, *S. echinocarpum* J. Agardh, *S. ligulatum* C. Agardh, *S. oligocystum* Montagne, *S. sandei* Reinbold, *S. subalatum* Sonder, *S. swartzii* C. Agardh, and *S. wightii* Greville. In this study, five of these 10 species are accepted and redescribed.

Materials and Methods

Materials used in this study were collected from several sites along the coast of the Philippines, Papua New Guinea, and Australia by the authors and deposited in the herbarium of the Faculty of Fisheries, Kagoshima University, Japan.

Specimens from the following herbaria were examined: Department of Botany, Adelaide University, Adelaide, Australia (ADU); Department of Botany, James Cook University, Townsville, Australia (JCT); National Herbarium of Victoria, Royal Botanic Garden, South Yarra, Australia (MEL); National Herbarium, Royal Botanic Gardens, Sydney, Australia (NSW); Western Australia Herbarium, Department of Agriculture, South Perth, W. A., Australia (PERTH); Department of Botany, University of Western Australia, Nedlands, W. A., Australia (UWA); and Faculty of Science, Hokkaido University, Sapporo, Japan (SAP).



Fig. 1. Sargassum echinocarpum J. Agardh (Oahu, Hawaii, leg. M. S. Doty, April 11, 1959; SAP 045925).

Fig. 2. Sargassum ligulatum C. Agardh (Rottnest Island, Western Australia, Australia, leg. T. Noro, January 22, 1991; KF 1001).

Fig. 3. Sargassum oligocystum Montagne (Mactan Island, Cebu, Philippines, leg. T. Noro, January 29, 1988; KF 1002).

Fig. 4. Sargassum swartzii (Turner) C. Agardh (Magnetic Island, Townsville, Queensland, Australia, leg. K. Edyvane, June 18, 1988; KF 1003).

Key to Species of Compressed Primary Branch group of subgenus Sargassum

1.	Receptacle compressed	
1.	Receptacle terete	
	2. Receptacle compressed slightly and branching separating into two divisions	S. oligocystum
	2. Receptacle compressed strongly and branching not as	
	above; endemic to Western Australia	S. ligulatum
3.	Receptacle spinous	
З.	Receptacle not spinous; distributed in Indian Ocean	S. wightii
	4. Leaves thick and strongly dentate; endemic to Hawaii	S. echinocaroum
	4. Leaves thin and shallowly dentate	S. swartzii

Description of the Species

Sargassum echinocarpum J. Agardh, Sp. gen. ordines algarum, vol. 1, p. 326, 1848. (Figs. 1,6)

Non Sargassum echinocarpum of Greville 1848, p. 274, pl. 5.

S. oligocystum sensu De Wreede, Ecol. Sarg. Hawaii, p. 45, figs. 43–47, 50, 60, 63, 1973.

Type Locality: Hawaiian Islands (as Sandwich Islands).

Type Specimen: Herbarium Agardh, Lund.

Thallus yellow to dark brown, 0.5–1.0 m long. Holdfasts conical to discoid, 0.5–1.0 cm across, with a simple, terete stem 1 cm high, 5 mm in diameter, bearing apically and radially one to six primary branches. Primary branches 0.5–1.0 m long, axes alternately and distichously branched, strongly compressed, without spines. Laterals 3–10 cm long, 2–8 mm wide, simple, linear, costate, more or less flat and smooth with entire margins, apices acute, with scattered cryptostomata, grading to upper laterals of similar form but 2–3 cm long and 2–4 mm wide. Vesicles axillary, petiolate, subspherical, 2–5 mm in diameter, mucronate or rounded.

Reproduction monoecious. Receptacles bisexual, simple initially, becoming highly branched clusters with spines, terete to slightly compressed, 3–10 mm long, 0.5–1.5 mm wide with rounded apices. Conceptacles unisexual.

Distribution: Hawaii, Fiji, New Caledonia, Samoa, Timor, Sumatra, Tonga, Saudi Arabia, Ethiopia, Kenya, Solomon Islands, and Taiwan (for references see Magruder 1988, p. 65). Most of the reported specimens from locations other than Hawaii are probably *S. oligocystum*.

Remarks: This is the most common species of *Sargassum* in Hawaii. Magruder (1988) described the range of morphological variations in Hawaiian populations. His photographs are useful and can be used to understand this species. Leaves of this species are often similar to those of *S. oligocystum*, but receptacles are terete in *S. echinocarpum* and compressed in *S. oligocystum*. *Sargassum echinocarpum* has been previously studied by Grunow (1874, p. 6;



Fig. 5. Sargassum wightii Greville (Indies orientale, MEL 696678).

1915, p. 383), De Wreede (1976, p. 178), and Magruder (1988, p. 66, figs. 1-14).

Sargassum ligulatum C. Agardh, Syst. algarum, p. 297, 1824.

(Figs. 2,7)

Synonym: S. subalatum Sonder, Bot. Zeitung 4:51, 1845.

Type Locality: Western Australia (MEL 687516).

Type Specimen: Herbarium Agardh, Lund (No. 2405).

Thallus medium brown, 15–30 cm long. Holdfasts discoid, 4 mm across, with a simple, terete stem 5 mm high, 2 mm in diameter, bearing apically and radially one to three primary branches. Primary branches alternately and distichously branched, 15–30 cm long, axes strongly compressed, without spines. Laterals 1–3 cm long, 2–6 mm wide, simple, costate, more or less flat and smooth with shallow dentate margins, apices acute, with scattered cryptostomata. Vesicles axillary, petiolate, subspherical, 2–5 mm in diameter, mucronate or round ended.

Reproduction monoecious. Receptacles bisexual, simple and strongly compressed, 3–4 mm long, 1–2 mm wide with spinous apices. Conceptacles unisexual.

Distribution: Western Australia.

Remarks: Sargussum ligulatum is difficult to distinguish from *S. oligocystum*, but receptacles of *S. ligulatum* are more strongly compressed than those of *S. oligocystum*. More detailed morphological study is necessary for this species from Western Australia, where *S. oligocystum* and *S. ligulatum* grow together (e.g., Kalbarii). Sargassum ligulatum has been studied by J. Agardh (1848, p. 335; 1889, p. 88, pl. 26.3) Kützing 1849 p. 620) and De Toni (1895, p. 48).

Sargassum oligocystum Montagne, Voy. Pol. Sud. Bot. 1:67. 1845.

(Figs. 3,8)

Synonym: *S. binderi* J. Agardh, Sp. gen. ordines algarum, vol. 1, p. 328, 1848 (Womersley and Bailey 1970, p. 299).

Type Locality: Lampung Bay, Sumatra, Indonesia.

Type Specimen: Cryptogamic herbarium, Museum of Natural History, Paris (PC). (Not examined).

Thallus medium brown, 20–50 cm long. Holdfasts discoid, 1 cm across, with a simple, terete stem 4 mm high, 3 mm in diameter, bearing apically and radially one to five primary branches. Primary branches alternately and distichously branched, 20–50 cm long, axes strongly compressed, without spines. Laterals 2–5 cm long, 0.5–1.5 cm wide, simple, costate, with shallow dentate margins, apices acute, with scattered cryptostomata. Vesicles axillary, petiolate, subspherical, 2–7 mm in diameter, mucronate or rounded.

Reproduction monoecious (mostly) or dioecious (rare). Receptacles bisexual, divided and strongly compressed, 2–5 mm long, 1–2 mm wide with spinous apices. Conceptacles bisexual or unisexual.

Distribution: Amami-Oshima Islands; Japan; Taiwan; Southeast Asia; tropical Australia; and Solomon Islands.

Remarks: This is the most common species of *Sargassum* in the Indo-Pacific area. It has been studied by Reinbold (1913, p. 156), Grunow (1915, p. 383), Pham (1967, p. 295), Ang and Trono (1988, p. 394), Silva et al., 1987, p. 86), Modelo (1988, p. 161), and Tseng (1983, p. 234, pl. 118, fig. 1).

Sargassum swartzii (Turner) C. Agardh, Sp. Algarum, vol. 1, 11. 1820.

(Figs. 4,9)

Basionym: Fucus swartzii Turner, Fuci, vol. 4, pl. 248, 1819.

Synonym: *S. acutifolium* Greville, Ann. Mag. Nat. Hist. vol. 3, ser. 2, p. 256, pl. 10, 1849 (J. G. Agardh 1889).

Type Locality: Indian Ocean.

Isotype Specimen: MEL 696669 as isotype.

Thallus light to medium brown, 25–45 cm long, with a simple stem 2–7 mm long, terete, 1–2 mm in diameter, bearing apically and radially one to five primary branches. Holdfast discoid-conical, 5–12 mm across. Primary branches 25–45 cm long, axes strongly compressed, without spines, alternately distichously branched. Laterals 3–8 cm long, 2–8 mm wide, simple, linear, costate, and smooth with



Fig. 6. Receptacle of *Sargassum echinocarpum* J. Agardh (Oahu, Hawaii, leg. M. S. Doty, April 11, 1959; SAP 045925).

Fig. 7. Receptacle of *Sargassum ligulatum* C. Agardh (Port Denison, Western Australia, Australia, leg. E. M. Gordon, November 8, 1968; ADU A33221). Fig. 8. Receptacle of *Sargassum oligocystum* Montagne (Mactan Island, Cebu, Philippines, leg. T. Noro, January 29, 1988; KF 1002).

Fig 9. Receptacle of *Sargassum swartzli* (Turner) C. Agardh (Magnetic Island, Townsville, Queensland, Australia, leg. K. Edyvane, June 18, 1988; KF 1003). Fig. 10. Receptacle of *Sargassum wightii* Greville (Indies orientale, MEL 696678).

entire margins, apices acute, with scattered cryptostomata, grading to upper laterals of similar form 2–3 cm long and 2–4 mm wide. Vesicles axillary, petiolate, subspherical, 4–5 mm in diameter, mucronate or rounded.

Reproduction monoecious. Receptacles bisexual, terete, and verrucose, simple initially, in clusters 3–5 mm long, 1–2 mm wide with rounded apices, with spines. Conceptacles unisexual.

Distribution: Indian Ocean, China, Vietnam, and tropical Australia.

Remarks: *Sargassum swartzii* has similarities with *S. oligocystum* but the two can be differentiated. The first has thin and linear leaves with entire margins and divided smooth linear receptacles. *Sargassum swartzii* has been studied by C. Agardh (1824, p. 296), J. Agardh (1848, p. 328, 1889, p. 85, pl. 26.1), Kützing (1861, p. 6, pl. 18), Reinbold (1913, p. 157), Grunow (1915, p. 381), Setchell (1935, p. 3, pl. 1), Yamada (1942, p. 25, fig. 1), Biswas and Sarma (1950, p. 87, fig. 3), Durairatnam (1961, p. 44, pl. 9, figs. 2-10), Misra (1966, p. 176), Pham (1967, p. 293d, fig. 13), Tseng (1983, p. 238, pl. 120, fig. 1), and Modelo (1988, 183, pl. 23a–23b, pl. 35b, pl. 62a).

Sargassum wightil Greville, Ann. Mag. Nat. Hist. vol. 3, ser. 2, p. 217, 1849 (Figs. 5,10) Type Locality: Indian Ocean. Type Specimen: Holotype in Herbarium of Wight (No. 12, 13 not examined); isotype in MEL (MEL 696678).

Thallus medium brown, 30 cm long, with a simple stem 1 mm long, terete, 2 mm in diameter, bearing apically and radially seven primary branches. Holdfast probably discoid. Primary branches 30 cm long, axes strongly compressed, without spines, alternately distichously branched. Laterals 4–5 cm long, 2–10 mm wide, simple, linear and smooth with entire margins, apices acute or rounded, with scattered cryptostomata, grading to upper lateral of similar form but 2–3 cm long and 2–4 mm wide. Vesicles axillary, ovate or elliptical, 3–5 mm in diameter, often mucronate at the apex, with flattened pedicels.

Reproduction monoecious. Receptacles bisexual, simple initially, becoming furcately or laterally branched, in clusters 2–5 mm long, terete, verrucose, 0.5–0.8 mm wide, with rounded apices; ostioles scattered. Conceptacles unisexual.

Distribution: East coast of India (Biswas and Sarma 1950), Ceylon (Durairatham 1961), and Kenya (ADU A40343).

Remarks: This species is closely related to *S. swartzii*. The only difference is in the receptacles, which are strongly compressed and spinous in *S. wightii* and terete and smooth in *S. swartzii* (Durairatnam 1961). However, the isotype specimen (MEL 696678) has terete and verrucose receptacles. More detailed study on *S. wightii* from the Indian Ocean is needed. *Sargassum wightii* has been studied by J. Agardh (1848, p. 329;1889, p. 86), De Toni (1895, p. 45), Grunow (1915, p. 382), Børgesen (1933, p. 13), Biswas and Sarma (1950, p. 88), Durairatnam (1961, p. 432, pl. 8, figs. 11–18, pl. 9, fig. 1), and Chennubhotla et al. (1987, p.11, fig. 7).

Discussion

Some *Sargassum* species with compressed primary branches belong to the subgenera *Phyllotrichia*, *Bactrophycus*, and *Arthrophycus* (Womersley 1987, Yoshida 1983). However, the species dealt with in this study are restricted to the members that belong to the subgenus *Sargassum*.

Among them, *S. berberifolium* J. Agardh (1889) and *S. sandei* Reinbold (1913) are also described as having a flat primary branch. The type specimen of *S. berberifolium*, which was collected from Admiralty Islands, Western Australia, by the naturalist J. J. Labillardiere (1755–1834), was not examined. However, specimens collected from the vicinity of the type locality and determined to be *S. berberifolium* by Mueller (MEL 688656) or Lucas (Lucas collection in NSW) could not be distinguished from *S. cristaefolium* C. Agardh (1820). *Sargassum cristaefolium*, however, resembles *S. crassifolium* and these two species are not difficult to distinguish from each other when they are fresh; however, the characters used for distinction are difficult to recognize in dried specimens. Fresh leaves are thick in *S. crassifolium*, and thin in *S. cristaefolium*, and the plants are monoecious in the first species and dioecious in the second. These two are probably independent species.

A photograph of the type specimen of *S. sandei*, collected by Dr. Van Der Sande from the south coast of Flores Sea, Indonesia, and deposited in Rijksherbarium, Leiden, Netherlands [L], shows a strong resemblance to *S. ilicifolium* (Turner) C. A. Agardh (1820). The type material of *S. sandei* shows small duplicated leaves and narrow primary branches, which are included in the range of morphological variations of *S. ilicifolium*. We think that *S. sandei* should be a synonym of *S. ilicifolium*.

In conclusion, of a total of 10 known species with compressed primary branches placed in the subgenus *Sargassum*, five species are retained and described in this chapter and five are placed in synonymy or moved elsewhere.

Literature Cited

- Abbott, I. A., Tseng, C. K., and Lu Baoren. 1988. Clarification of some subgeneric nomenclature in *Sargassum* subgenus *Sargassum*. In: Tax. Econ. Seaweeds 2, pp. 55–57.
- Agardh, C. 1820. Species algarum, vol. 1. iv + 168 pp. Berling, Lund.
- Agardh, C. 1824. Systema algarum, xxxviii + 312 pp. Berling, Lund.
- Agardh, J. 1848. Species, genera et ordines algarum I. Species, genera et ordines fucoidearum ... I. viii + 363 pp. Gleerup, Lund.
- Agardh, J. 1889. Species Sargassorum Australiae descriptae et dispositate. Kgl. Svenska Vet.-Akad. Handl. 23:1–133, pls. 1–31.
- Ang, P., Jr., and Trono, G., Jr. 1988. The genus *Sargassum* (Phaeophyta, Sargassaceae) from Balibago, Calatagan, Philippines. Bot. Mar. 30:387–397.
- Biswas, K., and Sarma, S. A. K. 1950. Sargassa of Indian Seas. J. R. Asiatic Soc. Bengal Sci. 16:79–97, pls. 1–3.
- Børgesen, F. 1933. Some Indian green and brown algae, especially
- from the shores of the presidency of Bombay. III. J. Indian Bot. Soc. 12:1-16, pls. 1-5.
- Chennubhotla, V. S. K., Kaliaperumal, N., and Kalimuthu, G. 1987. Economically important seaweeds (in India). Cen. Mar. Fish. Res. Inst. Bull. 41:3–19.
- De Toni, G. B. 1895. Sylloge algarum, vol. 3. Fuciodeae. Typis Semmminarii, Padua, pp. 1–638.
- De Wreede, R. E. 1976. The phenology of three species of Sargassum (Sargassaceae, Phaeophyta) in Hawaii. Phycologia 15:175–183.
- Durairatnam, M. 1961. Contribution to the study of the marine algae of Ceylon. Fish. Res. Sta. Ceylon Bull. 10:1–117, pls. 1–32.
- Grunow, A. 1874. Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. J. Mus. Godeffroy [Hamburg] 3:23–50.
- Grunow, A. 1915. Additamena ad cognitionem Sargassorum. K. K. Zool.-Bot. Gesell. Verhandl. Vienna 66:1-48, 136-185.
- Kützing, F. T. 1849. Species algarum. 922 pp. Brockhaus, Leipzig.
- Kützing, F. T. 1861. Tabulae phycologicae, vol. 11, pp. 1–31, pls. 1–100. W. Koehne and author, Nordhausen.
- Magruder, W. H. 1988. *Sargassum* (Phaeophyta, Fucales, Sargassuceae) in the Hawaiian Islands, In: Tax. Econ. Seaweeds 2, pp. 65–87.
- Misra, J. N. 1966. Phaeophyceae in India. vii + 203 pp. ICAR, New Delhi.
- Modelo, R. B., Jr. 1988. Studies on brown algae (Phaeophyceae) of the Philippines. Doctoral dissertation. University of Kyoto, Japan.
- Pham Hoang Ho. 1967. Contribution a l'étude des algues littorales d'Vietnam I: le genre

Sargassum. Ann. Fac. Sci. Saigon pp. 259-332.

Reinbold, T. 1913. *Sargassum*. In: Weber-van Bosse, A. Myxophyceae, Chlorophyceae, Phaeophyceae. Siboga Expeditie, vol. 59a. Brill, Leiden, pp. 150–174.

Setchell, W. A. 1935. Hong Kong seaweeds. IV. Hong Kong Nat. Suppl. 4:1-24, pls. 1-17.

- Silva, P. C., Meñez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contrib. Mar. Sci. 27:178 pp. Smithsonian Institution Press, Washington, D.C.
- Tseng, C. K. 1983. Common seaweeds of China. i–x + 316 pp., pls. 1–149. Science Press, Beijing.
- Womersley, H. B. S., and Bailey, A. 1970. Marine algae of the Solomon Islands. Phil. Trans. R. Soc. London 259B:257–352.
- Womersley, H. B. S. 1987. The marine benthic flora of Southern Australia. Part II. 484 pp.
- Yamada, Y. 1942. Notes on *Sargassum* from southern parts of Japan. I and II. J. Jpn. Bot. 18:369–381; 503–519.
- Yoshida, T. 1983. Japanese species of *Sargassum* subgenus *Bactrophycus* (Phaeophyta, Fucales). J. Fac. Sci. Hokkaido Univ., Ser. 5., 13:99–246.

A TENTATIVE IDENTIFICATION OF SOME SPECIMENS OF SARGASSUM FROM THE TROPICAL SOUTH PACIFIC

Tadahide Noro and Isabella A. Abbott

Abstract

Sixteen specimens were loaned for study by Claude Payri, Université Française du Pacifique, Tahiti. Twelve of the 16 had been obtained from Gabriel Valet, Noumea, New Caledonia. The two collections were examined at the Sea Grant workshop in Sapporo and looked at further by Dr. Noro. Six species of Sargassum are tentatively identified from New Caledonia: *S. decurrens, S. howeanum* (?), *S. ilicifolium, S. oligocystum, S. polyporum,* and *S. polycystum. Sargassum mangarevense* is tentatively identified in the present Tahitian collection. What is needed is many more specimens from these two places.

Introduction

The list of identifications that follows is offered apologetically, because the small number of specimens makes identification difficult. The literature on Tahitian *Sargassum* species dates to Setchell (1926), who listed four species. He raised three of them in rank from formae recognized by Grunow (1916), who, however, had indicated that those formae might represent parts of the same species, either *S. obtusifolium* or *S. vulgare*. The latter name, however, is no longer applicable to Pacific species. Such a possible relationship has never been investigated, and until it is, the three combinations of Setchell will remain in doubt (*S. boraborense, S. sociale, and S. mangarevense*).

The large numbers of names of species in *Sargassum* in the Pacific are names proposed by Grunow (1915, 1916) on the basis of very small numbers of specimens (some taxa have only one specimen). The burden of proof therefore rests on the shoulders of current phycologists as more corners of the Pacific are explored. Previously, *Sargassum* specimens may not have been collected in the islands of the Pacific because it was thought that no one would work on them. However, with current interest on the part of many, perhaps more headway will be made in classifying this polymorphic genus. It is toward that goal that these notes are offered.

Garrigue and Tsuda (1988) published a list of 25 species of *Sargassum* from New Caledonia, mostly a compilation of earlier published materials, but also containing several name changes (probably contributed by Dr. Tsuda). All pertinent specimens should be assembled in one place, and new material should be compared with them. It would be a worthwhile project. Garrigue and Tsuda (1988) report that New Caledonia has 336 species of marine algae, representing 137 genera, and that *Sargassum* now constitutes half the species of brown algae.

Species of Sargassum from New Caledonia

Sargassum decurrens C. Agardh. No. 90–61. Collected at Recif Ricaudy. (Also mixed with No. 90–54 at the same place.) (New record.)

(?) Sargassum howeanum Lucas. No. 90–57. Collected at Recif Ricaudy. More material is needed to be certain of the identification (if correctly identified, a new record).

Sargassum ilicifolium (Turner) C. Agardh. No. 1610 (two specimens). Collected at Anse Vata. Reported by Grunow (1915).

Sargassum oligocystum C. Agardh. No. 1684. Collected at Port N'Gea. According to Garrigue and Tsuda (1988), previously listed by Catala (1950) as *S. binderi*.

Sargassum polyporum Montagne. Nos. 90–54, 90–58, and 90–59. Collected at Recif Ricaudy. New record for New Caledonia. (Identified by C. K. Tseng and T. Ajisaka.)

Sargassum polycystum C. Agardh (basal portion of plant). No. 90-55. Collected at Recif Ricaudy. Previously reported by Grunow (1915) and Catala (1950).

Two specimens of *Hormophysa triquetra* (Nos. 90–56 and 1650) were included in the collection and one specimen of *Cystoseira muricatum* (No. 90–60), all from Recif Ricaudy.

Sargassum from Tahiti

Four specimens of *Sargassum* that appear to be alike were submitted by Claude Payri from Tahiti.

Sargassum mangarevense (Grunow) Setchell. All collected May 16, 1991 by Claude Payri (without numbers): One specimen from Paea, one from Atimaono, and two from Barriere Tipaerui.

Although these specimens resemble the illustrations of Tahitian specimens of *S. mangarevense* (Setchell 1926, pl. 15, fig. 6; pl. 16, figs. 1-2), they are young and do not have all the features necessary to be certain of identification.

Acknowledgments

We thank Claude Payri for sharing her specimens with us.

Literature Cited

- Catala, R. 1950. Contribution à l'étude ecologique des îlots coralliens du Pacifique Sud. Bull. Biol. 3:234–310.
- Garrigue, C., and Tsuda, R. T. 1988. Catalog of marine benthic algae from New Caledonia. Micronesica 21:53-70.
- Grunow, A. 1915. Additamenta ad cognitionem Sargassorum. Verh. Zooł. Bot. Ges. Wien 65:329-448.
- Grunow, A. 1916. Additamenta ad cognitionem Sargassorum. Verh. Zool. Bot. Ges. Wien 66:1-48, 136-185.
- Setchell, W. A. 1926. Tahitian algae ... Univ. Calif. Publ. Bot. 12:61–142 (including pls. 7–22).

Section II. Japanese Species of Gelidium

INTRODUCTION

Bernabé Santelices

The coast of Japan is one of the world's areas with a large diversified representation of the order Gelidiales. All the currently accepted genera in the order are reported from Japan, and several genera, such as *Gelidium* and *Pterocladia*, are represented by several species along these coasts.

Many of the Japanese species of *Gelidium* and *Pterocladia* were carefully described and illustrated by Okamura (1900, 1901, 1914, 1934). However, the specimens in Okamura's herbarium did not show the degree of morphological variation commonly found in these species, and, consequently, Okamura could not draw sharp limits to designate the species. Although later authors have studied type materials in several collections (e.g., Segi 1955, 1957, 1959) or quantitatively described morphological attributes in a few populations (e.g., Akatsuka 1982, 1983), patterns of morphological variation were not established. The result is much taxonomic confusion for the Japanese species of *Gelidium* and *Pterocladia*. Thus, whereas Akatsuka (1986) reported more than 25 species of *Gelidium*, some of them with several forms, Yoshida et al. (1990) restricted the number to 19 species.

The species of *Gelidium* and *Pterocladia* from Japan have a long tradition in the seaweed trade. In fact, the technology for the preparation of agar is traced to the coast of Japan. Even though industrial expansion and pollution in recent years have decreased the quantities of *Gelidium* harvested, Japan is still a major

producer of *Gelidium*, annually providing some 3100 tons of dry matter, which amounts to 14.5% of the world production (McHugh, 1991). Therefore, taxonomic clarification of this algal group is biologically as well as economically most important.

The following contributions deal with the little understood species of *Gelidium* found in Japan. One refers to *Gelidium pacificum*, which is known from its original description only. The other refers to *G. amansii*, whose identity and taxonomic limits have been questioned in recent years. As this last species is widespread in the Sino-Japanese-Philippines subarea of the Indo-West Pacific, a critical understanding of its taxonomic status will also help delimit the taxonomic boundaries of other species of *Gelidium* in the same geographical area.

Literature Cited

- Akatsuka, I. 1982. Preliminary observations and literature analysis of morphological variability in some Japanese species of *Gelidium* (Gelidiaceae, Rhodophyta) and an evaluation of criteria used in their discrimination. Nova Hedwigia 36:759-774.
- Akatsuka, I. 1983. The morphological relationships between *Gelidium japonicum* (Harvey) Okamura and *Gelidium pristoides* (Turner) Kützing. Nova Hedwigia 38:197–207.
- Akatsuka, I. 1986. Japanese Gelidiales (Rhodophyta), especially *Gelidium*. Oceanogr. Mar. Biol. Ann. Rev. 24:171–263.
- McHugh, D. J. 1991. Worldwide distribution of commercial resources of seaweeds including *Gelidium*. Hydrobiologia 221:19–29.
- Okamura, K. 1900. Illustrations of marine algae of Japan, Vol. 1, No. 1. Keigyosha, Tokyo, pp. 1–16, pls. 1–5.
- Okamura, K. 1901. Illustrations of marine algae of Japan, Vol. 1, No. 5. Keigyosha, Tokyo, pp. 57–79, pls. 21–25.
- Okamura, K. 1914. Icones of Japanese algae, Vol. 3, No. 6. Kazamashobo, Tokyo, pp. 99–120, pls. 126–130.
- Okamura, K. 1934. On *Gelidium* and *Pterocladia* of Japan. J. Imp. Fish. Inst. 29:47–67, pls. 16–33.
- Segi, T. 1955. The species of the genus *Gelidium* from Japan and its vicinity. I. Rep. Fac. Fish. Pref. Univ. Mie 2:124–137.
- Segi, T. 1957. The species of the genus *Gelidium* from Japan and its vicinity. II. Rep. Fac. Fish. Pref. Univ. Mie 2:456–462.
- Segi, T. 1959. On the type specimens of *Porphyra tenera* Kjellman and *Gelidium amansii* Lamouroux, Rep. Fac. Fish. Pref. Univ. Mie 3:251–256.
- Yoshida, T., Nakajima, Y., and Nakata, Y. 1990. Checklist of marine algae of Japan (revised in 1990). Jpn. J. Phycol. 38:269–320.

A REASSESSMENT OF THE TAXONOMIC STATUS OF GELIDIUM AMANSII (LAMOUROUX) LAMOUROUX

Bernabé Santelices

Abstract

Originally described from Mauritius and Madagascar, *Gelidium amansii* is reputed to be the most common species of *Gelidium* in the Sino-Japanese-Philippines subregion of the Indo-West Pacific. Morphological differences observed between the original illustrations and the plants generally assigned to this species have led several authors to suggest that there might be two or more species. This study reexamined the type materials in light of the morphological and anatomical variation shown by the species in Japan. It is concluded that the number of morphological and anatomical differences between the type materials and representative Japanese specimens of *Gelidium amansii* is too small to warrant more than one species. The binomial *Gelidium amansii* should be maintained for the populations from the Sino-Japanese-Philippines region. Critical studies should be made of material from Mauritius and Madagascar, as so far only drift material has been gathered in these two locations.

Introduction

Gelidium amansii was originally described and illustrated by Lamouroux (1805, pp. 48–50, pl. 26, figs. 2–5), as *Fucus amansii*, from materials collected on the coast of lle de France and Madagascar. Later (Lamouroux 1813), the species was transferred to the genus *Gelidium*, and Lamouroux indicated "Ind. Orient." (Indes orientales), which has come to mean the general vicinity of India and Sri Lanka, as the area inhabited by this species. The same locality was reported by Kützing (1849) on the basis of Lamouroux's reports.

In 1866, Martens ascribed to this species some specimens collected in Shimoda, Yokohama, and Nagasaki in Japan, and representative materials of those collections were illustrated as *G. amansii* by Kützing (1868, p. 16, pl. 44). In this same work, on the basis of materials also collected by Martens in Yokohama, Kützing (1868, p. 18, pl. 52) described and illustrated a new species of *Gelidium: G. elegans.*

The descriptions of *G. amansii* provided by Lamouroux (1805) and Kützing (1849, 1868) were too general to characterize the species precisely or illustrate its pattern of variation. Okamura (1914) first provided a complete description of *G. amansii* and later (Okamura 1934) described the variability shown by the species in various areas and habitats of Japan. He distinguished several forms in *G. amansii* and discussed similarities and differences between *G. amansii* and other species of *Gelidium* and *Pterocladia*. Okamura (1934) recognized that the forms illustrated by Kützing (1868) as *G. elegans* were abundant in Yokohama, as reported by Martens, but also widely found in other Japanese localities. Furthermore, he indicated the existence of many intermediate forms, concluding that *G. elegans* was a form of *G. amansii*. In Okamura's time (1934), no one had a clear

idea of the occurrence or identity of the type materials used by Lamouroux. Okamura based all his interpretations on the descriptions and illustrations provided by Lamouroux (1805) and Kützing (1868, pl. 44). The type materials remained unknown until Segi (1959) described and illustrated them. Inasmuch as these materials are rather fragmentary, and because the redescription of the type did not take into consideration the morphological variation shown by the species, Segi's contribution did not clarify whether the Japanese materials corresponded to materials collected in Mauritius, and Segi did not comment on the similarities or differences of materials classified with either *G. amansii* or *G. elegans*. In a subsequent study, Segi (1963) reproduced as part of the authentic materials of *G. amansii* some individuals collected at Yokohama (Martens 1866) and used by Kützing (1868, pl. 44) to illustrate *G. amansii*.

Working with the Chinese and Taiwanese species of *Gelidium*, Santelices (1988) called attention to the climatic differences between the type locality and the Sino-Japanese subregion of the Indo-West Pacific where *G. amansii* was abundant. He also noticed morphological differences between the illustrations provided by Lamouroux (1805) and the plants generally assigned to this species in China and Taiwan. The problem was likely to be solved only after extensive studies of field variation of the species now recognized as *G. amansii* in the Sino-Japanese subregion and after reevaluation of the type materials.

The morphological and climatic differences were noted also by Norris (1990). He compared Japanese specimens of *G. amansii* identified by Dr. I. Akatsuka with photographs of the holotype specimens in the Lamouroux Herbarium (CN) and with putative fragments of the type materials found at the Herbarium of the University of California. These fragments were used to examine anatomical details of the plants. Noting differences in branching patterns and in the shape (apiculate vs. spatulate) and length of sporophylls, Norris (1990) concluded that the plants described by Lamouroux (1805) and the plants represented by the Japanese materials corresponded to different species. Accordingly, he proposed that the name *G. amansii* be restricted in its application to the original materials (i.e., Lamouroux material from Indes orientales). With respect to the populations from Japan, China, and the Philippines, he suggested that they should be recognized as *G. elegans* Kützing.

Although Norris's (1990) proposal has been followed by other authors (Yoshida et al. 1990), the highly variable morphological features used to segregate these two taxa make the separation doubtful. The thorough study of Okamura (1934) of many Japanese specimens, reexamination of these materials, and an examination of the type material of *G. amansii* in the Lamouroux Herbarium showed a substantial number of variable features that required critical study.

Materials and Methods

The specimens used in this study include the type materials in Lamouroux Herbarium now at the Laboratoire de Biologie et Biotechnologie Marines, Université de Caen; the original materials used by Okamura (1934) to typify the several forms (*typica, elegans, elatum,* and *teretiusculum*) of *G. amansii*, now at the Herbarium of the Department of Botany, Faculty of Science, Hokkaido University (SAP); and 54 other specimens of *G. amansii* collected at several places in Japan. More than 100 additional specimens at SAP were judged to adequately represent the range of morphological variation exhibited by the species. Sections were cut from the specimens with a Leitz freezing microtome, stained with 1% aqueous aniline blue, acidified, and mounted in glucose syrup.

Results And Discussion

As Okamura (1934) recognized, the morphological variation shown by the Japanese populations of G. amansii can be extreme. Four such variants are illustrated in Figures 1-4. The plant reproduced in Figure 1 (SAP 23419) is representative of the most common morphology among the materials studied. The plants can be attached by rhizomatous holdfasts that produce many upright axes 10-15 cm long. The erect axes are up to 1 mm wide and invested with many lateral branches oppositely or alternately arranged, similar in shape and appearance to the erect axes. Branches, of up to four orders, are flexuous, pinnate, sometimes pyramidal, especially in portions close to the tips, or with long and short branches mixed without order. Characteristically, however, the terminal pinnae end in sharp and acute tips, about 0.8 mm wide in subapical portions. about 0.5 cm below the tip. The appearance of some of the larger plants in the collection (e.g., SAP 47728, Fig. 2) can be essentially similar to that of the one just described, except for size and branching. The most important differences between this morphology and that illustrated in Figure 1 are the wider erect axes (up to 2.5 mm wide) and the less dense branching of the plant shown in Figure 2. Still, the plants maintain the pinnate branching pattern and the narrow, terete, acute or filiform appearance of the terminal branchlets. Normally they are deep red, but some of them have lost their red pigments and appear bleached or yellowish.

The collection contains a few individuals (SAP 27143, Fig. 3) in which the erect axes have elongated, broad (up to 2 mm) basal portions, and branching is sparse, more abundant in the apical parts of axes. Branching is essentially simple, distichous, alternate or opposite, generally of one or two orders. Terminal pinnae are narrow and elongated or filiform and can be slightly incurved at the base.

Other specimens in the collection of Japanese plants are individuals (e.g., SAP 10238, Fig. 4) up to 20 cm long, with linear axes, compressed throughout, with sparse and simple branching. These morphological characteristics were described by Okamura (1934) in the form *elatum*, but a few plants are intermediate between that form and the form *teretiusculum*. Branches are linear or filiform and of one or two orders.



Figs. 1–4. Four variants of *Gelidium amansii*. Fig. 1, (SAP 23419) shows external morphology most commonly found among the Japanese specimens examined.



5cm

Fig. 2, (SAP 47728) has wider erect axis and less dense branching compared with the specimen in Fig. 1.



Fig. 3, (SAP 27143) has an elongated, broad erect axis and sparse branching.



Fig. 4, SAP 10238 is intermediate between the form *elatum* and the form *teretiusculum* described by Okamura.



Fig. 5. Details of terminal branching in *Gelidium amansii.* (A, SAP 23419; B, SAP 47728; C, SAP 27143; D, SAP 10238).

Details of the terminal branching exhibited by different plants of *G. amansii* are shown in Figure 5. Some specimens are regularly pinnate, with distichous, elegant branching. In other plants or in other plant parts, branching can be irregular, with long and short branches mixed along the axes, with elongated, terete, almost filiform terminal pinnae. Tetrasporangial sori have been found in individuals representing all the morphological variants described previously. The sori appear as spatulate or ovate swellings at the terminal portions of branches. Depending on the length of the branchlet and the width of the swollen tip, they appear to have a long or a short pedicel or to taper gradually or abruptly. The numerous tetrasporangial branches illustrated in Figure 6 indicate that the shape of the sporophyll and the length of the pedicel are essentially variable characters in the several individuals of *G. amansii* studied. Furthermore, in a few specimens, apical



Fig. 6. Specimen of *Gelidium amansil* from SAP shows variability in shape, size, and length of fertile branches (sporophylls).

growth continued after spore production; therefore the tetrasporangial sorus was, in a few cases, found beneath the branch tip. Tetrasporangia are rounded, cruciately divided, up to $25 \,\mu\text{m}$ in diameter, and arranged without order in the sori.

Cystocarpic plants (Fig. 7) generally are well branched. Cystocarps are spherical or slightly ovato-elongated, up to 0.6 mm in diameter, subterminal beneath a simple or branched lanceolate apex.

Without detailed ecological studies of this species, one can only guess at the factors that determine the external morphological variation. Abiotic factors such as light intensity, water turbulence, and nutrients are obvious candidates. In fact, Okamura (1934) associated some of the narrowly branched forms of *G. amansii* to certain habitats such as bays (forma *teretiusculum*) or deep waters (forma *elatum*). Additional variation seemingly arises from the reproductive process. Some specimens showed soral bleaching and apical decay after tetrasporangial production. This process should produce a reduction in the number of branches after the first reproductive period. If the plants live longer than 1 year and the main axes keep growing in breadth, the thalli of second and later years should be long, with broad axes and reduced branching. This is the main difference among the plants illustrated in Figure 1 and Figure 2. A similar pattern of morphological variation derived from reproduction and longevity is known for *Pterocladia caerulescens* from Hawaii (Santelices 1978).



Fig. 7. Specimen of Gelidium amansii from SAP shows subterminal cystocarps.

Unlike the highly variable external morphology, the internal structure of *G. amansii* is rather similar in most specimens studied, although it shows some ontogenic changes.

Å cross section through narrow branches (Fig. 8) shows a cortex formed by one to four rows of pigmented cells; the most external cells are 4–6 μ m in diameter, gradually enlarging in size internally. Medullary cells are 15–30 μ m in diameter, colorless and rounded and have few intercellular connections. In narrow branches, the rhizoidal filaments are characteristically aggregated in masses disposed in the internal cortex, in the border between the cortex and the medullary tissue. A few large cortical cells often are interposed between the masses of rhizoidal filaments. The greater abundance of rhizoidal filaments in the internal cortex and the compactness of the cortical cells contrast with



50 µm

Fig. 8. *Gelidium amansii.* Cross sections from narrow branches. Half section on the left is from a Japanese specimen (SAP 23419). Half section on the right is from type material in the Lamouroux herbarium.

the loose-lying nature and the large size of the medullary cells. Therefore, when observed under low magnification, transections through these narrow branches give the impression of branches formed by two quite different types of tissue.

Thick main axes and branches, in transection, are essentially similar to narrow branches. However, the cortical tissue is less compact than in narrow branches (Fig. 9), the groups of rhizoidal filaments include proportionately more internal cortical cells, and the rhizoidal filaments are also found among medullary cells. Therefore, under low magnification, the separation between cortical and medullary tissue is not as evident as in the narrow branches.



Fig. 9. *Gelidium amansii.* Cross sections from main axes. Half section on the left is from a Japanese specimen (SAP 47728). Half section on the right is from type material in the Lamouroux herbarium.

The materials of *F. amansii* Lamouroux (CN) are kept in two folders. One contains the two herbarium sheets reproduced in Figures 10 and 12. The largest plant in Figure 10 was reproduced by Segi (1959) as the type of *G. amansii*, but two other plant fragments are included on this herbarium sheet. A comparison of the present specimen with Segi's picture suggests that the two plant fragments are fragments of branches from the large plant. All the materials reproduced in Figures 10 and 12 were selected as lectotypes by Dr. Roger Meslin, who was the curator of Chauvin's herbarium at Archiv de Botanique in Caen.

The largest plant fragment in Figure 10 seems to be the one that most resembles the illustration of what might be considered the type (Lamouroux 1805, pl. 26, fig. 2, reproduced in Fig. 11). The branching pattern and the general disposition of the plant somewhat resemble Lamouroux's illustration. However, this herbarium specimen lacks a holdfast, which was illustrated by Lamouroux. In addition, the branches in the illustration are more filiform and pointed than the branches in the herbarium specimens. The two smaller plant fragments have cylindrical axes, with sparse, distichous branching along most of the axes. Most of the branching is lost, leaving short branch remains along the axis. Both the larger plant and the fragments are yellowish brown.

The second herbarium sheet also contains several plant fragments of different sizes (Fig. 12). All have narrow, filiform branches, with pointed ends. The branching pattern and external appearance are similar to those of the plants on the other herbarium sheets, although the axes of the plants on the second sheet are

5 cm MUSEUM BORSTOIRE NATED -No Cettinian Demonster Laws 2 hypo da Gelidina Amaani - aa Piss. Fixaa : 30.57 Rosen Mertin

Fig. 10. Specimen of *Gelidium amansil* in Lamouroux's collection, now at the University of Caen.



Fig. 11. A copy of pl. 26, fig. 2 of Lamouroux (1805) that accompanies the original description of the species *Fucus amansli* (about 0.75 natural size).



Fig. 12. Specimen of Gelidium amansii in Lamouroux's collection.



Fig. 13. Materials of *Gelidium amansii* from Lamouroux herbarium. Arrows indicate sporophylls.

narrower and the fragments are greenish blue. Like the other type materials, these specimens also lack attachment structures.

Under low magnification (Fig. 13), many of the filiform branches of the plants from both herbarium sheets appear somewhat similar to elongated terete branches of *G. amansii* (compare Fig. 13 with the narrow forms in Fig. 5). Furthermore, the tetrasporangial sporophylls in the type materials (arrows in Fig. 13) appear as swollen, spatulate branches, similar to the sporophylls found in the Japanese specimens of *G. amansii*. There is little doubt that the materials in these two herbarium sheets were used by Lamouroux (1805, pl. 26) to illustrate *G. amansii*. However, the present condition of these plants does not agree in all details with Lamouroux's (1805) illustrations. As mentioned, none of the plants has any of the attachment structures illustrated by him, or the filamentous, epiphytelike cover shown on the basal portions of erect axes and branches. Even though the terminal pinnae in these plants are terete, the filiform, extremely narrowed ends in the illustrations are exaggerated with respect to the original plant. The scarcity and small size of sporophylls in the original materials contrast with those illustrated by Lamouroux (1805, pl. 26, fig. 3).

Different reasons may account for these discrepancies. The extremely narrowed tips and the filamentous attachment structure may be due to inaccurate representation. Scarcity of sporophylls may arise from losses resulting from repeated handling and study of the type materials. Differences in general appearance between the herbarium specimens and the illustrations may be associated with remounting of the plants since Lamouroux's time and losses of fragments of branches. These differences notwithstanding, the small discrepancies between the plants in the illustrations of *G. amansii* provided by Lamouroux (1805) and the materials currently recognized as the type material do not support the notion of more than one species.

The second folder in the Lamouroux herbarium contains the materials used by Lamouroux (1805) to describe G. amansii var. simplicior. The collection includes two quite different plants. One (Fig. 14) corresponds to the specimens illustrated by Lamouroux (1805, pl. 26, fig. 5). It has a few branches devoid of branchlets, similar to the two fragments of branchlets preserved around the large plant in Figure 10. Lamouroux (1805) suggested that this might represent a decaying plant rather than a different species. As numerous branch remains are found along the axis, this interpretation seems to be correct. The second sheet included in the folder contains two plant fragments (Fig. 15). The larger fragment is an individual 8 cm high; the axis is flat and erect at the basal parts and cylindrical at the terminal parts, with alternate or opposite distichous branching. The second fragment is much smaller than the first, and it corresponds to the terminal portion of a branch, with narrowed, filiform terminal pinnae. The larger individual shows morphological continuity in general appearance and branching pattern with some of the branched variants of G. amansii from Japan. On the other hand, the fragment interpreted to be a terminal branch shows morphological continuity with some of the branches of the larger plant in this folder and with the narrower, terete plants presently



Fig.14. Gelidium amansii var. simplicior illustrated by Lamouroux (1805, pl. 26, fig. 2).

recognized as type materials of *G. amansii* (Figs. 10 and 12). In passing, it was noted that all these plant fragments lack adhesive structures.

Even though the plant in this second herbarium sheet was taken from Chauvin's herbarium and returned to Lamouroux's herbarium, evidence indicates that Lamouroux considered this plant part of the materials of *G. amansii* var. *simplicior*. The illustration reproduced here as Figure 16 was found with the herbarium specimen. It was prepared by Lamouroux but it was not published in Lamouroux (1805). The similarity between the larger plant fragment and the plant shown in the illustration is great, and most likely this illustration represents the large plant fragment. It is also noteworthy that in this illustration the artist exaggerated the fillform, narrowed tips of branches and added a hapteralike structure that does not exist on the herbarium specimen.



Fig. 15. Gelidium amansil var. simplicior taken from Chauvin's herbarium and returned to Lamouroux's herbarium.

The information provided by the large specimen of *G. amansii* var. *simplicior* (Fig. 15) indicates a link between the morphological characters exhibited by the various plant fragments in the type materials of *G. amansii* and *G. amansii* var. *simplicior*. Considered together, these materials suggest a significant degree of morphological variation in the species, mainly produced by the falling off of branches in some individuals. It is not known if this reduction in the number of branches is due to bad preservation of the materials after the original gathering, losses associated with reproduction, or both. The blue-green color, already reported by Lamouroux, suggests plant decoloration. In addition, all materials lack attachment structures. It seems likely, therefore, that these materials were not attached when collected, and perhaps they formed part of the drift. If that is the case, the species perhaps does not occur attached in Mauritius or Madagascar. It is certainly interesting to realize that Børgesen (1943) did not report this species





among the 10 species of *Gelidium* in his comprehensive treatise of the flora of Mauritius, and Andrimampandry (1988) did not consider *G. amansii* among the phycocolloid-producing red algae from Madagascar. Perhaps the species does not occur in Mauritius or Madagascar, or perhaps its ecological representation in any one of these areas is reduced and restricted to deep waters. Even though photosynthesis in the Japanese populations of *G. amansii* steadily increases with increasing temperatures up to 30°C (Yokohama 1972), growth increments correlate with increasing temperature up to 20°C only (Yamada 1978), unless the species grows under nutrient-rich and low-light-intensity conditions. The species disappears or becomes reduced at temperatures higher than 25°C. In Mauritius,

the sea temperature varies from 22°C in August–September to 27°C in January– April (Hodkins and Michel 1961).

Conclusions

It is concluded that the morphological and anatomical differences between the type materials of *G. amansii* Lamouroux and the Japanese materials under this name are insufficient to warrant recognition of more than one species. The range of variation found in the Japanese populations of *G. amansii* includes the morphological characteristics shown and reported by Lamouroux in his original descriptions, but close examination shows overlap between other features as well. The proposal by Norris (1990) to restrict the name of *G. amansii* to plants collected in Madagascar and to assign the populations from Japan, China, and the Philippines to *G. elegans* is not supported by the present results. No substantial evidence from an evaluation of features used in recognizing species of *Gelidium* was found whereby these two names could be applied to different populations. Two Japanese species, *G. vagum* and *G. subfastigiatum*, are also related to *G. amansii*, and studies of their morphological variability should be made so that their differences or similarities can be assessed.

As a result of these studies, it is also suggested that the *formae* pointed out by Okamura (1934) be eliminated, as they are merely steps in the variable pattern of branching, and some of them show overlapping of characters, as shown here.

Acknowledgments

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Literature Cited

- Andrimampandry, A. V. 1988. Beckerella pterocladioides sp. nov. et Gelidium madagascariense sp. nov.: deux espèces de Gelidiales-Rhodophytes de Fort-Dauphin (Madagascar). Cryptog. Algol. 9:243–259.
- Børgesen, F. 1943. Some marine algae from Mauritius. III. Rhodophyceae. Part 2. Gelidiales, Cryptonemiales, Gigartinales. Kgl. Dansk. Vidensk. Selsk. Biol. Meddel. 19:1–85.

Hodkins, E. P., and Michel, C. 1961. Zonation of plants and animals on rocky shores of Mauritius. Proc. R. Soc. Arts Sci. Mauritius 2:121–145.

Kützing, F. T. 1849. Species algarum. Brockhaus, Leipzig. 922 pp.

Kützing, F. T. 1868. Tabulae phycologicae. Nordhausen, vol. 18, 35 pp., 100 pls.

Lamouroux, J. V. F. 1805. Dissertations sur plusieurs espèces de Fucus. xxiv + 83 pp. Raymond Nouvel, Paris.

Lamouroux, J. V. F. 1813. Essai sur les genres de la famille des Thalassiophytes non articulées. Ann. Mus. Hist. Nat. Paris 20:21–47, 115–139, 267–293.

- Martens, G. von 1866. Die Tange. In: Die Preussische Expedition nacht Ost-Asien nacht amtlichen Quellen. Bot. Theil. 152 pp., 7 pls., Berlin.
- Norris, R. E. 1990. A critique on the taxonomy of an important agarophyte, *Gelidium amansii*. Jpn. J. Phycol. 38:35-42.
- Okamura, K. 1914. Icones of Japanese algae, vol. 3. Kazamashobo, Tokyo, pp. 1–218, pls. 51–90.
- Okamura, K. 1934. On *Gelidium* and *Pterocladia* of Japan. J. Imp. Fish. Inst. (Tokyo Fish. Univ.) 29:7–67.
- Santelices, B. 1978. The morphological variation of *Pterocladia caerulescens* (Gelidiales, Rhodophyta) in Hawaii. Phycologia 17:53–59.
- Santelices, B. 1988. Taxonomic studies on Chinese Gelidiales (Rhodophyta). In: Tax. Econ. Seaweeds 2, pp. 91–107.
- Segi, T. 1959. On the type specimens of *Porphyra tenera* Kjellman and *Gelidium amansii* Lamouroux. Rep. Fac. Fish. Pref. Univ. Mie 3:251–255.
- Segi, T. 1963. The type or authentic specimens of *Gelidium* in Europe. Rep. Fac. Fish. Pref. Univ. Mie 4:509–525, pls. 1–52.

Yamada, N. 1978. Current status and future prospects for harvesting and resource management of the agarophyte in Japan. J. Fish. Res. Board Canada 33:1024–1030.

- Yokohama, Y. 1972. Photosynthesis—temperature relationships in several benthic marine algae. Proc. Int. Seaweed Symp. 7:286–291.
- Yoshida, T., Nakajima, Y., and Nakata, Y. 1990. Check-list of marine algae of Japan (revised1990). Jap. J. Phycology 38:269–320.
OBSERVATIONS ON GELIDIUM PACIFICUM OKAMURA

Bernabé Santelices and Masahiko Miyata

Abstract

The identity of *Gelidium pacificum* Okamura was evaluated by studying the type materials and other Japanese specimens and comparing the external and internal morphology of these specimens with that of representative individuals of *G. amansii* and *G. robustum*. Numerous characters segregate *G. pacificum* from *G. amansii* and *G. robustum*. Therefore, it is proposed that the epithet *G. pacificum* should be retained to designate the Japanese populations of this large-sized *Gelidium*.

Introduction

Gelidium pacificum was described by Okamura (1914) as a large, subtidal plant 30–40 cm long. In his original description, Okamura recognized that this species was morphologically related to *G. cartilagineum* Greville and could be confused with *G. amansii* (Lamouroux) Lamouroux.

At the time of Okamura's descriptions, the concept of *G. cartilagineum* included the variety *robustum* Gardner, from central and southern California (USA) and the Pacific Coast of Mexico. Size and mode of branching were thought to be the fundamental characters in which the two species differed. *Gelidium cartilagineum* var. *robustum* had a more regularly pinnate branching pattern than *G. pacificum*; its fronds were longer and more stout, and the branches were broader, thicker, and slightly narrower at the base than those in the Japanese entity.

Gelidium pacificum was distinguished from *G. amansii* (Lamouroux) Lamouroux on the basis of the former's larger frond, broader branches, and aggregated disposition, and shape of fertile ramuli. However, Okamura (1934) also indicated that *G. pacifica* and *G. amansii* could be confused with each other, although some ecological distinction might be noted. The more robust *G. pacificum* preferred habitats with strong waves and fast tidal currents, whereas the more delicate *G. amansii* preferred rather calm habitats.

Later authors have generally discussed the similarities and differences between *G. pacificum* and *G. amansii* and ignored those between *G. pacificum* and *G. robustum*. When Gardner (1927) described *G. cartilagineum* var. *robustum* from California, he noted the general similarity of the new entity to the Japanese species. Without providing supporting data, he concluded that the Californian plants were more closely related to *G. cartilagineum* than to *G. pacificum*. Later studies (e.g., Hollenberg and Abbott 1965) have clarified the relationships between *G. cartilagineum* and *G. robustum*, but no additional data have been provided on the degree of similarity between *G. pacificum* and *G. robustum*. These last two species are recognized (Hommersand 1972) as one of several cases of morphological and ecological convergence between the marine floras of central California and Japan.

The relationship between G. pacificum and G. amansii has been examined more frequently than the relationship between G. pacificum and G. robustum, but results have not been conclusive. The validity of the taxonomic limits between G. pacificum and G. robustum was doubted by Suto (1954; see also Akatsuka 1982). Width and thickness of main axes and branches were, according to Akatsuka (1982), the only reliable characters segregating the two species. However, both characters are generally variable in species of Gelidium and often are of little taxonomic value. Working with the Chinese species of Gelidium, Santelices (1988) noticed that the range of variation exhibited by G. amansii included the morphologic characteristics described for G. pacificum. Because materials of G. pacificum were not available for examination at that time, Santelices (1988) recommended additional studies to characterize the morphological variations of G. pacificum and G. robustum and to critically evaluate their taxonomic limits. However, on the basis of Suto's and Santelices's comments and without examination of additional materials, Norris (1990) recommended placing G. pacificum as a synonym of G. elegans (= G. amansii),

Materials and Methods

We examined specimens of *G. pacificum* (see Table 1) from Okamura's collection containing the plants illustrated by him (Okamura 1934, pls. 126–127, figs. 9–11) in the original description of *G. pacificum*, several other specimens collected in different places in Japan, the type specimens of the various forms distinguished by Okamura within *G. amansii* (see study on *G. amansii*), and Californian materials of *G. robustum*.

Collection No.	Date and Place of Collection	Determined by	
Okamura's collection (no number)	No date Nemoto Awa	K. Okamura	
Okamura's collection (no number)	August 26 1898 Nemoto, Awa	K. Okamura	
*SAP 020719	April 1923	Y. Yamada	
	Osenkorogashi, Awa		
SAP 020714	May 1924	Y. Yamada	
	Misaki, Sagami		
SAP 025369	May 25 1944	T. Segi	
	Misaki, Sagami		
SAP 054233	April 12 1956	N. Tazawa	
	Ohara, Chiba Prefecture		
SAP 054889	August 1931	Y. Yamada	
	Futoomi, Awa		

Table 1.	. Specimens of	Gelidium	pacificum Okamura	Considered in	This Study
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*Note: SAP = Herbarium of Faculty of Science, Hokkaido University

Results

The specimens of *G. pacificum* are 5–35 cm long; the erect axes are flattened throughout and are 2–3 mm wide. Branching can be relatively sparse (Fig. 1) or abundant (Fig. 2). When the branching is abundant, it can be up to four orders, with branches alternate or opposite along the axis. The main branches are elon-gated, flexuous, and slightly narrower than the erect axes but otherwise similar in appearance and branching pattern. Often branches of different lengths and different degrees of branching are intermixed along the same axis. However, all branches are flattened and broad. Even terminal pinnules can be up to 1 mm wide. Although the branching to another, the branches of *G. pacificum* are directed upward, sometimes with the base of the branch slightly incurved.



Fig. 1. Sparsely branched individual of *Gelidium pacificum* (Specimen from Okamura herbarium, SAP).



Fig. 2. Well-branched individual of Gelidium pacificum (SAP 025369).

Comparison of Gelidium pacificum and Gelidium amansii

The size of the plant, the size and shape of main axes and branches, the mode of branching, and the texture of the plant set *G. pacificum* among the large-sized, robust species of *Gelidium*. Therefore *G. pacificum* Okamura resembles *G. robustum* from California much more than it resembles *G. amansii*. Even the abundantly branched specimens of *G. pacificum* are different from the specimens of *G. amansii*. The axes and especially the branches of *G. pacificum* are four to five times thicker than the branches of *G. amansii*, the branching of *G. pacificum* is much sparser than that of *G. amansii*, and cooccurrence of short and long branches along a given axis is found in *G. pacificum* but never in *G. amansii*. Therefore, the most needed comparison is between *G. pacificum* and *G. robustum*. Additional data on *G. amansii* and comparison with *G. pacificum* can be found in the study on *G. amansii* in this volume.

Comparison of Gelidium pacificum and Gelidium robustum

Although *G. pacificum* and *G. robustum* externally look quite similar, a close comparison of each species shows several important differences.

Plants of *G. pacificum* often arise from a fibrous base formed by creeping axes with peglike projections disposed at such short distances that they form a discoid attachment (Fig. 2). This base can be invested with branches that confer a fibrous appearance to the holdfast. Such a fibrous attachment structure does not occur in the materials of *G. robustum* examined. In *G. robustum*, attachment is by creeping axes with peglike structures disposed at some distances one from the other and not forming a discoid holdfast.

The erect axes of *G. pacificum* are compressed throughout (Fig. 3). At lower parts of the plants (e.g., 10 cm above the disc) they are up to 3-4 mm wide and 0.4 mm thick. The erect axes of *G. robustum* are cylindrical at the base and become compressed apically. At lower parts of the plants (e.g., 10 cm above the disc), the axis is up to 4 mm in diameter.



Fig. 3. Transection through erect axes of *Gelidium pacificum* (top) and *Gelidium robustum* (bottom). See enlargements of these sections in Fig. 8.

In both G. pacificum and G. robustum, the erect axes are invested with branches. However, in the former, branching starts from the base, whereas in the latter, the lower axes often are devoid of branches. Up to four orders of branches are found in both species, and those of the first and second orders often retain the appearance of the main erect axes. In G. pacificum, the branches are distichous. alternate, or opposite, and branches of different lengths are intermingled along the axis (Fig. 4). Therefore, erect axes often lack the pyramidal appearance typical of G. robustum that results from the basalmost branches being longer than the apical branches (Fig. 4). This difference in branching pattern between the two species is observed in all orders of branches. Although in both species the branches, especially those of lower orders, are directed upward, the branching angle of G. pacificum generally is wider than that of G. robustum (Fig. 4), especially in old branches. In addition, the branches of G. robustum are clearly geniculate, whereas those of G. pacificum generally lack any geniculation (Fig. 5). In both species, branching becomes multilobed and complex when the plants are fertile. However, in G. robustum, branches generally are longer, and the number is comparatively higher than in G. pacificum (Fig. 6). Sporophylls are rounded or ovate-lanceolate in G. pacificum and elongate in G. robustum (Fig. 7).



Fig. 4. Comparison of branching pattern of *Gelidium pacificum* (left) and *Gelidium robustum* (right).



Fig. 5. Comparison of terminal pinnules in *Gelidium pacificum* (left) and *Gelidium robustum* (right).



1**cm**

Fig. 6. Comparison of congested, fertile branching in *Gelidium pacificum* (left) and *Gelidium robustum* (right).



Fig. 7. Fertile branchlets in Gelidium pacificum (left) and Gelidium robustum (right).

Both species also differ in their internal organization. A transection through a middle portion of an erect axis of *G. pacificum* (Fig. 8) shows a cortex formed by two to three rows of subcuboidal or rounded cortical cells grading into a medulla formed by large, rounded, colorless cells. Elongated rhizines (or hyphae) are numerous in the central parts of the medulla, scarce in the external medulla, and completely absent from the cortex. In *G. robustum*, the cortex has three to four layers of transversely elongated cells (Fig. 8) that also grade into globose and large medullary cells. However, elongated rhizines are scarce. They are generally found in the medullary tissue (slightly more abundant in the central than in the external medulla), and are absent from the cortex. Intercellular connections among medullary cells are especially abundant in *G. robustum*.

Conclusions

The results of our study show that *G. robustum* and *G. pacificum* are two distinct species and support Okamura's decision (Okamura 1914) to segregate the Japanese population from the Californian populations. Size and gross external morphology support Hommersand's idea (Hommersand 1972) of morphological convergence for these two species of *Gelidium* that live along the rims of the Northern Pacific. However, evidence of numerous external and internal interspecific differences suggests that additional comparative studies are needed to determine patterns of morphological or ecological convergence in the genus *Gelidium*.

The morphological analysis of *G. pacificum* indicates that it is externally and internally quite different from *G. amansii* (see study on *G. amansii* in this volume). Internal and external morphological differences are so obvious that these two species can be distinguished from each other almost on the basis of qualitative characters. Therefore, the proposal by Norris (1990) to designate *G. pacificum* as a synonym of *G. amansii* is not supported by our results. The epithet *G. pacificum* should be retained to designate the Japanese populations of this large-sized *Gelidium*.

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Literature Cited

Akatsuka, I. 1982. Preliminary observations and literature analysis of morphological variability in some Japanese species of *Gelidium* (Gelidiaceae, Rhodophyta) and an evaluation of criteria used in their discrimination. Nova Hedwigia 36:759–774.
Gardner, N. L. 1927. New species of *Gelidium* on the Pacific Coast of North America. Univ. Calif. Publ. Bot. 13:273-318. pls. 36–54.



Fig. 8. Transections through middle portions of erect axes of *Gelidium pacificum* (above) and *Gelidium robustum* (below).

- Hollenberg, G. J., and Abbott, I. A. 1965. New species and new combinations of marine algae from the region of Monterey, California. Can. J. Bot. 43:1177–1188.
- Hommersand, M. 1972. Taxonomic and phytogeographic relationships of warm temperature marine algae occurring in Pacific North America and Japan. Proc. Int. Seaweed Symp. 7:66–71.
- Norris, R. E. 1990. A critique on the taxonomy of an important agarophyte, *Gelidium amansii*. Jpn. J. Phycol. 38:35–42.
- Okamura, K. 1914. Icones of Japanese algae. Vol. 3. Kazamashobo, Tokyo, pp. 99–120, pls. 126–130.
- Okamura, K. 1934. On *Gelidium* and *Pterocladia* of Japan. J. Imp. Fish. Inst. 29:47–87, pls. 16–33.
- Santelices, B. 1988. Taxonomic studies on Chinese Gelidiales. In: Tax. Econ. Seaweeds 3, pp. 91–107.
- Suto, S. 1954. Tengusa no zshoku. Suisan Zshoku Sho. 8:53 plus 4 pp. of corrections.

SOME SPECIES OF *GELIDIUM* (GELIDIALES, RHODOPHYTA) FROM KOREA

Hae-Bok Lee

Abstract

Six common species of *Gelidium—G. amansii* (Lamouroux) Lamouroux, *G. crinale* (Turner) Lamouroux, *G. divaricatum* Martens, *G. pusillum* (Stackhouse) Le Jolis var. *cylindricum* Taylor and var. *pacificum* Taylor, and *G. vagum—*from Korea were identified, and morphological and anatomical studies were done. The Asian plants identified as *G. amansii* include a nomenclatural problem with respect to the type material originally designated by Lamouroux. The two varieties of *G. pusillum* (var. *cylindricum* and var. *pacificum*) are reported for the first time from Korea.

Introduction

Korean plants of Gelidium were first mentioned by Cotton (1906) with records of G. australe (non J. Agardh = G. amansii f. teretiusculum) and G. latifolium. Later, Okamura (1915) reported G. amansii from the east coast of Korea. Kang (1956) reported two forms of G. amansii, f. typica (= f. amansii) and f. elegans from the east coast of Korea, and later added five species, G. amansii, G. divaricatum, G. pusillum, G. pacificum, and G. vagum, in his paper (Kang 1966) on the distribution of marine algae in Korea. Lee and Kim (1977) reported G. crinale in their study of marine flora, and Sohn and Kang (1978) described nine species of Gelidium, adding three taxa recorded for the first time in Korea. More recently, Lee and Kang (1986) listed a total of nine species and two forms of Korean Gelidium, and Lee (1988) described six species from Cheju Island, adding two newly listed taxa. Consequently, the Korean taxa of Gelidium reported so far include three forms, one variety, and 13 species: G. latifolium (Cotton 1906), G. amansii (Okamura 1915, Kang 1966), G. amansii f. amansii (Kang 1966), G. amansii f. elegans (Kang 1956), G. amansii f. teretiusculum (Cotton 1906, Okamura 1934), G. corneum var. pinnatum (Lee 1988), G. crinale (Lee and Kim 1977) G. decumbens (Lee and Kang 1986), G. divaricatum (Kang 1966), G. johnstonii (Sohn and Kang 1978), G. microphysa (Sohn and Kang 1978), G. pacificum (Kang 1966), G. pusillum (Kang 1966), G. sesquipedale (Lee 1988), G. tenue (Sohn and Kang 1978), and G. vagum (Kang 1966).

Other species of Gelidiales reported from Korea besides *Gelidium* are *Acanthopeltis japonica*, *Pterocladia capillacea*, *P. densa*, and *P. robusta*. As the morphological variation of the *Gelidium* plants is so great and the definition of a species among morphologically similar species is not distinct, the nature and number of *Gelidium* species in Korea are still not clear. One of the difficulties is that the type materials of most of the reported species are not kept in Korea, and the repeated use of names in the literature without examination of original material adds to the uncertainty of identification. Even the use of the name *G. amansii*, supposedly the most common species in Asia, is controversial (Santelices 1988,

Norris 1990). In this study, as a first step for the taxonomy of Gelidiales in Korea, six species of *Gelidium* were investigated. Further field (ecological) and laboratory studies will be needed to adequately circumscribe the taxa.

Description of the Species

Gelidium amansii (Lamouroux) Lamouroux, Ann. Mus. Hist. Nat. 20:129, 1813. Baslonym: Fucus amansii Lamouroux, Diss. Fucus, p. 48, 1805.

Plants are attached on rocks in the intertidal belt by fibrous, stout, linear rhizoids that bear many compressed erect branches 8–15 cm high and 1.0–2.5 mm wide. Erect axes are branched three to four times pinnately in alternate to, rarely, opposite manner and invested with lateral branches with a shape similar to that of erect axes. Lateral branches are long below and gradually shorter above; they are issued at 2- to 3-mm intervals and form an axis monopodially in the upper part of the frond. Terminal pinnae are subterete and long, gradually acute apically (Fig. 1).



Fig. 1. Dried specimens of Gelidium amansii (Lamouroux) Lamouroux from Namhae Island, south coast of Korea. A female gametophyte collected on November 3, 1991 (top), and a vegetative thallus collected on April 15, 1991 (bottom). In transverse section, erect axes in the middle parts of fronds are composed of a cortex and a medulla (Fig. 2). Cortices consist of four to five layers of cells that gradually become larger toward the center of the structure. The cells in the first and second layers (nearest the surface) are 4–6 μ m wide and spherical; those in the third and fourth layers are periclinally elongate, 7–16 μ m wide, 4–7 μ m long, and elliptical; and those in the fifth layer are of various sizes and spherical. Cortical cells in the apical portion are 4.5–5.0 μ m wide, 12–14 μ m long, anticlinally elongated, and elliptical. Secondary pit-connections occur frequently inside the third layer of cells. The thickness of the medulla is 70–80% the thickness of the thallus. Medullary cells are spherical, elliptical, or stellate, up to 12–30 μ m in diameter, with thick walls.

In longitudinal section, apical cells are 7–8 μ m in diameter, spherical, and divided into an upper dome-shaped cell and a lower cell that produces two pericentral cells. In surface view, the outermost cortical cells in the middle of the frond are 4–7 μ m wide, 5–8 μ m long, elliptical to ovoid, and arranged in lines (Fig. 4). Rhizoidal filaments are densely aggregated longitudinally in the innermost part of the cortex and the outer part of the medulla at midfrond (Fig. 3) and in the central part of the medulla in the lower part of the frond. They arise from the fourth to fifth layer of cortical cells. Filaments develop downwards only in erect fronds and in all directions in holdfasts.

Cystocarps are borne on ultimate branchlets with one or two acuminate ends; are elliptical, 250–400 μ m wide and 400–600 μ m long, and have a bilocular internal structure. Carposporangia are ovate, 40–55 μ m long and 10–15 μ m wide. Spermatangial mother cells develop from outermost cortical cells and cut off a single triangular to spherical spermatangium. Tetrasporangial branches are spatulate to clavate, up to 500 μ m long and 300 μ m wide. Tetrasporangia arise



Figs. 2-4. Vegetative structures of *Gelidium amansii*. Fig. 2, A transverse section of an erect axis. Fig. 3, A longitudinal section of an erect axis. Fig. 4, Surface view of outermost cortical cells.

from the fourth to fifth layer of cortical cells and are elliptical, cruciately divided, $25-35 \ \mu m$ wide, and $40-55 \ \mu m$ long.

Distribution: The plants identified as *G. amansii* are distributed along all the coasts of Korea. *Gelidium amansii* is the most abundant of the *Gelidium* species, especially on the south coast and Cheju Island. The plants grow on rocks well exposed to the sun in inter- to subtidal zones with clear seawater.

Remarks: Okamura (1934) divided Japanese plants of *Gelidium amansii* into four forms—f. *typica* (= *amansii*), f. *elegans*, f. *elatum*, and f. *teretiusculum* reducing Kützing's (1868) *G. elegans* as a form. Santelices (1988) pointed out that Chinese plants of *G. amansii* were different from the illustrations of ones described originally by Lamouroux (1805). Norris (1990) suggested that the Japanese *G. amansii* should bear the name *G. elegans* Kützing and that *G. amansii* should be restricted to Madagascar specimens. Yoshida et al. (1990) accepted the suggestion and changed the name of Japanese *G. amansii* to *G. elegans* in their list of Japanese algae. The final decision on the entity of east Asian plants currently adopted as *G. amansii* should await further comparative studies. The Korean plants so far are basically similar to Japanese "*G. amansii*."

Gelidium crinale (Turner) Gaillon, Thalassiophytes. Dictionnaire des Sciences Naturelles [LeVrault], 53, p. 362, 1828.

Basionym: Fucus crinalis Turner, Fuci...vol. 4, p. 4, pl. 198, 1819.

Plants are purple-red, cartilaginous, up to 5 cm high, composed of creeping and erect cylindrical axes, and attached to the substratum by conical holdfasts. Erect axes are cylindrical, narrow and without branches below, 400–600 μ m in diameter, and acute at the ends. Imbrications of segments are common. Branches are patent and pinnate for three to four times in alternate to, rarely, opposite manner and not in one plane (Fig. 5).



2 cm

Fig. 5. A vegetative thallus of *Gelidium crinale* (Turner) Lamouroux collected on the west coast of Korea on November 15, 1986. In transverse sections erect axes consist of a cortex and a medulla (Fig. 6). Cortices are red and 70–80 μ m thick and consist of five layers of cells that gradually become larger toward the center. The cells in the outermost layer are anticlinally elongate, ovoid to elliptical, and 7 μ m long. Cells in the second layer are ovoid to square and 6 μ m in diameter; those in the third layer are ovoid to spherical and 12 μ m in diameter; and those in the fourth to fifth layers are ovoid to elliptical and 16 μ m in diameter, with cytoplasmic connections. Medullary cells are round, 12–20 μ m in diameter, with thick walls. Rhizoidal filaments are long, 4–6 μ m thick, densely aggregated around the peripheral part of the medulla, and arranged mostly longitudinally.

In longitudinal sections of erect axes, the outermost cortical cells are anticlinally elongate, ovoid to elliptical, and 6–8 μ m long; the innermost cortical cells are periclinally directed, elliptical to cylindrical, and 20–26 μ m long. Medullary cells are longitudinally cylindrical and up to 160 μ m long, but mainly 50–70 μ m long (Fig. 7). The thickness of the medulla is 60–70% the breadth of thalli in the middle parts of fronds. In surface view, the outermost cortical cells are polygonal, 4–6 μ m wide, and 5–8 μ m long (Fig. 8) and are arranged in several lines. Reproductive organs are not observed.

Distribution: Plants of *G. crinale* are rarely observed in Korea and until now have not been reported in areas other than the west and south coasts.

Remarks: Materials examined in this study are all vegetative plants. Unlike the Japanese plants (Okamura 1934), they have scarcely compressed fronds and do not have two or three branches arising from the same place (glomerate). They are characterized by cylindrical erect axes; absence of branches at lower axes; and mainly longitudinal, but partially interlacing, rhizoidal filaments. Further study and observation of reproductive organs will be needed to clarify the characteristics and status of Korean plants.



Figs. 6–8. Vegetative structures of *Gelidium crinale* (Turner) Lamouroux. Fig. 6, A transverse section of the middle part of a frond. Fig. 7, A longitudinal section of the middle part of a frond. Fig. 8, Surface view of outermost cortical cells.

Gelidium divaricatum Martens, Preuss. Exped. Ost-Asien, p. 30, 1868.

Plants attach to and are prostrate on rocks in the upper intertidal belt. Many plants fuse to form entangled mats on a substratum, with small conical holdfasts issuing at contiguous points. Thalli are purple-red, cartilaginous, and 0.5–1.5 cm high. They have cylindrical to subcylindrical creeping axes 400–700 μ m in diameter and lateral branches 200–500 μ m wide, and 0.2–3.0 mm long. The lateral branches arise from the axes at almost a right angle, are long below and short above, and branch pinnately one to two times in opposite to alternate manner, not in one plane. Apices are round and slightly inflated or attenuate (Fig. 9). In longitudinal sections, holdfasts consist of rhizoidal filaments, which are compact and longitudinally elongate, issuing from cortical and medullary cells of lower fronds.

In transverse sections, creeping axes are composed of a cortex and a medulla (Fig. 10). Cortices are red and 50–75 μ m thick. They consist of four layers of cells that gradually become larger toward the center of the structure. The cells in the outermost layer are anticlinally long, ovoid to oblong, 4–6 μ m wide, and 6–10 μ m long. In the innermost layer, cells are lobed and 6–14 μ m in diameter. The thickness of the medulla is 40–60% the breadth of the thalli. Medullary cells are irregularly elongate, with three to four side arms, and sparse. Rhizoidal filaments are derived from cortical and medullary cells, are 2–4 μ m thick, and are arranged densely in all directions.

In longitudinal sections of the middle parts of fronds, the cortical cells are anticlinally elongate in the first to second layers and longitudinally elongate in the third to fifth layers (Fig. 11). Cortical cells become gradually longer toward the center of the cortex. Inner cortical cells are 6–9 μ m wide, and 10–40 μ m long. In surface view, outermost cortical cells are ovate to elliptical, 3–5 μ m wide, and 4–8 μ m long, and irregularly arranged (Fig. 12). The apical cell is single and triangular. The outermost cortical cells near the apex are long and cylindrical, 2–3 μ m wide, and 7–10 μ m long. Cystocarps are ovate to spherical, 450–650 μ m in diameter, frequently stalked, constricted at the base, ostiolated on both surfaces, and developed on ultimate branches. Tetrasporangia form sori on ultimate pinnae in compressed clavate form and are derived from the fourth to fifth layer of cortical cells. Tetrasporangia are long, elliptical, cruciately divided, 25–35 μ m wide, and 50–60 μ m long.

Distribution: The plants commonly grow on rocks in the upper intertidal belt together with *Caulacanthus okamurae* along all the coasts of Korea.

Remarks: Zonate tetrasporangia observed in Chinese plants (Santelices 1988) were not found. The Korean plants are characterized by creeping small fronds, cylindrical to subcylindrical axes with interlacing rhizoidal filaments in all directions, and divaricate pinnae.

Gelidium pusillum (Stackhouse) Le Jolis, Mem. Soc. Imp. Sci. Nat. Cherbourg 10, p. 139, 1863.

Basionym: Fucus pusillus Stackhouse, Nereis Britannica, vol. 3, p. 17, 1801.



Figs. 9–12. A vegetative thallus of *Gelidium divaricatum* Martens. Fig. 9, A general habit of a thallus. Fig. 10, A transverse section of a creeping axis. Fig. 11, A longitudinal section of a creeping axis. Fig. 12, Surface view of outermost cortical cells.

Gelidium pusillum var. *cylindricum* Taylor, Allan Hancock Pac. Exped. 12, p. 154, 1945.

Plants are purple-red, cartilaginous, up to 2 cm high, and attached to substratum by means of conical holdfasts, forming a mat of small bushes. Thalli consist of creeping and erect axes. Creeping axes are cylindrical and 180–320 μ m in diameter. They produce small holdfasts downward or adventitiously at irregular intervals and many erect axes densely upward (Fig. 13). Fronds branch pinnately three times in opposite, alternate, or, rarely, secund manner, not in the same plane. Erect axes are narrow and cylindrical below and above, but compressed and slightly broad in midfrond, where they are 110–150 μ m thick, and 200–500 μ m wide. Imbrications of segments are common. Upper parts of thalli are slender, elongate, and winding here and there, frequently forming a bush with many divaricate branchlets. Apices are normally attenuate.

In transverse sections, erect axes consist of a cortex and a medulla (Fig. 14). Cortices are red and 25–30 μ m thick and consist of three layers of cells. Cells in

the outermost layer (nearest the surface) are anticlinally elongated, ovoidal, elliptical or rectangular, and 6–10 μ m long. Cells in the second and third layers are periclinally elongate and 6–10 μ m long. Medullary cells are round, 10–16 μ m in diameter, with hyaline thick walls. Rhizoidal filaments are 4–5 μ m thick and dispersed around medullary cells.

In longitudinal sections of erect axes, cells in the outermost layer of the cortex are ovoid to cylindrical, 6–8 μ m long, and anticlinally elongated. Cells in the second and third layers of the cortex are ovoidal to irregularly globose, elongated periclinally, and 6–16 μ m long (Fig. 15). Medullary cells and rhizoidal filaments are very long and run periclinally in a bundle. In longitudinal sections, holdfasts consist of dense and longitudinal rhizoidal filaments derived from cortical cells. The thickness of the medulla is about 50% the breadth of the thalli in the middle parts of fronds, about 70% in creeping axes, and about 45% in the upper part of fronds. In surface view, cortical cells are irregularly arranged, ovate to elliptical, 5–7 μ m wide, and 6–11 μ m long, with thick walls (Fig. 16).



Figs. 13–16. A vegetative thallus of *Gelidium pusllum* var. *cylindricum* Taylor, Fig. 13, A plant from the east coast of Korea. Fig. 14, A transverse section of an erect axis. Fig. 15, A longitudinal section of erect axis. Fig. 16, Surface view of outermost cortical cells.

Cystocarps were not observed. Tetrasporangia develop from the third to fourth layer of cortical cells in ultimate branches in sori. Tetrasporangia are ovoid to elliptical, divided cruciately or irregularly, 20–35 μ m wide, and 45–60 μ m long.

Gelidium pusillum var. pacificum Taylor, Allan Hancock Exped. 12, p. 153, 1945.

Plants are purple-red, cartilaginous, up to 1 cm high, and 200–450 µm wide at the widest part. They attach to the substratum by means of conical holdfasts, forming matted bushes. Thalli are composed of creeping and erect axes. Creeping axes are cylindrical and 150–200 µm thick; they produce long conical holdfasts adventitiously downward at regular intervals and many erect axes densely upward (Fig. 17). Erect axes are narrow and cylindrical below, compressed and linearly oblanceolate to lanceolate above, with obtuse, acute, or cylindrical and long attenuate ends. Imbrications of segments are common. Fronds branch two to three times, mostly in the lower portions, in alternate, subdichotomous, or opposite manners. Regeneration of thalli is frequent, producing simple, dichotomous, or trichotomous branches.

In transverse sections, erect axes consist of a cortex and a medulla (Fig. 18). Cortices are red and 20–25 μ m thick and consist of three layers of cells. Cells in the outermost layer (nearest the surface) are spherical, ovoid, or rectangular, 6–8 μ m long. Cells in the second and third layers are periclinally elongated, ovoid to elliptical, 5–8 μ m wide, and 10–13 μ m long, with hyaline walls. Medullary cells are round, thick walled, and 10–14 μ m in diameter. Rhizoidal filaments are 3–4 μ m thick and restricted to medulla.

In longitudinal sections of erect axes, the outermost cortical cells are spherical, ovoid to rectangular, and 5–7 μ m long. Cells in the second to third layers of the cortex are periclinally elongate, ovoid, elliptical to cylindrical, and 8–22 μ m long. Holdfasts consist of dense and longitudinal rhizoidal filaments derived from cortical cells in lower fronds. Medullary cells and rhizoidal filaments are very long and run periclinally in a bundle (Fig. 19).

The thickness of the medulia is about 35% of the thickness in middle parts of fronds, more than 50% in cylindrical parts of creeping axes and lower erect axes, and about 40% in compressed upper parts of fronds. In surface view, cortical cells are irregularly arranged, 5–7 μ m wide, and 6–10 μ m long (Fig. 20). Reproductive organs were not observed.

Distribution: Plants of *G. pusillum* var. *pacificum* are distributed along all coasts of Korea.

Remarks: *Gelidium pusillum* was first reported without mention of the infraspecific taxa in Korea (Kang 1966, Sohn and Kang 1978). However, Lee (1988) recognized f. *foliaceum* Okamura from Cheju Island. In the present study, two varieties of *G. pusillum* were added, and they compare well with var. *cylindricum* Taylor and var. *pacificum* Taylor, as described by Santelices (1988) in a study of Chinese materials.

Korean plants of G. pusillum var. pacificum are characterized by conical



Figs. 17–20. A vegetative thallus of *Gelidium pusillum* var. *pacificum* Taylor. Fig. 17, A plant from Cheju Island, Korea. Fig. 18, A transverse section of an erect axis. Fig. 19, A longitudinal section of an erect axis. Fig. 20, Surface view of outermost cortical cells.

holdfasts at regular intervals on creeping axes, fronds that are cylindrical in lower parts but compressed in middle to upper parts, and rare branches arising mainly at lower parts of plants.

Plants of *G. pusillum* var. *cylindricum*, on the other hand, distinctively have holdfasts at irregular intervals. The erect axes are cylindrical in the lower parts of fronds, somewhat compressed in the middle parts, and cylindrical to compressed in the upper parts. Santelices (1988) mentioned that the erect axes of the Chinese plants of *G. pusillum* var. *cylindricum* consisted of many imbricate segments, which were not observed in other varieties of the species. The plants examined in the present study, however, did not have many imbricate segments. Truncate apices and imbricated segments are common among many species of Korean *Gelidium*.

Gelidium vagum Okamura, J. Imp. Fish. Inst. 29:58, 1934.

Plants attach solitarily to rocks in the intertidal belt by means of fibrous rhizoids and are up to 9 cm high. Plants are cartilaginous and purple-red and have

short, cylindrical stipes below. Branches are pinnate four to six times, compressed linearly, 0.8–2.0 mm wide at the widest part of the middle of the frond, abruptly becoming narrow at upper parts of main axes and forming thin, cylindrical, long ultimate branchlets (Fig. 21). Several fibrous rhizoids develop from the lower part of the stipe. Main axes are distinct or not and branch pinnately in alternate to opposite manner at an acute angle. The first lateral branches are long below and short above. They are broad and compressed, sometimes narrow and cylindrical to subcylindrical distally, curved adaxially. Branchlets often develop from surfaces of compressed middle parts of a frond. Apices are acute.

In transverse sections, main branches in the middle part of a frond are com-



Fig. 21. Female reproductive thalli of *Gelidium vagum* Okamura collected at Jumoonjin, the east coast of Korea, July 25, 1987.

posed of a cortex and a medulla (Fig. 22). Cortices are red and 60–70 µm thick and consist of four to five layers of ovate to elliptical cells that gradually become larger toward the center of the structure. The cells in the outermost layer (nearest the surface) are anticlinally elongated, ovate to rectangular, 4–6 µm wide, and 5–10 µm long. The cells in the innermost layer are ovoid, 15 µm wide and 24 µm long. The thickness of the medulla is about 50–60% of the thickness of the thalli. Medullary cells are spherical to ovoidal, 15–35 µm in diameter, and thickly walled. Rhizoidal filaments are derived from inner cortical cells and medullary cells, are 3-5 µm thick, and are grouped at the central part of the medulla, gradually becoming thickened toward the bottom part.

In longitudinal sections, medullary cells are long and cylindrical, with pitconnections at both ends, and 70–330 μ m long (Fig. 23). In surface view, outermost cortical cells are 4–6 μ m wide, and 6–10 μ m long, polygonal with thick walls, and arranged in several lines (Fig. 24).



Figs. 22–24. Vegetative structures of *Gelidium vagum* Okamura. Fig. 22, A transverse section of an erect axis. Fig. 23, A longitudinal section of an erect axis. Fig. 24, Surface view of outermost cortical cells.

Cystocarps are developed on the upper parts of ultimate branches that have acute ends. The cystocarps are long, stalked, spherical to elliptical, 300–400 μ m in diameter, with ostioles on both surfaces. Tetrasporangia are derived from the fourth to fifth layer of cortical cells and form sori on ultimate branchlets. They are ovoid to elliptical, cruciately divided, 30–40 μ m wide, and 50–60 μ m long.

Distribution: Plants of this species are distributed along all the coasts of Korea, including Cheju Island.

Remarks: Tetrasporangia of this species are normally divided cruciately. However, some of the materials investigated also have tetrahedral tetrasporangia. An ultimate branch develops a single cystocarp. Unicellular hairs, 3–4 μ m thick and about 100 μ m long, frequently arise from superficial cortical cells. In the Korean plants, branchlets rarely arise from surfaces of compressed parts in the middle of fronds, and abruptly narrowing branches arise from erect axes at the second to fourth pinnae.

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Literature Cited

Cotton, A. D. 1906. Marine algae from Corea. Kew Bull., pp. 366-373.

- Kang, J. W. 1956. Unrecorded species of marine algae in Korea. Bull. Pusan Fish. Coll. 1 (1):33–45.
- Kang, J. W. 1966. On the geographical distribution of marine algae in Korea. Bull. Pusan Fish. Coll. 7 (1,2):1–125, pls 1–12.
- Kützing, F. T. 1868. Tabulae phycologicae. Nordhausen, vol. 18, 35 pp., 100 pls.
- Lamouroux, J. V. F. 1805. Dissertations sur plusiers espèces de Fucus peu connues ou Nouvelles ... 83 pp., 36 pls. Raymond Nouvel, Paris.
- Lee, I. K., and Kim, Y. H. 1977. A study on the marine algae in the Kwang Yang Bay. 3. The marine flora. Proc. Coll. Nat. Sci. SNU 2 (1):113-153.
- Lee, I. K., and Kang, J. W. 1986. A check list of marine algae in Korea. Korean J. Phycol. 1 (1):311-325.
- Lee, Y. P. 1988. Taxonomic studies on the Gelidiaceae (Rhodophyta) in Cheju Island. I. Some members of *Gelidium*. Korean J. Plant Tax. 18 (2):95–113.
- Norris, R. E. 1990. A critique on the taxonomy of an important agarophyta, *Gelidium amansii*. Jpn. J. Phycol. 38:35–42.
- Okamura, K. 1915. On the marine algae of the east coast of Chosen. I. Bot. Mag. Tokyo 29(337):28–29.
- Okamura, K. 1934. On *Gelidium* and *Pterocladia* of Japan. J. Imp. Fish. Inst. (Tokyo Fish. Univ.) 29:47–67, pls. 16-33.
- Santelices, B. 1988. Taxonomic studies on Chinese Gelidiales (Rhodophyta). In Tax. Econ. Seaweeds 2, pp. 91–107.
- Sohn, C. H., and Kang, J. W. 1978. The classification of the family Gelidiaceae (Rhodophyta) in Korea. Publ. Inst. Mar. Sci. Natl. Fish. Univ. Pusan. 11:20–40.
- Yoshida, T., Nakajima, Y., and Nakata, Y. 1990. Check-list of marine algae of Japan. Jpn. J. Phycol. 38 (2):269–320.

Section III. Gracilaria

INTRODUCTION

Isabella A. Abbott

A decade ago, only scattered studies such as those of Weber-van Bosse, Dawson, and Pham were among the published works available to help us identify such common genera as *Sargassum* or *Gracilaria* in the western Pacific. The earlier work of Okamura (1936) had dealt mostly with the main islands of Japan, though the broader investigations of Yamada took in some of the southern regions (Formosa and Ryukyus among them). The work of Ohmi (1958) and Yamamoto (1978) on *Gracilaria* also included some southern species; but since more specimens were from central and northern Japan, greater attention was paid to them.

Chinese studies of marine algae from the coral reefs of the Xisha (Paracel) Islands and southern Hainan Island have added taxa from the warm waters of China. The recent contributions of Zhang and Xia (especially those in this work-shop series) have also increased the number known from the southern Chinese mainland, where the sandy-muddy habitats found in Guangdong and Guanxi provinces have been found suitable for *Gracilaria* species. As a result, *Gracilaria* species from south China are better known than are those from the north; moreover, more species of this alga seem to occur in the south than in the north. But, curiously, more species of *Gracilaria* seem to occur in Japan's northern latitudes than in China or adjacent Korea.

At the same time that he pursues the taxonomy of *Gracilaria*, Dr. Yamamoto is busy culturing and crossing many species. This slow work, however, has not permitted him (Yamamoto and Sasaki, 1987) to settle the problem of *Gracilaria "verrucosa"* as easily as did Zhang and Xia (1986) after the first workshop, when it became clear that plants outside the southern British Isles that were being called *verrucosa* probably were not. While he was seeking another appropriate name for the Japanese *verrucosa*, Yamamoto found several "look alikes," including *G. vermiculophylla* Ohmi, which had been thought to be a Japanese "endemic" plant

with verrucosa-type spermatangia. He found (Yamamoto and Sasaki, 1987) that under proper culture conditions, plants from different locations, although morphologically dissimilar could be hybridized. Further, he and Yabu (1988) showed that *verrucosa* plants from a habitat furnishing one of the parents of his crosses had 24 pairs of chromosomes. In this, they are similar to *verrucosa* from British Columbia, but different from European specimens, which have 32 pairs. How many "species" are there among the Japanese *verrucosa*?

Not to be outdone, Lynda Goff (unpublished current molecular studies) has a method by which she can extract DNA from dried herbarium specimens of *Gracilaria*. Although this might help segregate populations of given species, I think that we will have to continue our (sometimes unsatisfactory) morphological studies the old-fashioned way.

I am pleased to have Dr. Lewmanomont doing a study on *Gracilaria* of Thailand, because she is an excellent and careful observer. If she does not agree with everything I have done on Thai *Gracilaria*, it is probable that she is correct and I am not. I am also pleased to have Drs. Dinh and Phang of Viet Nam and Malaysia, respectively, working on *Gracilaria*. I find exciting the new distribution of species they are recognizing—10 years ago we did not even know the species were there.

A vexing problem still remains: how to identify sterile specimens. One practical solution to identifying sterile (and most tetrasporangial) specimens would be to recognize only the genus *Gracilaria*. This would satisfy those who grow agar-producing plants for commercial purposes, but it would surely not satisfy phycologists. Another suggestion is to place all species in *Gracilaria*, and let phycologists direct their attention to subgenera. With this approach, the phylogenetic relationships of groups of species would not be disturbed, but the intricacies of cystocarpic and spermatangial development would remain for trained persons to elucidate. I suggest, however, that students of *Gracilaria* should continue to seek features by which most phycologists can have some confidence in the identifications of these species.

The papers included in this section add six new species of *Gracilaria* (one in Thailand, by Lewmanomont; two in China, by Zhang and Xia; two in the Philippines, by Yamamoto and Trono; and one in Hawaii, by Hoyle). The paper by Hoyle (the author of three other Hawaiian species) was held up for about 10 years, while he waited for spermatangial plants to be collected. We still await the gametophytes of one other species in Hawaii in order to complete identification. Altogether, eight species of *Gracilaria* from Hawaii have been reported.

Additionally, three papers report new records and new distributions of species in Malaysia, Thailand, and the Philippines; and a paper from southern Japan gives phenological information from a field population that failed to produce gametophytes during the period of observation.

Literature Cited

- Dawson, E. Y. 1949. Studies of Northeast Pacific Gracilariaceae. Allan Hancock Found. Publ. Occ. Pap. 7:1–104, pls. 1–25.
- Ohmi, H. 1958. The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. Mem. Fac. Fish. Hokkaido Univ. 6:1–66, pls. 1–10.
- Pham Hoang Ho. 1969. Marine algae of south Vietnam. 558 pp. Ministry of Education and Youth, Saigon.
- Weber van Bosse, A. 1928. Liste des algues du Siboga, IV. Rhodophyceae. Siboga-Expeditie Mongraphie 59b:393–533, figs. 143–213, pls. XI–XVI. E. J. Brill, Leiden.
- Yabu, H., and Yamamoto, H. 1988. Chromosome number of *Gracilaria verrucosa* (Hudson) Papenfuss in the vicinity of Hakodate, Hokkaido. Bull. Fac. Fish. Hokkaido Univ. 39:4–5.
- Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25:97–152.
- Yamamoto, H., and Sasaki, J. 1987. Crossing experiments between populations of socalled *Gracilaria verrucosa* (Huds.) Papenfuss from two localities, Shinori and Kokonai in Hokkaido. Bull. Fac. Fish. Hokkaido Univ. 28:335–338.
- Zhang Junfu, and Xia Bangmei. 1986. On *Gracilaria asiatica* sp. nov. and *G. verrucosa* (Huds.) Papenfuss. Oceanol. Limnol. Sinica 16:175–180.

GRACILARIA DAWSONII SP. NOV. (RHODOPHYTA, GIGARTINALES): A SECOND FLATTENED SPECIES FROM THE HAWAIIAN ISLANDS

Mitchell D. Hoyle

Abstract

A new flattened species, *Gracilaria dawsonii* sp. nov., from fringing reefs on the islands of Oahu, Maui, and Kauai is described. It is the second compressed species of the genus to be reported from the Hawaiian Islands. The new species was compared with 10 other compressed, nonproliferous species of *Gracilaria* from other localities and was found to differ substantially in morphological and spermatangial characteristics, anatomy, and habitat, thus justifying its erection as a new species.

Introduction

The extent of nomenclatural problems within the genus *Gracilara* is well known to marine phycologists. These problems, for the most part, arise from weak morphological distinctions among many of the species. Taxonomic opinions and judgments differ over the generally terete to subcompressed taxa of *Gracilaria*, which greatly resemble one another. These, as well as flattened species, have been separated (Yamamoto 1975) into subgenera on the basis of spermatangial characteristics. However, in most encounters with the genus, male plants have been rare or overlooked, and in few cases have been compared with female and tetrasporic thalli. Nonetheless, many species are neither terete nor subcompressed, and their specific boundaries are often relatively clear and based on nonspermatangial characteristics. The new species described here is compressed and is defined on the basis of both morphological and spermatangial characteristics.

First collected in Hawaii by Prof. M. S. Doty in 1951, the new species was identified by E. Y. Dawson as *G. vivesii* Howe. Indeed, for a long time, I assigned that name to this alga. However, prolonged comparative studies both of exsiccata specimens and the literature have convinced me that the two entities differ sufficiently to justify the erection of the Hawaiian material as a new species, *G. dawsonii* sp. nov.

Description of the Species

Thalli perennes, solitarii vel caespitosi, ligulati, 4–7 cm alti. Coriaceae frondes cardinales colore. Frondes compressae plus minusve regulatim dichotome ramosae in uno planu; divaricatae. Laminae 4–6 mm latae, usque ad 1 mm crassae. Cortex monostromaticus. Subcortex monostromaticus. Medulla 10–13 cellulae diametro. Tetrasporangia cruciatim divisa; in una pagina solum. Gametophyta feminea ferentia dispersa cystocarpia globa in una pagina solum. Gametophyta mascula paucis dispersis late spermatangiis in vadosis

conceptaculis cupulatis (28 µm x 40 µm) in una pagina solum.

Thalli perennial, solitary or caespitose, ligulate, 4–7 cm tall. Coriaceous frond cardinal red in color. Fronds compressed, more or less regularly dichotomously branched in one plane; divaricate. Blades 4-6 mm wide, up to 1 mm thick. Cortex monostromatic. Monostromatic subcortex. Medulla 10–13 cells across. Tetrasporangia cruciately divided; on one surface only. Female gametophytes bearing scattered globose cystocarps on one surface. Male gametophytes with few, widely scattered spermatangia in shallow cup-shaped (28 μ m x 40 μ m) conceptacles on one surface only.

The species is named in memory of Elmer Yale Dawson (1919–1966), an important contributor to the systematics of *Gracilaria*.

Materials and Methods

Specimens of Gracilaria dawsonii Hoyle Examined

The holotype, *G. dawsonii* Hoyle (spermatangial, Doty 28976), was collected at Hauula Beach Park, Oahu, Hawaii, May 13, 1980, by G. A. Santos and deposited in the Bishop Museum (BISH). The holotype sheet contains seven specimens: one is spermatangial, three are cystocarpic, one is tetrasporangial, and three are sterile. An isotype sheet, prepared from previously liquid-preserved material, is deposited in the Herbarium of the University of California, Berkeley (UC). Syntypes, all collected at Hauula Beach Park, include Hoyle 737, June 1985 (BISH); J. W. Hunt 894, March 1975 (BISH); Hoyle 794, February 1976 (tetrasporic, UC); Hoyle 1083A and B, June 1978 (cystocarpic, UC); and Hoyle 795, 796, 834, 1074A–1074D, and 1160 A and B (BISH). Additional specimens studied were W. Magruder K-3 (loaned by W. Magruder) collected at Kipukai, Kauai, Hawaii, September 1979; Hoyle 1165 A and B collected at Oneloa Beach, Makena, Maui, Hawaii, March 1986; and *G. vivesii* Howe, identified by E. Y. Dawson, collected at Hauula Beach Park. February 1951 (Doty 8657, BISH).

Other Species Examined

Other species examined included the isotype *G. skottsbergii* Taylor collected from Archipelago de Colon, Ecuador, in January 1934 (Taylor 360, UC); *G. vivesii* Howe collected from Guaymas, Sonora, Mexico, in May 1946 (Dawson 1654, UC) and from Bahia Agua Dulce, Isla Tiburon, Mexico, in February 1946 (Dawson 877, UC); *G. textorii* (Suringar) J. Agardh collected from Sukumo, Shikoku, Japan, in March 1975 (Stren, in my herbarium) and from Akashi, Fujie Beach, Japan, in April 1974 (Stren 51, in my herbarium); *G. textorii* of Lucas (UC 466204); *G. textorii* of Yamada (UC 279922); *G. peruana* Piccone et Grunow collected at Talara, Peru (Dawson 22473, UC); *G. mammillaris* Greville of I. Calvijo (West Indies Laboratory, Fairleigh Dickinson University, St. Croix, Virgin Islands); and the type specimen of *G. vivipara* Setchell et Gardner, UC 221115.

Methods

Both fresh and exsiccata specimens were examined. For habit sketches, either fresh thalli or exsiccata material that had been soaked in 10% KNO₃ for about 1 hour were used. Sections prepared with a freezing microtome or by hand were used for anatomical drawings. Exsiccata material to be sectioned on the freezing microtome was first soaked in 10% KNO₃ in order to restore near-natural turgidity and size. Before free-hand sectioning was done, a drop of wetting agent was added to the dried specimens and immediately blotted up. Sections were stained either with 1% aniline blue, followed by fixation with 1% HCl, or, preferentially, with Delafield's hematoxylin and then washed and mounted in 25% corn syrup (Karo Brand, Corn Products, Inc., Chicago, Illinois).

Observations

Distribution

Gracilaria dawsonii is endemic to the Hawaiian Islands, where it has been found on Oahu, Kauai, and Maui. The type locality is the fringing reef at Hauula Beach Park on the north shore of Oahu, where the alga grows attached to the limestone substratum among *Laurencia parvipapillata* Tseng, *Rhodymenia leptophylloides* Dawson, and *Amansia glomerata* C. Agardh and underneath *Sargassum* sp. and entangled *Ulva reticulata* Førsskal. Typically, *G. dawsonii* is found in crevices at or just above zero tide level. On Kauai, it occurs in similar habitats at Kipukai (William Magruder, personal communication).

Habit

The thalli of G. dawsonii are perennial, solitary or caespitose, ligulate, up to 7 cm tall with thick (up to 1 mm) coriaceous fronds arising by means of terete stipes (usually less than 1 cm long and becoming elliptical and then compressed above) from scutate holdfasts (Fig. 1). Thalli are cardinal red, becoming greenish or buff where exposed to direct sunlight at low tide. Fronds are compressed (Fig. 2) and more or less regularly dichotomously branched three to six times in one plane. The divaricate branches are generally ascending; however, branches may sometimes become attached to the substratum via secondary holdfasts. Often the thalli are decidedly ligulate, with as few as two forks. Other thalli have more forks or bifurcations and are more spreading. Apices are rounded. Internodes are 0.5-3.0 cm long and up to 6 mm wide just below bifurcations. The margins are entire and nonproliferous. Where branches have been broken off or grazed on, new growth occurs, giving the thallus a constricted appearance. In some cases, the tetrasporophytes are identifiable by thickenings (Fig. 6) in the central part of the blade, excluding margins and older proximal parts. Female gametophytes (Fig. 7) bear scattered globose, ostiolate, nonrostrate cystocarps (up to 1.8 mm in diameter), which are constricted at the base.



Figs. 1–5. Gracilaria dawsonii sp nov. Fig. 1, Habit sketch of paratype shows its ligulate, caespitose form. Fig. 2, Diagrammatic representation of a transverse section of a thallus shows its compressed nature. Fig. 3, Transverse section of a sterile thallus shows the vegetative cortex and medulla. Fig. 4, Transverse section of a tetrasporic thallus shows a cruciate tetrasporanglum and the absence of significant nemathecial modification. Fig. 5, Surface view of a tetrasporic thallus shows the top pair of tetraspores in a tetrasporanglum, putative tetraspore mother cells (stippled), and smaller vegetative cortical cells.



Figs 6 and 7. *Gracilaria dawsonii* sp. nov. Fig. 6, Portion of a tetrasporic thallus shows sori as visible swellings on one surface. Fig. 7, A female gametophyte shows the disposition of cystocarps on the thallus.

Anatomy

The anatomical features of the new species are consistent with those of the genus. The fronds in transverse section (Fig. 3) are 650-800 µm thick (up to 1 mm in older parts) and consist of a cortex composed of mostly one cell layer (rarely two) of densely pigmented, anticlinally (or rarely periclinally) disposed, irregularly shaped cells. Cortical cells in one surface (presumably dorsal) are more deeply pigmented than those of the opposite surface. The cells may be ovoid or cuboidal (6-9 μm in diameter) or elongated (3-7 μm wide and 7-10 μm long). A colorless cuticle (6-12 µm thick) covers the cortex. In those places where the blade becomes appressed to the substrate, the outer cortical cells become elongate (up to 20 µm) and narrow (2 µm), thus protruding from the surface to form secondary holdfasts. In the cortex, basal cells of hairs are round to ovoid (8.3 μ m wide and 10.4 µm long) in surface view. They are scarce, but have been found embedded in the cortex of both surfaces. They are common on the sterile surface of tetrasporic thalli and rare on the opposite fertile surface. Hair cells are elongate (the longest observed was 17 µm long and 6 µm wide), with the hyaline portion protruding

12 μ m beyond the cuticle. The few observed were extensions of otherwise normal pigmented cortical cells. The cortex is subtended by an irregular layer of small subcortical cells, which are more or less densely pigmented (Fig. 4) and may contain numerous floridean starch grains about 2 μ m in diameter. Beneath this subcortex may be two to three irregular layers of more or less pigmented medul-lary cells (17–50 μ m in diameter), which also may contain floridean starch grains.
Changes in the size of these outermost medulla cells toward the inner part of the medulla are abrupt in most thalli (e.g., in Hoyle 737) but gradual in others (e.g., Hoyle 834). The pseudoparenchymatous medulla may be 10–13 cells across. These cells are rounded to slightly laterally compressed (ovoid) and increase in size centripetally to up to $100 \times 180 \ \mu m$ ($200-225 \ \mu m$). Cell walls between medullary cells are 6–12 μm thick. The stipe in transverse section 5 mm from the base consists of a cortex two to six cells across, enlarging gradually centripetally. In surface view, more darkly pigmented, irregularly shaped cells can be found scattered (Fig. 5) sparsely among smaller, lighter colored cortical cells. It is postulated that these somewhat enlarged cells are tetraspore mother cells. Other cells, not shown in Figure 5, somewhat larger than regular vegetative cells and yellowish, are basal cells of hairs.

Tetrasporophyte

Tetrasporangia are cruciately divided, rounded (15–30 μ m in diameter) or slightly elongated (e.g., 10 μ m × 13–20 μ m × 30 μ m). They occur on one surface only and are scattered or sometimes localized in well-defined swellings or sori (Fig. 6), which may be discernable on gross examination. Some thalli have little to no nemathecial modification, whereas others have additional cortical cells (Fig. 4) and are elongated or crescent shaped (7–15 μ m long and 3–11 μ m wide).

Carposporophyte

Carposporophytes are produced in globose (1.8 mm in diameter), ostiolate, basally constricted, nonrostrate cystocarps (Fig. 7). Rarely marginal, they usually occur only on the dorsal surface of the thallus. The thick (350 μ m) pericarp is constructed of many layers of anticlinally elongated cells, which surround a massive gonimoblast of large (75 μ m in diameter) cells with numerous slender absorbing (traversing) filaments (3–5 μ m wide and up to 300 μ m long) radiating deep (100–200 μ m) into the pericarp. Traversing filaments also extend from the placenta into the gonimoblast. Carpospores are rounded (15 μ m in diameter) and are produced in linear series.

Male gametophyte

Male gametophytes (Fig. 8) are rare or difficult to recognize because spermatangial conceptacles are few and widely scattered and occur on one surface only. Irregularly shaped spermatangia densely line the interior of shallow cup-shaped or globular cavities of the verrucosa-type. Spermatia are about 2 μ m in diameter. The conceptacles (Fig. 9) are generally about 30–78 μ m long and up to 40 μ m wide. Conceptacles open to the thallus surface through a canal in the surface gel via a pore about 5 μ m in diameter.



Figs. 8 and 9. Type specimen (MSD 28976) of *Gracilaria dawsonii* sp. nov. Fig. 8, Male gametophyte. Fig. 9, Cross section shows widely scattered, shallow, cup-shaped spermatangial conceptacles.

Discussion

The literature indicates that at least 35 flattened or compressed species of *Gracilaria* can be found throughout the world. For comparative purposes, these can be divided into three categories: (1) proliferous species, (2) nonproliferous species, and (3) species that are usually nonproliferous but sometimes have proliferations. Inasmuch as *G. dawsonii* has never been found with proliferations, it falls within the second category. When the status of a potential new species is determined, detailed comparisons must be made with species in category 2 and less detailed comparisons with certain species in category 3.

Table 1 lists the 10 nonproliferous species with which *G. dawsonii* was compared on the basis of morphological and anatomical characteristics and habitat. The new species most closely resembles a specimen in the herbarium at the University of California, Berkeley (Dawson 22473), collected and identified by E. Y. Dawson as *G. peruana* Piccone et Grunow from Talara, Peru. It is difficult to distinguish this strap-shaped specimen from the new species, except that *G. dawsonii* is 2–3 cm shorter. If Dawson's material is *G. peruana*, it is not as highly branched as the *G. peruana* described by Taylor (1945) as *G. brevis* or as flabellate or as wide as the thallus shown by Dawson et al. (1964). As can be seen in Table 1, apparently significant anatomical differences distinguish the two species. Howe (1911) examined a portion of Piccone and Grunow's collection and found that the thallus was as much as 1 mm thick, as thalli of *G. dawsonii* sometimes are, and had medullary cells up to 650 µm in diameter, or about three times the diameter of those in *G. dawsonii*.

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			Blade	No. of Cell		Medulla			
Snariae	Height	Width (mm)	Thickness	Layers in	Thelling Totation	Width	Cell Size	-	
dawsonii	6.5	4 (up to 6)	650-800 (1000)	1 (up to 2)	Coriaceous	(NO. 01 CENS) 10-13	225	Locality Hawaii	Intertidal
sp. nov.									
<i>abbottiana</i> Hoyle 1978	2-3	2.5-4.0	200		Coriaceous	10-12	220	Hawaii	Intertidal
<i>corallicola</i> Zanardini 1865	6	6	*	÷	Coriaceous	8-10	*	Adriatic	1020 m
<i>curtissiae</i> J. Agardh <i>in</i> Taylor 1967	64	35	750-1000	2-3	Membranous	*	120	Florida, Caribbean	m 0 -9
<i>ecuadoreanus</i> (Taylor) Dawson 1949	თ	ц	150	-	*	ω	60	Galapagos Archipelago	Intertidal
mammillaris (Mont.) Howe 1918	5-15	8-6 6-6	250	Ĩ	Membranous	*	125	Southeast Atlantic	Intertidal to 18 m
mannarensis Rao 1972	12	50-60	460-560	۲ 1	Coriaceous	*	380	India	Subtidal
<i>региапа</i> Piccone et Grunow <i>in</i> Howe 1911	10 (up to 20)	3-10	1000	ل	Coriaceous	œ	650	Peru	Tidepooł
skottsbergii Taylor 1945	8	20-30	250	-	Firmly Fleshy	ę	125	Ecuador	27 m
symmetrica Dawson 1949	8	24	280-300	1-2	Membranous	*	100	Costa Rica	Dredged
<i>tepocensis</i> Dawson 1961	5-13	1 -3	200-300	1-2	Membranous	1-2	200	Sonora, Mexico	71 m

Table 1. Comparison of Gracitaria dawsorni with Ten Other Nonproliferous Species

*Not known

Both *G. dawsonii* and *G. abbottiana* Hoyle are decidedly coriaceous, and both are intertidal. However, the new species grows in cracks and crevices in the lowest intertidal zone on calcium carbonate substratum, whereas *G. abbottiana* grows near the same level on the sides of basaltic boulders protected from the direct onslaught of breaking waves. At first glance (Table 1), it might be suspected that these two species are ecads, as the new species is about two to three times as large as *G. abbottiana*. However, *G. dawsonii* is not as highly branched as *G. abbottiana* and lacks the incurved apices and twisted branches characteristic of *G. abbottiana* (Hoyle 1978). The most distinguishing feature is the conceptacles. *Gracilaria dawsonii* has small, widely scattered, comparatively shallow (78 μ m), cup-shaped spermatangial conceptacles, whereas in *G. abbottiana*, they are dense, deep (up to 120 μ m), and pocketlike. Furthermore, unlike *G. abbottiana*, *G. dawsonii* has conceptacles on one surface only. Finally, agar gels extracted from the two species differ significantly (G. Santos, personal communication).

Because Dawson first identified the alga from Hauula as *G. vivesii* Howe, that name required special attention in this study. Treating the various species of *Gracilaria* from Pacific Mexico, Dawson (1949) said that the thalli of *G. vivesii* showed extreme vegetative variability but that anatomically the plants were quite uniform. At that time Dawson suspected that *G. vivesii* and *G. textorii* (Suringar) J. Agardh were conspecific, even though the former is coriaceous and the latter generally membranous. Ohmi (1955) noted earlier that *G. vivesii* is less proliferous, less dissected, and more coriaceous than *G. textorii*, and he considered such differences "local." Therefore, he placed *G. vivesii* in synonymy with *G. textorii*, a species complex with great morphological variability, as shown by the number of taxa now included in synonymy with it. Previously Dawson (1944) united *G. johnstonii* Setchell et Gardner with *G. vivesii* Howe.

When *G. dawsonii* is compared with the wide range of current morphological characteristics (Howe 1911; Setchell and Gardner 1924; Dawson 1949, 1961; Ohmi 1955, 1958) of *G. textorii*, the new species is shorter (4–7 cm vs. 9–5 cm) and at the lower end of the spectrum in width (4–6 mm vs. 6–47 mm). Thalli in the new species are generally thicker (650–1000 μ m vs. 230–800 μ m) than thalli reported for *G. textorii*. The maximum size of medullary cells (255 μ m in diameter) in *G. dawsonii* is less than that reported (250–500 μ m) for *G. textorii* (Howe 1911; Dawson 1949, 1961; Ohmi 1958). Furthermore, unlike *G. textorii*, the new species is never proliferous, and its tetrasporangia are found on one surface only, often in sori vaguely discernible to the unaided eye as localized swellings. The new species looks very much like the Hawaiian species of *Rhodymenia*: *R. leptophylloides*.

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Literature Cited

Dawson, E. Y. 1944. The marine algae of the Gulf of California. Allan Hancock Pac. Exped. 3:189–454, pls. 1–47.

Dawson, E. Y. 1949. Studies of Northeast Pacific Gracilariaceae. Allan Hancock Found. Publ. Occ. Pap. 7:1–104, pls.1–25.

Dawson, E. Y. 1961. Marine red algae of Pacific Mexico. Pt. 4. Gigartinales. Pac. Nat. 2:191–343.

Dawson, E. Y., Acleto, C., and Foldvik, N. 1964. The seaweeds of Peru. Nova Hedwigia, 13:1–111, pls. 1–80.

Howe, M. A. 1911 Phycological studies. V. Some marine algae of Lower California, Mexico. Bull. Torrey Bot. Club 38:498–514, fig. 1, pls. 1–8.

Howe, M. A. 1918. Algae. In Britton, N. L. Flora of Bermuda. C. Scribners, New York, pp. 489–540.

Hoyle, M. D. 1978. *Gracilaria abbottiana* sp. nov. (Rhodophyta, Gigartinales): a second intertidal species of *Gracilaria* from the island of Oahu, Hawaii. Phycologia 17:297–301.

Ohmi, H. 1955. Contributions to the knowledge of Gracilariaceae from Japan. 1. Critical notes on the structure of *Gracilaria textorii* Suringar. Bull. Fac. Fish. Hokkaido Univ. 5:320–331.

Ohmi, H. 1958. The species of *Gracilaria* from Japan and adjacent waters. Mem. Fac. Hokkaido Univ. 6:1–66, pls. 1–10.

Rao, U. M. 1972. On the Gracilariaceae of the seas around India. J. Mar. Biol. Assoc. India 14:671–696.

Setchell, W. A., and Gardner, N. L. 1924. The marine algae expedition of the California Academy of Sciences to the Gulf of California in 1921. Proc. Calif. Acad. Sci. Series 4 12:695–949, pls. 1–77.

Taylor, W. R. 1945. Pacific marine algae of the Allan Hancock expeditions to the Galapagos Islands. Allan Hancock Pac. Exped. 12:1–528.

Taylor, W. R. 1967. Marine algae of the eastern tropical and sub-tropical coasts of the Americas. 780 pp., 80 pls. Univ. of Michigan Press, Ann Arbor.

Yamamoto, H. 1975. The relationship between *Gracilariopsis* and *Gracilaria* from Japan. Bull. Fac. Fish. Hokkaido Univ. 26:217–222.

Zanardini, G. 1865. Iconographia phycologia adriatica 2:127, pl. 71.

TWO NEW SPECIES OF GRACILARIA FROM THE PHILIPPINES

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Abstract

Gracilaria manilaensis sp. nov. and *G. sullivanii* sp. nov. are described from materials collected in the Philippines. *Gracilaria manilaensis* is characterized by sharp constrictions at the branch bases, abundant, long branches, and reddish fronds. *Gracilaria sullivanii* is distinctive in its regular dichotomous branching, blunt tips of the branches, prostrate habit, and attachment to the substrate by hapters originating from the ventral side of the branches.

Introduction

Twenty-five species of *Gracilaria* and one species of *Polycavernosa* have been reported from the Philippines (Silva et al. 1987). This list and that of Abbott (1985) represent compilations of species previously reported. Several of these species probably have not been identified correctly and have been left for detailed study by future researchers.

We collected *Gracilaria* species in various localities of the Philippines in 1986– 1990. Among these collections and the specimens deposited in the herbarium of the Marine Science Institute, the University of the Philippines, we recognized two new species: *G. manilaensis* Yamamoto et Trono and *G. sullivanii* Yamamoto et Trono, which we describe in this paper.

Materials and Methods

The materials preserved in formalin-seawater were used for anatomical study. In vitro cultures were used for reciprocal crosses (Yamamoto and Sasaki 1987, Yamamoto 1991) with Japanese *G. "verrucosa"* (= *G. vermiculophylla*) (Yamamoto and Sasaki 1988) collected in Kagoshima Prefecture, southern Japan. Some of the F₁ tetrasporophytes raised in vitro were fixed in alcohol-acetic acid (3:1) and stained with Wittmann's solution (Wittmann 1965) for chromosome counts.

Description of the species

Gracilaria manilaensis Yamamoto et Trono sp. nov. (Figs. 1–3; 5–8; 12–15) Frondes caespitosae, 60 cm vel plus altae, axes principales plerumque percurrentes, teretes, 1.5 mm diametro; ramificatio alterna, secunda, vel irregularis; rami accedentes ad axes principales amplitudine et longitudine; bases ramorum et ramulorum valde constrictae. Cortex 1–2 stratorum, cellulae basales pilorum dispersae super superficie; transitus inter corticem et medullam abruptus. Cystocarpia globosa, usque ad 1 mm diametro, filamentis absorbentibus penetrantibus in pericarpium; spermatangia formata in conceptaculis (verrucosa typus); tetrasporangia circumcincta aliquot stratis elongatarum cellularum vegetativarum.

Etymology: Named for Manila Bay, the type locality.

Fronds caespitose, up to 60 cm or more tall; main axes up to 1.5 mm thick, cylindrical throughout, usually percurrent; branching alternate, sometimes secund or irregular; branches abundant, long, similar to main axis, with lateral branchlets; bases of branches and branchlets sharply constricted at their point of attachment; purplish red or sometimes greenish; fleshy to somewhat cartilaginous (Figs. 1-3). Cortical layer consisting of one to two rows of densely protoplasmic cells; outermost cells 7.2-12.8 µm high, 8.8-13.6 µm wide, with primary pit connections only; hair basal cells about 16 μm high, about 15 μm wide, scattered (Fig. 5), Medulia consisting of polygonal cells, increasing in size toward center, up to 570 um. Outer layer of medulla more or less compressed parallel to frond surface; transition in cell size from cortex to medulla abrupt (Fig. 5). Cystocarps globose, up to 1000 μ m in diameter, gonimoblast cells elongated, up to 23 × 71 μ m; absorbing filaments present, penetrating into pericarp. Spermatangia formed in conceptacles (verrucosa type); conceptacles cup-shaped, roundish, or oval, up to 71 µm deep, up to 50 µm wide, crowded but separated by vegetative tissue (Figs. 7-8). Tetrasporangia 35-40 µm high, 24-27 µm wide, regularly cruciate, surrounded by several tiers of elongated vegetative cells (Fig. 6).

Life history is typical Polysiphonia type (Yamamoto 1991).

Chromosome Number: n = 24 (Figs. 12–15).

Habitat: This species grows on muddy bottom in shallow water together with *Gracilaria* species No. 2, described by Trono et al. (1983).

Holotype: No T2243.1, cystocarpic, leg. G. C. Trono, Jr., Hali Beach, Parañaque, Manila Bay, June 15, 1969.

Other Materials: T8450, leg. R. A. Corrales, Bo. Kaingin, November 20, 1977; T8022, leg S. Vannajan, Parañaque Beach, July 15, 1974; T7745, leg. R. A. Corrales, Bacoor, January 16, 1977; T8017, leg. R. A. Corrales, Bacoor, April 25, 1977; T8020, leg. S. Vannajan, Parañaque, March 6, 1974; T8403, leg. G. C. Trono, Jr., Bacoor, October 23, 1977; T1502, leg. G. C. Trono, Jr., January 6, 1969; T7768, leg. R. A. Corrales and D. Manuel, Bacoor, February 20, 1977. All the specimens are deposited in the herbarium of the Marine Science Institute, the University of the Philippines at Quezon City, Philippines.

Remarks: This species had been identified as *G. verrucosa* (Trono et al. 1983). However, its extreme constriction at branch bases is distinctive (Fig. 3) for species in the verrucosa group. Yamamoto (1991) showed that the constriction was retained in generation-to-generation culture (two cycles of life history in vitro).

This species is similar to *G. blodgettii* (in the sense of Fredericq and Norris 1992) in the marked constriction at the branch bases, but is different in the frond length, the width, and the number of branches. *Gracilaria blodgettii* tends to have shorter stubby branches in contrast to the long, gradually tapering to almost filiform branches in *G. manilaensis*. Similar observations and comparisons can be generally made of *G. changii* (Xia et Abbott) Zhang, Xia, and Abbott from the



Figs. 1–3. *Gracilaria manilaensis.* Fig. 1, Habit of holotype. Fig. 2, Habit of male frond raised in culture. Fig. 3, Close-up of branch bases, showing marked constriction. Fig. 4. *Gracilaria sullivanil.* Habit of holotype, showing hapters (arrowed). (Figs. 2–3 after Yamamoto 1991; Fig. 4 after Yamamoto 1989). Scale bars = 5 cm for Figs. 1 and 2, 2 cm for Fig. 4, and 5 mm for Fig. 3.



Figs. 5–8. *Gracilaria manilaensis.* Fig. 5, Cross-sectional view of sterile portion, showing a hair basal cell (arrow). Fig. 6, Cross-sectional view of a tetrasporophyte, showing tetrasporangia surrounded by somewhat elongated vegetative cells. Fig. 7, Cross-sectional view of a mature male frond, showing deep cup-shaped spermatangial conceptacles (verrucosa type) that are crowded but separated by modified vegetative cells. Fig. 8, Surface view of a mature male frond. Scale bars = 50 μ m for all.

western Pacific. No specimens previously identified as *G. verrucosa*, however, show the consistent presence of the sharp constriction at the branch base. In the generalized habit of long, thin axes with many branches attached in a variety of ways, *G. manilaensis* resembles *G. lemaneiformis* (chorda-type spermatangia) and *G. tenuispitata* (textorii-type spermatangia). *Gracilaria blodgettii* has textorii-type spermatangia also (Fredericq and Norris 1992) and *G. changii* has verrucosa-polycavernosa type. It is therefore important to have spermatangial plants for critical identification.

We confirmed that this taxon is incompatible in reciprocal crosses with Japanese *G. verrucosa* (= *G. vermiculophylla*), which is similar in general appearance.

Gracilaria sullivanii Yamamoto et Trono sp. nov. (Figs. 4, 9-11)

Frondes prostratae, usque ad 10 cm longae, affixae per haptera e latere ventrali. Axes principales compressi, usque ad 5 mm lati, 3 mm crassi; axes ramificantes dichotome, partibus superis ramorum factis teretibus. Cortex 1–2 stratorum; cellulae basales pilorum locatae in gregibus 20 ad 40; transitus inter corticem et medullam abruptus. Tetrasporangia formata in nemathecio super latere dorsali frondis, ordinate cruciata, circumcincta seriebus elongatarum cellularum vegetativarum.

Etymology: Named for James J. Sullivan, director of the California Sea Grant program, who has aided enormously in promoting the study of taxonomy of useful algae.

Fronds prostrate, attaching to substrate by hapters originating from ventral side of the fronds, up to 10 cm long; main axes compressed, up to 5 mm wide and 3 mm thick; branching dichotomously in opposite manner; upper portion of branches almost cylindrical, branch tips blunt; reddish brown; cartilaginous (Fig. 4). Cortical layer consisting of one to two rows of densely protoplasmic cells; outermost cells 5.6–16 μ m high, 4–8 μ m wide, with primary pit connections only; hair basal cells about 20 μ m high, about 18 μ m wide, in groups of 20–40 cells (Fig. 9). Medulla consisting of polygonal cells, increasing in size toward center, reaching up to 410 μ m. Outer layer of medulla more or less compressed parallel to frond surface; transition in cell size from cortex to medulla abrupt. Tetrasporangia formed in upper half portion of nemathecium-like elevation on dorsal side of the frond, regularly cruciate, 44.5–50.5 μ m high, 20–26.3 μ m wide, surrounded by rows of elongated vegetative cells; nemathecium-like structure consisting of layers of up to eight cells, up to 140 μ m thick (Figs. 10–11). Cystocarps and spermatangia unknown.

Habitat: This species grows prostrate on rock at depth of 2–3 m, beyond the edge of coral reef.

Holotype: No. T18986, tetrasporic, Matabungkay (Batangas, Luzon Island), February 5, 1988.

Isotypes: No. T18987; tetrasporic; No. T18988, tetrasporic. All the specimens are deposited in the herbarium of the Marine Science Institute, the University of the Philippines at Quezon City, Philippines.



Figs. 9–11. *Gracilaria sullivanii.* Fig. 9, Cross-sectional view of sterile portion, showing hair basal cells (solid cells). Fig. 10, Cross-sectional view of a tetrasporophyte, showing tetrasporangial nematheciumlike structure (solid part), that is located on dorsal side only (arrow). Fig. 11, Cross-sectional view of a mature tetrasporophyte, showing tetrasporangia formed in upper half of nematheciumlike structure. Scale bars = 50 μ m for Figs. 9 and 11 and 1 mm for Fig. 10.



Figs. 12–15. Chromosome number of *Gracilaria manilaensis*. Figs. 12–14, Meiotic late prophase I at three different focuses in a tetrasporangium. Fig. 15, Combination sketch of Figs. 12–14. Scale bars = $20 \,\mu m$ for all.

Remarks: This species is characterized by regular dichotomous branching and prostrate habit (Fig. 4). The several layers of elongated vegetative cells that surround the tetrasporangia form prominent and distinctive nemathecium-like elevated structures not present in other Gracilaria species (Fig. 10-11). These features appear to be distinctive enough for separating this species from other taxa, notwithstanding the absence of cystocarps and male reproductive organs. Yamamoto (1989) earlier reported this alga as Gracilaria sp.

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Literature Cited

- Abbott, I. A. 1985. Gracilaria from the Philippines: list and distribution of the species. In: Tax. Econ. Seaweeds 1, pp. 89-90.
- Fredericq, S., and Norris, J. N. 1992. Studies on cylindrical species of western Atlantic Gracilaria (Gracilariales, Rhodophyta): G. cylindrica Børgesen and G. blodgetti Harvey. In: Tax. Econ. Seaweeds 3, pp. 211-232.
- Silva, P. C., Meñez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines, Smithsonian Contrib, Mar. Sci. 27:1-179.
- Trono, G. C., Jr., Azanza-Corrales, R., and Manuel, D. 1983. The genus Gracilaria (Gigartinaloes, Rhodophyta) in the Philippines. Kalikasan Philipp. J. Biol. 12:15-41.
- Wittmann, W. 1965. Aceto-iron-haematoxylin-chloral hydrate for chromosome staining. Stain Technol. 40:161-164.
- Yamamoto, H. 1989. Gracilaria and Polycavernosa species of the Philippines. In: Umezaki, I., ed. Scientific survey of marine algae and their resources in the Philippine Islands. Kvoto University Press, Kyoto, Japan, pp. 35-40.
- Yamamoto, H. 1991. Relationship between Gracilaria "verrucosa" and Gracilaria sp. (Gracilariaceae) of Manila Bay, Philippines. Bull. Fac. Fish. Hokkaido Univ. 42:81-84.
- Yamamoto, H., and Sasaki, J. 1987. Crossing experiments between populations of socalled Gracilaria verrucosa (Huds.) Papenfuss from two localities. Bull. Fac. Fish. Hokkaido Univ. 38:335-338.
- Yamamoto, H., and Sasaki, J. 1988. Interfertility between so-called Gracilaria verrucosa (Huds.) Papenfuss and G. vermiculophylla (Ohmi) Papenfuss in Japan. Bull. Fac. Fish. Hokkaido Univ. 39:1-3.

THREE FOLIOSE SPECIES OF GRACILARIA FROM CHINA

Zhang Junfu (C. F. Chang) and Xia Bangmei

Abstract

Two new species, *Gracilaria glomerata* and *G. yamamotoi*, and a newly recorded species of foliose *Gracilaria* are recognized from new material deposited in the herbarium of the Institute of Oceanology, Academia Sinica. One of the new species, *G. glomerata*, differs from other species of *Gracilaria* in its unique morphology, that of glomerate branches. The other new species, *G. yamamotoi*, is characterized by small gonimoblast cells, by two kinds of cell layers in the pericarp, and by the lack of traversing filaments in the cystocarp. The new record, *G. cuneifolia*, is a rare plant, collected only once before: in Japan.

Introduction

Twenty-one species and two varieties of *Gracilaria* have been reported from mainland China (Zhang and Xia 1992), and most of them belong to terete species. Only two foliose species of this genus have previously been reported from China: *Gracilaria spinulosa* (Okamura) Chang et Xia and *G. textorii* (Suringar) De Toni. This is probably due to the subtidal habitat of foliose *Gracilaria* and their easy confusion with other foliose red algae, for example, species of *Rhodymenia*. Recently, we examined some new samples and found that they represent three foliose species of *Gracilaria*, including two species new to science and one new record for China.

Description of the Species

Gracilaria cuneifolia (Okamura) Lee et Kurogi, Bull. Jpn. Soc. Phycol. (Sorui) 25:113–118, figs. 1–3, 1977. (Figs. 1–2, 5–12)

Basionym: *Rhodymenia cuneifolia* Okamura, Rec. Oceanogr. Works Japan 6:16, pl. 7, 1934.

Thallus erect, solitary or caespitose, flattened, 4–7 cm tall, arising from a small disc by a short, slender subterete stipe 2–6 mm long; purplish red; thin, membranous, adhering imperfectly to paper on drying; two to three times dichotomously branched, segments 1.5–9.0 mm wide, with broad, round, patent axils, ending in blunt or notched apices, with entire margins. Thallus in transverse section consisting of a medulla of two to three layers of large parenchymatous cells, 112–224 µm × 66–120 µm in diameter, with walls 6 µm thick, surrounded by one to two layers of small cells, 10–33 µm × 17–43 µm in diameter, the outermost layer 4–7 µm × 3.3–6.6 µm in diameter, pigmented and with surface jelly 10 µm thick; sterile thallus in transverse section 297–322 µm thick.

Tetrasporangia cruciately divided, scattered among the surface layers of frond, circular or ovoid in surface view, 26–33 μ m × 23–30 μ m in diameter, ovoid or oblong in transverse section, 26–36 μ m × 17–23 μ m, surrounded by modified



Figs. 1–2. Gracilaria cuneifolia (Okamura) Lee and Kurogi. From Xinhai, Haikou, Hainan Island, China (AST 80-2633). Fig. 1, Tetrasporangial thallus. Fig. 2, Cystocarpic thallus. Scale bars = 1 cm.

cortical cells. Cystocarps on both surfaces of frond, prominently protruding, hemispherical, domelike in appearance, slightly rostrate, up to 0.7 mm × 1.23 mm in diameter, nonconstricted at base; gonimoblast consisting of branched pseudo-parenchymatous filaments developing from a fusion cell; gonimoblast cells polygonal, 46–92 μ m × 26–46 μ m, upper traversing filaments abundant, connecting gonimoblast to the pericarp; carposporangia rounded to ovoid, 13–23 μ m × 10–13 μ m. Pericarp of one kind of tissue, 191–198 μ m thick, consisting of 13–16 layers of cells, the cells with obscure cell walls, the contents star-shaped. Spermatangia textorii-type in cortical depressions, 23–30 μ m × 20–33 μ m deep.

Habitat: Drift at Xinhai, Haikou, Hainan Province, China in May (AST 80-2633, tetrasporangial, cystocarpic, spermatangial).

Remarks: Okamura (1934) originally established *R. cuneifolia* on the basis of specimens from Chiba Prefecture in Honshu, Japan. It was not reported again after its first collection. When the Fourth taxonomy workshop was held in Sapporo, Japan, in 1991, we had an opportunity to study the specimens of *R. cuneifolia* Okamura in the Herbarium of Faculty of Science, Hokkaido University. One of Okamura's specimens (Lee and Kurogi 1977, p. 144, fig. 1b) has been selected as the lectotype of this species. Lee and Kurogi (1977) found that the Japanese materials identified as *R. cuneifolia* Okamura (Okamura 1934) are a species of *Gracilaria* and made the combination *G. cuneifolia* (Okamura) I. K. Lee et Kurogi on the basis of the textorii-type spermatangial configuration (Lee and Kurogi 1977,

figs. 3a–3h) of *Gracilaria* subgenus *Textoriella*. Cystocarpic plants were not found in the Okamura collection.

A few cystocarpic specimens, together with spermatangial and tetrasporangial plants, are in the Hainan collections and add to our knowledge of this species. This rare plant collected only once from the Bay of Tateyama, Japan, is now more completely described, and its placement in *Gracilaria*, as suggested by Lee and Kurogi, is further confirmed. Our material agrees well with the Japanese specimens and the species described by Lee and Kurogi. The plant has a membranous, thin frond and shallow, saucer-shaped spermatangial configurations. However, the Chinese specimen is smaller than the Japanese specimens, has a narrower thallus, and has fewer dichotomies in branching, only two to three times. Some specimens show new branches generated from the thick stipe of an old plant.

Gracilaria glomerata Zhang and Xia, sp. nov. (Figs. 3, 13–15)

Planta erecta, 4.0–4.5 cm longi, haptero discoidea parvo. Axes et rami complanates; ramificatio 6-7 ordinum, in fasciculos glomeratiformes et confertos terminantibus; compositus ex strato externo 1-2 cellularum corticalium 3.0–6.6 μ m × 5–6 μ m, et medulla cellularum globosarum 79–145 μ m × 73–112 μ m diametro. Conceptacula spermatangiorum typi textorii, spermatangia in conceptaculis corticalibus 23–30 μ m profundo. Cystocarpia et tetrasporangia non observata.

Holoype: AST 82-440 (Fig. 3), spermatangial, growing in intertidal rock pools, collected by Lu Baoren and Xu Fali at Yinggehai, Hainan Island, Hainan Province, China, April 28, 1982.

Etymology: This species has compound divaricate branches that aggregate at the upper portion of the plants and takes its specific name, *glomerata*, from that characteristic.

Plants 4.0–4.5 cm tall, complanate, dark purplish brown, attached below by a discoid holdfast, with a short and slender subterete stipe 1–2 mm long; frond 1–2 mm wide, irregularly dichotomously branched, to six to seven orders, usually branching one to three times subdichotomously below, otherwise naked for 1.0–2.5 cm in basal and median parts, bearing toward their apices dense branches, often somewhat glomerate; texture cartilaginous, with entire margins and blunt apices. Frond in transverse section consisting of a medulla of large, thin-walled cells 79–145 μ m \times 73–112 μ m in diameter, and one to two layers of small pigmented cortical cells 3.0–6.6 μ m \times 5–6 μ m; transection 448–481 μ m thick. Spermatangia textorii-type in cortical depressions, 23–30 μ m deep. Tetrasporangial and female plants unknown.

Remarks: The dense branches in the upper parts together with rather thick segments are so distinctive as to separate this species readily from all others now reported in this genus. None of the other complanate species is reported as having glomerate branches. Although tetrasporophytes and female material have not been seen, the habit of these male plants is different from that of other species, and the plants represent an independent species.



Fig. 3. *Gracilaria glomerata* Zhang and Xia, sp. nov. Spermatangial thallus, holotype sheet (AST 82-440), from Yinggehai, Hainan Island, China. Scale bar = 1 cm Fig. 4. *Gracilaria yamamotoi* Zhang and Xia, sp. nov. Spermatangial thallus, isotype sheet (AST 80-2293), from Yinggehai, Hainan Island, China. Scale bar = 1 cm

Gracilaria yamamotoi Zhang and Xia, sp. nov. (Figs. 4, 16–21)

Plantae 3–7 cm altae, foliatae, frondibus pluribus ex haptero discoide basali ortis; dichotome et irregulariter ramosae, apicibus acutis; thallus 310–320 µm crasso, in sectione transversali medullam cellulis 99–106 µm diametro, subcorticem celluis parvis et corticem 1-2 stromaticem cellulis pigmentosis 7–10 µm longis et 3–7 µm latis. Conceptacula spermatangiorum typi textorii; spermatangia in conceptaculis corticalibus 30–33 µm profundo; cystocarpia globoidea non vel leviter rostrata, 1.2–1.5 mm diametro; gonimoblastus cellulis vacuolatis; carposporangium terminalia, rotundae vel ovales, 40–53 µm diametro. Tetrasporangia non observata.

Holotype: AST 80-2301, cystocarpic, growing on surf-beaten rocks in low intertidal zone, collected by Zhang Junfu and Xia Bangmei at Yinggehai, Hainan Island, Hainan Province, China, April 28, 1980.

Isotype: AST 80-2293 (Fig. 4), spermatangial.

Etymology: The new species is named in honor of Dr. Hirotoshi Yamamoto, Hokkaido University, Faculty of Fisheries, for his major contributions in the studies of Gracilariaceae.

Plants 3–7 cm tall, foliose, dark purplish red, attached below by a discoid holdfast, with a short and slender subterete stipe 2–6 mm long; blades 1–3 mm wide, irregularly dichotomously branched in one plane, thick, coriaceous to cartilaginous, with entire margins and attenuate apices; branches of one to two (up to three) orders; never adhering to paper on drying. Frond in transverse section consisting of a medulla of large, thin-walled cells, 99–106 µm in diameter, and one to two layers of small pigmented cortical cells, 7–10 µm × 3–7 µm; transection 310–320 µm thick.



Figs. 5–12. *Gracilaria cuneifolia* (Okamura) Lee and Kurogi (AST 80-2633). Fig. 5, Transection of thallus showing large medullary cells. Fig. 6, Transection of cortex showing tetrasporangia. Fig. 7, Transection of cortex, showing textoril-type spermatangial configuration. Fig. 8, Surface view of male frond. Fig. 9, Carpospores. Fig. 10, Surface view of tetrasporangla. Fig. 11, Longitudinal section of pericarp. Fig. 12, Longitudinal section of cystocarp.







Figs. 16–21. *Gracilaria yamamotoi* sp. nov. Fig. 16, Transection of thallus showing large medullary cells (AST 80-2293). Fig. 17, Longitudinal section of pericarp (AST 80-2301). Fig. 18, Transection of cortex, showing textorii-type spermatangial configuration (AST 80-2293). Fig. 19, Longitudinal section of cystocarp (AST 80-2301). Fig. 20, Carpospores (AST 80-2301). Fig. 21, Surface view of male frond (AST 80-2295).

Spermatangia (textorii-type) in individual to confluent saucerlike depressions, 30–33 µm deep, surrounded by modified cortical cells, distributed over thallus surface. Cystocarps nearly globose, 1.2–1.5 mm in diameter, prominently protruding, not rostrate to only slightly rostrate, unconstricted at the base; gonimoblast consisting of many small cells, 20–36 µm × 10–17 µm, with several cells toward the apex of each filament developing into carposporangia; carpospores roundish, ovoid or oblong, 40–53 µm in diameter, traversing filaments absent; pericarp 264–304 µm thick, consisting of two kinds of tissue, the outer of six to seven rows of smaller, dense, oblong shaped contents, the inner 10–11 rows of larger, loose, horizontally oblong cells.

Remarks: This species is similar to slender forms of *G. textorii* (Suringar) De Toni in external appearance. It is distinguishable, however, by the lack of traversing filaments in the cystocarp, by the small gonimoblast cells, and by two kinds of cell layers in the pericarp. In *G. textorii*, the traversing filaments are conspicuous, and the pericarps are constructed of only one kind of cells.

Literature Cited

- Lee, I. K., and Kurogi, M. 1977. On the taxonomic position of *Rhodymenia cuneifolia* Okamura (Rhodophyta). Bull. Jpn. Soc. Phycol. (Sorui) 25 ((Suppl.):113–118.
- Okamura, K. 1934. Notes on algae dredged from the Pacific Coast of Chiba Prefecture. Rec. Oceanogr. Works Japan 6:13–18, figs. 1–3, pl. 7(1).
- Zhang Junfu (Chang, C. F.), and Xia Bangmei. 1991. Studies on two new *Gracilaria* from south China and a summary of *Gracilaria* species in China. In: Tax. Econ. Seaweeds 3, pp. 195–206.

NEW RECORDS AND A REASSESSMENT OF *GRACILARIA* (RHODOPHYTA) FROM THE PHILIPPINES

Isabella A. Abbott

Abstract

Although approximately 25 species of *Gracilaria* are listed for the Philippines, about half are misidentified or have had their names changed recently. Nine taxa with new geographic distributions within the Philippine Archipelago are discussed in this chapter. Three of the nine are added as new records: *G. firma, G. lemaneiformis,* and *G. tenuistipitata* var. *liui*

Introduction

The 23 species and two varieties of *Gracilaria* and *Polycavernosa* reported for the Philippines by Silva et al. (1988) represent compilations from old and fairly recent literature. Among the first of the reports was that of Montagne (1844) of *G. "confervoides,"* which has been moved (as a name) to a variety of species, without examination of the specimen or specimens to which this name was given. Also nearly as early are the reports by Dickie (1876) of the Challenger expedition specimens with the names of *G. dactyloides* and *G. eucheumoides*. The more recent articles (Cordero 1981, Trono et al. 1983, Abbott 1985) in some cases repeat the old names, but add new ones also. Nevertheless, nearly all the *Gracilaria* species reported for the Philippines require critical reexamination; most of those that I have seen, moreover, lack sufficient numbers of specimens for an evaluation of the boundaries of species, and many names have been applied to sterile specimens.

The purpose of my examination of *Gracilaria* specimens in major herbaria and of specimens sent to me was mostly to try to understand the life forms (morphology) of the species and to compare herbarium specimens with more recently collected ones. As with any genus that is widely distributed (e.g., *Ulva, Sargassum*, and *Fucus*), *Gracilaria* species vary a great deal, even within a given habitat and the same population. Until large numbers of specimens can be examined, it is hazardous to name new species in a genus that already has more than 100 described taxa. A sorting out of named species depends on the study of type specimens. This is not as easy as it sounds, for unlike *Liagora* (Abbott 1990a, 1990b), for which most types are in few herbaria, type specimens of *Gracilaria* are widely distributed, and many specimens are difficult to find.

Moreover, although each geographical region has some species in common with other areas (near or far), each also has some species that, if not endemic, at least have a narrow distribution. On this basis, a number of species listed by Silva et al. (1988) are from the warm Atlantic-Caribbean (*G. damaecornis, G. disticha, G. venezuelensis,* and *P. debilis*). I have not seen material from outside of this

region that I would identify with these names, and I question whether these species exist in the western Pacific. Other names have been placed in the synonymy of other taxa: G. cylindrica with G. blodgettii by Fredericq and Norris (1992) and G. canaliculata and G. minor with G. salicornia by Xia (1986). Gracilaria papenfussii, G. spinigera, and G. turgida are species from the North Pacific and Gulf of California with which I am familiar, but have not seen collections from the western Pacific. Some plants previously identified with G. blodgettii and G. cylindrica in the warm Pacific have been transferred, after examination, to G. changii (Xia and Abbott) Abbott, Zhang et Xia. G. cylindrica in the sense of Weber van Bosse (1928) was placed with G. vanbosseae (Abbott) Abbott (1991). As shown by Zhang and Xia (1992), three "look-alike" species fall into the broad characterization of G. bursa-pastoris of the Atlantic. The two Pacific entities are G. parvispora (Abbott 1985) of the Hawaiian Islands and G. chouae (Zhang and Xia 1992) of southern China. All three can be distinguished from one another on the basis of the structural features of the cystocarp and pericarp. The Japanese specimens, which are illustrated in Okamura (1928, pl. 242, fig. 5) as G. compressa and to which the Philippine specimens of Meñez (1961, p. 74) were compared, could certainly be allied with G. bursa-pastoris of Yamamoto (1985, p. 78). Yamamoto, however, has not subsequently commented on the Japanese specimens bearing this identification. I examined the Okamura specimen (SAP), which was not gametophytic and therefore not particularly informative for systematic purposes. It could be any one of a number of taxa now disguised as "G. verrucosa." | do not think that G. compressa will be found in the western Pacific. Finally, G. lacinulata, listed by Weber van Bosse (1928), has been synonymized with G. foliifera (Forsskal) Børgesen. If I understand the boundaries of the species from the Caribbean and the Pacific coast of North America (including the Gulf of California) mentioned here, I have not recognized them in the numerous Gracilaria collections from the Philippines that I have examined. If all the 14 species listed here were removed from the Philippine flora, a rigorous study of large numbers of specimens and comparison with type specimens would still be necessary before a clear understanding could emerge.

This chapter contains an annotated list of Philippine species that were identified in Sapporo with the help of Xia Bangmei and H. Yamamoto. We examined specimens that had been collected in the Philippines and loaned to me by Dr. Trono, and other specimens that Drs. Trono and Yamamoto had collected in the Philippines in recent years.

At this writing, all species are listed in *Gracilaria* because the integrity of *Hydropuntia* (= *Polycavernosa*) has been questioned (Abbott et al. 1991), and the definition of *Gracilariopsis* as elucidated by Fredericq and Hommersand (1989) was found to be too technical for any but the most highly trained. Inasmuch as one of the aims of the taxonomy workshops is to make identification (i.e., taxonomy) of algae within reach of those who are not specialists on marine algae, we continue to search for usable criteria by which non-*Gracilaria* specialists can identify these useful plants.

Materials and Methods

Dried herbarium material from the collections of M. S. Doty (at B. P. Bishop Museum, Honolulu, Hawaii); G. C. Trono, Jr. (University of the Philippines); H. Yamamoto (Faculty of Fisheries, Hokkaido University, Hakodate); and my own herbarium, collected by my late husband, Donald P. Abbott, were examined. Sections were cut by hand, rehydrated, and then stained with a mixture of about 0.3% aniline blue in glucose syrup to which a drop of 1% HCl is added when used. Sections were mounted in about 35% glucose syrup with phenol crystals added.

Observations

Gracilaria arcuata Zanardini, Mem. R. Inst. Veneto Sci. Lett. Arts 7:265, pl. 5, fig. 2, 1858.

This species was previously listed for the Philippines by Cordero (1981) and Trono et al. (1983) and by others cited in Abbott (1985). Recognition of this taxon appears to be consistent among workers in the western Pacific (Chang and Xia 1976, Yamamoto 1978, Trono et al. 1983). However, as shown by me (Abbott 1988b, figs. 3, 4), the Weber van Bosse material from Indonesia of this species is clearly flattened, being linear in cross section, whereas other illustrations (Chang and Xia 1976, fig. 13, 1, 2; Yamamoto 1978, pl. 47, figs. 4, 5; Trono et al. 1983, fig. 7; and Abbott 1985, fig. 17, identified by M. Doty) show cylindrical to subcylindrical plants that are terete or oval in cross section. Material of *G. arcuata* from the Red Sea, its type locality, is scarce or not helpful in solving the problems of identification. As knowledge of the type and of other Red Sea material is limited, recognition of varieties of *G. arcuata* appear to be inappropriate.

New Philippine Records: Tapaan Island, Siasi, Sulu Archipelago. T4091 and T4110 collected December 29, 1970 by G. C. Trono, Jr., and T5107 collected by G. C. Trono, Jr., April 26, 1972 at the same place as T4091 and T4110.

Gracilaria changii (Xia et Abbott) Abbott, Zhang, and Xia, Pac. Sci. 45:23, 1991.

Very large plants (about twice the size of the Malaysian type material) from Pieto Diaz, Bicol, collected by V. Alvarez, were examined. *Gracilaria changii* was earlier reported (as *P. changii*) (Xia and Abbott 1987) from the central Philippines.

Gracilaria vieillardii Silva, Smithsonian Contrib. Mar. Sci. 27: 44, 1988. (Replaced name for *G. denticulata* (Kützing) Weber van Bosse, Siboga Exped. 59d:432, 1928, a later homonym of *G. denticulata* Schmitz ex Mazza).

Only one plant was collected by V. Alvarez from Dancalan, Sorsogon, May 5, 1988. It shows typically frondose apices with dentate margins. The species was previously reported by Cordero (1981).

Gracilaria edulis (Gmelin) Silva, Univ. Calif. Publ. Bot. 25:293, 1952.

Included under this name are most of the specimens (*in herbario*) from the western Pacific under the name of *G. lichenoides* of various authors. Abbott et al.

(1991) also placed specimens previously identified as *P. fastigiata* with this species; as this species is the type species of the genus *Polycavernosa*, this move placed *Polycavernosa* (= *Hydropuntia*, its older name) with *Gracilaria*.

A "typical" short specimen of this species, which is terete to somewhat compressed with a small number of laterals, was collected at Cavite, Manila Bay, May 23, 1989, by an unknown collector (UPI). Other newly recorded collections include those from Laminusa Island, Siasi (Sulu Archipelago), leg. D. P. Abbott (IA 17896), and from Taganak Island, Turtle Island Group, from southeast shore, leg. D. P. Abbott (IA 17882). The species was previously reported from the Philippines as *P. fastigiata* (Xia and Abbott 1987) with distribution from Cebu to Mindanao.

Remarks: Polycavernosa was described in 1963, but lack of communication between China and the West prevented the publication from being distributed until the mid 1970s. The original description of P. fastigiata has been expanded to include plants that are nearly twice as tall as and more laxly branched than the original plants from Hainan Island. Xia and I (Xia and Abbott 1987) transferred H. urvillei to Polycavernosa, overlooking the fact that Hydropuntia, the genus name, was older than Polycavernosa. Later, both genera were reduced to the synonymy of Gracilaria and P. fastigiata was recognized as G. edulis (Abbott et al. 1991). Only experience with a large number of specimens from various herbaria gave the clue that if the spermatangial differences used to separate the two genera previously were only ontogenetic, then it was not practical to recognize two species: edulis and fastigiata. In terms of external morphology, it is the former, G. edulis, that must be expanded to include the variability of the latter, because P. fastigiata is far better known than is G. edulis (in a strict sense). The most comprehensive, because based on more than 100 specimens, description of this taxon is found under P. fastigiata in a paper written by Xia and me (Xia and Abbott 1987).

Although *G. edulis* is the oldest published name for this widespread species, the roots of *G. edulis* are found in the pre-Linnean publication of Rumphius (Herbarium Amboinense, vol. 6, pl. 74, fig. 3, and pl. 76, figs. a–c, 1750). Referred to as "alga coralloides" by this legendary botanist, the plant in the illustration is clearly the species we now call *G. edulis*. Before equating *P. fastigiata* with this species, I thought that Rumphius's illustrations matched the type material of *P. fastigiata*. The fact that Rumphius's material was probably from the harbor of Ambon (Amboina), about 128° E and 4° 40' S, now in Indonesia, puts "alga coralloides" well within the center of the presently known distribution of *G. edulis*. Figures 1–4 are photographs of Rumphius's pl. 74, fig. 3, and pl. 76, figs. a–c. I have not seen the specimen, collected by Robinson in 1913 in Amboina, that Merrill (1917) refers to as *G. lichenoides* (= *G. edulis*), but it is probably correctly identified.

Gracilaria firma Chang et Xia, Stud. Mar. Sinica 11:143–145, fig. 38, 1–8; fig. 39, 1–4, pl. 2, fig. 4, 1976.

The four specimens from Sorsogon, collected by V. Alvarez in 1988, and two from Bagacoy, Gubat, Sorsogon, also collected by V. Alavarez on May 18, 1988,



Figs. 1–4. Photographs of Rumphius (1750) "alga coralloides" (*Gracilaria edulis*). Fig. 1, pl. 74, fig. 3. About natural size. Figs 2–4, pl. 76, figs. a–c. About one-half natural size.

are thicker than the type material (Chang and Xia 1976) from China and the plants recognized as *G. firma* from Thailand (Abbott 1988a), and appear to be common plants in the north central Philippines. The plants are frequently straw colored in collections. When entangled with other species (e.g., Danjon Reef, Bohol, leg. Walter Dino, February 15, 1986), they can be picked out easily because of their color. They become nearly black when they grow in fishponds under the influence of fresh water. Whatever their color, all specimens have a thickened axis, with somewhat angular lateral edges when dried. This species is a new record for the Philippines.

Gracilaria gigas Harvey, Proc. Am. Acad. Arts Sci. 4:331, 1860.

This species was reported by Trono et al. (1983) from Bulusan. Another specimen is from the inner coral reef at Calatagan, Batangas, collected by A. Albano and A. Gutierrez on June 12, 1979.

Of the erect species, the individual plants of *G. gigas* are robust, more so than those of *G. salicornia* even when both are fresh. As such, it is not a common morphology for western species of *Gracilaria*.

Gracilaria lemaneiformis (Bory) Weber van Bosse, Siboga Exped. 59d:435, fig. 176, 1928.

This is a common species throughout the warm Pacific. In outlying areas, which would include regions with slightly cooler surface seawater temperatures, such as the type locality (Paitá, Peru), northeast China, and the North American Pacific coast, the form most commonly encountered is what was formerly recognized as *Gracilariopsis sjoestedtii* (Kylin) Dawson. These plants are more robust than the usual plants found in areas with warmer water, such as the Philippines, Hawaii, and Thailand.

In habit, the tropical plants frequently have a percurrent, filiform axis with few to many short laterals, short-spinous to elongate. In temperate areas, the laterals may be as elongate and as thick as the axes, with few laterals, or may be bushy plants.

Philippine Records: T2245, Manila Bay, leg. Danilo Sanchez and Lilia Silva, July 17, 1969; Juban, Sorsogon, leg. V. Alvarez, May 18, 1988. These are new records for the Philippines.

Remarks: G. lemaneiformis can be confused with three other species: Gracilariopsis heteroclada Zhang et Xia¹ with chorda-type spermatangia, Gracilaria tenuistipitata var. liui Zhang et Xia with textorii-type spermatangia, and G. manilaensis. Generally, G. heteroclada has more orders of branching, lacks a percurrent axis, and has laterals of sharply different diameters from those of the axes. Gracilaria tenuistipitata var. liui favors areas with an intrusion of fresh water (which makes it a fine candidate for aquaculture conditions); it is a slender, tall plant with several orders of branching. In Manila Bay, another species, named in this volume as G. manilaensis (see Yamamoto and Trono) resembles both of these taxa (relatively thin, with rather delicate branches) but has verrucosa-type spermatangia. Cystocarps of G. heteroclada and G. lemaneiformis are similar, with small-celled gonimoblast filaments and no traversing filaments (i.e., Gracilariopsis-type), whereas the new Manila Bay species contains traversing filaments in the cystocarp (i.e., verrucosa-type cystocarps). It is too early to know whether the agar characteristics of these taxa can give a clue to the correct names, and we are reminded (again) that even with careful attention to the details of spermatangia and cystocarps, we are not certain how much weight to give to these features. Moreover, the systematics must take into consideration both field and laboratory features by which the separate species can be recognized even if sterile. This is a goal that does not appear to be in sight.

Gracilaria salicornia (C. Agardh) Dawson, Bull. S. Calif. Acad. Sci. 53:4, fig. 3, 1954.

Basionym: *Sphaerococcus salicornia* C. Agardh, Icones algarum inedit, pl. 8, 1820.

Included under this name are previous Philippine records of G. canaliculata

¹ *Gracilariopsis heteroclada* (Zhang and Xia) Zhang and Xia. In: Abbott, I. A., Zhang Junfu, and Xia Bangmei. 1991. Pac. Sci. 45:22.

and *G. crassa* encompassed by Xia (1986) in the synonymy of *G. salicornia*. This species, whose type locality is Manila Bay (although reported as being from Alaska because of a mix-up of labels), is widely distributed in the Philippines (Abbott 1985). The new collections are from the southern Sulu Sea.

IA 17933, 17875, 17889, and 17929 were all collected from Gnat Reef, southwest Balabac Island, by D. P. Abbott.

Gracilaria tenuistipitata var. *liui* Zhang et Xia, Tax. Econ. Seaweeds 2, pp. 131–132; figs. 1, 3–9; 1988.

The five specimens on three sheets, collected at Buguey, Cagayan, by Susan Rabana on June 24, 1989, resemble the illustration of Zhang and Xia (1988, p. 132, fig. 1). These are finely and repeatedly branched plants, usually growing in sandy mud, on pebbles and shells, and easily detached, because of the small, slender stipe. Plants are frequently found cast ashore. This species is a new record for the Philippines.

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Literature Cited

- Abbott, I. A. 1985. *Gracilaria* from the Philippines: list and distribution of the species. In: Tax. Econ. Seaweeds 1, pp. 89–90.
- Abbott, I. A. 1988a. Some species of *Gracilaria* and *Polycavernosa* from Thailand. In: Tax. Econ. Seaweeds 2, pp. 137–150.
- Abbott, I. A. 1988b. Some species of *Gracilaria* and *Polycavernosa* from the Slboga expedition. In: Tax. Econ. Seaweeds 2, pp. 151–156.
- Abbott, I. A. 1990a. A taxonomic assessment of the species of *Liagora* (Nemaliales, Rhodophyta) recognized by J. Agardh, based upon studies of type specimens. Cryptog. Bot. 1:308–322.
- Abbott, I. A. 1990b. A taxonomic and nomenclatural assessment of the species of *Liagora* (Rhyodophyta, Nemaliales) in the herbarium of Lamouroux. Cryptog. Algol. 11:111-136.
- Abbott, I. A., Zhang Junfu, and Xia Bangmei. 1991. *Gracilaria mixta* sp. nov. and other Western Pacific species of the genus (Rhodophyta: Gracilariaceae). Pac. Sci. 45:12–27.
- Chang, C. F. [Zhang Junfu], and Xia Bang Mei. 1976. Studies on Chinese species of *Gracilaria*. Stud. Mar. Sinica 11:91–163.
- Cordero, P. 1981. Studies on Philippine marine red algae. 258 pp., 28 pls. National Museum of the Philippines, Manila.
- Dickie, G. 1876. Algae, chiefly Polynesian, In: Contributions to the botany of the expedition of the HMS *Challenger*. J. Linn. Soc. (Bot.) 155:235–246.
- Fredericq, S., and Hommersand, M. 1989. Comparative morphology and taxonomic status of *Gracilariopsis* (Gracilariales, Rhodophyta). J. Phycol. 25:228–241.
- Fredericq, S., and Norris, J. N. 1992. Studies on cylindrical species of western Atlantic

Gracilaria (Gracilariales, Rhodophyta): *G. cylindrica* Børgesen and *G. blodgettii* Harvey. In: Tax. Econ. Seaweeds 3, pp. 211–231.

- Meñez, E. 1961. The marine algae of the Hundred Islands, Philippines. Phil. J. Sci. 90:37– 86, pls. 1–12.
- Merrill, E. D. 1917. An interpretation of Rumphius's Herbarium Amboinense. Publ. No. 9: 595 pp., 2 maps. [Philippines] Dept. Agriculture and Natural Resources, Bureau of Science, Manila.
- Montagne, C. 1844. Plantae cellulares quas in insulis Philippinensibus a cl. Cuming collectae recensuit ... Lond. J. Bot. 3:658–662.
- Okamura, K. 1928. Icones of Japanese algae vol. 5. Published by Author, Tokyo, pls. 201–240.
- Silva, P. C., Meñez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contrib. Mar. Sci. No. 27:178 pp. Smithsonian Institution Press, Washington, D.C.
- Trono, G. C., Jr., Azanza-Corrales, R., and Manuel, D. 1983. The genus *Gracilaria* (Gigartinales, Rhodophyta) in the Philippines. Kalikasan Philip. J. Biol. 12:15–41.
- Weber van Bosse, A. 1928. Liste des algues du Siboga, IV. Rhodophyceae. Siboga-Expeditie Mongraphie 59d:393–533, figs. 143–213, pls. XI–XVI. E. J. Brill, Leiden.
- Xia Bangmei. 1986. On *Gracilaria salicornia* (C. Agardh) Dawson. Chin. J. Oceanol. Limnol. 4:100–106, pl. 1.
- Xia Bangmei, and Abbott, I. A. 1987. New species of *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta) from the western Pacific. Phycologia 26:405–418, figs. 1–14.
- Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25:97–152.
- Yamamoto, H. 1985. *Gracilaria* from Japan: vegetative and reproductive keys and list of the species. In: Tax. Econ. Seaweeds 1, pp. 77–80.
- Zhang Junfu, and Xia Bangmei. 1988. On two new *Gracilaria* (Gigartinales, Rhodophyta) from south China. In: Tax. Econ. Seaweeds 2, pp. 131–136.
- Zhang Junfu, and Xia Bangmei. 1992. Studies on two new *Gracilaria* from south China and a summary of *Gracilaria* species in China. In: Tax. Econ. Seaweeds 3:195–206.

OCCURRENCE OF A DIFFERENT GRACILARIA IN JAPAN

Anong Chirapart, Masao Ohno, and Hirotoshi Yamamoto

Abstract

A species of *Gracilaria* that grows on the coast of Shikoku Island, southern Japan, is described as a new member of Japanese *Gracilaria*. This taxon is similar to *G. chorda* in morphology but has smaller tetrasporangia and larger medullary cells.

Introduction

Species of *Gracilaria* are distributed throughout Japan. In a previous study, Ohmi (1958) noted 15 species of *Gracilaria* and three species of *Gracilariopsis*. In 1975 and 1978, Yamamoto merged the genus *Gracilariopsis* into genus *Gracilaria* (Papenfuss 1966) and reported 16 species of *Gracilaria*. However, some taxa are still taxonomically uncertain. A species of *Gracilaria* that grows along the coasts of Tosa Bay and the Inland Sea and is harvested in large quantities for agar is one of these taxa. This alga was previously identified as a local type (ecotype) of *G. chorda*, but it appears to be distinguishable from *G. chorda* in ecological habit and in some morphological features.

We present descriptions and notes on the ecology and morphology of this species of *Gracilaria* and compare its features with those of *G. chorda*.

Materials and Methods

Materials were collected along the coast of Tosa Bay (Kochi Prefecture), Nakajima (Tokushima Prefecture) and Horie Bay (Ehime Prefecture) in Shikoku Island, southern Japan. Sections of the materials were prepared by hand or by using a freezing microtome and were stained with 1% aqueous aniline blue intensified with 1% HCI. The sections were then washed with fresh water to remove excess stain and mounted in glycerin on glass slides.

The specimens examined are deposited in the herbarium of Usa Marine Biological Institute, Kochi University.

Description Of The Species

Plants (Fig. 1) solitary, slender and delicate, cylindrical throughout, 30–200 cm or, rarely, up to 450 cm long; main axes 0.4–2.0 mm in diameter, attenuated toward bases and tapering to the apex, generally furnished with luxuriant branches, sometimes with a few branches. Branches arising alternately or on all sides or unilaterally at irregular intervals, occasionally two to three branches arising at the same place (fasciated) (Fig. 2); branch bases slightly or markedly constricted and sometimes becoming compressed and broader (Fig. 3). First- and second-order branches bearing branchlets. Main axes and branches greenish, but branchlets brownish. Cartilaginous in texture. Cortex consisting of two to three layers of cells, 25–45 µm thick; outermost cells 8–10 µm; medulla consisting of





Fig. 1. New *Gracilaria* species from Japan. Sterile fronds from Shikoku Island. A, From Tosa Bay, Kochi Prefecture. B, From Nakajima, Tokushima Prefecture. C, From Horie Bay, Ehime Prefecture.



Fig. 2. New *Gracilaria* species from Japan. Fasciated branching, showing two to three branches arising from the same part.



Fig. 3. New *Gracilaria* species from Japan. Fasciated branching, showing branch base constricted and becoming compressed and broader.



large polygonal cells, 850–950 μm in diameter; transition in cell size from cortex to medulla abrupt. Tetrasporangia (Fig. 4) cruciate, scattered among cortical layer, ovoid or oblong, 25–50 μm high, 15–40 μm wide, generally 36–40 μm high and 21–25 μm wide (Fig. 5), surrounded by elongated cortical cells. Male and female reproductive organs unknown.

Remarks: This species of Gracilaria grows at a depth of 1–3 m in Tosa Bay and at a depth of 2–10 m on the coasts of Nakajima. It attaches by small holdfasts to pebbles, shells, and the other substrata such as rope, as well as anchoring on sandy-muddy bottom. Sometimes it is found on other seaweeds. Generally, lower parts of the thalli are buried under sand or mud, but sometimes thalli also occur in free-living form.

Fig. 4. New *Gracilaria* species from Japan. Part of vertical section of asexual frond, showing cruciate tetrasporangium.

Fragments of plants are usually found at the habitat. At Tosa Bay in January, 20% of the fragmented thalli collected had holdfasts. However, 45.7% were fragments without holdfasts that were torn off at constricted branch bases, and 34.3% were from the midpart of branches. Almost all the specimens were vegetative throughout the year; no gametophytes were found in any of the populations, and only a few tetrasporophytes were found at Tosa Bay in May.

Gracilaria chorda has been divided into two local types in morphology. One is thick and has few branches and grows in warmer regions. The other is slender and has abundant branches and is found in colder regions (Yamamoto 1978). The types appear to be different in external morphology, although fasciated branching, which is distinctive in this species, is a common feature in both. Like the latter type, the new species has slender axes, luxuriant branches, and fasciated branching. However, it differs in having more branches and branchlets, and in color. *Gracilaria chorda* is always reddish, and thus by color the two species can be distinguished from each other. Tetrasporangia of this new alga are smaller than those of *G. chorda*, and medullary cells are larger (Yamamoto 1978). Additionally,



Fig. 5. New Gracilaria species from Japan. Variation in height (A) and width (B).

this taxon prefers lower salinity and sandy-mud bottom, whereas *G. chorda* grows on pebble-sand bottom in comparatively high salinity. The populations of both taxa are segregated in the field. Consequently, we suggest that this new *Gracilaria* species is distinctive from *G. chorda* and other species, and is a new member of Japanese *Gracilaria*.

We are attempting to find gametophytes of this taxon in the field and in culture in order to finalize its taxonomic position. The new name will be given after plants with male and female reproductive organs have been found.

Literature Cited

- Ohmi, H. 1958. The species of *Gracilaria* and *Gracilariopsis* from Japan and adjacent waters. Mem. Fac. Fish. Hokkaido Univ. 6:1–66.
- Papenfuss, G. F. 1966. Notes on algal nomenclature. V. Various Chlorophyceae and Rhodophyceae. Phykos 5:95–105.
- Yamamoto, H. 1975. The relationship between *Gracilariopsis* and *Gracilaria* from Japan. Bull. Fac. Fish. Hokkaido Univ. 26:217–222.
- Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25:119–120.

SOME SPECIES OF *GRACILARIA* FROM PENINSULAR MALAYSIA AND SINGAPORE

Siew-Moi Phang

Abstract

The habitats and distribution of five species of *Gracilaria* from Malaysia and Singapore are reported: *G. salicornia, G. changii, G. edulis, G. firma*, and *G. coronopifolia. Gracilaria firma* and *G. coronopifolia* are new records. These five species are added to *G. subtilis* and *G. urvillei*, previously known from Malaysia.

Introduction

The first record of marine algae from the Asian region resulted from the collections made during the *Preussische Expedition nach Ost-Asien*, 1860–1862, by Eduard von Martens. The collection, which was from Java, the Philippines, Singapore, Taiwan, Hong Kong, and other east Asian regions, was enumerated and published by Georg von Martens in 1866. In 1899 and 1900, collections were made in the Indonesian region during the Siboga Expedition, and the results were documented in monographs on *Halimeda* (Barton 1901), Codiaceae (Gepp and Gepp 1911), and Corallinaceae (Weber van Bosse and Foslie 1904). Recently, Abbott (1988) reexamined the Gracilariaceae collected during the Siboga expedition and described six taxa, including a new species *Polycavernosa vanbosseae* (renamed *Gracilaria vanbosseae* (Abbott) Abbott, Zhang et Xia (Abbott et al. 1991). Checklists of the marine algae of Malaysia and Singapore have been compiled (Teo and Wee 1983; Phang 1984, 1986; Phang and Wee 1991).

Related literature on the Gracilariaceae of Malaysia has been sporadic, and related chiefly to the genus's agarophytic potential (Burkill et al. 1968; Doty et al. 1983; Santos and Doty 1983; Doty and Fisher 1987; Phang and Maheswary 1990). Ten taxa have been reported: *G. salicornia* (including *G. crassa, G. cacalia,* and *G. minor*), *G. changii* (including the reidentified *G. cylindrica* first reported by Doty et al. in 1983 and *G. blodgettii* reported by Phang in 1986 and by Phang and Maheswary in 1990), *G. edulis, G. subtilis, G. urvillei, G. textorii, G. eucheumoides, G. taenoides, G. lichenoides* and *G. confervoides*. The identity of the last four species has been questioned (I. A. Abbott, personal communication), and as no material is available for examination, these are not in the following discussions.

Fifty-five specimens of *Gracilaria* from Malaysia, belonging to the collection at the Institute of Advanced Studies, University of Malaya, Kuala Lumpur, have been found to belong to five species: *G. salicornia*, *G. changii*, *G. edulis*, *G. firma*, and *G. coronopifolia*. The last two are new records.

PSM specimens were collected by Phang Siew-Moi; WYC specimens by Wee Yeow-Chin.
Vegetative Key to the Malaysian Species of Gracilaria

1. 2.	 Plant flat and leafy Plant cylindrical to compressed A. Branches constricted at bases 1. Plant segmented 			G. textorii
		a.	Segments and branches clavate	salicornia
		b.	Segments and branches flattened to terete with irregular to	
			dentate margins	G. urvillei
	2.	Pla	int not segmented	
		a.	Densely branched delicate plant with ultimate branches	
			attenuate, at times ending in bifurcate tips	G. subtilis
		þ.	Densely branched robust plant with irregularly alternate	
			branching; branches thicker distal to constriction at the base	
			and tapering towards the tip	G. changii
		C.	Sparsely branched plant with short main axis and short	· · · · ·
			irregularly alternate branching; tertiary branches short, fine.	
			and hairlike	G. firma

Description of the Species

Gracilaria salicornia (C. Agardh) Dawson, Bull. South Calif. Acad. Sci. 53(1):1-7, 1954.

Basionym: Sphaerococcus salicornia C. Agardh, C. A. Agardh pl. 8, p. 302, 1822.

Synonyms: As reported in Xia Bangmei, Chin. J. Oceanol. Limnol. 4(1):100–106, pl. 1., 1986.

Plants have regular branching that forms tightly entangled masses when internodes are long and low prostrate clumps when internodes are short. Long internodes are associated with plants growing in silted muddy mangroves. Plants found on rocks and corals in intertidal areas have short prominently clavate internodes. Two specimens collected from sandy substrate (PSM 880 from Pantai Dickson and PSM 1142 from Cape Rachado, both in Negeri Sembilan) have minimal to no constrictions and long branches. The first (PSM 880) is characterized by secondary and tertiary branches curving away from each other, with axillary angles reaching 115° (Fig. 1). Sterile and cystocarpic plants are found. *Congracilaria* is common on plants from the mangroves at Morib, Selangor.

Distribution: Mangrove estuary at Sungei Kisap, Pulau Langkawi (PSM 797); mangrove at Sementa, Selangor (PSM 116, PSM 772); mangrove at Morib, Selangor (PSM 904, PSM 1172); intertidal sandy substrate at Port Dickson, Negeri Sembilan (PSM 834–836, PSM 1130); intertidal sandy substrate, Pantai Dickson, Negeri Sembilan (PSM 880); rocks at Pantai Dickson, Negeri Sembilan (PSM 184, PSM 186, PSM 265, PSM 849, PSM 856, PSM 1115, PSM 1116); intertidal corals at Cape Rachado, Negeri Sembilan (PSM 154, PSM 1142); intertidal corals at Pulau Besar, Melaka (PSM 298); mangrove estuary at Sungei Pulai, Johor (PSM 1084); intertidal corals at Pulau Tioman, Johor (PSM 1029); intertidal corals at Pulau Sentosa, Singapore (WYC 5027).

Remarks: Gracilaria salicornia collected from the rocky shores of Pantai Dickson have poor quality agar of 345 g/cm² gel strength and maximum agar yield of 10% dry weight.

Gracilaria changii (Xia et Abbott) Abbott, Zhang et Xia, Pac. Sci. 45(1):12–27, 1991.

Basionym: *Polycavernosa changii* Xia et Abbott, Phycologia 26:407. 1987. Synonym: *Hydropuntia changii* (Xia et Abbott) Wynne, Taxon 38:476, 1989.

Plants are generally bushy, with the main branches much thicker than the third-order branches (Fig. 2) Two exceptions were found. The collection (PSM 1179) from a sandy substrate at Mersing, Johor, has a very fine little-branched plant that either has almost no tertiary branches or the very fine (0.1 mm) tertiary branches have dropped off (Fig. 3). The collection (PSM 1121) found attached on fish cages in Kukup, Johor, has very thick (1–2 mm) main branches but also almost no tertiary branches.

Distribution: Intertidal mudflats, Middle Bank, Gelugor, Pulau Pinang (JRF 1056, PSM 1184); mangroves at Sementa, Selangor (PSM 98, PSM 115, PSM 771, PSM 892, PSM 930); mangroves at Morib (PSM 905, PSM 1122, PSM 1171, PSM 1176); mangroves at Pantai Dickson, Negeri Sembilan (PSM 269, PSM 875, PSM 1066); attached to fish cages at Kukup, Johor (PSM 1121, PSM 1181); mangrove estuary at Sungei Pulai, Johor (PSM 1085); sandy beach at Johor Baru, Johor (PSM 908); sandy beach at Mersing, Johor (PSM 1179); washed onto shore at Changi Beach, Singapore (WYC 437).

Holotype: Fisher 1022, intertidal mudflat at Pulau Pinang.

Remarks: This species has often been misidentified as *G. cylindrica* (Doty et al. 1983, Santos and Doty 1983, Doty and Fisher 1987) and as *G. blodgettii* (Phang 1986, Phang and Maheswary 1990) because of the constrictions at the branch bases. *Gracilaria changii* is quite widely distributed in Malaysian waters. The agar content and gel strength vary with locality. Plants from the mangroves at Sementa have a maximum agar content of 29% dry weight but a low gel strength of 344 g/cm². Plants from the mangroves at Morib have average agar content and gel strength: 26% and 500 g/cm², respectively. Plants attached to fish cages in Johore have high agar content (39%) but low gel strength.

Gracilaria edulis (Gmelin) Silva, Univ. Calif. Berkeley Publ. Bot. 25:293, 1952. Basionym: *Fucus edulis* Gmelin, Hist. Fuc. p. 113, 1768.

Synonyms: *Polycavernosa fastigiata* Chang et Xia, Stud. Mar. Sinica 3:125, 1963. *Hydropuntia fastigiata* (Chang et Xia) Wynne, Taxon 38:477, 1989.

Plants are much-branched, wiry, and entangled. Ultimate branches may be short and spinelike or with tendrils (Fig. 4). Plants growing attached to fish cages have thicker primary branches (1.5 mm) than the plants found in mangroves (0.5–1.0 mm). Plants found on corals, however, appear to be bushy because of



Fig. 1. Gracilaria salicornia (C. Agardh) Dawson. A specimen (PSM 800) collected from an intertidal rock pool. Note wide axillary angles.

Figs. 2 and 3. *Gracilaria changii* (Xia et Abbott) Abbott, Zhang et Xia. Fig. 2, Plants attached to *Avicennia* root in the mangroves. Fig. 3, A specimen (PSM 1179) growing on a sandy substrate. Plant is very fine, with few branches. Original magnification \times 1.

Figs. 4 and 5. *Gracilaria edulis* (Gmelin) Silva. Fig. 4, A typical specimen (PSM 1185). Fig. 5, A specimen (PSM 1152) growing on corals. Note short, spinelike ultimate branches.

Fig. 6. Gracilaria firma Chang et Xia. A specimen (PSM 1127) collected from a fishcage.

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the short branches that have very short, fine, almost spinelike ultimate branches (Fig. 5).

Distribution: Intertidal mudflats at Gelugor, Pulau Pinang (PSM 1185); on fish cages at Sungei Merbok, Perak (PSM 1124); mangroves at Morib, Selangor (PSM 1173, 1174); on corals at Pulau Besar, Melaka (PSM 1152); on fish cages at Kukup, Johor (PSM 1186); mangrove estuary at Sungei Pulai, Johor (PSM 1066); intertidal pools at Pulau Tekong Besar, Singapore (WYC 434).

Remarks: This species is often found with *G. changii*, sharing the same intertidal muddy substrate. The two can be easily distinguished because the plants of *G. edulis* are bushier than those of *G. changii* and are red when dry rather than black. The average agar content and gel strength of agar from *G. edulis* plants from Morib are 10% and 120 g/cm², respectively.

Gracilaria subtilis (Xia et Abbott) Xia et Abbott, Pac. Sci. 45:23, 1991.

Basionym: *Polycavernosa subtilis* Xia et Abbott, Phycologia 26:413, 1987. Synonym: *Hydropuntia subtilis* (Xia et Abbott) Wynne, Taxon 38:477, 1987.

Holotype: Doty 32423, cystocarpic, growing on the lines of an experimental mariculture farm in Pulau Pinang, Malaysia.

Remarks: This species has not been collected by me, indicating that it is probably not a commonly found species. An isotype (MSD 32423) specimen brought to the taxonomy workshop in Sapporo by Professor Abbott was examined.

Gracilaria urvillei (Montagne) Abbott, Zhang et Xia, Pac. Sci. 45:23, 1991.

Basionym: *Hydropuntia urvillei* Montagne, Prodromus generum, specierumque phycearum novarum, p. 7, 1842.

Synonyms: *Corallopsis urvillei* (Montagne) J. Agardh, Sp. gen. ordines algarum 3(1):583, 1876. *Polycavernosa urvillei* (Montagne) Xia et Abbott, Phycologia 26:414, 1987.

Remarks: This species, distinctly characterized by large multisegmented plants, has not been collected by me. Collections by Doty and Burkill came from Sabah, east Malaysia; Melaka, peninsular Malaysia; and Singapore, indicating a wide distribution in the region.

Gracilaria textorii (Suringar) De Toni, Sylloge algarum III, p. 27, 1895.

Synonyms: *Sphaerococcus (Rhodymenia) textorii* Suringar, Ann. Bot. Mus. Bot. Lugd. Bat. p. 259, 1867; *Gracilaria vivesii* Howe, Bull. Torr. Bot. Club 38:503, 1911; *Gracilaria vivipara* Setchell et Gardner, Proc. Calif. Acad. Sci. ser. 4, 12:750, 1924; *Gracilaria sinicola* Setchell et Gardner, Proc. Calif. Acad. Sci. ser. 4, 12:752, 1924; *Gracilaria johnstonii* Setchell et Gardner, Proc. Calif. Acad. Sci. ser. 4, 12:752, 1924; *Gracilaria johnstonii* Setchell et Gardner, Proc. Calif. Acad. Sci. ser. 4,

Remarks: This species with distinctly flat leafy plants has not been collected by me. Doty and Fisher (1987) reported that it was found growing on "debris at the deepest intertidal levels but [under] natural conditions grows on muddy shores." A specimen (JRF 1016) brought to the Sapporo workshop by Professor Abbott was examined. Gracilaria firma Chang et Xia, Stud. Mar. Sinica 11:143-144, 162-163, 1976.

Plants are erect, terete, 0.5–2.0 mm thick, firm, and reddish to dark brown when dry. Branches are sparse, irregularly alternate; tertiary branches are short, fine, and hairlike (Fig. 6). The base of the branch narrows to form a short stipe. Transition in cell size from cortex to medulla is gradual. Tetrasporangial plant is similar in size and branching pattern, with cruciate tetrasporangia scattered on surface of plant. Cystocarps are prominent and densely scattered over plants, rostrate at ostiole and constricted at base. Pericarp consists of smaller cells near surface and larger cells inside. Gonimoblast cells are very small; absorbing filaments are few, and grow upward and sideways. No male plants have been collected.

Distribution: Attached to fish cages at Sungei Merbuk, Perak, northern peninsular Malaysia (PSM 1127).

Remarks: The species resembles *G. firma*, *G. changii*, and *G. edulis*. It can be separated from *G. edulis* on the basis of the abundance of basal absorbing filaments (few in *G. firma*) and structure of pericarp cells. It has a less branched plant than *G. changii*, with gradual transition from cortex to medulla, cystocarp constricted at base, and no horizontally oriented inner pericarp cells.

Three non-Malaysian specimens of *G. firma* were examined at the Sapporo workshop: a typical *G. firma* from Trat, Thailand, collected by Lewmanamont on May 5, 1985; a nontypical specimen (KL 5201) from Laem Tien, Trat, Thailand, collected by Lewmanomont on April 18, 1986; and a specimen from the Philippines (MSD 33352) collected by Alvarez. The Malaysian material is most similar to the Philippine specimen in plant form, size, and branching. The nontypical specimen (KL 5201) has numerous tertiary branches and is most different from all the rest.

Sungei Merbuk is quite close to Thailand where *G. firma* has been reported from Songkhla, which is at the southwestern part of the Gulf of Thailand (Abbott 1988). It is also found in South China; the type locality is Guangdong Province (Chang and Xia 1976).

Gracilaria coronopifolia J. Agardh, Sp. gen. ordines algarum, vol. 2, p. 692, 1852.

Plants are short, from 4–6 cm, irregular, and subdichotomous, branching to form an entangled mass; purplish-red when fresh but red when dry. Tertiary branches (up to 1.5 m) are much thicker than main branches (0.5 mm), probably because of anastomosing of the branches (Fig. 7); ultimate branches have pointed apices. Cuticle is thick, one to two rows of small cortical cells before large medullary cells, and transition from cortex to medulla is abrupt. Only young cystocarps are found, rostrate at ostiole and constricted at the base. No distinct size variation is found in pericarp cells, gonimoblast cells are small and compressed, and upward-growing absorbing filaments are present. No male plants or sporophytes were available for examination.

Distribution: In intertidal rock pools at muddy beach of Pulau Tekong Besar, Singapore (WYC 273, WYC 432).



Fig. 7. Gracilaria coronopifolia J. Agardh. A specimen (WYC 273) collected from an intertidal rock pool.

Fig. 8. *Gracilaria salicornia* (C. Agardh) Dawson. Typical plants growing attached to a rope in the mangroves (one-half natural size).

Fig. 9. Gracilaria edulis (Gmelin) Silva. Typical plants attached to Avicennia root in the mangroves (one-half natural size).

Remarks: This species resembles *G. edulis* in having subdichotomous branching, rostrate ostiole, and constricted base in the cystocarp. However, unlike *G. edulis*, it has no "thick-walled bricklike cells" in the pericarp and no basal absorbing filaments (Xia and Abbott 1987). It resembles closely the description by Yamamoto (1978). Also, Yamamoto observed that branches of young plants anastomose, which is observed in most of the Malaysian specimens described here. WYC 237 and WYC 432 are similar in appearance to Yamamoto's specimens (see Yamamoto 1978, p. 49, figs. 2, 3).

The following non-Malaysian specimens of *G. coronopifolia* were examined at Sapporo: MSD 33253 from Haleiwa Beach Park, Oahu, Hawaii; MSD 33257 from Oahu, Hawaii; IA Abbott 16117 from Kaneohe Bay, Oahu, Hawaii; IA Abbott 16638 purchased from Honolulu Fish Market, Oahu, Hawaii. WYC 273 and WYC 432 resemble MSD 33253 most. Other specimens had thicker plants. WYC 273 and WYC 432 resemble the specimens shown in figures 44 (from Japan) and 48 (from Hainan Island, China) but differ from figures 46 (from Philippines) and 47 (Hawaii) in Abbott and Norris (1985). Two other specimens, PSM 1180 collected from intertidal rock pools at Tanjung Bunga, Pulau Pinang, and PSM 1183 collected from rock pools at Tanjung Tokong, Pulau Pinang, resemble the currently described specimens in plant morphology, especially the anastomosing branches. PSM 1180 has no reproductive structures. PSM 1183 has cystocarps with rostrate ostiole and constricted base and small gonimoblast cells. It also has abrupt transition from cortex to the medulla. Until male and sporophytic plants are collected, these plants may also be identified with *G. coronopifolia*.

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Literature Cited

- Abbott, I. A. and Norris, J. N., eds. 1985. Taxonomy of economic seaweeds: with reference to some Pacific and Caribbean species. California Sea Grant Program, La Jolla, Calif.
- Abbott, I. A. 1988. Some species of *Gracilaria* and *Polycavernosa* from the Siboga Expedition. In: Tax. Econ. Seaweeds 2, pp. 151–156.
- Abbott, I. A., Zhang, J., and Xia, B. 1991. *Gracilaria mixta*, sp. nov.and other western Pacific species of the genus (Rhodophyta: Gracilariaceae). Pac. Sci. 45(1):12–27.
- Barton, E. S. 1901. The genus Halimeda. Siboga Exped. Monogr. 60.
- Burkill, H. M., Greenwood-Barton, L. H., and Crowther, P. C. 1968. Some studies of Malayan agarophytic and alginophytic seaweeds. Gardens Bull. Singapore 22:429–441.
- Chang, C. F., and Xia, B. M. 1976. Studies on Chinese species of *Gracilaria*. Stud. Mar. Sinica 11:157–163.
- Doty, M. S., and Fisher, J. 1987. Experimental culture of seaweeds (*Gracilaria*) in Penang, Malaysia. Bay of Bengal Program. Working paper No. 52. Food and Agriculture Organization, Madras, India.
- Doty, M. S., Santos, G. A., and Ong, K. S. 1983. Agar from *Gracilaria cylindrica*. Aquat. Bot. 15:299–306.

Gepp, A., and Gepp, E. S. 1911. The Codiaceae of the Siboga Expedition, including a monograph of Flabellariaceae and Udoteae. Siboga Exped. Monogr. 62.

- Martens, G. von. 1866. Die Preussische Expedition nach Ost-Asien. Bot. Theil, Berlin.
- Norris, J. N. 1985. *Gracilaria* and *Polycavernosa* from the Caribbean and Florida: key and list of the species of economic importance. In: Tax. Econ. Seaweeds 1, pp. 101–113.
- Phang, S. M. 1984. Seaweed resources of Malaysia. Wallaceana 33:3-8.
- Phang, S. M. 1986. Malaysia's seaweed flora. In: Proceedings Ninth Annual Seminar Malaysian Society of Marine Sciences, pp. 17–45.
- Phang, S. M., and Maheswary, V. 1990. Phycocolloid content of some Malaysian seaweeds. In: Proceedings Twelfth Annual Seminar Malaysian Society of Marine Sciences, pp. 65–78.

- Phang, S. M., and Wee, Y. C. 1991. Benthic marine algae. In: Kiew, R., ed. The state of nature conservation in Malaysia, pp. 51–61.
- Santos, G. A., and Doty, M. S. 1983. Agarose from *Gracilaria cylindrica*. Bot. Mar. 26:31–34.
- Teo, L. W., and Wee, Y. C. 1983. Seaweeds of Singapore. Singapore University Press, Singapore.
- Weber van Bosse, A., and Foslie, M. 1904. The Corallinaceae of the Siboga-Expedition. Siboga Exped. Monogr. 61:78–110.
- Xia Bangmei, and Abbott, I. A. 1987. New species of *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta) from the western Pacific. Phycologia 26(4):405–418.
- Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25(2):97–152.

THE SPECIES OF GRACILARIA FROM THAILAND

Khanjanapaj Lewmanomont

Abstract

Thirteen species of *Gracilaria* from Thailand are described. Eight were previously reported by Abbott in 1988, four are new records for Thailand, and one is newly described as *G. minuta*.

Introduction

Knowledge of the red algal genus *Gracilaria* from Thailand was not seriously pursued until 1986, when the project Seaweed Production and Processing was started. In this project, specimens of *Gracilaria* were collected, and herbarium sheets were prepared and sent to Dr. Abbott for identification. In 1988, four species of *Gracilaria* and four species of *Polycavernosa* from Thailand were described by Abbott, of which two were described as new: *G. irregularis* and *P. percurrens*. All species described in *Polycavernosa* have subsequently been assigned to *Gracilaria* (Abbott et al. 1991).

This chapter reports 13 species of *Gracilaria* collected from the Gulf of Thailand and the Andaman Sea. Eight have been previously reported (Abbott 1988), four are new records for Thailand, and one is newly described.

Key to the Species of Gracilaria from Thailand

1.	Thallus cylindrical (terete) throughout2
1.	Thallus compressed or flattened 12
	2. Thallus delicate, main axis less than 1 mm in diameter
	2. Thallus slender or robust, main axis nearly 1 mm or more in diameter 4
3.	Cystocarp markedly rostrate and constricted at the base, nearly the
	same diameter or larger than bearing branches G. tenuistipitata
	With numerous delicate lateral branchletsvar. liui
	• With few elongate lateral branches, branching mostly basal var. tenuistipitata
3.	Cystocarp globular, rostrate, not constricted at the base G. minuta
	4. Main axis and branches nearly the same diameter
	4. Diameter not the same throughout 10
5.	Thallus dichotomously or trichotomously branching, spermatangia in
	groups or polycavernosa type
5.	Thallus not dichotomously or trichotomously branching, spermatangia
	verrucosa or chorda type
	6. Thallus clustered or fastigiate, branch intervals long G. edulis
	6. Thallus corymbose, branches dense and at short intervals G. bangmeiana
7.	Thallus bushy, more than two orders of branching, spermatangia
	verrucosa type
7.	Thallus of few long slender branches, branching mostly basal,
	spermatangia in superficial layer or chorda type G. lemaneiformis

8. Thallus robust, more than 2 mm wide	9
8. Thallus slender, less than 2 mm wide	ri
9. Branches inflated with tapering ends and constricted at bases G. chang	ļÜ
9. Branch apices blunt or acute, branches of first order constricted at bases G. firm	а
10. Thallus erect, branches without articulation1	1
10. Thallus prostrate to semierect, branches with articulation	a
11. Thallus succulent, branching mostly secund G. irregular	is
11. Thailus not succulent, branches percurrent, lower part slender and	
broadened distally G. percurren	s
12. Thallus flat, membranous, branching dichotomous in one plane	rii
12. Thallus compressed, prostrate, and succulent	5

Description of the Species

Gracilaria bangmeiana Zhang et Abbott, Pac. Sci. 45:23, 1991.

(Figs. 1, 2)

Basionym: *Polycavernosa ramulosa* Chang et Xia, Stud. Mar. Sinica 3:125, 1963. (Non *Gracilaria ramulosa* J. Agardh, Sp. gen. ordines algarum epicr., p. 417, 1876).

Synonym: *Hydropuntia ramulosa* (Chang et Xia) Wynne, Taxon 38:477, 1989. Thallus rigid, 5–13 cm tall, with many orders of short branches, intervals short, forming a dense tuft, somewhat corymbose; branching dichotomous, branches 0.5–1.0 mm in diameter; dark red. Frond in transverse section consisting of large thin-walled medulla, 100–250 µm in diameter, one to two layers of small cortical cells; transition from medulla to cortex abrupt. Tetrasporangial plant not found. Spermatangia in groups of deep saclike cavities (polycavernosa type), slightly elevated from surface of thallus. Cystocarps globose, 0.8–1.4 mm in diameter, rostrate, constricted at bases; gonimoblasts consisting of elongate cells; basal absorbing filaments robust with many branches, lateral absorbing filaments few; carpospores roundish, 18–25 µm in diameter; pericarp consisting of eight to ten rows of cells, oval and horizontally compressed. Male and female plants distinguished by the dense and quite short intervals of branching in the female plants.

Habitat: Growing on rocks in clear water of sublittoral zone and on fish cages together with *G. edulis*.

Distribution: Ban Phe, Rayong Province, and Palian, Trang Province. This is a new record for Thailand.

Gracilaria changii (Xia et Abbott), Abbott, Zhang, and Xia, Pac. Sci. 45:23, 1991.

(Fig. 3)

Basionym: *Polycavernosa changii* Xia et Abbott, Phycologia 26:407, fig. 3, 1987.

Thalli 5–7 cm tall, with many branches arising from a small discoid holdfast or from a percurrent axis; branching alternate or irregular of two to four orders; branches cylindrical or inflated, 1.0–2.5 mm in diameter, abruptly constricted at



Figs. 1–2. *Gracilaria bangmeiana*. Fig. 1, A specimen from fish cage, Trang Province, Thailand. Fig. 2, Fragments of female plant from Rayong Province, Thailand. Fig. 3. *Gracilaria changli* from Trat Province, Thailand.

Fig. 4. *Gracilaria edulis*, a specimen from sandy mud, Trat Province, Thailand. Fig. 5. *Gracilaria eucheumoides* found growing on a fragment of dead coral, from Phuket Province, Thailand.

Fig. 6. Gracilaria irregularis with secund branches, from Trat Province, Thailand.

bases and tapering toward apices. Fronds in transverse section consisting of large medullary cells with thick cell walls, two to three layers of cortical cells; transition of cells abrupt. Tetrasporangia ovoid, $13-17 \times 28-36 \mu m$ in diameter, cruciately divided. Spermatangial conceptacles verrucosa type, adjoining ones frequently coalescing, forming polycavernosa-type spermatangia. Cystocarps conical or semiglobose, 1.0-1.4 mm wide, 0.5-0.8 mm high, some slightly rostrate, not constricted at bases; gonimoblasts consisting of numerous small cells; absorbing filaments few, lateral and upper; carpospores rounded, $18-24 \mu m$ in diameter; pericarps thick, consisting of two kinds of cells, the outer five to six rows rounded, the inner six to nine rows compressed.

Habitat: Growing on gravel, shells, rock fragments, mangrove roots, or fish cages in sandy-muddy to muddy areas with high turbidity.

Distribution: This species is rather common along the east coast of the Gulf of Thailand. It is abundant in Trat Province and grows in some areas in Chantaburi and Rayong Province. In Chon Buri Province, where it had not been found before, it was introduced at Si Racha Fisheries Research Station in 1986. This species is not common along the west coast of the Gulf of Thailand but is commonly found growing on fish cages in Trang, Satun, Krabi, and Phangnga provinces along the Andaman Sea. It was first described from Malaysian material by Xia and Abbott (1987) and from Thailand by Abbott (1988).

Gracilaria edulis (Gmelin) Silva, Univ. Calif. Publ. Bot. 25:293, 1952.

(Fig. 4)

Basionym: Fucus edulis Gmelin, Hist. Fuc., p. 113, 1768.

Synonyms: *Polycavernosa fastigiata* Chang et Xia, Stud. Mar. Sinica 3:125, 1963; *Hydropuntia fastigiata* (Chang et Xia) Wynne, Taxon 38:477, 1989; Abbott et al., Pac. Sci. 45:20, 1991.

Thallus growing from a disclike holdfast, with prostrate rhizome forming a tuft or a cluster 6–27 cm tall; branching dichotomous or trichotomous, five to seven orders; branches 0.4–1.0 mm in diameter. Two groups of plants can be distinguished. The first grows in fastigiate tufts with five to seven (up to 10) orders of branches with narrow-angle furcations, branch intervals gradually decreasing in length, the last order ending in bifurcate or trifurcate apices. This group is found growing on fish cages or on rocks in rather clear water. The second group grows on rocks or mud surface in sandy mud areas, forming an entangled mass or loose clump with hooks or rootlike discs on branch apices; branching of five to seven orders with wide-angle furcation, lower branch intervals much longer than the last two orders; branch cylindrical, lower branches about 1 mm thick and becoming thinner, to 0.3 mm, for terminal segments with attenuate apices.

Frond in transverse section consisting of roundish thin-walled medulla, 100–250 μ m in diameter, one to two rows of small cortical cells; transition from medulla to cortex abrupt. Tetrasporangia ovoid in transverse section 20–60 × 32–38 μ m, surrounded by elongate cortical cells. Spermatangia in groups of six to ten deep saclike cavities (polycavernosa type), slightly elevated from surface of thallus.

Cystocarps globose, 0.7–1.2 mm in diameter with rostrate tips and constricted at bases; gonimoblasts consisting of elongate cells; carpospore roundish, $15 \times 22 \,\mu$ m in diameter; pericarps thick consisting of nine to 14 rows, cells of the outer rows oval, inner cells horizontally compressed; basal absorbing filaments robust with many branches, lateral absorbing filaments rare.

Habitat: Growing in loose clumps on rocks or mud surface in muddy areas of intertidal zone, in dense tufts when growing on fish cages, and in loose fastigiate tufts on rocks in clear water.

Distribution: Trat Province, the east coast of the Gulf of Thailand; Trang, Phuket, and Satun provinces along the coast of the Andaman Sea. *Gracilaria edulis* was first attributed to Thailand by Abbott (1988, as *P. fastigiata*).

Gracilaria eucheumoides Harvey, Proc. Am. Acad. Arts Sci. 4:331, 1859. (Fig. 5)

Thallus compressed, prostrate, thick and succulent; branching pinnate to dichotomous; branches 1–3 cm long, 0.5–1.0 cm wide, 0.2–0.9 (up to 1.1) cm thick, with dentate margins, attaching by discoid holdfasts. Fronds in transverse section consisting of many layers of cells with stellate plastids, transition of cells from medulla to cortex gradual, medullary cells 100-200 μ m in diameter. Only a few specimens of tetrasporic plants found; tetrasporangia roundish on surface view and elongate in transverse section. Gametophytic plants not found.

Habitat: Growing on dead coral fragments.

Distribution: *Gracilaria eucheumoides* is newly reported from Thailand. This species is not common in Thai waters; only a few thalli were found at Rawai Beach, Phuket Province.

Gracilaria firma Chang et Xia, Stud. Mar. Sinica 11:143, 162, 1976.

(Figs. 7, 8)

Thallus erect, caespitose, with many branches coming from a small discoid holdfast or from a percurrent axis, 5–20 cm tall; branching alternate or irregular or secund of two to five orders, 1.0–2.5 mm in diameter, first-order branches always constricted at bases, others with or without constrictions, apices blunt or acute; plants yellowish-brown. Two groups of plants can be distinguished. The first group has few orders of branching; branches long, cylindrical, terminal branches without or with some furcations and blunt apices. The second group has many orders in branching, branch intervals of the last two orders short and forming a cluster with acute or blunt apices.

Frond in transverse section consisting of medulla of many layers of thin-walled cells, cortex only one to two cells thick; transition of medulla to cortex gradual. Tetrasporangia ovoid to spherical, 18–38 μ m in diameter. Spermatangial conceptacles oval (verrucosa type), 35–58 μ m wide, 50–80 μ m deep. Cystocarps conical, rostrate not constricted at bases, 0.5–0.7 mm high, 0.8–1.2 mm wide; gonimoblasts consisting of filaments of numerous small elongate cells with obscure cell walls and reticulate pit connections, occupying almost the whole cavity; absorbing



Figs. 7–8. Gracilaria firma. Fig. 7, A specimen from Laem Tian, Trat Province, Thailand, with few orders of branching. Fig. 8, A specimen from Laem Sok, Trat Province, Thailand, with many orders of branching.

Fig. 9. Gracilaria fisheri from Songkhla Province, Thailand

Fig. 10. Gracilaria lemaneiformis from fish cage, Trang Province, Thailand. Fig. 11. Gracilaria percurrens from Trat Province, Thailand.

filaments scarce, upper, lateral, or basal; carpospores spherical, 16–25 μ m; pericarps thick, almost one third the size of cystocarp, 10–15 rows of cells with distinct cell walls.

Habitat: Growing on shells, gravel, and rock fragments in muddy areas of turbid water.

Distribution: This species occurs only in Trat Province at Laem Tian, Laem Hin, Laem Sok, Ao Cho, and Ao Len. It was first reported for Thailand by Abbott (1988).

Gracilaria fisheri (Xia et Abbott) Abbott, Zhang, and Xia, Pac. Sci. 45:23, 1991. (Fig. 9)

Basionym: *Polycavernosa fisheri* Xia et Abbott, Phycologia 26:411–413, figs. 5, 13, 1987.

Synonym: Hydropuntia fisheri (Xia et Abbott) Wynne, Taxon 38:477, 1989.

Thallus bushy, 13–30 (up to 45) cm tall, with many branches coming from a short stipe or from percurrent axis; branching alternate, three to four orders; branches cylindrical, 0.6–2.3 mm in diameter, constricted at bases and tapering toward apices. Frond in transverse section consisting of medulla 220–620 μ m in diameter, with thick layers of cortex; transition from medulla to cortex gradual. Tetrasporangia ovoid, tetraspores 20–25 μ m in diameter. Spermatangia ovoid, single or in groups of two to three cavities. Cystocarps conical, rostrate, unconstricted at bases, 0.3–0.7 mm high, and 1.0–1.3 mm wide; gonimoblasts consisting of many small cells; absorbing filaments lateral and upper; pericarp thick with inconspicuous cell walls and star-shaped contents; carpospores rounded, 18–24 μ m in diameter, or ovoid, 8–14 × 14–20 μ m.

Habitat: Commonly found growing on living and empty shells (*Cerithium* sp.) and on broken rocks, gravel, polyethylene bags, and fish cages in sandy-muddy areas of turbid water.

Distribution: This species is abundant in Ao Pattani (type locality); Pattani Province; and Talesap Songkhla, Songkhla Province, and was introduced in many provinces along the coasts of the Gulf of Thailand. It was first reported by Xia and Abbott (1987).

Gracilaria irregularis Abbott, Tax. Econ. Seaweeds 2, p. 141, figs. 1, 5–6, 1988. (Fig. 6)

Thalli erect, succulent, 2.5–13.8 cm tall, percurrent axes 1–5 mm in diameter; branching mostly secund; branches always smaller than main axes, the last order of branches sometimes clustered. Fronds in transverse section consisting of medulla of large cells, 300–775 μ m in diameter, cortex one to two cells thick, sometimes three to five cells; transition of cells from medulla to cortex abrupt. Tetrasporangia cruciate, 23–36 μ m in diameter, tetrasporic plants with many large "gland" cells. Spermatangia in superficial layer (chorda type); male plants pale. Cystocarps conspicuous, dome-shaped, 0.6–0.8 mm high and 0.9–1.6 mm wide, not constricted at bases; gonimoblast consisting of many small cells with obscure cell walls and star-shaped contents, giving a reticulate appearance; pericarps roundish or slightly compressed, nine to 12 rows; absorbing filament lacking; carpospores oval to rounded, 21–25 μ m in diameter.

Habitat: Growing on gravel, shells, and rock fragments in sandy-muddy areas together with *G. changii* and *G. firma*.

Distribution: Ao Len and Ao Cho, Trat Province. The species was described from Thailand by Abbott (1988).

Remarks: Abbott (1988) described the male plants as having spermatangial conceptacles of the verrucosa type, oval to obovate, numerous, adjoining ones frequently coalescing. I have been unable, so far, to find any verrucosa type male plants. I have seen the chorda type only. In order to confirm the male type, gametophytic plants from tetraspores were cultured. They showed the chorda type spermatangial arrangement. *Gracilaria irregularis* can be distinguished from other

Gracilaria species in Thailand by its short and succulent axis and secund branching.

Gracilaria lemaneiformis (Bory) Weber-van Bosse, Siboga Exped. 59b:435, 1928 (as *lemanaeformis*). (Fig. 10)

Basionym: *Gigartina lemaneiformis* Bory, In: Duperrey, L. E. (ed.), Voyage autour du monde...sur...La Coquille, p. 151, 1828. (as *lemanaeformis*).

Synonyms: Specimens of the several synonyms of this widely distributed species have not previously been reported from Thailand. Their names are omitted here because they have been repeatedly listed elsewhere [Editor].

Thallus solitary or caespitose, up to 46 cm tall, with few to several long branches 0.5–1.4 mm in diameter; branching irregular, mostly from lower portion, branches simple, two to five branchlets frequently occurring from a single branch apex. Frond in transverse section consisting of medulla of large thin-walled cells, 130–260 μ m in diameter, two layers of cells in cortex; transition from medulla to cortex abrupt. Tetrasporangia ovoid 15–28 × 30–50 μ m. Spermatangia superficial (chorda type). Cystocarps spherical, 0.7–0.9 μ m in diameter, slightly rostrate or nonrostrate and constricted at bases; gonimoblasts consisting of filaments of many small cells with obscure cell walls and reticulate contents; carpospores roundish to ovoid, 18–25 μ m in diameter; pericarp 10–14 layers; without absorbing filaments.

Habitat: Growing on fish cages.

Distribution: Trang Province. This is a new record for Thailand.

Remarks: *Gracilaria lemaneiformis* resembles *G. tenuistipitata* var. *liui* and can be separated with certainty only on basis of spermatangial configuration. Spermatangia are superficial in *G. lemaneiformis* (chorda type) and in shallow saucerlike depressions in *G. tenuistipitata* var. *liu.* The latter species is grown under mariculture conditions in Taiwan and South China.

Gracilaria percurrens (Abbott) Abbott, Pac. Sci. 45:23, 1991.

(Fig. 11)

Basionym: *Polycavernosa percurrens* Abbott, Tax. Econ. Seaweeds 2, pp. 146–148, fig. 13, 1988.

Synonym: Hydropuntia percurrens (Abbott) Wynne, Taxon 38:477, 1989.

Thallus erect, with percurrent axis, 12–21 cm tall; branching alternate to irregular, branches constricted at bases and broadened distally, 0.5–2.2 mm in diameter, with blunt apices. Frond in transverse section consisting of large thin-walled medullary cells, 123–370 μ m in diameter, two layers of cells in cortex; transition of cells from medulla to cortex abrupt. Tetrasporangia 15–18 × 25–29 μ m. Spermatangial conceptacles saclike, single (verrucosa type) and in groups of two to four cavities (polycavernosa type). Cystocarps conical, rostrate, not constricted at bases, 0.5–0.8 mm high, 0.7–1.0 mm wide; gonimoblast filaments consisting of small cells; basal absorbing filaments few, lateral and upper absorbing filaments few to many; carpospores roundish to ovoid, 13–20 μ m in

diameter; pericarps thick, 10-14 rows of cells.

Habitat: Growing on rock fragments in intertidal zone of turbid water at Laem Sok, Trat Province, and on fish cages at Ko Yo, Songkhla Province. Abbott (1988) reported the occurrence of the materials found on fish cages and collected by J. R. Fisher from Phe Fisheries Station, Rayong Province.

Distribution: Laem Sok, Trat Province; Ko Yo (type locality), Songkhla Province; and Phe, Rayong Province. The species was first described from Thailand by Abbott (1988).

Gracilaria salicornia (C. Agardh) Dawson, Bull. South. Calif. Acad. Sci. 53:4, 1954. (Fig. 12)

Basionym: Sphaerococcus salicornia C. Agardh, Sp. algarum, vol. 1, p. 302, 1822.

Synonyms: See synonyms in Xia Bangmei (1986).

Thalli prostrate to semierect; branching of prostrate form dichotomous to irregular; branches cylindrical, 3–5 mm in diameter, partly constricted; forming a rough entangled mass of various sizes with rootlike discs on branch apices; in semi-erect form, segments constricted throughout, with two to four branches at each node, 10–15 cm tall; yellow to bright orange. Fronds in transverse section consisting of many layers of thin-walled cells, 150–400 μ m in diameter, cortical layer of two to four cells with abundant "gland" cells; transition of cells from medulla to cortex gradual. Tetrasporangia cruciately divided, 25–30 × 37–45 μ m in diameter, scattered over surface of thallus. Spermatangial conceptacles oval (verrucosa type), single or in group of two to three cavities. Cystocarps globose, nonrostrate, slightly constricted at bases, 0.8–2.0 μ m in diameter; gonimoblasts consisting of many small cells; pericarp thick, consisting of two kinds of cells, six to eight elongate cells in outer layer, five to eight rounded cells in inner layer; absorbing filaments lateral and upper; carpospores spherical, 16–24 μ m in diameter.

Habitat: Growing on various kinds of substrates, rocks, gravel, shells, and mangrove roots, in clear to turbid water. Specimens growing in clear water are always orange; those growing in muddy areas are dark brown.

Distribution: This species is common in Thai waters. It is found in almost every province along the sea coasts. As *G. cacalia*, it was reported by Velasquez and Lewmanomont (1975), a species later merged by Xia (1986) with *G. salicornia*.

Gracilaria tenuistipitata Chang et Xia, Stud. Mar. Sinica 11:161, 1976.

(Figs. 13, 14)

Thallus slender, 21–54 cm tall, with few orders of branching, lateral branchlets delicate, few to numerous; branching alternate; branches 0.4–1.0 mm in diameter. Frond in transverse section consisting of a few layers of cells, medulla of large cells at the center 155–320 μ m in diameter, one to two layers of small cortical cells; transition from medulla to cortex abrupt. Tetrasporangia ovoid in transverse section, 20–30 × 30–46 μ m. Spermatangia in shallow depressions (textorii type)



Fig. 12. Gracilaria salicornia from Ko Samui, Skurat Thani, Thailand. Fig. 13. Gracilaria tenuistipitata var. tenuistipitata from Songkhla Province, Thailand. Fig. 14. Gracilaria tenuistipitata var. Ilui from Ban Dato, Pattani Province, Thailand. Fig. 15. Gracilaria textorii from Trang Province, Thailand.

surrounded by elongate cortical cells. Cystocarps markedly rostrate and constricted at bases, diameter nearly the same or greater than that of bearing branches, 0.4–1.0 mm high, 0.6–1.2 mm wide; gonimoblasts consisting of large cells; carpospores rounded to ovoid, 17–24 µm in diameter; absorbing filaments lateral; pericarp eight to ten layers, cells rounded with distinct cell walls.

Gracilaria tenuistipitata var. tenuistipitata Chang et Xia, Stud. Mar. Sinica 11:161, figs. 6 and 7, pl. 1, 1976.

Typical *tenuistipitata* specimens have one to two orders of elongate branches with same diameter, 0.6–1.0 mm as main axes; branching from near bases, or along axes.

Habitat: Growing naturally on shells and gravel in sandy-muddy areas.

Gracilaria tenuistipitata var. *liui* Zhang et Xia, Tax. Econ. Seaweeds 2, pp. 131–132, figs. 1, 3–9, 1988.

Plants of variety *liui* slender, with branching more dense than that of variety *tenuistipitata* and with two to three orders, the second order attached alternately or irregularly, with ends of branches curling away from percurrent axes; numerous delicate branchlets 0.2 mm in diameter. Variety more common than *tenuistipitata* in the field, detaching and forming large masses of contorted thalli.

Distribution: Commonly found in Ao Pattani, Pattani Province, and Talesap Songkhla, Songkhla Province, in southern Thailand. This species was previously reported from Thailand by Zhang and Xia (1988) and by Abbott (1988).

Gracilaria textorii (Suringar) DeToni, Mem. R. Inst. Veneto Sci. Lett. Art. 25:259, 1867. (Fig. 15).

Basionym: Sphaerococcus textorii Suringar, Ann. Mus. Bot. Lugduno-Batavi 3:259, 1868.

Synonyms: Many species have been placed in the synonymy of *G. textorii*, but as they have not been reported from Thailand previously, they do not create confusion with the recognition of this species.

Thallus foliose, attached below by a small discoid holdfast, 4.2–13.2 cm tall and 6.1–18.8 cm wide; blade branched dichotomously or subdichotomously in one plane, segments 0.7–2.0 cm wide, membranous when dried, with entire margins or proliferous, apices blunt, bifurcate; dark red to greenish red. Frond in transverse section 147–185 μ m thick, consisting of a few layers of medullary cells, transition of cells from medulla to cortex abrupt. Gametophytic plants, both male and female, smaller than tetrasporic plants; male plants very rare, tetrasporic plants abundant. Tetrasporangia ovate, scattered on both surfaces, 16–25 × 23–27 μ m, surrounded by elongate cortical cells. Male frond pale, spermatangia in shallow or saucerlike depressions (textorii type). Cystocarps large and prominent, semiglobose to globose, 0.7–1.0 mm in diameter, slightly rostrate, not constricted at bases; gonimoblast cells small, numerous, almost occupying the cystocarpic cavity; absorbing filaments upper and lateral.

Habitat: Growing on rocks and fish cages.

Distribution: Trang Province. This is a new record from Thailand.

Gracilaria minuta sp. nov. (Figs. 16–22)

Plantae erectae; subtiles, 1–2 cm altae (raro usque ad 5 cm); axes percurrentes, usque ad 0.7 mm diametro, non ramosae, vel paucis ramosis. Tetrasporangia elongatis cellulis corticalibus circumcincta. Spermatangia in depressionibus vadosis (textorii typus). Cystocarpium rostratum, filis absorbentibus.

Etymology: This species is named for the size of the plants, which usually are less than 2 cm tall when reproductive.



Fig. 16. Gracilaria minuta, showing forms of thalli.

Plants erect, delicate, 1–2 (rarely up to 5) cm tall, axes percurrent, up to 0.7 mm in diameter; unbranched, or with few branches. Tetrasporangia surrounded by elongate cortical cells; spermatangia in shallow depressions (textorii type); cystocarps rostrate, with absorbing filaments.

Frond in transverse section consisting of a few layers of medullary cells, 33– 96 µm in diameter, one to two layers of small cortical cells; transition from medulla to cortex abrupt. Tetrasporangia ovoid, $27-30 \times 34-45 \mu m$, surrounded by elongate cortical cells; tetraspores roundish to ovoid, $12-22 \mu m$ in diameter. Spermatangia in shallow depressions (textorii type), the depressions $22-32 \mu m \times 22-45$ µm, surrounded by elongate cortical cells. Cystocarps globular, rostrate, not constricted at bases, diameter nearly the same as or larger than that of bearing branches, 0.4-1.2 mm; gonimoblasts consisting of large cells, ovoid to oblong with obscure cell walls; basal absorbing filaments with few branches; lateral and upper absorbing filaments scarce; carpospores roundish with a stellate plastid, $29-32 \mu m$ in diameter; pericarp thin, five to eight rows of rounded cells.



Figs. 17–22. Fig. 17, Mature thall growing on rock fragment. Fig. 18, Transverse section of cortex with tetrasporangium. Fig. 19, Longitudinal section of cystocarp. Fig. 20, Longitudinal section of pericarp. Fig. 21, Basal absorbing filament. Fig. 22, Transverse section of spermatangial conceptacles (textoril type).

Holotype: KL 5616, collected January 30, 1988, growing on rock fragments, gravel, and shells in sandy mud of the upper littoral zone, which is exposed during low tide, at Ao Cho, Trat Province. It is deposited in the Kasetsart University Museum of Fisheries, Bangkok. Other specimens include KL 6517, collected from Ao Yang, Trat Province, April 11, 1989, and KL 7017, topotype collected from Ao Cho, January 26, 1991.

Remarks: This species is similar to *G. tenuistipitata* in external and internal structures, except that *G. minuta* is much smaller, the cystocarp is not constricted at the base, and branched basal absorbing filaments have few branches.

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Literature Cited

- Abbott, I. A. 1988. Some species of *Gracilaria* and *Polycavernosa* from Thailand. Tax. Econ. Seaweeds 2, pp. 137–150, figs. 1–14.
- Abbott, I. A., Zhang Jungfu, and Xia Bangmei. 1991. Gracilaria mixta, sp. nov. and other western Pacific species of the genus (Rhodophyta: Gracilariaceae). Pac. Sci. 45:12– 27, figs. 1–25.
- Velasquez, G. T., and Lewmanomont, K. 1975. A checklist on the study of the benthic marine algae of Thailand. Kasetsart Univ. Fish. Res. Bull. 8:1–25.
- Xia Bangmei 1986. On *Gracilaria salicornia* (C. Agardh) Dawson. Chin. J. Oceanol. Limnol. 4:100--106.
- Xia Bangmei, and Abbott, I. A. 1987. New species of *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta) from the western Pacific. Phycologia 26(4):405–418.
- Zhang Junfu, and Xia Bangmei. 1988. On two new *Gracilaria* (Gigartinales, Rhodophyta) from South China. Tax. Econ. Seaweeds 2:132.

Section IV. Ahnfeltiopsis (Rhodophyta, Phyllophoraceae)

INTRODUCTION

Michio Masuda and Richard E. Norris

The red algal family Phyllophoraceae includes small- and large-sized species, some of which are used commercially as sources of phycocolloids (Chapman and Chapman 1980, Santelices et al. 1989) or locally for food (Magruder and Hunt 1979, Tseng 1983). This family is characterized by multiaxial plants with a compact and pseudoparenchymatous medulla, rod-shaped spermatangia, a single procarp consisting of a three-celled carpogonial branch provided with a sterile branchlet and a large supporting cell serving as an auxiliary cell, inward or outward development of gonimoblasts, unbranched chains of tetrasporangia, and iota or iota-kappa carrageenans in gametophytes and lambda carrageenans in sporophytes (Guiry et al. 1984).

The family has comprised the following eight genera: *Phyllophora* Greville, *Gymnogongrus* Martius, *Stenogramme* Harvey, *Ceratocolax* Rosenvinge, *Ozophora* J. Agardh, *Petroglossum* Hollenberg, *Besa* Setchell, and *Schottera* Guiry et Hollenberg. The medulla of plants in the genus *Besa* Setchell is composed of somewhat elongated cells (Abbott and Hollenberg 1976, Kim 1976) or is filamentous (Setchell 1912, DeCew and West 1981, p. 240, footnote). It is sometimes difficult to determine whether the medulla is filamentous or pseudoparenchymatous solely by using formalin-seawater–fixed or dried materials. Living material should be sectioned (Brodie et al., unpublished observations on some *Chondrus* species). The occurrence of a species with a filamentous medulla in

Phyllophoraceae is possible. The Phyllophoraceae, Gigartinaceae, and Petrocelidaceae may show a close phylogenetic lineage.

DeCew and West (1981, p. 240, footnote) described the gametophytes and tetrasporophytes of *B. papillaeformis* Setchell et Gardner, the type species of the genus, as isomorphic. The origin of tetrasporangia, however, has not been described. It is one of the major differences between the Phyllophoraceae and Gigartinaceae. Tetrasporangia arise in rows in superficial nemathecia in the Phyllophoraceae, whereas they develop in groups within the plant in the Gigartinaceae. The current placement of *Besa* in Phyllophoraceae is based on the presence of a sterile cell on the lowest cell of a carpogonial branch (Kim 1976) and the presence of iota carrageenan (Guiry et al. 1984).

Three genera, *Erythrodermis* Batters (Guiry and Garbary 1990, Maggs 1990), *Ahnfeltiopsis* Silva et DeCew (Silva and DeCew 1992), and *Coccotylus* Kützing (Wynne and Heine, 1992), were recently added or substituted. These genera have been characterized by the position of reproductive structures (in specialized outgrowths or not, or restricted to the median line of branches or not) and types of life history (isomorphic *Polysiphonia* type, tetrasporoblastic, or heteromorphic). The genus *Ahnfeltia* Fries, long a member of this family, has been removed to a new family, the Ahnfeltiaceae in a new order Ahnfeltiales (Maggs and Pueschel 1989). The female reproductive system and postfertilization stages of this new family differ from those of the Phyllophoraceae. Considering all the characters collectively, Maggs and Pueschel (1989) concluded that the two families are phylogenetically remote from one another.

Life-History Patterns of Ahnfeltiaceae

The members of the family Ahnfeltiaceae show a great diversity of life-history patterns, as is well known. Three basic types can be found. The first, the *Polysiphonia* type, has morphologically similar gametophytic and tetrasporophytic phases and diploid carposporophytes on the female gametophyte. Results of laboratory experiments and observations on plants collected in the field indicate that the following members may show this type of life history: *Stenogramme* (Abbott and Hollenberg 1976), *Besa* (DeCew and West 1981), *Ozophora* (Abbott 1969), *Petroglossum* (Abbott and Hollenberg 1976), *Schottera* (Guiry and Hollenberg 1975), and *Phyllophora* (Newroth 1972).

The second type, the tetrasporoblastic type, has morphologically dissimilar gametophytic and tetrasporophytic phases; the latter phase develops in monoecious gametophytes instead of carposporophytes. Results of laboratory experiments and observations on plants collected in the field indicate that this type of life history is known for *G. griffithsiae* (Turner) Martius (Gregory 1934, Schotter 1968), *G. crenulatus* (Turner) J. Agardh (= *G. norvegicus* of Schotter 1968 and Ardré 1978), *G. chiton* (Howe) Silva et DeCew (= *G. platyphyllus* of Doubt 1935 and McCandless and Vollmer 1984), *G. dilatatus* (Turner) J. Agardh (Anderson and Bolton 1990), *G. "tetrasporiferus*" (undescribed species of Anderson and Bolton 1990), and *Coccotylus truncata* (Pallas) Wynne et Heine 1992 (= *Phyllophora truncata* of Newroth 1971).

The third type, the heteromorphic type, has alternation of upright dioecious gametophytes with a crustose tetrasporophyte and has diploid carposporophytes on the female gametophyte. The results of laboratory experiments indicate that the following members have this type of life history: *E. traillii* (Holmes ex Batters) Guiry et Garbary (= *Phyllophora traillii* of Maggs 1989), *Ahnfeltiopsis concinna* (J. Agardh) Silva et DeCew (= *Ahnfeltia concinna* of Magruder 1977, Masuda 1983), *A. gigartinoides* (J. Agardh) Silva et DeCew (= *Ahnfeltia gigartinoides* of DeCew 1983), *A. furcellata* (C. Agardh) Silva et DeCew (= *G. furcellatus* of Candia and Kim 1977, Lewis et al. 1991), *A. flabelliformis* (Harvey) Masuda (= *G. flabelliformis* of Masuda et al. 1979, Masuda 1981), *A. leptophylla* (J. Agardh) Silva et DeCew (= *G. leptophyllus* of DeCew and West 1981), *A. linearis* (C. Agardh) Silva et DeCew (= *G. leptophyllus* of DeCew and West 1981), *A. complicata* (Kützing) Silva et DeCew (= *G. longardas* of Anderson and Bolton 1990), *A. glomerata* (J. Agardh) Silva et DeCew (= *G. longardas* of Anderson and Bolton 1990), and *A. polyclada* (Kützing) Silva et DeCew (= *G. glomeratus* of Anderson and Bolton 1990). Other species of *Ahnfeltiopsis* may also have the heteromorphic-type life history (Masuda 1993; Masuda et al., this volume; Norris, this volume).

Furthermore, a direct type of life history involving only female gametophytes that apomictically produce carposporophytes is known for some populations of four Ahnfeltiopsis species: A. leptophylla from California (= G. leptophyllus of DeCew and West 1981), A. devoniensis (Greville) Silva et DeCew from Roscoff, France (= *G. devoniensis* of Ardré 1978) and Ireland, England, and northern Spain (= *G. devoniensis* of Maggs et al. 1992), an undescribed species of *Ahnfeltiopsis* from Nova Scotia and Ireland (= Gymnogongrus sp. of Maggs 1988), and A. flabelliformis from Japan (Masuda, unpublished observations). This type may be derived from species with the heteromorphic type of life history, as in the case of Mastocarpus of the Petrocelidaceae as pointed out by Masuda et al. (1984). The relationship between the populations with a heteromorphic type of life history and those with a direct type in any species of Mastocarpus has not been resolved. According to Masuda et al. (1984), only a single tetraspore germling from a fieldcollected Petrocelis crust grew into a female plant of M. pacificus (as Gigartina *pacifica*) that reproduced directly. This suggests that change from heteromorphic type to direct type actually occurs in nature, although the frequency may be extremely low and the mechanism has not yet been elucidated. It also suggests that plants with a direct type of life history have been derived from populations with a heteromorphic type and may represent clones. These clones of an undescribed species of *Mastocarpus* from central Japan have some characteristic features, such as blade morphology, reproductive phenology, and geographical distribution, that differ from those of "parent" populations (Masuda et al. 1987). Recently, Maggs (1988) reported that female gametophytes of *M. stellatus* from Nova Scotia with the direct type of life history are diploid and that development of their carposporophyte is apomictic. This type of life history is thought to be a

consequence of a double female genetic complement rather than a male and a female genome as in diploid tetrasporophytes, and it may be due to failure of meiosis (Maggs 1988). Maggs et al. (1992) recently showed that both heteromorphic- and direct-type populations of *A. devoniensis* (as *G. devoniensis*) have almost identical DNA sequences in the Rubisco spacer. This suggests that a high degree of genetic differentiation is not necessarily involved in the development of the direct type of life history (Maggs et al. 1992). The species of *Ahnfeltiopsis* and *Mastocarpus* consisting of populations with both heteromorphic and direct-types of life history are somewhat similar to the agamic complex known in flowering plants (Grant 1981) and are an interesting topic.

The type of life history of *Ceratocolax*, with a single species, *C. hartzii* Rosenvinge, is unknown. Although separate tetrasporangial and gametangial plants have been reported, cystocarpic plants have never been found (Rosenvinge 1931, Taylor 1957). The familial status also is uncertain, although the affinity to the Phyllophoraceae has been traditionally suggested by the similarity of tetrasporangial nemathecia. Taylor (1957) placed it in the Choreocolacaceae.

Crucial differences between Ahnfeltiopsis Silva et DeCew validated recently and Gymnogongrus Martius should be examined thoroughly. In G. griffithsiae, the type species of the genus (Schotter 1968), G. crenulatus (= G. norvegicus of Schotter 1968), and in G. chiton (Doubt 1935), gonimoblasts (= tetrasporoblasts) develop from auxiliary cells that presumably have received fertilized nuclei and then grow outwardly through the gametophytic medulla, outward and through the cortex, giving rise to the external nemathecial structure over the surface of the monoecious gametophyte. Meiosis may occur during tetrasporogenesis (McCandless and Vollmer 1984). In plants with this life history, formation of carposporangia is suppressed, and the tetrasporophyte is parasitic. On the other hand, in Ahnfeltiopsis, gonimoblasts developing from the auxiliary cells produce carposporophytes within the female gametophytic medulla. Released carpospores germinate and grow into crustose tetrasporophytes. Gonimoblasts of this group do not penetrate the cortex and do produce carposporangia. Thus, a striking difference exists between the species with the tetrasporoblastic type of life history (Gymnogongrus) and those with a heteromorphic type (Ahnfeltiopsis) in postfertilization development, although other vegetative and reproductive features are similar. This difference should be emphasized in comparison with Nemaliales species, such as Liagora, in which carpotetrasporophytes form four-spored sporangia, and with other species in which carposporophytes form single-spored sporangia. The postfertilization development of species with these carpotetrasporophytes is similar to that of closely related species with "normal" carposporophytes (Guiry 1987). Cordeiro-Marino and Poza (1981) reported that in G. griffithsiae from Brazil, carposporangia borne on inwardly growing gonimoblasts and medullary cells within the gametophytic plant and the carpospores germinated within the gametophyte and reached the surface of the plant by growth of filaments from the gonimoblast or by an irregular and localized crack on the surface of the plant. This type may represent an intermediate stage between

the tetrasporoblastic and heteromorphic types as pointed out earlier (Masuda et al. 1987). Unfortunately, however, the illustrations of Cordeiro-Marino and Poza (1981) do not include any evidence of carposporangial formation and carpospore germination. Even if these authors' interpretation was incorrect, or their material aberrant, it is likely that species with a tetrasporoblastic type of life history have been derived from species with a heteromorphic type (Guiry 1987). Two hypotheses have been proposed to account for the evolutionary divergence in the species group under discussion: (1) The divergence occurred once, and subsequent speciation has occurred within each group. (2) The divergence occurred independently several times and has formed several couples of closely related species, an ancestor with a heteromorphic type of life history and a descendant with the tetrasporoblastic type. We think that the first hypothesis is more likely; the second was suggested by Schotter (1968). This is one reason for supporting the establishment of *Ahnfeltiopsis*.

Key to Genera of Phyllophoraceae

The following synoptical key to genera of Phyllophoraceae can be given on the basis of several papers (Kylin 1956, Abbott 1969, Guiry and Hollenberg 1975, Abbott and Hollenberg 1976, Maggs 1990).

1. 1.	Plants parasitic
••	2. Plants primarily crustose; upright axes less than 2 mm tall with isomorphic gametophytes and sporophytes
	 Plants not primarily crustose; gametophytes and sporophytes isomorphic or heteromorphic or lacking independent sporophytes (tetrasporoblastic)
З.	Cystocarps formed in conspicuous median lines of branches; with isomorphic gametophytes and tetrasporophytes
3.	Cystocarps not formed in median lines of any branches or of special outgrowths; with isomorphic or heteromorphic gametophytes and
	tetrasporophytes or with tetrasporoblastic life history
	 Cystocarps formed in onspecialized ordinary branches and/or marginal Cystocarps formed in nonspecialized ordinary branches and/or marginal
E	proliterations/
э. 5	Spermatangia in surface son, each species with somorphic me history
0.	 Plants with isomorphic upright gametophytes and tetrasporophytes Phyllophora Plants with heteromorphic, upright gametophytes and crustose
	tetrasporophytes Erythrodermis
	 Plants with tetrasporoblastic life history; tetrasporangia borne in nemathecial pustules Coccotylus
7.	Plants with isomorphic upright gametophytes and tetrasporophytes
7.	Plants with heteromorphic, upright gametophytes and crustose
	tetrasporophytes Ahnteltiopsis
7.	Plants with tetrasporoblastic life history; tetrasporangia borne in
	nemathecial pustules Gymnogongrus

8.	Carposporangia formed in pairs on elongated, sterile cells;	
	tetrasporangial sori formed in series on diminutive plants	Schottera
8.	Carposporangia aggregated in irregular groups; tetrasporangial	

sori formed singly on mature plants

Description of the Genus Ahnfeltiopsis

In the fourth taxonomy workshop, the species of Phyllophoraceae from western Pacific and Hawaiian waters were investigated (see Masuda et al. and Norris, this volume). The occurrence of only two genera has been confirmed for these waters: *Stenogramme* (in Japanese waters) and *Ahnfeltiopsis*. The genus *Ahnfeltiopsis* is circumscribed as follows on the basis of published and unpublished observations on many western Pacific and some eastern Pacific species by Masuda and his coworkers.

Plants having heteromorphic, independent gametophytes and tetrasporophytes. Single gametophytes with many upright plants arising from a common basal disc, lacking stolons; the basal disc with or without extra basal tissue. Upright plants terete to flattened, dichotomously to subdichotomously branched, usually with adventitious branches (proliferations). Medulla of upright plants compact and pseudoparenchymatous, the cells large to small, elliptical to angular in longitudinal section, elliptical to circular in transverse section; in some species medullary cells producing very slender, anastomosing filaments. Cortex of upright plants composed of short anticlinal filaments of small, pigmented cells. Unicellular colorless hairs formed from the outermost cortical cells.

Gametophytes dioecious, forming reproductive structures on unspecialized ordinary and adventitious branches. Spermatangia formed from outermost cortical cells (spermatangial parent cells), usually in pairs in distal sori on branches; mature spermatangia anticlinally elongated; spermatangia rod-shaped. Procarps formed in the inner cortex of distal parts of branches; a single three-celled carpogonial branch borne on a supporting cell; the lowest cell usually with a sterile branchlet. Cystocarps immersed within the medulla, with inwardly directed gonimoblasts; the cortex around a cystocarp becoming thicker than adjacent vegetative parts; mature cystocarps slightly to conspicuously prominent, usually with several carpostomes consisting of short periclinal filaments formed from anticlinal cortical filaments of the thickened cortex. Tetrasporophytes crustose, circular to elliptical, closely attached to the substratum by the whole lower surface, usually without rhizoids. Single crustose plants composed of a radiating monostromatic basal layer constituting a hypothallus and short erect filaments constituting a perithallus; in some species extra basal tissue occurring beneath the hypothallus; perithallial filaments tightly or loosely coalescent, dichotomously branched a few times. Tetrasporangia occurring in intercalary short chains in sori; mature sori slightly to conspicuously bulging; the tetrasporangia divided cruciately.

Taxonomic features of the species examined can be summarized as follows. Each taxonomic feature is discussed through the stages of life history shown in Figure 1. In stage I (vegetative gametophytes), the following features can characterize each species: (1) nature of upright axes (terete, compressed, or flattened, and their width); (2) size of upright plants; (3) presence or absence of extra basal tissue beneath the basal holdfasts; (4) branching intervals and angles, which



Fig. 1. Diagram of the heteromorphic life history of Ahnfeltiopsis, stages I-V, (see text).

contribute to the plant shape; (5) abundance of proliferations; (6) dimensions and numbers of medullary cells and numbers of anticlinal rows of cortical cells; (7) presence or absence of hyphalike filaments from medullary cells; and (8) plant color.

In stage II (reproductive gametophytes), the features are (9) numbers of sterile branchlet-cells on carpogonial branches; and (10) dimensions of spermatangia (or spermatia). In stage III (carposporophytes), the features are (11) position of carposporophytes in the medulla (central or lateral); (12) numbers of anticlinal rows of cells around carposporophytes; and (13) dimensions of carpospores.

In stage IV (vegetative tetrasporophytes), the features are (14) association of perithallial filament (tightly or loosely coalescent); and (15) presence or absence of extra basal layers can characterize each tetrasporophytic crust. In stage V (reproductive tetrasporophytes), the features are (16) numbers of tetrasporangia in series; and (17) numbers of cap cells can characterize crusts of each species.

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Literature Cited

- Abbott, i. A. 1969. Some new species, new combinations, and new records of red algae from the Pacific coast. Madrono 20:42–53.
- Abbott, I. A., and Hollenberg, G. J. 1976. Marine algae of California. 827 pp. Stanford Univ. Press, Stanford.
- Anderson, R. J., and Bolton, J. J. 1990. Reproductive morphology and life histories of southern African *Gymnogongrus* species (Rhodophyta, Phyllophoraceae). Br. Phycol. J. 25:381–390.
- Ardré, F. 1978. Sur les cycles morphologiques du *Gymnogongrus crenulatus* (Turn.) J. Ag. et du *Gymnogongrus devoniensis* (Grev.) Schott. (Gigartinales, Phyllophoracées) en culture. Rev. Algol. N. S. 13:151–176.
- Candia, A. I., and Kim, D. H. 1977. Resultados preliminares de los estudios de ciclo de vida de *Gymnogongrus furcellatus* (C. Agardh) J. Agardh (Phyllophoraceae, Gigartinales). Gayana Misc. Prim. J. Nac. Acuicult. 5:77–78.
- Chapman, V. J., and Chapman, D. J. 1980. Seaweeds and their uses, 3rd ed. 334 pp. Chapman & Hall, London.
- Cordeiro-Marino, M., and Poza, A. C. 1981. Life history of *Gymnogongrus griffithsiae* (Turner) Martius (Phyllophoraceae, Gigartinales). Proc. Int. Seaweed Symp. 10:155–161.
- DeCew, T. C. 1983. Culture studies in the Hildenbrandiales, Cryptonemiales, Gigartinales and Palmariales (Rhodophyta). 208 pp. Ph.D. thesis, University of California, Berkeley.
- DeCew, T. C., and West, J. A. 1981. Life histories in the Phyllophoraceae (Rhodophyta: Gigartinales) from the Pacific coast of North America. I. *Gymnogongrus linearis* and *G. leptophyllus*. J. Phycol. 17:240–250.
- Doubt, D. G. 1935. Notes on two species of Gymnogongrus. Am. J. Bot. 22:294-310.
- Grant, V. 1981. Plant speciation, 2nd ed. 563 pp. Columbia Univ. Press, New York.
- Gregory, B. D. 1934. On the life-history of *Gymnogongrus Griffithsiae* Mart. and *Ahnfeltia plicata* Fries. J. Linnean Soc. London Bot. 49:531–551.
- Guiry, M. D. 1987. The evolution of life history types in the Rhodophyta: an appraisal. Cryptog. Algol. 8:1–12.

- Guiry, M. D., and Garbary, D. J. 1990. A preliminary phylogenetic analysis of the Phyllophoraceae, Gigartinaceae and Petrocelidaceae (Rhodophyta) in the north Atlantic and north Pacific. In: Garbary, D. J., and South, G. R., eds. Evolutionary biogeography of the marine algae of the north Atlantic. Springer-Verlag, Berlin, pp. 265–290.
- Guiry, M. D., and Hollenberg, G. J. 1975. *Schottera* gen. nov. and *Schottera nicaeensis* (Lamour. ex Duby) comb. nov. (= *Petroglossum nicaeense* (Lamour. ex Duby) Schotter in the British Isles. Br. Phycol. J. 10:149–164.
- Guiry, M. D., West, J. A., Kim, D. H., and Masuda, M. 1984. Reinstatement of the genus *Mastocarpus* Kützing (Rhodophyta). Taxon 33:53–63.
- Kim, D. H. 1976. A study of the development of cystocarps and tetrasporangial sori in Gigartinaceae (Rhodophyta, Gigartinales). Nova Hedwigia 27:1–146.
- Kylin, H. 1956. Die Gattungen der Rhodophyceen. 673 pp. Gleerup, Lund.
- Lewis, N. I., Avila, M., and McLachlan, J. L. 1991. Life history of *Gymnogongrus furcellatus* (C. Ag.) J. Ag. (Rhodophyta, Phyllophoraceae) from Chile. Bot. Mar. 34:145–152.
- Maggs, C. A. 1988. Intraspecific life history variability in the Florideophycidae (Rhodophyta). Bot. Mar. 31:465–490.
- Maggs, C. A. 1989. *Erythrodermis allenii* Batters in the life history of *Phyllophora traillii* Holmes ex Batters (Phyllophoraceae, Rhodophyta). Phycologia 28:305–317.
- Maggs, C. A. 1990. Taxonomy of phyllophoroid algae: the implications of life history. Hydrobiologia 204/205:119-124.
- Maggs, C. A., Douglas, S. E., Fenety, J., and Bird, C. J. 1992. A molecular and morphological analysis of the *Gymnogongrus devoniensis* (Rhodophyta) complex in the north Atlantic. J. Phycol. 28:214–232.
- Maggs, C. A., and Pueschel, C. M. 1989. Morphology and development of *Ahnfeltia plicata* (Rhodophyta): proposal of Ahnfeltiales ord. nov. J. Phycol. 25:333–351.
- Magruder, W. H. 1977. The life history of the red alga Ahnfeltia concinna (Rhodophyta, Gigartinales). Phycologia 16:197–203.
- Magruder, W. H., and Hunt, J. W. 1979. Seaweeds of Hawaii. 116 pp. Oriental Publishing Co., Honolulu.
- Masuda, M. 1981. Further observations on the life history of *Gymnogongrus flabelliformis* Harvey (Rhodophyta) in culture. J. Fac. Sci. Hokkaido Univ. Ser. V Bot. 12:159–164.
- Masuda, M. 1983. The life history of *Ahnfeltia concinna* J. Agardh (Rhodophyta, Gigartinales) from Japan. Jpn. J. Phycol. 31:180–189.
- Masuda, M. 1993. The taxonomic status of the western Pacific species of *Gymnogongrus* and *Ahnfeltia* (Gigartinales Rhodophyta). Jpn. J. Phycol. 41:1–6.
- Masuda, M., DeCew, T. C., and West, J. A. 1979. The tetrasporophyte of *Gymnogongrus flabelliformis* Harvey (Gigartinales, Phyllophoraceae). Jpn. J. Phycol. 27:63–73.
- Masuda, M., West, J. A., Ohno, Y., and Kurogi, M. 1984. Comparative reproductive patterns in culture of different *Gigartina* subgenus *Mastocarpus* and *Petrocelis* populations from northern Japan. Bot. Mag. Tokyo 97:107–125.
- Masuda, M., West, J. A., and Kurogi, M. 1987. Life history studies in culture of a *Mastocarpus* species (Rhodophyta) from central Japan. J. Fac. Sci. Hokkaido Univ. Ser. V Bot. 14:11–38.
- McCandless, E. L., and Vollmer, C. M. 1984. The nemathecium of *Gymnogongrus chiton* (Rhodophyceae, Gigartinales): immunochemical evidence of meiosis. Phycologia 23:119–123.
- Newroth, P. R. 1971. Studies on life histories in the Phyllophoraceae. I. *Phyllophora truncata* (Rhodophyta, Gigartinales). Phycologia 10:345–354.

- Newroth, P. R. 1972. Studies on life histories in the Phyllophoraceae. II. *Phyllophora pseudoceranoides* and notes on *P. crispa* and *P. heredia* (Rhodophyta, Gigartinales). Phycologia 11:99–107.
- Rosenvinge, L. K. 1931. The marine algae of Denmark: contributions to their natural history. Part IV. Rhodophyceae (Gigartinales, Rhodymeniales, Nemastomatales). Kgl. Danske Vidensk. Selsk. Skrifter 7 Raekke Nat. Mat. 7:491–627.
- Santelices, B., Camus, P., and Hoffmann, A. J. 1989. Ecological studies for harvesting and culturing *Gymnogongrus furcellatus* (Rhodophyta, Gigartinales) in central Chile. J. Appl. Phycol. 1:171–181.
- Schotter, G. 1968. Recherches sur les Phyllophoracées. Bull. Inst. Oceanogr. Monaco 67:1–99.

Setchell, W. A. 1912. Algae novae et minus cognitae. 1. Univ. Calif. Publ. Bot. 4:229-268.

Silva, P. C., and DeCew, T. C. 1992. *Ahnfeltiopsis*, a new genus in the Phyllophoraceae (Gigartinales, Rhodophyceae). Phycologia, 31:576–580.

Taylor, W. R. 1957. Marine algae of the northeastern coast of North America, revised ed. Univ. 509 pp. Univ. Michigan Press, Ann Arbor.

Tseng, C. K., ed. 1983. Common seaweeds of China. 316 pp. Science Press, Beijing.

Wynne, M. J., and Heine, J. N. 1992. Collections of marine red algae from St. Matthew and St. Lawrence Islands, the Bering Sea. Nova Hedwigia 55:97.

AHNFELTIOPSIS FROM THE WESTERN PACIFIC: KEY, DESCRIPTION AND DISTRIBUTION OF THE SPECIES

Michio Masuda, Zhang Junfu, and Xia Bangmei

Abstract

Thirteen species of *Ahnfeltiopsis* from the western Pacific, including the South China Sea, the East China Sea, the Yellow Sea, the Sea of Japan, and the Sea of Okhotsk, were studied. These species have the following features in common: (1) many upright plants arising from a common basal holdfast and lacking stolons, (2) plants with compact pseudo-parenchymatous medullae either terete or compressed and dichotomously or subdichotomously divided, (3) gametangia borne on nonmodified, ordinary branches and proliferations, (4) three-celled carpogonial branch provided with a sterile branchlet, and (5) internal cystocarps provided with multiple carpostomes. The specific status of some taxa, however, has not been confirmed, and further investigations are necessary. Morphological features of gametophytic plants were chiefly used to circumscribe each species, as tetrasporophytic crusts have not been known for many species concerned. Nine of the 13 species of *Ahnfeltiopsis* are endemic to the western Pacific. Of the remaining five species, *A. concinna* and *A. flabelliformis* are also distributed in Hawaiian waters, *A. densa* grows in the Bay of Bengal, *A. pygmaea* also occurs in the Bay of Bengal and in Hawaiian waters, and *A. serenei* is known on the Pacific coast of Mexico.

Introduction

In the western Pacific, only two of 11 genera of Phyllophoraceae (see Masuda and Norris, this volume) are known: Ahnfeltiopsis and Stenogramme. Yendo (1920) described Phyllophora japonica Yendo on the basis of specimens from Goto and Koshikijima, southern Japan. His description lacks information on reproductive features, and his voucher specimens have not been found in his herbarium in Tokyo (TI, the University Museum, University of Tokyo). Pham (1969) reported Gymnogongrus griffithsiae (Turner) Martius from Vietnam, but no description of reproductive structures was given. The occurrence of these two species in the western Pacific is uncertain. In the cooler regions of the western Pacific, some species assignable to Phyllophora and Coccotylus have been reported (Zinova 1940; Zinova and Makijenko 1972). Species of Ahnfeltiopsis in the areas studied can be found from high intertidal to upper subtidal zones, whereas Stenogramme interrupta grows in deeper waters (Okamura 1936). Ahnfeltiopsis is common, and the species are often dominant members of marine algal communities in the western Pacific: A. concinna is the most luxuriant highest growing alga at some localities of Hachijo Island, central Japan, as is the Hawaiian representative (Magruder and Hunt 1979); A. chnoosporoides overwhelmingly dominates in the middle to lower intertidal communities at some localities in central Vietnam; and A. paradoxa is the most dominant alga in the upper subtidal zone in many localities of central Japan.

In this study, we dealt with 13 species of *Ahnfeltiopsis* from the western Pacific. As mentioned earlier (Masuda and Norris, this volume), taxonomic

features of the species of this genus should be analyzed through the life history. However, life histories of many species have not been elucidated, which has hampered us in drawing conclusions. In our future studies, more species will be described from the areas concerned.

Materials and Methods

Historical and contemporary specimens, including liquid-preserved specimens deposited in the following herbaria, were examined: the herbarium of the Faculty of Science, Hokkaido University, Sapporo (SAP), the herbarium of the Institute of Oceanology, Academia Sinica, Qingdao (AST), and the herbarium of B. P. Bishop Museum, Honolulu (BISH). Abbreviations for herbaria follow Holmgren et al. (1981). Recent collections from Vietnam after the fourth taxonomy workshop were also used (Masuda et al., unpublished observations). Sections were made by hand by using a razor blade and pith stick and were stained with 0.5% (w/v) cotton blue in a lactic acid/phenol/glycerol/water (1:1:1:1) solution and mounted in 50% glycerol-seawater on microscope slides.

Key to the Western Pacific Species of Ahnfeltiopsis

1.	Upright plants terete to subterete throughout; hyphalike filaments absent in the medulia
1.	Upright plants compressed at least at the middle portion; hyphalike filaments
	present or absent in the medulla
	 Plants small, less than 1 cm tall, cystocarps central in the medulla A. gracilis Plants large, 3–11 cm tall, cystocarps hemispherically prominent
	(not restricted centrally) A. concinna
З.	Upper portions of plants terete to subterete
З.	Upper portions of plants compressed5
	Plants small and narrow (up to 3 cm tall and 700 μm wide);
	proliferations common, secund, pinnate, or fasciculate;
	hyphalike filaments absent in the medulia A. densa
	Plants large and broad (more than 5 cm tall and 1.2 mm wide);
	proliferations rare; hyphalike filaments abundant in the medulla A. okamurae
5.	Cystocarps hemispherically prominent
5.	Cystocarps central in the medulla
	6. Axes divided a few times (up to three) A. serenei
	6. Axes divided many times (more than four)7
7.	Axes 700-800 µm thick A. quinhonensis
7.	Axes 300–600 µm thick A. chnoosporoides
	Axes conspicuously channelled in living and fixed material;
	hyphalike filaments abundant in the medulla A. yamadae
	8. Axes not channelled; hyphalike filaments absent in the medulla
9.	Axes less than 1 mm wide 10
9.	Axes more than 1 mm wide 11
	10. Plants large, 6-14 cm tall; the cortex of axes thick, 10-18 layers A. catenata
	10. Plants small, up to 4 cm tall; the cortex of axes thin, 5-9 layers A. pygmaea

11.	. Plants large, 20-80 cm tall; axes sparsely branched at long	
	intervals, with many, large, simple to flabellate proliferations	A. paradoxa
11.	. Plants less than 15 cm tall; axes profusely branched at short	•
	intervals, with or without small proliferations	
	12. Plants pale red; axes 2.0-2.5 mm wide except at forks	A. divaricata
	12. Plants dark red to purplish red; axes less than 2 mm wide	
	except at forks	A. flabelliformis

Description and Distribution of the Western Pacific Species of Ahnfeltiopsis

Ahnfeltiopsis catenata (Yendo) Masuda, Jpn. J. Phycol. 41:2, 1993. (Figs. 1, 29, 37)

Basionym: *Gymnogongrus catenatus* Yendo, Bot. Mag. Tokyo 34:4, 1920. Type Locality: Ijika, Mie Prefecture, central Japan.

Lectotype Specimen: TI, collected March 22, 1894 (examined, see Masuda 1987, fig. 14).

Distribution: Endemic to Pacific coast of central to southern Japan (Masuda 1987, fig. 19), common.

Reference: Masuda 1987.

Upright plants (Fig. 1) rigid, dark red, 6-14 cm tall. Axes terete just above the basal disc, 500-850 µm in diameter, gradually becoming compressed upward; narrowly linear, but becoming slightly broader toward each fork, 800-950 µm wide and 300-500 µm thick except at forks, where 1.2-1.7 mm wide; divided six to 15 times in a regularly dichotomous manner from the middle to distal portions at angles of 40-90° at intervals of 3-12 mm; a few proliferations developing from lower portions of plants. Medulla consisting of closely appressed rows of thickwalled cells (walls, 3-5 µm thick), with many secondary pit connections between adjacent cells; 26-30 rows in lowest terete portion and 18-22 in lower to upper compressed portions; cells angular to elliptical in longitudinal section, 50-165 µm long (length/thickness, 1.6-6.6), elliptical to circular in transverse section, 20–40 μ m wide and 15–35 μ m thick in the center of medulla throughout plant. No hyphalike filaments evident throughout upright plant; short filaments with free tips sometimes present in medulla of lower terete portion, but do not elongate; filaments may be fused with a medullary cell. Medullary cells becoming gradually shorter and more slender toward anticlinal cortical rows of cells: rows in cortex closely packed and consisting of thin-walled cells with less frequent secondary pit connections between adjacent cells; 20-30 rows in lowest terete portion, 12-18 rows in lower to middle portions, and 6-10 rows in upper portion; cells in outer cortex rectangular, 5-7 µm wide.

Spermatangia formed in a distal sorus of ordinary branches; mature spermatangia 13–17 μ m long and 2.5–3.0 μ m wide. Procarps formed in groups in center of distal branches. A three-celled carpogonial branch provided with a two-celled sterile branchlet on the lowest cell (Fig. 29); cystocarps usually formed in two to seven catenate series; almost central in the medulla, 600–1000 μ m long,


Figs. 1–7. Herbarium specimens of species of *Ahnfeltiopsis*. Fig. 1. *A. catenata* (Yendo) Masuda (Iwaizaki, Mie Prefecture; in SAP). Fig. 2, *A. densa* (J. Agardh) Silva et DeCew (Nha Trang, Vietnam; in SAP). Fig. 3, *A. pygmaea* (J. Agardh) Silva et DeCew (Hainan Island, China; in AST). Fig. 4, *A. chnoosporoides* (Tanaka et Pham) Masuda (holotype; Nha Trang, Vietnam; in SAP). Fig. 5, *A. serenei* (Dawson) Masuda (isotype; Nha Trang, Vietnam; in BISH). Fig. 6, *A. divaricata* (Holmes) Masuda (Shimoda, Shizuoka Prefecture; in SAP). Fig. 7, *A. flabelliformis* (Harvey) Masuda (Shimoda, Shizuoka Prefecture; in SAP).

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700–1000 μ m wide, and 500–750 μ m thick; cystocarpic parts broader and thicker than adjacent vegetative parts (Fig. 37); thickened parts of cortex around a cystocarp composed of 18–24 anticlinal rows of cells, cortex of one side slightly thicker than other sides; multiple carpostomes developing in thickened cortex of both flat surfaces. Tetrasporophytes crustose; but not reaching reproductive maturity for about 1 year (Masuda, unpublished observations).

Remarks: The taxonomic history of *A. catenata* was given by Masuda (1987). This species is characterized by the repeatedly branched flabellate plant with narrow, linear segments. Although this feature is shared with *A. flabelliformis*, *A. catenata* is distinguished by its narrow medullary cells and thick cortices. In the field, this species can be discriminated on the basis of the rigid plant.

Ahnfeltiopsis chnoosporoides (Tanaka et Pham) Masuda, Jpn. J. Phycol. 41:2, 1993. (Figs. 4, 30, 35).

Basionym: *Gymnogongrus chnoosporoides* Tanaka et Pham, Mem. Fac. Fish. Kagoshima Univ. 11:26; figs. 3, 4; 1962.

Type Locality: Con, Nha Trang, Vietnam.

Holotype Specimen: SAP 052162, collected on April 22, 1961 (Fig. 4, examined).

Distribution: Endemic to central Vietnam.

References: Dawson 1954 (as G. flabelliformis in part), Pham 1969.

The following description is based on specimens collected at the type locality in March 1992 (Masuda et al., unpublished observations). Upright plants semirigid and flexible, yellowish brown in living state, 3-9 cm tall. Upright axes terete or subterete just above the basal disc, 0.6-1.1 mm in diameter, abruptly becoming compressed to flattened upward, and up to 1.6–4.0 mm wide at lower to middle portions except at forks; flattened portions $300-600 \ \mu m$ thick; axes divided four to nine times in a dichotomous or a subdichotomous manner at angles of 40-90° at intervals of 4-18 mm. Proliferations developing from margins and surfaces on older plants and from lower terete to subterete portions on younger plants, frequently formed on grazed ends and margins of branches, distinguished from ordinary branches on basis of terete or subterete proximal portions. Medulla consisting of 16-22 rows of cells in lowest terete portion and nine to 13 rows in lower to upper flattened portions; cells elliptical in longitudinal section, 65–150 μ m long (length/thickness, 1-3) in center of medulla in lower terete to subterete portions, 60–175 μ m long (length/thickness, 1–3) in middle portion, 60–115 μ m long (length/thickness, 1-2) in upper portion; elliptical or sometimes circular in transverse section, 30-50 μ m wide and 30-45 μ m thick in center of medulla in lower terete to subterete portions, 55–110 μm wide and 45–75 μm thick in middle portion, 55-110 µm wide and 30-85 µm thick in upper portions; walls of medullary cells 6–10 μ m thick. Slender hyphalike filaments 3–5 μ m wide developing from medullary cells in lower portion and less abundant than those formed for A. okamurae and A. yamadae; not found in small upright plants or in younger reproductive plants; filaments divided irregularly, bearing secondary pit connec-tions with medullary cells and having free ends. Cortex consisting of 12–16 rows

of cells in lower terete to subterete portion, seven to nine rows in middle portion, and five to six rows in upper portion; cells in outer cortex rectangular, 4.5–5.5 μm wide.

Spermatangia formed in a distal sorus of ordinary branches and proliferations; mature spermatangia 9–12 μ m long and 1.8–2.0 μ m wide. Procarps scattered at tips of branches and proliferations, each procarp consisting of a large supporting cell and a three-celled carpogonial branch with lowest cell bearing a one-celled sterile branchlet. Cystocarps formed in single or double catenate series; mature cystocarps not restricted centrally in the medulla and showing hemispherically prominent (warty) features (Fig. 35); 700–1000 μ m wide and 500–900 μ m thick; prominent part having a thicker cortex composed of 18–20 anticlinal rows of cells; five to 10 carpostomes formed in thickened cortex. Tetrasporophytes unknown.

Remarks: The specimens examined in this study were in agreement with the holotype specimen. Spermatangia were found on the specimen (Fig. 30). Dawson (1954) wrote that cystocarps of Vietnamese A. flabelliformis identified by him as G. flabelliformis were much more prominent on one side of the plant than on the other. This means hemispherically prominent cystocarps. Dawson's illustration (fig. 51b) clearly shows this feature, and his A. flabelliformis must include A. chnoosporoides. The occurrence of the genuine A. flabelliformis in Vietnam has been confirmed by Masuda (unpublished observations). Tanaka and Pham (1962) emphasized the presence of pinnate proliferations in A. flabelliformis as a feature that could be used to distinguish it from A. chnoosporoides. However, the two species cannot always be distinguished from each other on the basis of this feature. They can be distinguished on the basis of hemispherically prominent cystocarps and the presence of hyphalike filaments in the medulla, which are found in A. chnoosporoides but not in A. flabelliformis. Furthermore, in the field, these two species can be discriminated on the basis of color: A. chnoosporoides is a peculiar vellowish brown, whereas A. flabelliformis is dark red to purplish red.

Ahnfeltiopsis concinna (J. Agardh) Silva et DeCew, Phycologia 31:577, 1992.

(Figs. 8, 14, 15, 40)

Basionym: Ahnfeltia concinna J. Agardh, Öfvers Kongl. Vet. Akad. Forh. 4:12, 1847.

Type Locality: Hawaii

Holotype Specimen: LD (not examined).

Western Pacific Distribution: Pacific coast of central Japan (Shizuoka Prefecture, Izu Islands, Kanagawa Prefecture).

References: Okamura 1922, 1936; Mikami 1965; Masuda 1983.

Upright plants (Fig. 8) cartilaginous, rigid, 3–11 cm tall; usually dark purple to brown, but yellowish-brown plants found growing in uppermost intertidal regions at Hachijo Island and bleached yellow plants at same levels in Hawaii (Abbott, personal communication). Axes terete to subterete, 0.8–2.0 mm wide, dichoto-mously to subdichotomously divided four to eight times at intervals of 1–13 mm at angles of 40–90°; simple axes or those with a few dichotomies capable of



Figs. 8–11. Herbarium specimens of species of *Ahnfeltiopsis*. Fig. 8, *A. concinna* (J. Agardh) Silva et DeCew (Jogashima, Kanagawa Prefecture; in SAP). Fig. 9, *A. okamurae* Silva et DeCew (lectotype, Owase, Mie Prefecture; in SAP). Fig. 10, *A. paradoxa* (Suringar) Masuda (Miyake Island, Tokyo; in SAP). Fig. 11, *A. yamadae* (Segawa) Masuda (Jogazaki, Shizuoka Prefecture; in SAP).

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becoming fertile; first branching occurring in lower third to half of plants, intervals irregular with development of proliferations obscuring basic branching; proliferations from forked position resembling trichotomous branching. Medulla consisting of 32–40 rows of cells throughout upright plant except for apices of branches; cells elliptical to angular in longitudinal section, $35-140 \mu m \log (length/thickness, 1.4-6.0)$ in central medulla in lower to upper portions; circular to elliptical in transverse section, $15-35 \mu m$ wide and $17-28 \mu m$ thick in lower portion, $20-60 \mu m$ wide and $20-55 \mu m$ thick in middle portion, $18-43 \mu m$ wide and $22-37 \mu m$ thick in upper portion; cell walls $5-10 \mu m$ thick; no hyphalike filaments evident throughout upright plant. Cortex consisting of 16-20 anticlinal rows of cells in lowest portion; 10-12 rows in middle portion, seven to eight rows in upper portion; cells $3.5-5.0 \mu m$ wide in outer cortex.

Spermatangia formed in a distal sorus of ordinary branches and proliferations; mature spermatangia 7–15 μ m long and 2.5–3.8 μ m wide. Procarps formed in groups on corresponding portions to spermatangia; a three-celled carpogonial branch provided with a single-celled sterile branchlet. Cystocarps hemispherically prominent, 800–1100 μ m wide and 500–800 μ m thick; thickened parts of cortex composed of 14–20 anticlinal rows of cells, 100–150 μ m thick; each cystocarp provided with five to eight carpostomes (Fig. 40); released carpospores 15-20 μ m in diameter. Crustosc tetrasporophytes producing nemathecial sori in which intercalary tetrasporangia formed in two to three successive cells of single erect filaments; mature tetrasporangia ellipsoid, 37.5–42.5 μ m long and 17.5–22.5 μ m wide, divided cruciately; released tetraspores 12–16 μ m in diameter.

Remarks: Okamura (1922, pl. 191, fig. 4) illustrated a specimen from Saganoseki, Ooita Prefecture, Kyushu. The specimen deposited in his herbarium in SAP shows regular dichotomous branching occurring more often and densely at the upper portion than in the specimen in the illustration and is more similar in gross morphology to *A. okamurae*. The occurrence of *A. concinna* in southern Japan has not been verified. According to Mikami, the cystocarp of the Japanese *A. concinna* has an aperture (1965, fig. 6C). However, our present observations show multiple carpostomes (Fig. 40). These carpostomes are closely situated, suggesting that multiple carpostomes may be provided for a single cystocarp.

Masuda (1983) pointed out some differences between the Hawaiian and Japanese plants of *A. concinna*. The Hawaiian plant lacks a sterile branchlet on the carpogonial branch, and the Japanese plant has a nonnemathecial sorus (Magruder 1977). Reexamination of specimens of Hawaiian *A. concinna* collected at Makapuu Point, Oahu, Hawaii, and of laboratory grown plants showed a three-celled carpogonial branch with a sterile cell on the lowest cell and bulging mature tetrasporangial sori. Furthermore, results of hybridization experiments between Japanese and Hawaiian strains indicate that interbreeding is potentially free between these geographically distant populations (Masuda, unpublished observations). Although the Japanese plants are smaller than the Hawaiian plants, both kinds belong to the same biological species.

Ahnfeltiopsis densa (J. Agardh) Silva et DeCew, Phycologia 31:577, 1992.

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(Fig. 2)
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Basionym: *Gymnogongrus densus* J. Agardh, Sp. gen. ordines algarum 2:315, 1851.

Type Locality: Coast of Pakistan, Bay of Bengal.

Holotype Specimen: LD (not examined).

Western Pacific Distribution: Vietnam.

References: Kützing 1869.

The following description is based on specimens collected at Nha Trang, central Vietnam in March 1992 (Masuda et al., unpublished observations). Upright plants (Fig. 2) soft, dark red, 0.2-3.0 cm tall. Axes terete just above basal holdfast, 200-400 µm in diameter, becoming compressed upward, reaching 450-700 um wide and 200-400 um thick in lower to middle portions and then becoming terete to subterete upward, 280-500 µm in diameter; dichotomously to subdichotomously divided two to six times at intervals of 1-8 mm at angles of 50-90°; simple axes sometimes becoming fertile. Proliferations developing from many positions of axes and appearing on small axes less than 1 cm tall; formed irregularly and arranged secundly, pinnately, or fasciculately; usually subterete to terete, up to 1.5 cm long, often bearing secondary proliferations; basic dichotomous branching often obscured by development of proliferations, with distinction between branches and proliferations sometimes unclear. Medulla consisting of rows of cells, 14-22 from lower to upper portions of plant; cells elliptical in longitudinal section, 35-100 µm long (length/thickness, 1.6-6.3), and elliptical to circular in transverse section, 10-35 µm wide and 10-30 µm thick in the center of medulla in lower to upper portions of plant; cells walls 2.0-2.5 µm thick; no hyphalike filaments evident throughout the upright plant. Cortex consisting of eight to 14 anticlinal rows of cells in lower to middle portions, six to eight rows in upper portion: cells 5-6 µm wide in outer cortex.

Spermatangia formed in distal sori on ordinary branches and proliferations, 6–10 μ m long and 1.8–2.0 μ m wide. Procarps borne in groups at the uppermost portion of ordinary branches and proliferations; each procarp composed of a large supporting cell and a three-celled carpogonial branch, with lowest cell in branch provided with a one-celled sterile branchlet. Cystocarps produced in catenate series of four to six; formed solitarily or in a few catenate series on shorter branches and proliferations less than 5 mm long; mature cystocarps almost central or not restricted centrally in the medulla, 450–600 μ m wide and 400–550 μ m thick; thickened cortex around cystocarps consisting of eight to 12 rows of cells on carpostomal side and five to seven rows on the other side; multiple carpostomes (up to 10) formed in thickened cortex. Tetrasporophytes unknown.

Remarks: This species was originally characterized as having the following features: (1) dichotomous to fastigiate branches with wide angles; (2) plants mostly terete and less than 0.5 mm in diameter; (3) secundly arranged and patent, upper segments; and (4) somewhat solitary cystocarps formed in knotted, inflated upper segments and immersed in the middle of the plant (Agardh 1851). The

fastigiate branching and secund, patent upper segments are equivalent to the proliferations described here. Somewhat solitary cystocarps are equivalent to those formed on short proliferations and branches. On the basis of these characteristic features, the Vietnamese alga is referred to as *A. densa*, although the type materials of this species have not been examined. Slender medullary cells also characterize the species examined.

Ahnfeltiopsis divaricata (Holmes) Masuda, Jpn. J. Phycol. 41:577, 1993.

(Figs. 6, 20, 21, 32).

Basionym: *Gymnogongrus divaricatus* Holmes, J. Linn. Soc. Bot. 31:255, pl. 8, figs. 3a–3b, 1896.

Type Locality: Shimoda, Shizuoka Prefecture, central Japan.

Holotype Specimen: BM, collected in March 1894 (examined, see Masuda 1987, fig. 10.)

Distribution: Endemic to Pacific coast of southern to central Japan, common. References: Okamura 1934, 1936; Masuda 1987.

Upright plants semirigid texture, pale red, 4-11 cm tall; dichotomously divided seven to 13 times at angles of 70-90° at intervals of 2-10 mm in lower to middle portions and at angles of 45--65° in upper portion; divaricate-flabellate (Fig. 6) in outline. Upright axes terete just above the basal disc, 600-900 µm in diameter, abruptly becoming compressed to flattened upward and becoming 2.0-2.5 mm wide at the lower to middle portions except at forks, which are broader than other parts and 3.0-3.5 mm wide; compressed to flattened portions 400-500 µm thick. Many short proliferations formed from the margins (sometimes from the surface) throughout the plant. Medulla consisting of eight to 10 rows of cells throughout the plant; cells elliptical in longitudinal section (Fig. 20), 100-300 µm long (length/thickness, 1-5), and elliptical to circular (Fig. 21) in transverse section, 60-170 µm wide and 50-110 µm thick in center of medulla in lower to upper portions of the plant; cell walls 4-10 µm thick; no hyphalike filaments evident throughout upright plant. Cortex consisting of 17-25 rows of cells in lowest terete portion, eight to 11 in lower portion, and five to eight in middle to upper portions; cells in outer cortex 4-5 µm wide .

One or two spermatangia produced from a single spermatangial parent cell; mature spermatangia 10–12 μ m long and 2–3 μ m wide. Procarps formed in groups in the slightly depressed center of apices of distal portions of branches; each procarp consisting of a large supporting cell and a three-celled carpogonial branch, with the lowest cell in branch bearing a two-celled sterile branchlet. Cystocarps usually formed in catenate series of three to six, almost central in the medulla; mature cystocarps ellipsoid, 550–750 μ m long, 500–950 μ m wide, and 300–580 μ m thick; thickened parts of cortex around a cystocarp composed of eight to 14 anticlinal rows of cells on the carpostomal side and six to 12 rows on other sides. Tetrasporophytes crustose and forming nemathecial sori (Masuda, unpublished observations).

Remarks: This species is characterized by widely flabellate and dense branching of upright plants that have broad segments, pale red color, and large medullary cells. A previous record of this alga from the Pacific coast of central America (Dawson 1944) requires further examination.

Ahnfeltiopsis flabelliformis (Harvey) Masuda, Jpn. J. Phycol. 41:2, 1993.

(Figs. 7, 33)

Basionym: *Gymnogongrus flabelliformis* Harvey, in Perry, Narrative Exped. China Sea and Japan, vol. 2, p. 332, 1857.

Synonym: *Gymnogongrus japonicus* Suringar, Ann. Bot. Mus. Bot. Lugd.-Batavi., 3:259, 1867.

Type Locality: Shimoda, Shizuoka Prefecture, central Japan.

Lectotype Specimen: Collected in April 1854, deposited in TCD (examined, see Masuda 1987, fig. 1)

Distribution: Common in Vietnam, China, Korea, and Japan.

References: Okamura 1921, 1936; Tokida and Masaki 1959; Mikami 1965; Kang 1966; Tseng 1983; Masuda 1987.

Upright plants dark red to purplish red, semirigid texture, 3–6 cm long. Upright axes terete just above basal disc, 550–800 μ m in diameter, abruptly becoming compressed upward, 1.1–1.3 mm wide and 400–500 μ m thick in lower to middle portions, 800–900 μ m wide and 300–400 μ m thick in upper portion; dichotomously branched eight to 14 times at angles of 40–80° at intervals of 1–5 mm, showing a fan-shaped outline (Fig. 7). Short proliferations developing from both margins of lower to middle portions of upright plants. Medulla consisting of 18–20 rows of cells in lowest terete portion and 12–15 rows in lower to upper compressed portions; cells elliptical to angular in longitudinal section, 75–200 μ m long (length/ thickness, 1.6–4.4), and elliptical in transverse section, 40–110 μ m wide and 30–70 μ m thick, in center of medulla throughout plant; cell walls 4–8 μ m thick; no hyphalike filaments evident throughout upright plant. Cortex consisting of 16–24 anticlinal rows of cells in lowest portions; cells in outer cortex 4–5 μ m wide.

Spermatangia 9–10 μ m long and 2.5–3.0 μ m wide, formed in distal sori on ordinary branches and proliferations. Procarps borne in groups at uppermost portion of ordinary branches and proliferations; each procarp composed of a large supporting cell and a three-celled carpogonial branch, with lowest cell in branch provided with a two-celled sterile branchlet. Cystocarps produced on ultimate and penultimate branches in catenate series of three to five; mature cystocarps almost central in medulla, 500–600 μ m long, 400–550 μ m wide, and 300–500 μ m thick; thickened cortex around cystocarps consisting of 10–14 rows of cells on carpostomal side and seven to 11 rows on other side; multiple carpostomes formed in thickened cortex.

Remarks: This description is based on specimens collected at the type locality. This species is distributed widely and shows considerable variation in gross morphology. For example, plants growing along the coast of the Sea of

Japan reproduce under short-day regimens at a temperature range of 10–20°C and have more sparsely branched plants. This taxonomic species may include several biological species that are reproductively isolated (Masuda, unpublished observations). These data will be presented elsewhere. Tetrasporophytes reported earlier (Masuda et al. 1979, Masuda 1981) are referred to one such species.

Ahnfeltiopsis gracilis (Yamada) Masuda, Jpn. J. Phycol. 41:2, 1993.

Basionym: *Besa gracilis* Yamada, J. Fac. Sci. Hokkaido Imp. Univ. ser. 5, 1:73, fig. 3. 1931.

Synonym: *Ahnfeltia gracilis* (Yamada) Yamada et Mikami in Mikami, Sci. Pap. Inst. Alg. Res. Fac. Sci. Hokkaido Univ. 5:198, pl. 4 (1), figs. 11, 12, 1965.

Type Locality: Enoshima, Kanagawa Prefecture, central Japan.

Holotype Specimen: SAP 9798, collected in October 1923 by Y. Yamada (examined).

Distribution: Endemic to the Pacific coast of central Japan; uncommon, only known from the type locality.

References: Okamura 1936, Mikami 1965.

No liquid-preserved specimens are available. The following description is largely based on that given by Mikami (1965). Upright plants small, up to 6 mm long, fleshy-cartilaginous, terete, 1 mm in diameter; simple or once to twice dichotomous, usually having no proliferations. Medulla pseudoparenchymatous, composed of 18–20 rows of cells; cells elliptical in longitudinal section, 20–35 μ m long (length/thickness, 1-3) in center of medulla in lower to middle portions, circular to elliptical in transverse section, 15-25 µm wide and 10-20 µm thick; cell walls 2-3 µm thick; no hyphalike filaments evident throughout upright plant; medullary cells becoming shorter and more slender toward cortex. Cortex consisting of eight to 10 anticlinal rows of cells in lower to middle portions, five to six rows in upper portion; cells rectangular, 3-5 µm wide in the outer cortex. A three-celled carpogonial branch provided with a sterile cell on lowest cell; cystocarps swollen in upper portion of simple plants; thickened parts of cortex around cystocarps consisting of eight to 12 rows of cells; no carpostomes evident in thickened cortex, probably because of young stages of carposporophytic development. Tetrasporophytes unknown.

Remarks: This species is characterized by the diminutive upright plant. In relation to the plant's size, this species has very slender and short medullary cells.

Ahnfeltiopsis okamurae Silva et DeCew, Phycologia, 31:578, 1992.

(Figs. 9, 16-19, 27, 36)

Synonym: Ahnfeltia furcellata Okamura, Icon. Jpn. Alg. 7:16, pl. 310, figs. 6–10, 1934.

Type Locality: Kajika, Owase, Mie Prefecture, central Japan.

Lectotype Specimen: Okamura Herbarium in SAP, collected February 12, 1933, at Kajika (examined and designated here).

Distribution: Endemic to the Pacific coast of central to southern Japan (Mie, Kochi, and Ehime prefectures), uncommon, known from several localities only.

Reference: Okamura 1936, Mikami 1965.

The following description is based on liquid-preserved specimens collected at Mimaizaki, Misaki-cho, Ehime Prefecture, in the Seto Inland Sea, Upright plants semirigid, flexible (not cartilaginous), dark red to dark purple, 6-12 cm high. Axes dichotomously divided eight to 10 times from the lower third to lower half toward upper portion; branching regular up to four dichotomies, but becoming irregular distally; axes terete in lower portion (1.5-3.5 cm above basal disc), 1.2-1.6 mm in diameter (Fig. 16), gradually becoming subterete to compressed toward first fork. reaching maximum width and thickness of 1.8-2.2 mm × 1.4-1.6 mm before first dichotomy, then gradually becoming narrower and thinner, 1.6-1.9 mm × 0.9-1.2 mm (Fig. 17) after first dichotomy; axes slightly channelled throughout compressed portion; bearing subterete to terete branches 0.8-1.2 mm wide distally (Fig. 18), but also producing compressed branches 1.0-1.3 mm × 0.5-0.8 mm; upright axes usually devoid of proliferations. Medulla consisting of 40-50 rows of cells in lower terete portion, 34-40 rows in center of middle compressed portion, 23-30 rows in upper subterete to terete portion; cells elliptical to angular in longitudinal section, 55-100 µm long (length/thickness, 1.7-4.4) in center of medulla in lower terete portion, 90-330 µm long (length/thickness, 3-11) in middle compressed portion, 50-150 µm long (length/thickness, 3-8) in upper subterete to terete portion; elliptical to circular in transverse section, 25-40 µm wide and 15-35 um thick in center of medulla throughout plant; cells becoming gradually shorter and more slender toward cortex; cell walls 2.5-5.0 µm thick; slender hyphalike filaments 5-7 µm wide developing from medullary cells (Fig. 27) very abundant in medulla of lower portion. can be found in young upright axes 8-12 mm tall, divided irregularly, bearing secondary pit connections with medullary cells and having free ends. Cortex consisting of 10-12 anticlinal rows of cells in lower terete portion, eight to 10 rows in middle compressed portion, seven to nine rows in upper subterete to terete portion; cells rectangular, 5-7 µm wide in outer cortex.

Reproductive structures not found in the materials mentioned above. Cystocarps found on the lectotype and other specimens deposited in Okamura herbarium housed in SAP; latter specimens collected at type locality April 25, 1933. Cystocarps formed singly in terminal branchlets; ellipsoidal, swollen in medullary layer (Fig. 36), 1.6–2.2 mm long, 0.5–0.8 mm wide, 0.5–0.6 mm thick, provided with multiple carpostomes in thickened cortex (Fig. 36); thickened cortex composed of 18–22 anticlinal rows of cells 120–150 μ m thick on the carpostomal side, 12–14 rows of cells 70–80 μ m thick on the other side. Tetrasporophytes unknown.

Remarks: Silva and DeCew (1992) proposed a new name, *Ahnfeltiopsis* okamurae, for *Ahnfeltia furcellata* Okamura (1933) when it was transferred to *Ahnfeltiopsis*, because of the earlier proposal of the combination *Ahnfeltiopsis furcellata* (C. Agardh) Silva et DeCew. In establishing *A. furcellata*, Okamura (1934) did not designate the holotype specimen. A herbarium sheet including the specimen shown in his illustration (Okamura 1934, pl. 310, fig. 6) is deposited in

his herbarium in SAP; this sheet is designated here as the lectotype specimen (Fig. 9). The International Code of Botanical Nomenclature (ICBN) allows the type to consist of more than one individual preserved on one herbarium sheet for small herbaceous plants and for most non-vascular plants (Greuter et al., 1988, Article 9.1). Okamura (1934) and Mikami (1965) described the upright plants as almost cylindrical or almost terete. However, the lectotype specimen and specimens collected at the type locality April 25, 1933, have upright plants that are compressed in the middle portion (Fig. 19). Thus, this species shows an intermediate condition between species with terete plants and those with compressed to flattened plants. Slender hyphalike filaments were also found in the medullae of these specimens.

Mikami (1965, p. 194) mentioned that "the present alga (*Ahnfeltia furcellata*) is...closely related to *A. concinna* from which it differs by the regularly decompound-dichotomous divergence and by the gonimoblast embedded in the central portion of the frond." However, the production of hyphalike filaments from medulary cells, ellipsoid cystocarps, and noncartilaginous plants of *A. okamurae* distinguish it from *A. concinna*.

Ahnfeltiopsis okamurae previously reported from China (Tseng 1983) as Ahnfeltia furcellata should be discounted. We have never found specimens similar to A. okamurae in Chinese collections.

Ahnfeltiopsis paradoxa (Suringar) Masuda, Jpn. J. Phycol. 41:2, 1993. (Figs. 10, 12, 13, 22, 23, 26)

Basionym: *Gymnogongrus paradoxus* Suringar, Mus. Bot. Leide 2:13, pl. 21, 22, 1874.

Synonym: *Gymnogongrus furcellatus* (C. Agardh) J. Agardh var. *japonicus* Holmes, J. Linn. Soc. Bot. 31:256, pl. 11, fig. 2, 1896. *Ahnfeltia paradoxus* (Suringar) Okamura, Icon. Japan Alg. 7:13, 1934.

Type Locality: One of Izu Seven Islands in Japan.

Holotype Specimen: L 942.69.48 (examined, see Masuda 1987, fig. 5) Distribution: Endemic to Pacific coasts of northern to central Japan (Masuda 1987, fig. 9), common.

References: Okamura 1936, Mikami 1965, Masuda 1987.

Upright plants rigid in texture, coral red to dark red, 20–80 cm tall. Upright axes terete only at lowest portion (1–10 mm above basal disc), 0.7–1.0 mm in diameter (Fig. 12), gradually becoming compressed to flattened upward (Fig. 13); 1.6–2.7 mm wide, 800–900 μ m thick in lower to upper portions and 1.5–1.7 mm wide, 480–500 μ m thick 5 mm below apex. Axes sparsely branched two to nine times, mostly at intervals of 2–6 cm (sometimes less than 1 cm or 10 cm or more), dichotomously or subdichotomously at angles of 20–50° (Fig. 10), first dichotomy usually 3–12 cm (sometimes 20 cm or more) above basal disc; extra basal tissue developing beneath lower surface of basal holdfasts (Fig. 26). Often many proliferations between main branches (Fig. 10), up to 8 cm long, regularly dichotomously divided four to six times at short intervals and often bearing secondary



Figs. 12–19. Transverse sections of axes of species of *Ahnfeltiopsis*. Figs. 12, 13, *A. paradoxa* from Miyake Island: Fig. 12, lower terete portion; Fig. 13, upper portion. Figs. 14, 15, *A. concinna* from Shimoda: Fig. 14, lower portion; Fig. 15, upper portion. Figs. 16–19, *A. okamurae* from Mimaizaki: Fig. 16, lower portion; Fig. 17, middle portion; Fig. 18, upper portion; Fig. 19, middle portion of the lectotype specimen. Scale in Fig. 19 also applies to Figs. 12–18.

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proliferations; various forms differing mainly in degrees of elongation of main axes and in stages of development; plants with elongated axes and short, less frequently divided proliferations very different from those with less elongated axes and frequently branched proliferations. Medulla consisting of 20–24 rows of cells in center of axis in lower to upper portions; cells angular to elliptical in longitudinal section (Fig. 22), 50–175 μ m long (length/thickness, 1.8–7.0), circular to elliptical in transverse section (Fig. 23), 20–45 μ m wide and 20–35 μ m thick in center of medulla in lower to upper portions; cell walls 5–6 μ m thick; no hyphalike filaments evident throughout upright plant, short filaments with free tips sometimes present in medulla in lower terete portion, but do not elongate; filaments may be fused with a medullary cell, as in the case of *A. catenata*. Cortex thick, 20–44 anticlinal rows of cells in lower portion to 10 cm below apex of plants, 10–12 rows 2–5 cm below apex, and six to eight rows 5 mm below apex; cells rectangular, 4–7 μ m wide in outer cortex.

Spermatangia formed in a distal sorus of proliferations; mature spermatangia $12-15 \ \mu m$ long and $2.5-3.0 \ \mu m$ wide. Procarps formed in groups on apices of proliferations; a three-celled carpogonial branch provided with a one-celled sterile branchlet on lowest cell. Cystocarps usually formed in catenate series of two to six, sometimes in small groups on broad parts of proliferations; almost central in medulla, $650-900 \ \mu m$ long, $650-800 \ \mu m$ wide, and $300-600 \ \mu m$ thick; cystocarpic parts thicker than adjacent vegetative parts; thickened parts of cortex around a cystocarp composed of 12-16 anticlinal rows of cells, $110-150 \ \mu m$ thick (cortex slightly thicker on carpostomal side than on other side). Tetrasporophytes crustose and forming nemathecial sori; crusts forming extra basal tissue beneath basal layer; intercalary tetrasporangia formed in three to five successive cells of single erect filaments (Masuda and Shimizu, unpublished observations).

Remarks: *A. paradoxa* is a large, upright plant with axes little branching at long intervals and at narrow angles, and with many large simple to flabellate proliferations. This species is also characterized by the production of extra basal tissue beneath the basal layer of both the gametophytic holdfast and the tetrasporangial crust. This tissue has been found only in *A. paradoxa* among the western Pacific species examined. However, it is not easy to detect this tissue in field-collected plants. Further culture studies may show such tissue for other species.

Ahnfeltiopsis pygmaea (J. Agardh) Silva et DeCew, Phycologia 31:578, 1992.

(Figs. 3, 24, 25, 39)

Basionym: *Gymnogongrus pygmaeus* J. Agardh, Sp. gen. ordines algarum, vol. 2, p. 317, 1851.

Type Locality: Coast of Pakistan, Bay of Bengal.

Holotype Specimen: LD (not examined).

Western Pacific Distribution: Vietnam, China (Hainan Island), and Hawaii (see Norris, this volume).

References: Kützing 1869, Børgesen 1936, Dawson 1954.

A few specimens from Hainan Island were examined. Upright plants (Fig. 3) dark red to purplish red, semirigid in texture, 2-4 cm tall. Upright axes terete in lowest portion only, 450-550 µm in diameter, abruptly becoming compressed upward, 600-700 µm wide and 300-450 µm thick in lower to middle portions. 400-600 µm wide and 260-300 µm thick in upper portion (2 mm below apex); dichotomously branched 10-12 times from near base to distal tips at short intervals of 1-4 mm at angles of 50-80°; forming a flabellate plant. Medulla consisting of 14-18 rows of cells in center of axis throughout plant; cells elliptical to angular in longitudinal section (Fig. 24), 35-88 µm long (length/thickness, 1.5-3.5) in lower portion, 50-75 µm long (length/thickness, 1.2-2.5) in middle portion. and 30-80 µm long (length/thickness, 1.1-3.8) in upper portion (2 mm below apex): circular to elliptical in transverse section (Fig. 25), 17-40 µm wide and 17-40 μm thick in lower portion, 27-45 μm wide and 20-45 μm thick in middle portion, and 20-50 µm wide and 17-35 µm thick in upper portion; cell walls 3-4 um thick; no hyphalike filaments evident throughout upright plant. Cortex composed of 12-18 anticlinal rows of cells in lower portion, six to nine rows in middle portion, and five to six rows in upper portion (2 mm below apex); cells rectangular, 4-5 µm wide in outer cortex.

Cystocarps solitarily formed in middle to upper portions of plant; mature cystocarps almost central in medulla, 400–450 μ m in diameter and 280–300 μ m thick, with layer of eight to ten cells in cortex on carpostomal side and a layer of five to six cells on other sides; multiple carpostomes (up to six) formed on a cystocarp (Fig. 39).

Remarks: On the basis of Greville's unpublished name *Chondrus pygmaeus*, J. Agardh (1851) established *G. pygmaeus*. This species has been characterized by slender compressed upright plants that are repeatedly branched in a regular dichotomous manner. We have never examined the type material of this species. Our present circumscription of the species is provisional. Currently, we refer specimens of flabellate plants with narrow, compressed axes to this species. These specimens, on the other hand, are similar to a slender form of *A. flabelliformis*.

Ahnfeltiopsis quinhonesis (Pham) Masuda, Jpn. J. Phycol. 41:3, 1993.

Basionym: *Gymnogongrus quinhonensis* Pham, Marine Algae South Vietnam, p. 201, fig. 2.133, 1969.

Type Locality: Qui Nhon, central Vietnam.

Holotype Specimen: Unknown.

Distribution: Endemic to central Vietnam.

The following description is based on dried spermatangial specimens collected at the type locality in May 1992 (Masuda et al., unpublished observations). Upright plants subcartilaginous in texture, brownish to dark red, 6–12 cm tall. Axes terete just above basal disc only, 1.2–1.4 mm in diameter, abruptly becoming compressed to flattened upward, up to 3.8–4.3 mm wide in lower to middle portions except at forks; flattened portions 700–800 μ m thick; axes branched



Figs. 20–25. Longitudinal (Figs. 20, 22, 24) and transverse (Figs. 21, 23, 25) sections of axes of species of *Ahnfeltiopsis* showing different dimensions of medullary cells and different thicknesses of cortices. Figs. 20, 21, Middle portions of *A. divaricata* from the type locality show large medullary cells. Figs. 22, 23, Middle portions of *A. paradoxa* from Miyake Island show slender medullary cells and thick cortices. Figs. 24, 25, *A. pygmaea* from Hainan Island show slender medullary cells and thin cortices: Fig. 24, lower portion; Fig. 25, middle portion. Scale in Fig. 25 also applies to Figs. 20–24.

eight to nine times dichotomously or subdichotomously at angles of $20-50^{\circ}$ at intervals of 5–30 mm; proliferations formed on grazed ends and from lower portion of axes. Medulla consisting of 20-25 rows of cells in lowest terete portion and 12-14 rows in lower to upper flattened portions; cells elliptical in longitudinal section, $60-180 \mu$ m long (length/thickness, 1.4-3.7) in center of medulla in lower portion of upright plants, $150-225 \mu$ m long (length/thickness, 1.4-2.6) in middle portion, $40-80 \mu$ m long (length/thickness, 1.0-1.8) in upper portion; elliptical to circular in transverse section, $60-160 \mu$ m wide and $55-100 \mu$ m thick in center of medulla in lower portion, $75-180 \mu$ m wide and $50-100 \mu$ m thick in middle portion, $40-100 \mu$ m wide and $30-50 \mu$ m thick in upper portions; cell walls $7.5-10.0 \mu$ m thick; slender hyphalike filaments $2.5-7.5 \mu$ m wide developing from medullary cells, abundant in medulla in lower portion. Cortex consisting of 20-30 rows of cells in lowest terete portion; cells rectangular, $3.8-5.0 \mu$ m wide in outer cortex.

Spermatangia formed in a distal sorus of branches; mature spermatangia $9-12 \,\mu\text{m}$ long and $1.8-2.5 \,\mu\text{m}$ wide. Cystocarps hemispherical and formed on upper surface (Pham 1969).

Remarks: According to Pham (1969), this species closely resembles *A. serenei. A. quinhonensis*, however, has larger, thicker, more luxuriant plants and smaller cystocarps and the dimensions of its medullary cells are different, 1.0–3.7 times longer than broad vs. two to three times longer than broad in *A. serenei*. It is also related to *A. chnoosporoides*. Both have broad axes and hemispherically bulging cystocarps, but the axes in *A. quinhonensis* are thicker axes because of its larger medullary cells and narrow-angled branching. A detailed comparative study of ample specimens of these species is needed to elucidate their taxonomic relationship. Among the western Pacific *Ahnfeltiopsis* with compressed plants, only these three Vietnamese species produce hemispherically bulging cystocarps.

Ahnfeltiopsis serenei (Dawson) Masuda, Jpn. J. Phycol. 41:3, 1993.

(Fig. 5)

Basionym: *Gymnogongrus serenei* Dawson, Pac. Sci. 8:441, fig. 52d, 1954. Type Locality: Hon Tre, Nha Trang, central Vietnam.

Holotype Specimen: US (not examined). Isotype specimen: collected February 6, 1953 by E. Y. Dawson, BISH 499793 (examined).

Western Pacific Distribution: Vietnam.

Reference: Dawson, 1961.

Only a single sheet of Dawson's voucher specimens (= isotype, Dawson 11268) deposited in BISH was examined. Upright plants up to 4 cm tall, brownish red when dried. Axes terete just above basal disc, 1.0-1.2 mm in diameter, abruptly becoming compressed to flattened upward, up to 4 mm wide in middle portion except at forks, flattened portions $300-400 \mu$ m thick; axes simple or once to thrice dichotomously branched, mostly at intervals of 1 cm; proliferations formed on grazed ends only. Medulla consisting of 14–18 rows of cells in lowest terete portion, 10-12 in lower to upper flattened portions; cells elliptical in longitudinal

section, 50–175 μ m long (length/thickness, 2–7) in center of medulla in lower portion of upright plants, 75–200 μ m long (length/thickness, 2–6) in middle portion, 38–60 μ m long (length/thickness, 2–4) in upper portion; cells elliptical in transverse section, 58–125 μ m wide and 38-63 μ m thick in lower portion, 60–150 μ m wide and 40–70 μ m thick in middle portion, 25–75 μ m wide and 20–40 μ m thick in upper portion; cell walls 5.0–7.5 μ m thick; slender hyphalike filaments 2.5– 5.0 μ m wide weakly developing from medullary cells of lower portion. Cortex consisting of 14–18 rows of cells in lowest terete portion, five to six rows in middle portion, and three to four rows in upper portion; cells rectangular, 3.8–5.0 μ m wide in outer cortex.

Spermatangia formed in a distal sorus of branches; mature spermatangia 8–10 μ m long and 2.0–2.5 μ m wide. Cystocarps formed in single or catenate series in middle to upper portions of the plant; mature cystocarps not restricted centrally in medulla, hemispherically prominent, 600–800 μ m in diameter, 500–550 μ m tall; provided with multiple carpostomes in thickened cortex. Thickened cortex composed of 14–18 anticlinal rows of cells, 125–175 μ m thick, on carpostomal side and eight to 10 rows, 75–100 μ m thick, on other side. Tetrasporophytes unknown.

Remarks: This species is characterized by a few branches, thinner axes, and prominent hemispherical cystocarps. Because few herbarium specimens are available for study, it is impossible to describe the range of variation for morphological features of *A. serenei*.

Ahnfeltiopsis yamadae (Segawa) Masuda, Jpn. J. Phycol. 41:3, 1993. (Figs. 11, 28, 31, 34, 38)

Basionym: *Chondrus yamadae* Segawa, Sci. Pap. Inst. Alg. Res. Fac. Sci. Hokkaido Imp. Univ. 2:262, pl. 57, fig. 9. 1941.

Synonym: Ahnfeltia yamadae (Segawa) Mikami, Sci. Pap. Inst. Alg. Res. Fac. Sci. Hokkaido Univ. 5:201, pl. 1, fig. 13, 1965.

Type Locality: Shirahama, Shimoda, Shizuoka Prefecture, central Japan. Holotype Specimen: Herbarium of the Faculty of Agriculture, Kyushu University, collected July 31, 1937 (examined).

Distribution: Endemic to the Pacific coast of central Japan (Mie and Shizuoka prefectures); uncommon, known from several localities only.

Upright plants rigid, dark red, 10–30 cm tall. Main axes terete just above basal holdfast, 0.8–1.2 mm in diameter, becoming abruptly compressed upward, and reaching maximum width of 3–6 mm and thickness of 0.8–1.0 mm before first dichotomy; axes sparsely divided one to nine times dichotomously or subdichotomously at intervals of 2–8 cm except in upper portion and at angles of 30-70° (Fig. 11); channelled throughout compressed portion (Fig. 38) and producing numerous proliferations from both margins. Proliferations pinnate, filling intervening spaces between main branches; in fully grown upright plants also developing from both surfaces; terete to subterete in lower portion and compressed in middle to upper portion; up to 1.5 cm long, simple to thrice dichotomous; often bearing secondary



Fig. 26. Longitudinal section of an axis with the basal holdfast of *Ahnfeltiopsis* paradoxa from Jogashima shows the hypobasal tissue (h), basal holdfast (b) and medullary layer (m). Fig. 27. *Ahnfeltiopsis okamurae* from Mimaizaki, transverse section of an axis at the lower portion. Fig. 28. *Ahnfeltiopsis yamadae* from Kamishima, longitudinal section of an axis at the lower portion. Siender hyphalike filaments (arrowheads) developed secondarily from medullary cells. Scale in Fig. 26 also applies to Figs. 27 and 28.

proliferations in lower terete portions. Medulla consisting of 26–32 rows of cells in center of medulla throughout plant; cells elliptical to angular in longitudinal section, 50–200 μ m long (length/thickness, 1.6–8.8) in center of medulla in lower portion, 50–500 μ m long (length/thickness, 2-9) in middle portion, 50–250 μ m long (length/thickness, 2-9) in middle portion, 50–250 μ m long (length/thickness, 2-9) in middle portion, 50–250 μ m long (length/thickness, 2-9) in wide and 20–35 μ m thick in center of medulla in lower portion, 20–45 μ m wide and 20–35 μ m thick in center of medulla in lower portion, 20–85 μ m wide and 20–50 μ m thick in middle portion, 20–50 μ m wide and 20–45 μ m thick in upper portion; cell walls 4–5 μ m thick; slender hyphalike filaments 3–8 μ m wide developing from medullary cells and becoming anastomosing within medulla (Fig.



Figs. 29–33. Reproductive structures of species of *Ahnfeltioposis*. Fig. 29, Procarp of *A. catenata* from Toba consisting of a supporting cell, three-celled carpogonial branch (cb1, cb2, c), and two-celled sterile branch (st). Figs. 30, 31, Spermatangial sori show anticlinally elongated spermatangia: Fig. 30, from the holotype specimen of *A. chnoosporoides*; Fig. 31, from Atami specimen of *A. yamadae*. Figs. 32, 33, Developing cystocarps: Fig. 32, several gonimoblasts (arrowheads) issuing from an auxiliary cell in *A. divaricata* (after Masuda 1987, fig. 11F); Fig. 33, more advanced stage in *A. flabelliformis* from the type locality. Scale in Fig. 29 also applies to Figs. 30 and 31.

28), abundant in lower portion. Cortex consisting of 30–36 rows of cells in lowest terete portion, 16–18 rows in lower portion, 12–14 rows in middle portion, and seven to nine rows in upper portion; cells rectangular, 4–5 μm wide in outer cortex throughout plant.

Spermatangia formed in a distal sorus on ordinary branches and proliferations; mature spermatangia $11-13 \mu m$ long and $2.0-2.5 \mu m$ wide (Fig. 31). Procarps are formed in groups on distal portions of ordinary branches and proliferations; a three-celled carpogonial branch provided with a one- to three-celled sterile branchlet (Mikami 1965). Cystocarps central in medulla (Fig. 34, 38) with



Figs. 34–40. Longitudinal (Figs. 34, 37) and transverse (Figs. 35, 36, 38–40) sections of cystocarps of species of *Ahnfeltiopsis*. Figs. 34, 38, *A. yamadae* from Atami; Fig. 34, an elongated ellipsoid cystocarp, which is centrally located; Fig. 38, relationship of cystocarp to canaliculate surface (arrowheads). Fig. 35, Hemispherically prominent cystocarp of *A. chnoosporioides* from the type locality. Fig. 36, Lectotype specimen of *A. okamurae* with multiple carpostomes (arrowheads). Fig. 37, Ellipsoid cystocarp of *A. catenata* from Toba. Fig. 39, Portion of a cystocarp of *A. pygmaea* from Hainan Island showing two carpostomes (arrowheads). Fig. 40, Portion of a cystocarp of *A. concinna* from Shimoda showing three carpostomes (arrowheads). Scale in Fig. 34 also applies to Fig. 38; scale in Fig. 37 also applies to Figs. 35 and 36.

cystocarpic parts prominent; ellipsoidal (Fig. 34), 2–6 mm long, 0.9–1.2 mm wide, 0.5–0.7 mm thick; most thickened parts of cortex around cystocarps composed of 20–26 anticlinal rows of cells 160–180 μ m thick, other parts composed of 10–14 rows of cells 70–80 μ m thick; multiple carpostomes found in thickened cortex. Tetrasporophytes unknown.

Remarks: This species has a characteristic upright plant with conspicuously channelled axes, which are sparsely branched at long intervals at relatively narrow angles and have numerous pinnately arranged proliferations. Both this species and *A. okamurae* produce hyphalike filaments from medullary cells and have large ellipsoid cystocarps. However, the gross morphological features of these two species are quite different (see Figs. 9 and 11).

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Literature Cited

Agardh, J. G. 1851. Species genera et ordines algarum, vol. II. 351 pp. Gleerup, Lund. Børgesen, F. 1936. Some marine algae from Ceylon. Ceylon J. Sci. Sec. A. Bot.

12:57–996.

- Dawson, E. Y. 1944. The marine algae of the Gulf of California. Allan Hancock Pacific Exped. 3:189–452.
- Dawson, E. Y. 1954. Marine plants in the vicinity of the Institut Oceanographique de Nha Trang, Viet Nam. Pac. Sci. 8:373–481.
- Dawson, E. Y. 1961. Marine red algae of Pacific Mexico, Part 4. Gigartinales. Pac. Nat. 2:189–343.
- Greuter, W., et al. 1988. International Code of Botanical Nomenclature. Regnum vegetabile 118:1–328.

Holmgren, P. K., Keuken, W., and Schofield, E. K. 1981. Index herbariorum. Part I. The herbaria of the world, 7th ed. 452 pp. Bohn, Scheltema & Holkema, Utrecht.

- Kang, J. W. 1966. On the geographical distribution of marine algae in Korea. Bull. Pusan Fish. Coll. 7:1–138.
- Kützing, F. T. 1869. Tabulae phycologicae. 19:36, Taf. 1-100. Nordhausen.
- Magruder, W. H. 1977. The life history of the red alga *Ahnfeltia concinna* (Rhodophyta, Gigartinales). Phycologia 16:197–203.
- Magruder, W. H., and Hunt, J. W. 1979. Seaweeds of Hawaii. 116 pp. Oriental Publishing Co., Honolulu.

- Masuda, M. 1981. Further observations on the life history of *Gymnogongrus flabelliformis* Harvey (Rhodophyta) in culture. J. Fac. Sci., Hokkaido Univ. Ser. V (Botany) 12:159–164.
- Masuda, M. 1983. The life history of *Ahnfeltia concinna* J. Agardh (Rhodophyta, Gigartinales) from Japan. Jpn. J. Phycol. 31:180–189.
- Masuda, M. 1987. Taxonomic notes on the Japanese species of *Gymnogongrus* (Phyllophoraceae, Rhodophyta). J. Fac. Sci. Hokkaido Univ. Ser. V (Botany) 14:39–72.
- Masuda, M., DeCew, T. C., and West, J. A. 1979. The tetrasporophyte of *Gymnogongrus flabelliformis* Harvey (Gigartinales, Phyllophoraceae). Jpn. J. Phycol. 27:63–73.
- Mikami, H. 1965. A systematic study of the Phyllophoraceae and Gigartinaceae from Japan and its vicinity. Sci. Pap. Inst. Alg. Res. Fac. Sci. Hokkaido Univ. 5:181–285.
- Okamura, K. 1921, Icones of Japanese algae, 4(7):127-149, pl. 181-185.
- Okamura, K. 1922. Icones of Japanese algae. 4(9):173-184, pl. 191-195.
- Okamura, K. 1933. Icones of Japanese algae. 7(2):9-16, pl. 306-310.
- Okamura, K. 1936. Nippon kaiso Shi. 964 pp. Uchidarokakuho, Tokyo (in Japanese).
- Pham H. H. 1969. Marine algae of South VietNam. 559 pp. Ministry of Education and Youth, Trung-Tam Hoc-Liew Xuat-Btan, Saigon (in Vietnamese).
- Silva, P. C., and DeCew, T. C. 1992. *Ahnfeltiopsis*, a new genus in the Phyllophoraceae (Gigartinales, Rhodophyceae). Phycologia 31:576–580.
- Tanaka, T., and Pham H. H. 1962. Notes on some marine algae from VietNam. I. Mem. Fac. Fish. Kagoshima Univ. 11:24–40.
- Tokida, J., and Masaki, T. 1959. Studies on the reproductive organs of red algae. III. On the structure and development of female organs in *Schizymenia dubyi, Gymnogongrus flabelliformis*, and *Rhodymenia pertusa*. Bull. Fac. Fish. Hokkaido Univ. 10:87–96.
- Tseng, C. K., ed. 1983. Common seaweeds of China. 316 pp. Science Press, Beijing.
- Yendo, K. 1920. Novae algae Japoniae. Decas I-III. Bot. Mag. Tokyo 34:1-12.
- Zinova, E. S. 1940. Algae of the Sea of Japan. Trans. Pac. Committee Acad. Sci. USSR 5:1–164 (in Russian).
- Zinova, A. D. and Makijenko, V. F. 1972. Species nova generis *Phyllophora* (Rhodophyta) e Mari Japonico. Nov. syst. plant. non vasc. 9:60–64 (in Russian).

HAWAIIAN PHYLLOPHORACEAE

Richard E. Norris

Abstract

Hawaiian species of Phyllophoraceae are known mostly from gametophytes, which are dioecious upright, cylindrical to flattened, dichotomously branched plants mostly occurring on intertidal basaltic rock in moderate to strong surf. Cystocarps are enclosed within the thallus and have one to several carpostomes. Male plants produce sori of spermatangia in distal parts of branches. Because of the absence of large tetrasporophytes in many collections and because the results of a previous study indicate that the life history includes an alternation of heteromorphic phases, the Hawaiian species are placed in a new genus: *Ahnfeltiopsis* DeCew et Silva. Three species occur in Hawaii: *A. concinna*, the largest and most conspicuous red alga in the intertidal region on the major islands; *A. pygmaea*, a species previously known in India and on the southeast Asian coast and now also known from Oahu; and *A. flabelliformis*, a species previously known from Vietnam to Korea and Japan and now known to occur also on all major islands of Hawaii.

Introduction

The cartilaginous large plants of Phyllophoraceae are found in many tropical and subtropical intertidal regions of the world, including Hawaii, and often form a conspicuous upper subtidal to intertidal yellow to dark-colored zone. Such midintertidal zones are often present in Hawaii, mostly caused by growth of one of the larger of the phyllophoroid red algae, *Ahnfeltia concinna* J. Agardh, a species usually restricted to a black basaltic lava substratum exposed to surf.

Species assigned to *Gymnogongrus* also occur in habitats similar to those of *A. concinna* and on the outer parts of coral reefs in the Hawaiian Archipelago. *Gymnogongrus* ? *dendroides* Harvey et Bailey was listed from the island of Hawaii (Harvey and Bailey 1851), but examination of the type specimen (TCD) shows that it is the same as *A. concinna*. Two species, *G. vermicularis* var. *americana* J. Agardh and *G. disciplinaris* (Bory) J. Agardh, were listed by Reed (1907) from Hawaii. These species were originally described from South America, and their range currently does not include Hawaii. Therefore, three species of phyllophoroid algae were thought to occur in the Hawaiian region: *A. concinna* and two unidentified species of *Gymnogongrus*.

Materials and Methods

Sections of dried specimens were made by hand with a razor blade and transferred to deionized water. The water was then blotted off and replaced by 50% corn syrup containing 1% aniline blue, a few drops of HCl, and approximately 2% formalin. Reproductive structures mounted in this medium become stained within 24 hr, and the slides are usually semipermanent. Specimen numbers preceded by IA are in the herbarium of Dr. Isabella Abbott at the Botany

Department, University of Hawaii, and will be transferred to the Bishop Museum. Specimen numbers identified by BISH are now in the herbarium of the Bernice P. Bishop Museum, Honolulu, Hawaii.

Description of the Hawaiian Species

In a survey of the Phyllophoraceae from Hawaii in the Bishop Museum Herbarium and in the herbarium of I.A. Abbott, three species that should be assigned to the new genus Ahnfeltiopsis DeCew et Silva (Silva and DeCew 1992) have been discovered. Two are terete plants, more or less dichotomously branched; the third is a flattened plant that usually has dichotomous to fanlike branching. Cystocarps of all species are internal in the thallus, and carpostomes are present. Two of the species, A. concinna and flabelliformis, have alternative heteromorphic phases in their life histories (Magruder 1977, Masuda et al. 1979; Masuda 1981, 1983). The alternative phase is a plant with a prostrate crust similar to that of Erythrodermis Batters, a genus now synonymous with Phyllophora (Batters 1900; Maggs 1989, 1990). Ahnfeltiopsis pygmaea, which is mostly terete and is a small plant, sometimes distally compressed, fits well into a species originally described from the Indian coast, G. pygmaeus J. Agardh (Agardh 1851), a species that is known to also occur in the western Pacific on the Vietnam coast (Dawson 1954, Pham 1969), in the Philippines (Silva et al. 1987), and in the Cape Verde Islands (Price et al. 1986). Ahnfeltiopsis flabelliformis is probably the same as G. flabelliformis (Harvey) Masuda, which was formerly known to occur from Vietnam to Korea and Japan (Masuda 1993).

Ahnfeltiopsis concinna (J. Agardh) Silva et De Cew, Phycologia 31:577, 1992. (Fig. 1)

Basionym: Ahnfeltia concinna J. Agardh, Öfvers, Kgl. Svenska Vet.-Akad. Handl. 4:12, 1847.

References: Mikami 1965, figs. 5, 6; Magruder 1977, figs 1–17; Masuda 1983, figs. 1–5; Price et al. 1986 (all as *A. concinna* J. Agardh).

Synonym: *Gymnogongrus* ? *dendroides* Harvey et Bailey Proc. Boston Soc. Nat Hist. 3:370–373, 1851.

Gametophytic plants growing in dense tufts of erect thalli from prostrate crusts, sometimes forming more or less continuous bands in the midtidal region on basalt rocks. Plants dark reddish black to red-brown, becoming yellowed in distal regions of branches when growing in exposed areas with bright sunlight. Branches terete, with elongate unbranched proximal regions and several distal dichotomies (Fig. 1); up to 600 mm long and 1.5 mm wide. Medulla consisting of pseudo-parenchyma, with all cells approximately the same shape and size; cortex consisting of small-celled filaments perpendicular to the thallus surface.

Male plants having transverse bands of spermatangia produced in the outer cortex, giving a somewhat striped appearance to the fertile branch tips. Procarps occurring in small groups near branch apices. Cystocarps up to approximately

2 mm in diameter, often strongly projecting from the thallus surface, and when mature having one to several carpostomes (McFadden 1911). The cystocarps I have examined have up to three or four very small carpostomes, and they seem to be formed by degeneration of tissues. Japanese plants are somewhat smaller and have smaller cystocarps (Masuda 1983).

Tetrasporophytes are small crusts, without attaching rhizoids, up to approximately 2 mm in diameter and slightly more than 100 μ m thick in Magruder's and Masuda's cultures. Tetrasporangia borne in an intercalary position, in short catenate series. According to Masuda's comparison (1983) of this species from the two regions, the only other significant difference between them is the nonnemathecial arrangement of tetrasporangia in the Hawaiian species compared with tetrasporangia borne in nemathecia in the Japanese specimens.

Distribution: Hawaii, Japan, Cape Verde Islands.

Hawaiian Collections: Wailupe, Oahu, leg. D. P. and I. A. Abbott, July 1, 1945, IA 806; Kihei, Maui (drift at Lipoa Street), leg. I. A. Abbott, September 2, 1976, IA 14626; Hanamaulu Bay, Kauai, leg. M. Hoyle, March 18, 1973, BISH 517102; Moloaa Bay, Kauai, leg. M. S. Doty, February 8, 1952, BISH 525611.

Remarks: Magruder (1977) described procarps for *A. concinna*, with sterile cells not normally present, whereas a single sterile cell is always present on Japanese specimens assigned to this species (Masuda 1983). I found a sterile cell on the first cell of the carpogonial branch in *A. concinna* procarps from Hawaii. The Hawaiian plants may be a different species from the Japanese plants assigned to *A. concinna* because (1) Japanese specimens are smaller than the Hawaiian ones; and (2) tetrasporangia are nonnemathecial in the Hawaiian plants according to Magruder (1977), whereas Japanese tetrasporophytes bear sporangia in nemathecia (Masuda 1983). The material used for the report of this species from the Cape Verde Islands needs to be critically reexamined.

Ahnfeltiopsis pygmaea (J. Agardh) Silva et DeCew, Phycologia 31:578, 1992.

(Fig. 2)

Basionym: *Gymnogongrus pygmaeus* J. Agardh, Sp. gen. ordines algarum, p. 317, 1851

References: Børgesen 1937, Dawson 1954, Durairatnam 1961, Pham 1969 (as *G. pygmaeus*).

Plants up to approximately 3 cm tall, 0.5 mm wide, terete to compressed, repeatedly dichotomously branched, forming a bushy plant (Fig. 2). Procarps composed of five cells, the supporting cell bearing a three-celled carpogonial branch, the first cell of which has a single-celled branch. Cystocarps intercalary on slightly widened parts of branches, often present proximal to a dichotomy; deeply embedded in the branches, with a thickened cortex on the carpostomate side. Large medullary cells near cystocarps often filled with nutrients. Males and tetrasporophytes not observed.

Distribution: India, Sri Lanka, Vietnam, Philippines, Hawaii.

Hawaiian Collections: Koloa, Oahu, leg. M. S. Doty, October 9, 1955, BISH 519961; Waikiki, Oahu, leg. A. J. Bernatowitz, March 15, 1958, BISH 520002 and 523258; Haleiwa, Oahu, leg. M. S. Doty, September 14, 1959, BISH 488025.

Remarks: These are the first records for this species remote from the shores of the Asian continent. In addition to their small size, they are different from most other species in the genus because of their mostly cylindrical to compressed branches and the presence of embedded cystocarps. Small species are not well known, however, and future investigations may show that other narrow species such as *G. nigricans* P. Dangeard (Dangeard 1952) may be indistinguishable.

Ahnfeltiopsis flabelliformis (Harvey), Jpn. J. Phycol. 41:2, 1993.

(Figs. 3, 4)

Basionym: *Gymnogongrus flabelliformis* Harvey, Perry, Narrative Exped. China Sea and Japan, vol. 2, p. 332, 1857.

Synonym: *Gymnogongrus japonica* Suringar, Ann. Bot. Mus. Bot. Lugd.-Batavi, 3:259, 1867.

Plants forming shrubby upright branches, up to 10 cm tall and 1.5 mm wide, dichotomously to palmately divided (Figs. 3 and 4); branches mostly flat and dichotomously branched in proximal regions but sometimes becoming terete and finely palmately divided in distal parts; branches often with proliferous small branchlets at more or less right angles to axes. Procarps on narrow margins of flattened branches, with a form typical for the Phyllophoraceae, composed of five cells, a supporting cell bearing a three-celled carpogonial branch, a single sterile cell attached to its first cell. Cystocarps not protruding or protruding very little from surface in distal regions, if in a series, sometimes causing the plant to become slightly catenate, each with a single carpostome.

Plants dioecious, male plants with fertile bands of spermatangia-bearing cells encircling or in patches on distal branches. Tetrasporophytes as described by Masuda et al. (1979) and Masuda (1981).

Habitat: intertidal on basalt or occasionally on coral outcroppings in surf-swept areas.

Published Hawaiian Records: Not previously recorded from Hawaii.

Hawaiian Distribution: Kauai: Poipu Beach (County Park), Weliweli, leg. M. S. Doty, BISH 188431. Oahu: Halona, leg. I. A. Abbott, April 23, 1968, BISH 519951; Kaloko, May 14,1983, IA 16260; Diamond Head, May 1, 1941, IA 1202; Sans Souci, Waikiki, September 13,1987, IA 18427; Maui: Makiwa Park, August 17,1978, IA 14363; 1 mi. north of Launiupoko Point, September 7,1971, IA 14774. Hawaii: Shipman Estate, Keaau, September 19–21, 1975, IA 17616.

Remarks: Similarities exist between *A. flabelliformis* and *A. catenata* (Yendo) Masuda and *A. divaricata* (Holmes) Masuda (see Masuda et al., this volume, for descriptions of these species). Characters in common are (1) wide-angled dichotomous branching of compressed to flattened plants; (2) presence of marginal proliferations; (3) anatomical characteristics of the medulla and cortex; and (4) sometimes an arrangement of cystocarps, sunken in the medulla, in a catenate



Fig. I. Ahnfeltiopsis concinna. cystocarpic plants from Hanamaulu Bay, Kauai, Hawaii (BISH 517102).

Fig.2. Ahnfeltiopsis pygmaea, a cystocarpic plant from Walkiki, Oahu, Hawaii (BISH 523258).

Figs. 3 and 4. Ahnfeltiopsis flabelliformis, cystocarpic plants from Diamond Head, Oahu, Hawaii (IA 1202).

series. Potentially, what I think is *A. pygmaeus* in Hawaii may be a growth form of *A. flabelliformis.* The presence of cystocarps, however, on these small plants signifies maturity on plants with a structure, suggesting a different species.

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Literature Cited

Agardh, J. G. 1851. Species genera et ordines algarum, vol. 2. 351 pp. Gleerup, Lund.

- Batters, E.A. L. 1900. New or critical British marine algae. J. Bot. (London) 38:369-379.
- Børgesen, F. 1937. Contributions to a south Indian marine algal flora. II. J. Indian Bot. Soc. 16:311-357.
- Dangeard, P. 1952. Algues de la presqu'île du Cap Vert (Dakar) et ses environs. Botaniste 36:193-329.
- Dawson, E. Y. 1954. Marine plants in the vicinity of the Institut Océanographique de Nha Trang, Viet Nam. Pac. Sci. 8:373–470.
- Durairatnam, M. 1961. Contribution to the study of the marine algae of Ceylon. Bull. Fish. Res. Sta. Ceylon 10:1–181.
- Harvey, W. H., and Bailey, J. W. 1851. Descriptions of seventeen new species of algae, collected by the United States Exploring Expedition. Proc. Boston Soc. Nat. Hist. 3:370–373.
- McFadden, A. S. 1911. The nature of the carpostomes in the cystocarp of Ahnfeldtia gigartinoides. Univ. Calif. Publ. Bot. 4:137–142.
- Maggs, C. A. 1989. *Erythrodermis allenii* Batters in the life history of *Phyllophora traillii* Holmes ex Batters (Phyllophoraceae, Rhodophytae, Phycologia 28:305–317.
- Maggs, C. A. 1990. Taxonomy of phyllophoroid algae: the implications of life history. Hydrobiologia 204/205:119–124.
- Magruder, W. H. 1977. The life history of the red alga *Ahnfeltia concinna* (Rhodophyta, Gigartinales) Phycologia 12:197–203.
- Masuda, M. 1981. Further observations on the life history of *Gymnogongrus flabelliformis* Harvey (Rhodophyta) in culture. J. Fac. Sci. Hokkaldo Univ. ser. 5, 12:159–164.
- Masuda, M. 1983. The life history of *Ahnfeltia concinna* J. Agardh (Rhodophyta, Gigartinales) from Japan. Jpn. J. Phycol. (Sôrui) 31:180–189.
- Masuda, M. 1993. The taxonomic status of the western Pacific species of *Gymnogongrus* and *Ahnfeltia* (Gigartinales, Rhodophyta). Jpn. J. Phycol. 41:1–6.
- Masuda, M., DeCew, T. C., and West, J. A. 1979. The tetrasporophyte of *Gyumnogongrus flabelliformis* Harvey (Gigartinales, Phyllophoraceae). Jpn. J. Phycol. 27:63–73.
- Mikami H. 1965. A systematic study of the *Phyllophoraceae* and *Gigartinaceae* from Japan and its vicinity. J. Fac. Sci. Hokkaido Univ. ser. 5. 5:181–285.

- Pham Hoàng Hô. 1969. Rong biên Viêtnam: Marine algae of South Vietnam. [vi] + 558 pp. Ministry of Education and Youth, Trung-Tam Hoc-Liew Xuat-Btan, Saigon (in Vietnamese).
- Price, J. H., John, D. M., and Lawson, G. W. 1986. Seaweeds of the western coast of tropical Africa and adjacent islands: a critical assessment. IV. Rhodophyta (Florideae).
 1. Genera A–F. Bull. Br. Mus. Nat. Hist. (Bot) 15:1–122.
- Reed, M. 1907. The economic seaweeds of Hawaii and their food value. Ann. Rep. Hawaii Agric. Exp. Sta. 1906:61-88.
- Silva, P. C., and DeCew, T. C. 1992. *Ahnfeltiopsis*, a new genus in the Phyllophoraceae (Gigartinales, Rhodophyceae). Phycologia 31:576–580.
- Silva, P. C., Meñez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contrib. Mar. Sci. 27:1–179.

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