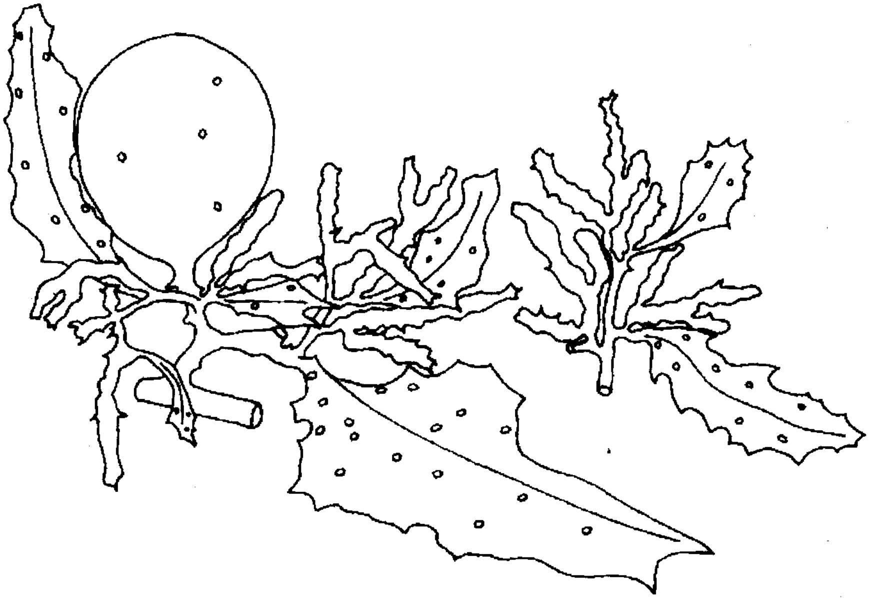
# TAXONOMY OF ECONOMIC SEAWEEDS
## With reference to some Pacific species
## Volume V

Isabella A. Abbott, Editor



A Publication of the
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Published by the California Sea Grant College System, University of California, La Jolla, California, 1995. Publication No. T-CSGCP-035. Additional copies are available for $10 (U.S.) each, prepaid (check or money order payable to "UC Regents") from: California Sea Grant College, University of California, 9500 Gilman Drive, La Jolla, CA 92093-0232. (619) 534-4444.

This work is funded in part by a grant from the National Sea Grant College Program, National Oceanic and Atmospheric Administration, U.S. Department of Commerce, under grant number NA36RG0537, project number A/P-1, and in part by the California State Resources Agency. The views expressed herein are those of the authors and do not necessarily reflect the views of NOAA, or any of its subagencies. The U.S. Government is authorized to produce and distribute reprints for governmental purposes.

Published on recycled paper.

**Publication: October 1995**

# TAXONOMY OF ECONOMIC SEAWEEDS
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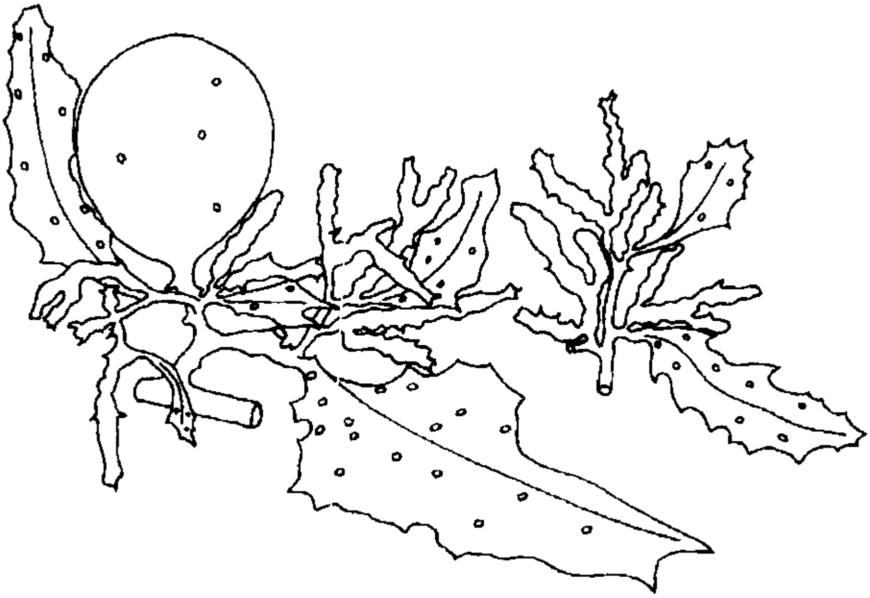
Results of an international workshop sponsored by the California Sea Grant College System in cooperation with the Pacific Sea Grant College Programs of Alaska, Hawaii, Oregon, and Washington and hosted by the University of Hawaii, Honolulu, July 1993.



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California Sea Grant College System

Report No. T-CSGCP-035

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# Dedication

This volume is dedicated
to the memory of
Zhang Junfu (C. F. Chang)

who died shortly after many of us had seen him at the International Phycological Congress in Qingdao in 1994.

Zhang Junfu graduated from the Biology Department of the Catholic University in Beijing in June 1941. He first taught Biology at the Qingdao City Girls' High School. In 1946, when C. K. Tseng arrived in Qingdao to teach at what is now Shandong Oceanographic University, Zhang started his study of the taxonomy of Chinese seaweeds with Tseng. When the Institute of Oceanology, Academia Sinica, opened in 1950, he accompanied Dr. Tseng to the Institute as a research associate. Eventually, Zhang became a senior research fellow (equivalent to Professor in China).

During the Cultural Revolution, Zhang continued to do research and publish. During that perilous period, he (with his long-time colleague Xia Bangmei) published an important paper on Chinese *Gracilaria* species which, while written in Chinese, had exemplary illustrations. He loved taxonomy and had a good eye for differences in species. He was a persistent and tenacious worker, showing excellent judgment in drawing species boundaries. We will miss the twinkle in his eyes and his shy humor, as well as his thoughtfulness and kindness.

We honor him now as a respected colleague who always had time to help us, and to offer an opinion when asked. We salute him in friendship, richer for having known him.

Isabella A. Abbott

# Preface

James J. Sullivan
Director, California Sea Grant College System

The series of workshops of which this one was part rests on the conviction that progress in seaweed aquaculture and marine natural products chemistry will advance appreciably once the taxonomy of commercially interesting species is better understood.

California Sea Grant funded the first of these biennial workshops more than a decade ago—in 1984, at the University of Guam. From the first, Dr. Abbott served as organizer and motivator. Her vision was to bring together leading systematists from around the Pacific Rim to direct their knowledge and insight to the enormous ignorance that prevails about warm-water Pacific algae. She recognized that many of these eminent specialists were not being succeeded by younger generations and thus represented an irreplaceable resource. Further, she believed that the enthusiasm and dedication of workshop participants would overcome any difficulties presented by language and cultural differences.

The progress made at these workshops has been considerable, and we at California Sea Grant, and our colleagues in the other Pacific Sea Grant Colleges, are pleased to have been able to play some small part in making them possible.

# Introduction

Isabella A. Abbott, Workshop Convener and Editor

Acting as convener and major hostess for the fifth Sea Grant workshop in Honolulu left some of the details and experiences in a kind of blur, I must admit. I think I was most worried about not being able to find everyone coming through customs near the times of arrival. Luckily, I had told everyone that one of the graduate students helping me with transportation was very tall—and being very tall was indeed a help. As it turned out, no one was left behind, so I was worrying needlessly.

Everyone from the Orient said that they enjoyed the clean campus and city and the clear Hawaiian air. They also enjoyed the field trip led by Professor Celia Smith and her graduate students while I was home preparing dinner. Dr. Sullivan brought enough appetizers of Chinese, Japanese, and Korean derivation to feed an army, but he made wonderful choices—they disappeared in minutes.

So what about the scientific sessions? Because workshop participants had seen one another several times before, even the most shy were brave about asking for help or sharing opinions. If Zhang Junfu of China and Hae Bok Lee of Korea are the "last" ones who would volunteer an opinion, they are among the first who will answer and help if asked. If the *Sargassum* group is so involved in the intricacies of nomenclature and unexpected variations shown by those "terrible" plants that they do not hear anyone talking about other species, at least (I am confident) they are on the brink of making significant taxonomic breakthroughs in that genus. It has taken them 10 years of sharing specimens and ideas and studying that genus to get to the stage of recognizing that you have to question the opinions and interpretations of others.

On the other hand, both the gelidioids and gracilarioids have their own problems, problems of recognition at the level of genus and other problems at the level of species. One of the good things about working with species that have economic importance is that there also exist people who work with them at a different, less specialized level than do phycologists. These more commercially oriented people are interested in getting the plants to grow, knowing when and how to harvest them, and turning them into something that has a monetary value.

If you, as a highly trained phycologist, can only identify genera on the basis of extremely detailed ontogenic events, no one without your training can follow you. This is the situation in *Gracilaria* and, to a lesser extent, in *Gelidium*.

What we must guard against, however, is arguing over the fine points of genus recognition while dozens of species remain unexamined and poorly known. In the relatively small basin of the Caribbean Sea, along with immediately adjacent regions, about 20 species of *Gracilaria*/*Gracilariopsis* can reportedly be found. In the Indian Ocean, a larger area, there are reportedly about 65 species. Probably no resident phycologist in either geographical area could recognize with certainty any more than half the number of reported species, however; and none of the *Gracilaria* "specialists" in the Sea Grant group would probably know more than two or three. Wouldn't it be fun to get all the specimens together and see what we could do? (The most difficult barrier to complete success is that many specimens of the older described species are sterile, or at least not spermatangial or cystocarpic.)

When the *Gelidium* group finishes the "big" species, I hope that it will give concerted attention to the "small" species that are usually relegated to *G. pusillum* or *G. crinale*. Whether only *Gelidium* is recognized for all *Gelidium* and *Pterocladia* species (a situation that should be avoided) or the genera are reconstituted or reinterpreted, those plants of small stature still need to be critically examined.

In closing, I am pleased to observe that Dr. Masuda's studies on the Phyllophoraceae reported in volume 4 added a new dimension to our taxonomic "holdings" as well as contributing to economic potentials, as these organisms are excellent producers of iota-carrageenan. He did such a thorough job that scarcely any species in the warm Pacific is unknown. I hope that he will again join a Sea Grant group.

We are happy to publish Dr. Doty's new genus, *Betaphycus*, in this volume. His previous *Eucheuma* contributions in volumes 1 and 2 are probably the most cited of all of the papers we have published.

# Acknowledgments

The fact that species of *Sargassum* and *Gracilaria* have been named in honor of Dr. James Sullivan, director of the California Sea Grant College System, and chief honcho of these extremely successful Sea Grant workshops on taxonomy, should tell him and the world how grateful the participants of the workshops are. Five of us (Tseng, Xia, Yoshida, Santelices, and I) who were at the first workshop are still with the group 10 years later. Some who were at the first (Yamamoto, Chiang, and J. Norris) have been in and out, and a few others joined us later and have continued to contribute. The ones in the "permanent party" appreciate the effort that must be expended to make these workshops a success, both in serving as hosts and in producing papers after attending a workshop. It would be an understatement to say that the invitations to the workshops are treasured; moreover, many researchers want to invite themselves.

I thank Joan Yamada of the Hawaii Sea Grant office, Anne Fieberling of the Marriott Food Services, Fay Horie and Carrie Matsuzaki of the College of Engineering, and the Botany Department, University of Hawaii, for help in hosting the workshop at the University of Hawaii. I thank Diane Durney of Dr. Sullivan's office for helping to make things run so smoothly.

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.

Isabella A. Abbott

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Workshop participants. (Front row, left to right): T. Yoshida, C. K. Tseng, I. A. Abbott, Phang Siew Moi, I. K. Lee, H. Yamamoto . (Second row, left to right): G. Trono, N. H. Dinh, K. Lewmanomont, Xia Bangei (behind Dr. Phang). (Third row, left to right): T. Noro, M. Baba, J. N. Norris, Lu Baoren, Zhang Junfu. (Top row, left to right): H.-B. Lee, G. R. South, T. Ajisaka, H. Q. Nang, B. Santelices, M. Miyata. (Not present for photograph: James J. Sullivan)

# 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). For another example, Lu Baoren's *first name* is Baoren.

Listing Species Names

In accordance with the practices of the international journal *Taxon* and the adoption of this practice in volume 4 of the workshop series, 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,* for example, in the discussion, 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), plate or figure number(s), and date. If this style is followed, no one will ever create an illegitimate name, many of which occur because an author did not provide the *exact reference* in which the species are described. Article 33.2 of the International Code of Botanical Nomenclature states: "A new combination ... for a previously and validly published name is not validly published unless its basionym ... is clearly indicated and a *full and direct reference given to its author and place of valid publication with page or plate reference and date.*"

**Literature Cited**

In this volume, all references to volumes (1–4) from the first four workshops are listed in nomenclature setups and in Literature Cited as "Tax. Econ. Seaweeds 1 (or 2, 3, 4)," followed by page and figure numbers, instead of giving the whole citation including editor, place of publication, and so forth. Inasmuch as the entire citation for each volume takes five lines of type, it will save a lot of ink and paper if we shorten the references within the volume. 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, eds. [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, ed. [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, ed. [i–ii] + iii–xiv + 1–241, 1992. California Sea Grant College, University of California, La Jolla, Calif. Report No. T-CSGCP-023.

*Taxonomy of economic seaweeds: with reference to some Pacific species*, vol. 4. I.A. Abbott, ed. [i–ii] + iii–xvii + 1–200, 1994. California Sea Grant College, University of California, La Jolla, Calif. Report No. T-CSGCP-031.

# Section I. *Sargassum* Species

## INTRODUCTION

Isabella A. Abbott

Three interesting things are apparent in the *Sargassum* contributions. First, the taxonomic level has moved from the subgenus to sections or other categories among the subgenera. As examples of what has been done previously, the subgenera *Bactrophycus* and *Sargassum* of the western warm Pacific (and central Pacific at Hawaii) have been examined and enumerated. The focus on subgeneric categories means that taxonomists are now examining details of smaller groups, which suggests that soon species will be placed in synonymy. This will be met with great pleasure by a lot of phycologists. Second, a suite of specimens of *S. siliquosum* J. Agardh is described from the region of its type locality, Singapore. This is a species widely distributed in the western Pacific. The species of *Sargassum* in Vietnam are being collected and new species established for these relatively uncharted coasts. Third, a comprehensive review of the biogeographical distribution of *Sargassum* species in the Pacific is contributed by Naomi Phillips, a graduate student at the University of Hawaii who filled in the spot that we usually have for a student who is interested in systematics.

# *SARGASSUM HENSLOWIANUM* VAR. *CONDENSATUM* YAMADA IN JAPAN: A SYNONYM OF *SARGASSUM YENDOI* OKAMURA ET YAMADA

Tadahide Noro, Tetsuro Ajisaka, and Tadao Yoshida

## Abstract

*Sargassum henslowianum* var. *condensatum* Yamada. which has not been reported since its first collection, is a synonym of *S. yendoi* Okamura et Yamada.

## Introduction

*Sargassum henslowianum* var. *condensatum* Okamura et Yamada was described on the basis of a specimen collected from Nomo, Nagasaki Prefecture, southern Japan (Yamada 1942). However, this variety has not been reported since it was first collected.

During the fifth Sea Grant workshop on taxonomy of economic seaweeds, held in Honolulu, Hawaii, in 1993, we were privileged to examine specimens of *S. henslowianum* C. A. Agardh that had been collected from northern Vietnam. By comparing the morphological characteristics, we found that Japanese *S. henslowianum* var. *condensatum* was quite different from *S. henslowianum* found in Vietnam and South China.

This chapter considers the taxonomy of *S. henslowianum* var. *condensatum.*

## Materials and Methods

Specimens of *S. henslowianum* used in this study were collected from Do Son, Hai Phong Province, Vietnam, in May 1967 by Nguyen Huu Dinh, and from Vinh Thuc Island, Quang Ninh Province, Vietnam, in March, 1969 by Huynh Quang Nang. Specimens of *S. henslowianum* var. *condensatum* (SAP 026414) were collected from Nomo, Nagasaki Prefecture, Japan, by S. Narita in April 1921. Specimens of *S. yendoi* were collected from various parts of Japan by many phycologists and were deposited in the herbarium of the Faculty of Science, Hokkaido University (SAP). Some specimens collected from Kagoshima Prefecture were deposited in the herbarium of the Faculty of Fisheries, Kagoshima University, Japan.

## Results and Discussion

*Sargassum henslowianum* was originally recognized by C. A. Agardh and a description published by J. G. Agardh (1889). However, type materials have not been located in the Agardh Herbarium at Lund, so Macao was then proposed as the type locality of this species (Setchell 1936). Therefore, neotypification based on the specimens collected in Macao is needed.

Until now, *S. henslowianum* had been reported from Vietnam and China (Agardh 1889, Grunow 1915, Setchell 1936, Pham 1967, Tseng 1983). In Nagasaki, Japan, Yamada (1942) found *Sargassum* with vesicles with extremely long stalks. This feature is also a prominent characteristic of *S. henslowianum*. He might have confirmed what Okamura (1936) had predicted about the occurrence of *S. henslowianum* in southern Japan. However, unlike *S. henslowianum*, the Japanese *Sargassum* with long stalked vesicles had densely clustered receptacles. Because of this, Yamada (1942) proposed a new variety: *S. henslowianum* var. *condensatum*. The type specimen of *S. henslowianum* var. *condensatum* (SAP 026414) is deposited in the SAP.

In examining the Vietnamese specimens brought by Nguyen Hun Dinh and Huynh Quang Nang to the fifth Sea Grant workshop, we found some *Sargassum* with long stalked vesicles (Fig.1). The characteristics of these Vietnamese specimens agreed well with the original description of *S. henslowianum* (Agardh 1889), and the specimens were identified as *S. henslowianum*. This identification was strongly supported by C. K. Tseng and Lu Baoren, who had studied *S. henslowianum* from the Fujian and Guangdong provinces of China, and Hong Kong (Tseng 1983).

The difference between *S. henslowianum* from Vietnam and *S. henslowianum* var. *condensatum* from Japan was the presence of densely clustered receptacles in the Japanese plant. However, a comparison of both materials showed a difference not only in the receptacles but also in the size of the leaves and the width of the main branches. For example, *S. henslowianum* is not as wide as *S. henslowianum var. condensatum* (Table 1, Figs. 1 and 2). These differences, especially the morphological difference in the receptacles, make it difficult to include *S. henslowianum* var. *condensatum* in *S. henslowianum* var. *henslowianum*. For these reasons, *S. henslowianum* var. *condensatum* is to be excluded from *S. henslowianum* and must be transferred to an independent species.

The type specimen (SAP 026414) of *S. henslowianum* var. *condensatum* is a female plant without basal parts. This was the first and only collection of this variety. After examining *S. henslowianum,* we thought that the type materials of *S. henslowianum* var. *condensatum* were similar to the upper part of a female plant of *S. yendoi* Okamura et Yamada (Yamada 1938). For example, a comparison (Table 1) of the flattened primary branch, the size of leaves, and the condensed female receptacles shows that *S. henslowianum* var. *condensatum* (e.g., Fig. 2b) has many morphological similarities with *S. yendoi* (e.g., Fig. 3b).

On the basis of these similarities, we propose that *S. henslowianum* var. *condensatum* is a synonym of *S. yendoi,* which is distributed in the middle and southern parts of Japan.

*Sargassum yendoi* has also been reported in the Philippines (Domantay 1962; Velasquez et al. 1975), but we have not examined these specimens. Specimens of *S. yendoi* from the Philippines could be confused with specimens of *S. henslowianum*. Both *S. henslowianum* and *S. yendoi* have vesicles with

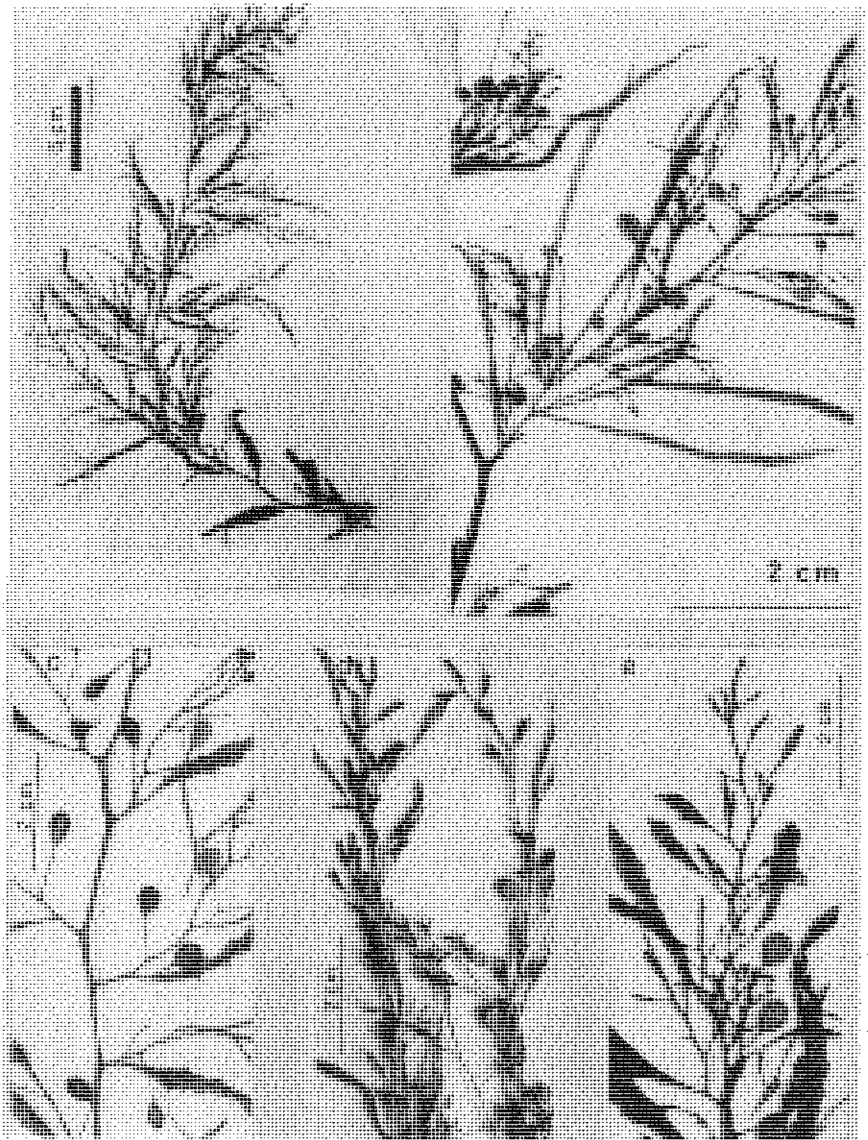

Fig. 1. *Sargassum henslowianum* C. A. Agardh ex J. G. Agardh. a., Whole thallus (Vinh Thuc Island, Quang Ninh Province, Vietnam, leg. Huynh Quang Nang, May 1968). b and c, Middle part of thallus (b) and vesicles (c) (Vinh Thuc Island, Quang Ninh Province, Vietnam, leg. Huynh Quang Nang, April 1969). d and e, Female (d) and male (e) receptacles (Do Son, Hai Phong Province, Vietnam, leg. Nguyen Hun Dinh, May 1967).

**Table 1. Morphological characteristics of *S. henslowianum* from Vietnam and *S. henslowianum* var. *condensatum* and *S. yendoi* from Japan***

| | *S. henslowianum* | *S. henslowianum* var. *condensatum* | *S. yendoi* |
|---|---|---|---|
| Holdfast | discoid | ? | discoid |
| Primary branch | compressed, 2 mm | compressed, 2 mm | compressed, 5 mm |
| Leaves | | | |
| Basal | lanceolate<br>50–100 mm × 5–8 mm | ? | lanceolate<br>50–100 mm × 5–12 mm |
| Upper | narrowly elliptic<br>50–80 mm × 3 mm | narrowly elliptic<br>80 mm × 8 mm | narrowly elliptic<br>50–100 mm × 3–10 mm |
| Vesicles | obovate-spherical<br>3–5 mm | obovate-spherical<br>8 mm | obovate-spherical<br>3–8 mm |
| Apices | round | round | round |
| Stalk | <10 mm | <24 mm | <15 mm |
| Receptacles | plant dioecious | plant dioecious? | plant dioecious |
| Male receptacle | branching<br>cylindrical<br>smooth<br>3–10 mm × 1 mm | ? | densely branching<br>cylindrical<br>smooth<br>3–5 mm × 1 mm |
| Female receptacle | branching<br>cylindrical<br>smooth<br>5–10 mm × 1 mm | densely branching<br>cylindrical<br>smooth<br>5–8 mm × 1 mm | densely branching<br>cylindrical<br>smooth<br>3–8 mm × 1 mm |
| Type locality | Macao | Nagasaki, Japan | Kanagawa or Shizuoka, Japan |
| Distribution | Southern China to northern Vietnam | Nagasaki, Japan (southern Japan) | Middle and southern Japan |

*Note—measured on dry materials

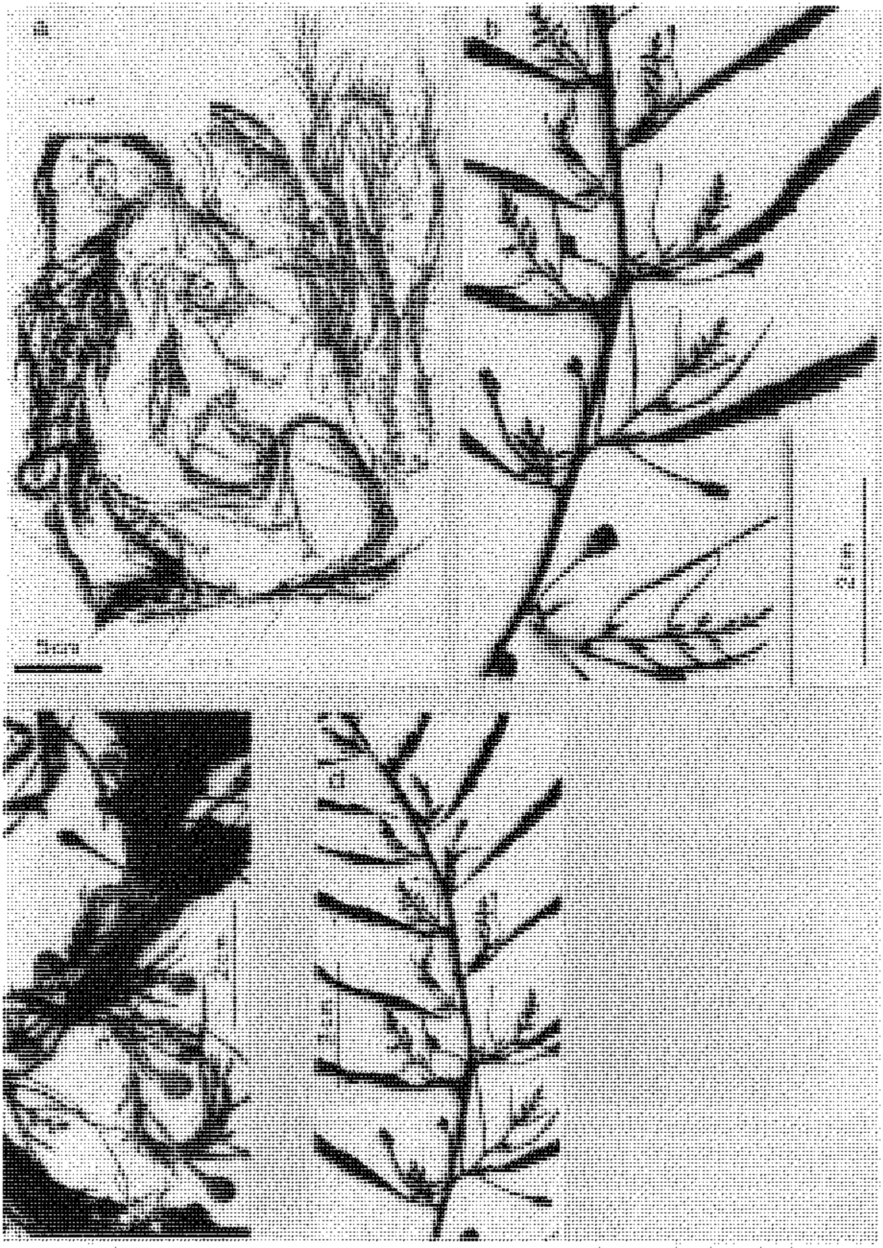

Fig. 2. *Sargassum henslowianum* var. *condensatum* Yamada (Nomo, Nagasaki, Japan, leg. S. Narita, April 1921; SAP 026414 ). a, Whole thallus. b, Middle part of thallus. c, Vesicles. d, Female receptacles.

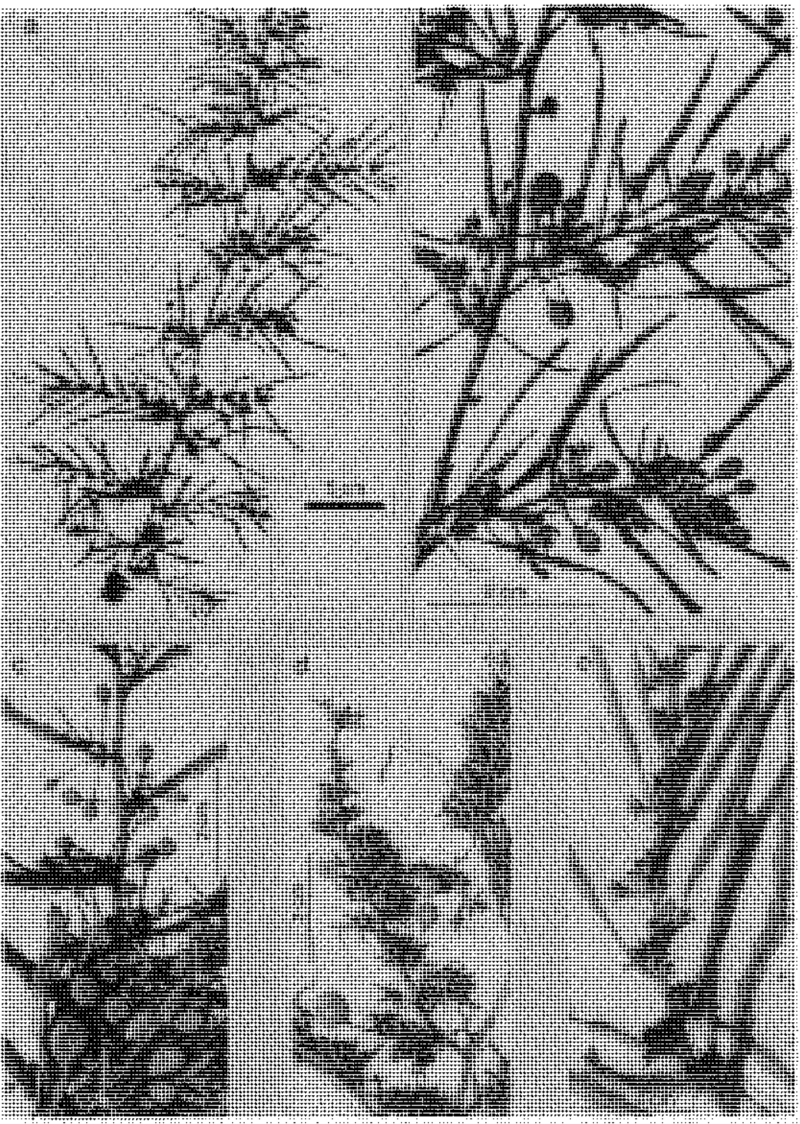

Fig. 3. *Sargassum yendoi* Okamura et Yamada ex Yamada. a and b, Whole thallus (a) and middle part (b) (Akune, Kagoshima, Japan, leg. T. Terawaki, May 1980). c, Vesicles (Bonotsu, Kagoshima, Japan, leg. T. Noro, July 1982). d, Female receptacles (Akune, Kagoshima, Japan, leg. T. Yoshida, June 1980). e, Male receptacles (Akune, Kagoshima, Japan, leg. T. Kima, June 1980).

elongated stalks, but *S. henslowianum* has condensed receptacles, and the texture of primary branches and leaves is harder.

*S. henslowianum* var. *condensatum* must be reduced in synonym as follows:

*Sargassum yendoi* Okamura et Yamada ex Yamada, Sci. Pap. Inst. Algol. Res. Fac. Sci. Hokkaido Imp. Univ. 2:121–123, pls. 21–22, figs. 1–2, 1938.

Type: Enoshima, Shimoda, or Hayama, Japan (a lectotype needs to be selected from Yamada's specimens in SAP).

=*Sargassum henslowianum* var. *condensatum* Yamada, J. Jpn. Bot. 18:372–374, fig. 2, 1942.

Type: Nomo, Nagasakl, Japan (holotype SAP 026414).

When Yamada (1938) originally described *S. yendoi,* he did not give a subgeneric attribution of this species. Later, he reported this species as a member of subgenus *Phyllotrichia* (Yamada 1955). According to Agardh (1889), the pinnate branching of lower laterals on the primary branch is the prominent characteristic of subgenus *Phyllotrichia.* However, in *S. yendoi,* the lower laterals on primary branches are not pinnate and can easily be distinguished from the primary branch. On the basis of other morphological characteristics, such as vesicles with rounded ends and dense clustered receptacles, *S. yendoi* is not a member of subgenus *Phyllotrichia,* but of subgenus *Sargassum (=Eusargassum ).* On the basis of vesicles with rounded ends and cymosely arranged receptacles, we propose that *S. yendoi* be assigned to subsection *Cymosae* section *Malacocarpicae* of subgenus *Sargassum.*

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# ZYGOCARPIC *SARGASSUM* SPECIES (SUBGENUS *SARGASSUM*) FROM JAPAN

Tetsuro Ajisaka, Tadahide Noro, and Tadao Yoshida

## Abstract

Ten species of the section *Zygocarpicae* (J. G. Agardh) Setchell of subgenus *Sargassum* from Japan are described. Holozygocarpic receptacles were observed in *S. carpophyllum* J. G. Agardh, *S. longifructum* Tseng et Lu, *S. myriocystum* J. G. Agardh, *S. polycystum* J. G. Agardh, *S.* sp. 1, and *S.* sp. 2. Additionally, pseudozygocarpic receptacles were observed in *S. bulbiferum* Yoshida, *S. crispifolium* Yamada, *S. glaucescens* J. G. Agardh, and *S. incanum* Grunow.

Keys to Japanese species and a proposal of a new systematic arrangement for the species in *Sargassum* section *Zygocarpicae* (J. G. Agardh) Setchell from the western Pacific area are also given.

## Introduction

The Japanese species of *Sargassum* subgenus *Sargassum* have been studied and descriptions published by Yendo (1907) and Yamada (1925, 1942, 1944). Through the workshops on taxonomy of economic seaweeds organized by the California Sea Grant Program since 1984, Yoshida (1988) summarized previous reports, and Kilar et al. (1992), Ajisaka (1992), Ajisaka, Noro, Trono, Chiang, and Yoshida (1994); and Noro et al. (1994), reported several species from Japan.

Tseng and Lu (1988) reported 17 species of section *Zygocarpicae* from China, and Abbott et al. (1988) clarified the subgeneric nomenclature in this section. Abbott, in an editorial clarification in Tseng and Lu (1988, p. 26), described *Pseudozygocarpicae* as "a subsection of the section *Zygocarpicae* in which pedicels of receptacles are usually constant (present), whereas they may be absent in the subsection *Holozygocarpicae*; and in which receptacles are paired with leaves, or receptacles paired with vesicles, whereas in subsection *Holozygocarpicae*, compound receptacles may be paired with leaves only, or with both leaves and vesicles."

At this time, we report 10 zygocarpic species from Japan. Six species belong to the subsection *Holozygocarpicae* Setchell, and 4 belong to the subsection *Pseudozygocarpicae* Setchell.

## Key to Japanese Species of Zygocarpic *Sargassum*

1. Plant with bulbous structure formed from stunted primary branches .......... *S. bulbiferum*
1. Plant without stunted primary branches .......... 2
  2. Laterals muricated with spines .......... 3
  2. Laterals without spines .......... 4
3. Plant with rhizoidal branches from stem .......... *S. polycystum*
3. Plant without rhizoidal branches .......... *S. myriocystum*
  4. Holozygocarpic, certain receptacles giving rise to leaf or vesicle .......... 5
  4. Pseudozygocarpic, receptacles intimately intermingled with leaf or vesicle .......... 7
5. Plant dioecious .......... *S. longifructum*
5. Plant monoecious .......... 6
  6. Receptacles without spines .......... *S. carpophyllum*
  6. Receptacles sometimes with a few spines .......... *S.* sp. 2
7. Plant monoecious, receptacles androgynous .......... 8
7. Plant dioecious .......... 9
  8. Primary branch compressed .......... *S.* sp. 1
  8. Primary branch terete .......... *S. incanum*
9. Female receptacles compressed .......... *S. glaucescens*
9. Female receptacles terete .......... *S. crispifolium*

## Description of the Species

*Sargassum bulbiferum* Yoshida, Jpn. J. Phycol. 42:48, figs. 9–13, 1994.
(Fig. 1)

Holdfast discoid, up to 2 cm in diameter. Stem terete, 1 cm high, 2 mm in diameter, often once forked at the distal portion; surface warty with vestiges of deciduous branches. Several primary branches radially produced from the distal portion of stem, 50 cm or more long, compressed, 2 mm wide, smooth on the surface, producing alternately leaves and lateral branches 10 cm or more long; several primary branches formed later in season not growing longer and becoming thicker, about 8 mm long and 3 mm in diameter, with a few small appendages on the surface. Leaves on the lower part of primary branch linear to linear-lanceolate, up to 10 cm long, up to 1 cm wide, margin entire or dentate with sparse and small teeth, papyraceous, midrib reaching the apex, lower leaves often once forked, leaves on distal portions of primary and lateral branches thinner in texture, becoming narrower and shorter; cryptostomata very small, scattered throughout the surface of leaves. Vesicles spherical to round-obovate, up to 3 mm in diameter; stalks filamentous and terete, up to 3 mm long.

Plants monoecious. Receptacles androgynous, slender, cylindrical, up to 7 mm long, forked once to twice, pseudozygocarpic.

Remarks: Specimens of this species were collected at Oburi Island, Hamasaka, Hyogo Prefecture, August 3, 1990. The species is characterized by the formation of a bulbous structure due to stunted primary branches. The upper part of the branches is somewhat similar to the upper parts of branches of *S.*

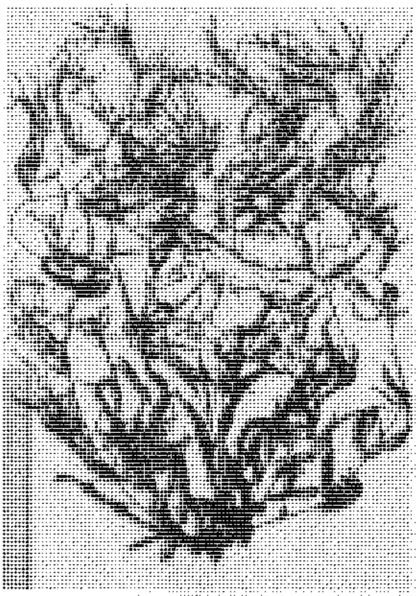

**Fig. 1. Holotype specimen (SAP 059011) of *Sargassum bulbiferum* Yoshida from Oburi Island, Hamasaka, Hyogo Prefecture.**

*carpophyllum* and *S. tenerrimum*, with thin and narrow leaves, but leaves on the lower part of primary branches in *S. bulbiferum* are much larger than in the other two species and are often once furcated. Interestingly, *S. bulbiferum* has been collected from the coast of the Sea of Japan, central part of Honshu, which is a temperate region.

*Sargassum carpophyllum* J. G. Agardh, Sp. gen. ordines algarum, vol. 1, p. 304, 1848. (Figs. 2, 3)

Holdfast discoid, up to 9 mm in diameter. Stem terete, up to 12 mm high, up to 2 mm in diameter, with a warty surface, bearing up to seven primary branches. Primary branches more than 1 m long, with a smooth surface, terete to slightly compressed, 1–2 mm wide, giving rise to spirally arranged secondary branches. Leaves on primary and secondary branches usually deciduous; leaves on tertiary branches thin and papyraceous, linear to linear-lanceolate, simple, with an asymmetrical base, 13.0–34.0 (average, 23.4) mm long, 1.7–5.2 (average, 3.0) mm wide, 4.4–13.6 (average, 8.2) in length-to-width ratio (100 leaves), with an acute or obtuse apices, margins irregularly dentate with shallow teeth or nearly entire, midrib distinct, reaching near the apex; cryptostomata scattered or arranged in one row on both sides of the midrib on linear leaves. Vesicles nearly spherical to obovoid or elongated, 3.0–5.8 (average 4.7) mm in long axis, 2.5–5.0 (average, 3.8) mm in short axis, entire (60%) or short apiculate (21%) or crowned (19%) (100 vesicles); stalks terete, 1.5–5.0 (average, 2.7) mm long, usually shorter than vesicles themselves (94%) but sometimes longer (6%).

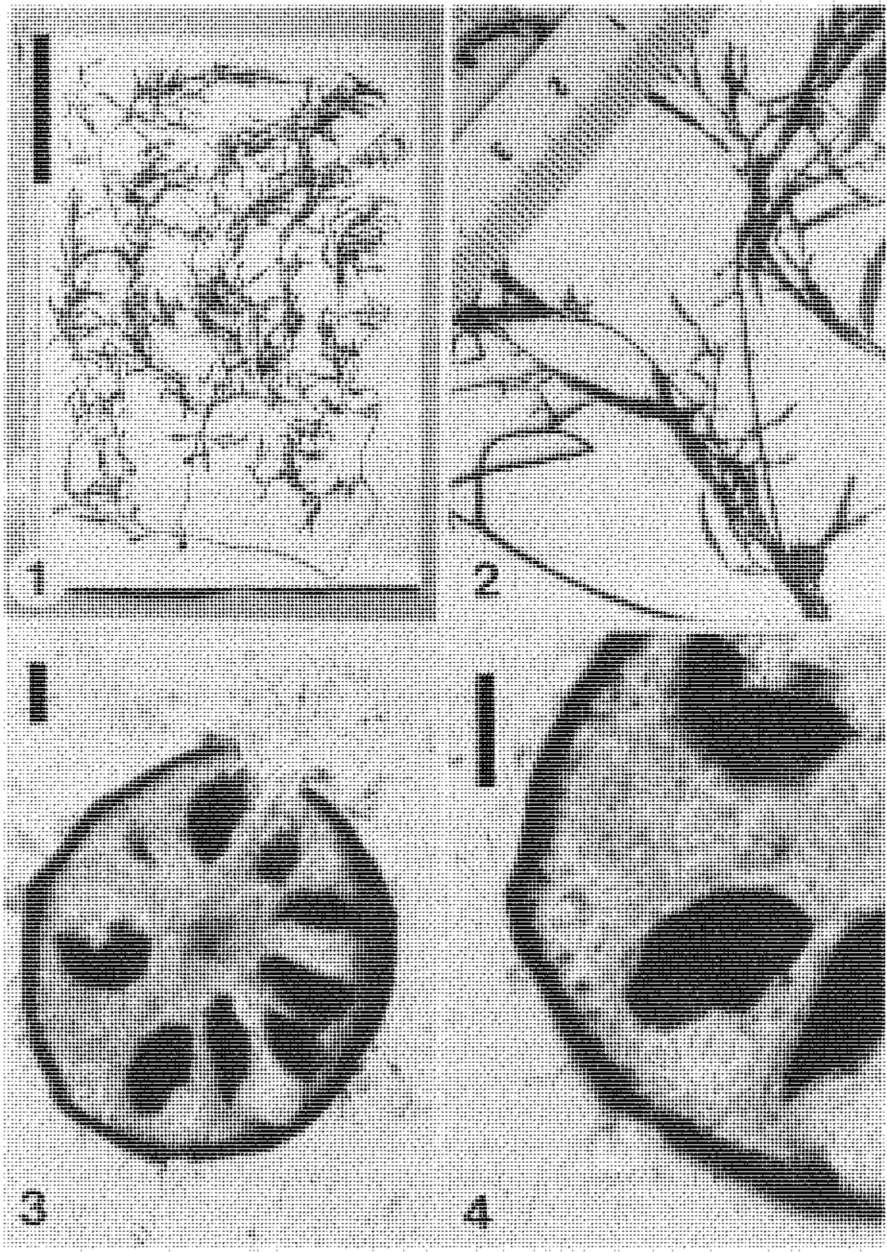

Fig. 2. *Sargassum carpophyllum* J. G. Agardh from Nagasaki Prefecture. 1, Whole plant of dried specimen. 2, Holozygocarpic receptacles. 3, and 4, Transverse section of an androgynous receptacle showing an antheridium among five oogonia. Scale bars: 1, 10 cm; 3 and 4, 100 μm.

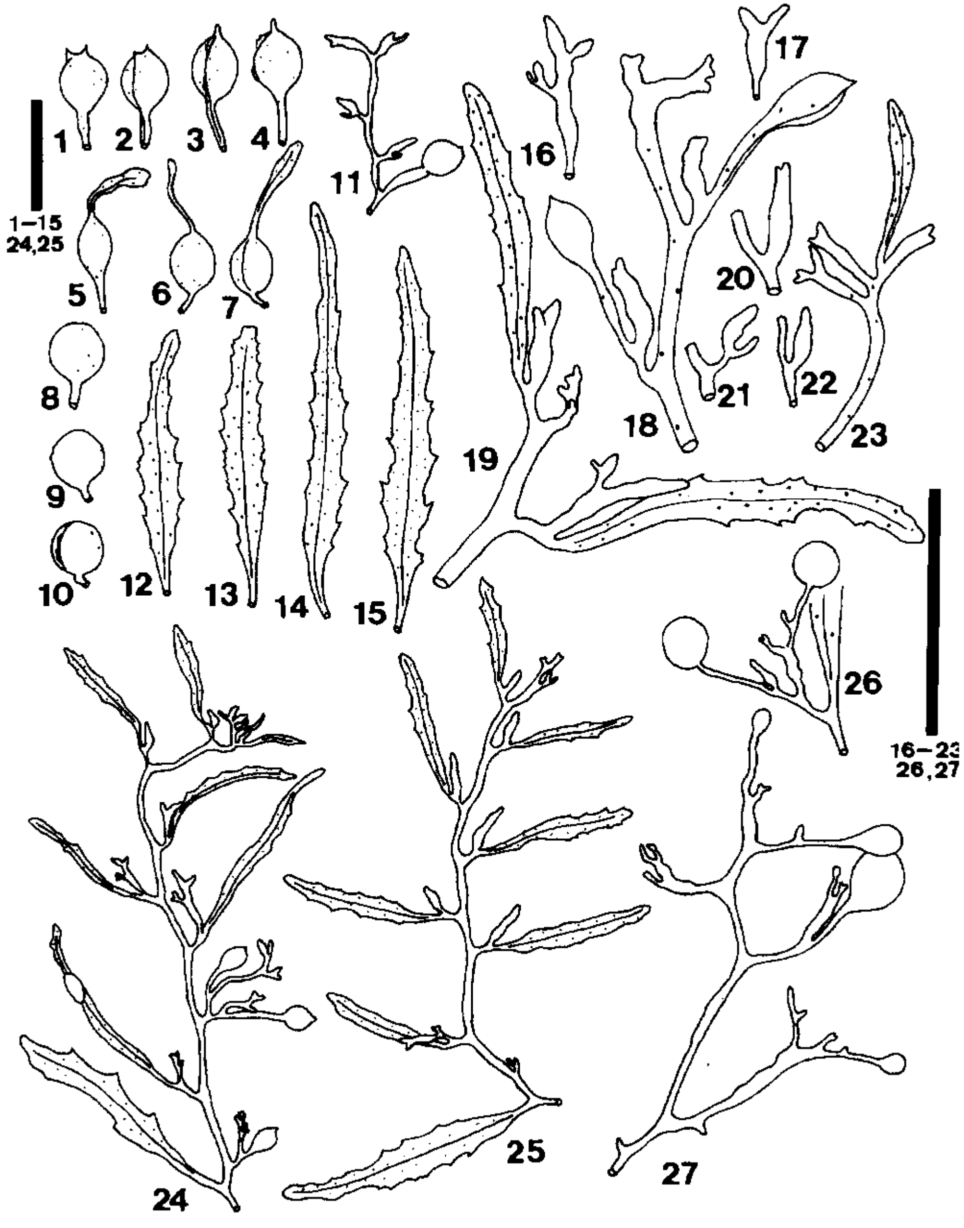

Fig. 3. *Sargassum carpophyllum* J. G. Agardh from Nagasaki Prefecture. 1–10, Morphological variations of vesicles. 11, Receptacles and vesicles on tertiary branch. 12–15, Linear to linear-lanceolate secondary leaves. 16–23, Pseudozygocarpic receptacles with small leaves and vesicles. 24 and 25, Secondary branches on upper part of plant. 26 and 27, Holozygocarpic receptacles with vesicles. Scale bars = 1 cm.

Plants monoecious. Receptacles androgynous, cylindrical to fusiform, up to 5.0 mm long, 1–2 mm in diameter, solitary or forked two to three times, smooth on the surface, racemosely arranged, holozygocarpic or pseudozygocarpic.

Remarks: *Sargassum carpophyllum* was reported from Taiwan and Tottori Prefecture in Japan (Yamada 1942), but those specimens were only parts of plants and ones that had drifted. After Yamada's records, this species has not been reported from Japanese coasts. The drifted materials of this species were collected by T. Ajisaka from Koe in Nagasaki Prefecture on May 25 (immature) and June 9 (mature), 1992. The immature plants were collected by Y. Yoshida from Gushikawa in Okinawa Prefecture on April 27, 1993. He also collected drifted immature plants from Kushima, Kagoshima Prefecture, on June 18, 1992. The materials collected by Ajisaka at Koe on June 9, 1992, were used for measurements and drawing of this species.

Androgynous, cylindrical to fusiform and holozygocarpic receptacles have been reported in *S. angustifolium* C. A. Agardh and *S. carpophyllum*. The main difference between these two species is the width of their leaves (Tseng and Lu 1988). The former has slender (up to 2 mm wide) leaves, and the latter has leaves up to 6 mm wide. In Japanese *S. carpophyllum*, we measured widths of 1.7–5. 2 mm (average, 3.0) mm on leaves of tertiary branches. Ranges of variation should be further checked on more material. In Japanese *S. carpophyllum*, we sometimes found receptacles with a few spines on their tips. These materials have been identified as *S. tenerrimum* J. G. Agardh by C. K. Tseng. However, this characteristic seems to be more variable in the populations from the Okinawa area than in those from the Hong Kong area, according to observations on specimens identified by Setchell, which are deposited in the herbarium at Hokkaido University (SAP).

*Sargassum angustifolium* was reported by Yamada (1942) from the Shikoku area in Japan. On the basis of our critical examination of the specimens identified by Yamada deposited in SAP, we cannot discriminate *S. angustifolium* from *S. carpophyllum*.

*Sargassum crispifolium* Yamada, J. Fac. Sci. Hokkaido Imp. Univ. Ser. 5, 1, p. 92, pl. 20, 1931. (Figs. 4, 5)

Holdfast small, discoid, about 5 mm in diameter. Stem very short, about 0.5–1.0 cm long, terete, bearing one to three primary branches. Primary branches terete, filiform, with smooth surface, giving rise to alternately pinnate or bipinnate secondary branches. Leaves with very shortly petiole or nearly sessile, linear-spatulate, 3–5 cm long, 0.5–1.0 cm wide, membranaceous, with obtuse or somewhat acute apices, with fine and sharp dentations at the margin, usually strongly crispate; midrib conspicuous, vanishing near the apex; cryptostomata conspicuous, scattered sparingly throughout the surface. Vesicles spherical, but rarely elliptical, 5–8 mm in diameter, smooth on the surface, with a few cryptostomata; stalks shorter than vesicles themselves.

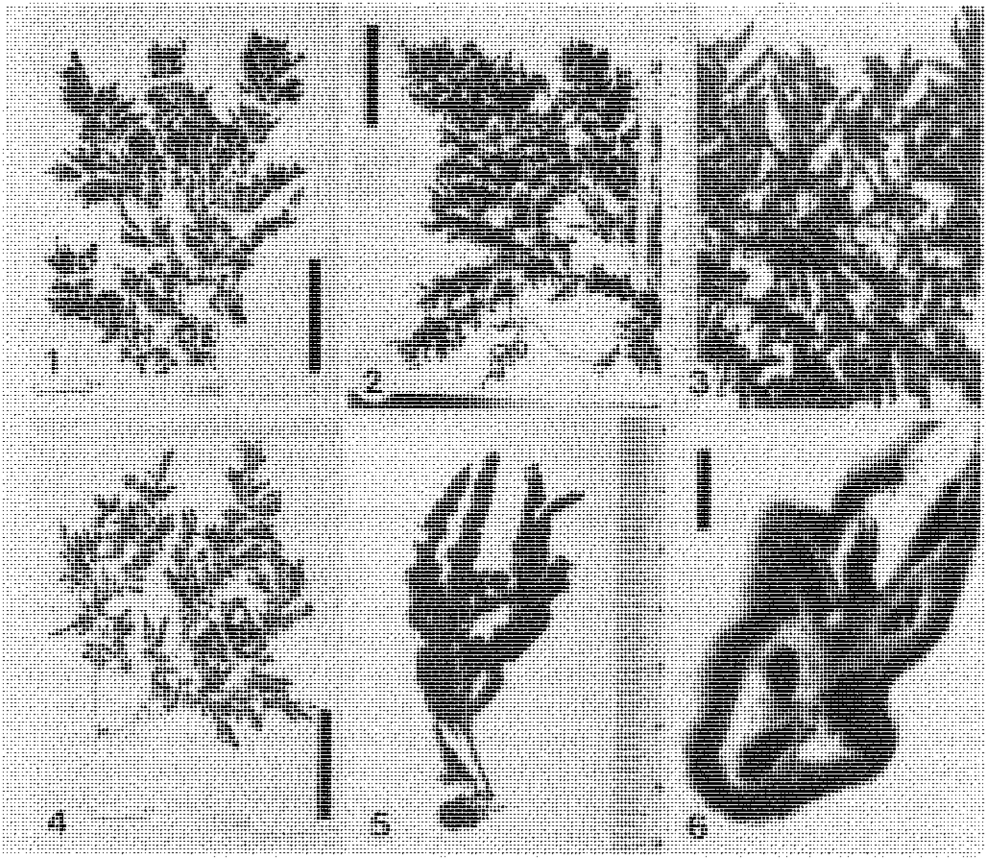

Fig. 4. *Sargassum crispifolium* Yamada. 1, Dried female specimen of holotype (SAP 9265) from Kochi Prefecture. 2 and 3, Dried specimen of male plant (SAP 048833) from Kagoshima Prefecture. 4, Dried female specimen of isotype (SAP 9877) from Kochi Prefecture. 5, Female receptacles on the secondary branches of isotype specimen. 6, Transverse section of female receptacles of isotype specimen. Scale bars: 1, 2, and 4, 10 cm; 6, 100 μm.

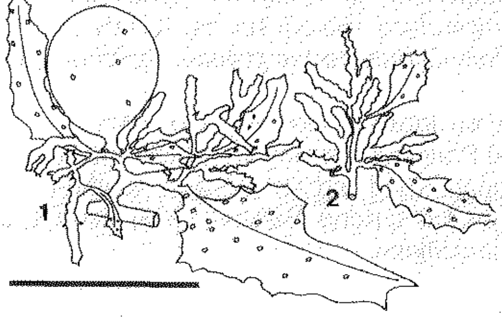

Fig. 5. *Sargassum crispifolium* Yamada from Kochi Prefecture. 1 and 2, Holozygocarpic female receptacles on isotype specimen (SAP 9877). Scale bar = 1 cm.

Plants dioecious. Female receptacles terete, 2–5 mm long, 0.5–0.8 mm in diameter, warty and sometimes with a few acute spines, solitary or forked one to four times; male receptacles terete, more than 1 cm long, 0.5–0.8 mm in diameter, warty and sometimes with acute spines, solitary or forked one to four times; female receptacles pseudozygocarpic.

Remarks: We observed female receptacles on the isotype specimen (SAP 9877, Figs. 4:4–6 and Fig. 5). The holotype specimen (SAP 9265, Fig. 4:1) and this isotype specimen were collected from Kashiwajima, Kochi Prefecture, in August 1925 by Y. Yamada. We found pseudozygocarpic, terete receptacles with a few spines in the isotype specimen. In the same herbarium are a male plant (SAP 048833, Figs. 4:2 and 4:3), which was collected from Uchinoura, Kagoshima Prefecture in August 1940 by Y. Nakamura, and a female plant (SAP 028129), which was collected by Y. Yamada from Kashiwajima, Kochi Prefecture, in July 1941. In the original description (Yamada 1931), the sex was not described. However, we found dioecious receptacles.

*Sargassum glaucescens* J. G. Agardh, Sp. gen. ordines algarum, vol. 1, p. 304, 1848. (Figs. 6, 7)

Holdfast small, discoid, up to 5 mm in diameter. Stem terete, 5–8 mm tall, up to 2 mm in diameter, with a warty surface, bearing two to three primary branches. Primary branches up to 30 cm long, with a smooth surface, terete to slightly compressed, up to 1.5 mm in diameter, giving rise to alternately arranged secondary branches; secondary branches 5–7 cm long, terete, up to 1 mm in diameter. Leaves on primary branches deciduous; secondary and tertiary leaves thin and membranous, glaucescent on their surface, lanceolate to elongate-lanceolate, simple, with an asymmetrical base, 8.8–45.0 (average, 25.8) mm long, 3.4–10.0 (average, 6.7) mm wide, 2.3–5.7 (average, 3.8) in length-to-width ratio (100 leaves), with round apices, margin dentate with sharp teeth, midrib distinct, reaching near the apex, cryptostomata scattered. Vesicles spherical, 2.2–8.8 (average, 4.3) mm in diameter, entire at the apex (100 vesicles); stalks terete, 1.0–5.5 (average, 2.9) mm long, usually shorter than the vesicles themselves.

Plants dioecious. Female receptacles compressed to flattened, up to 5 mm long, up to 1 mm wide, margin with dentate teeth or spines, solitary or forked once to twice, warty on the surface; male receptacles terete to fusiform, up to 4 mm long, 0.5–0.7 mm in diameter, with a warty surface, without spines, solitary or forked one to four times; both male and female receptacles pseudozygocarpic with leaves and vesicles.

Remarks: This species was collected on June 30, 1991, by S. Ui, from Shimaura Island, Nobeoka City, Miyazaki Prefecture, for the first time from Japan. This species has been reported from Hainan Island and Xisha Island, southern China (Tseng and Lu 1979, 1988) and from Hong Kong (Setchell 1935). Japanese specimens agree well with the Chinese specimens.

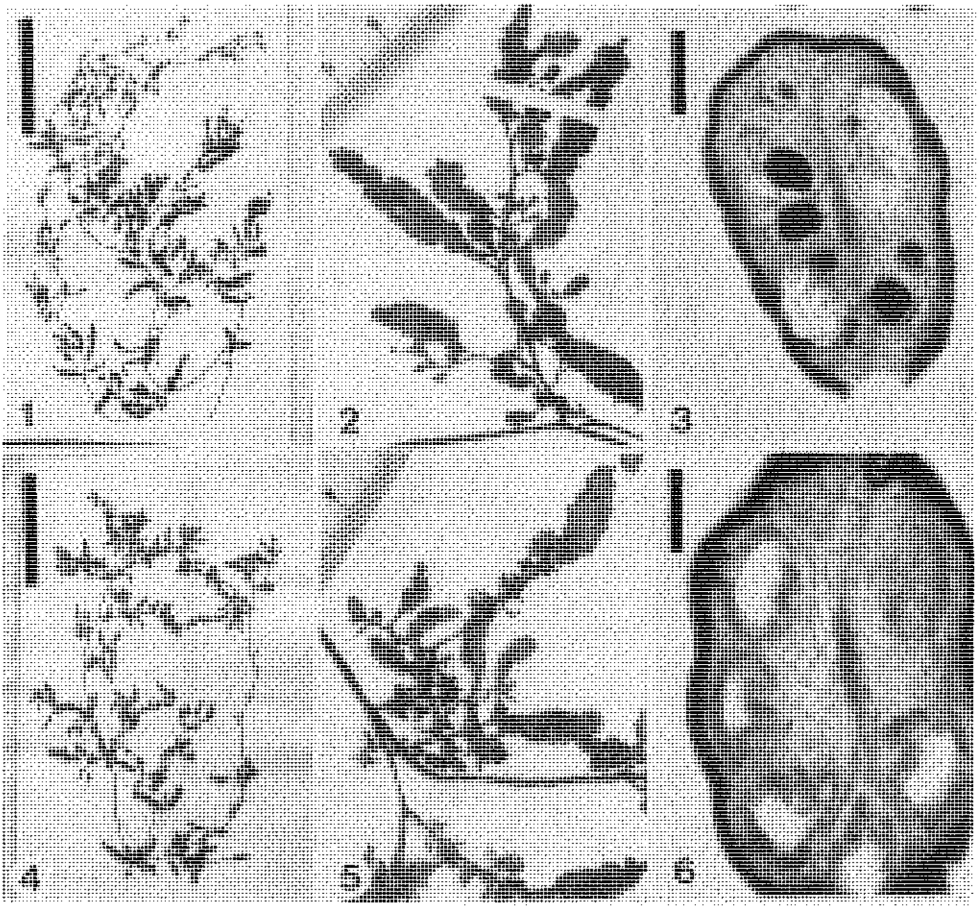

**Fig. 6.** ***Sargassum glaucescens*** **J. G. Agardh from Shimaura Island, Miyazaki Prefecture. 1, Whole plant of dried female specimen. 2, Compressed female receptacles. 3, Transverse section of female receptacle. 4, Whole plant of dried male specimen. 5, Cylindrical male receptacles. 6, Transverse section of male receptacle. Scale bars: 1 and 4, 10 cm; 3 and 6, 200 μm.**

*Sargassum incanum* Grunow, Verh. Zool. Bot. Gesell. Wien. 65:379, 1915.

(Figs. 8, 9)

Holdfast small discoid, up to 5 mm in diameter. Stem terete, 5–8 mm tall, up to 2 mm in diameter, with a warty surface, bearing two to three primary branches. Primary branches up to 40 cm long, with smooth surface, terete to slightly compressed, up to 1 mm in diameter, giving rise to alternately arranged secondary branches; secondary branches 5–7 cm long, terete, up to 1 mm in diameter. Leaves on primary branches mostly deciduous; leaves on secondary and tertiary branches thin and membranous, lanceolate to elongate-lanceolate, without

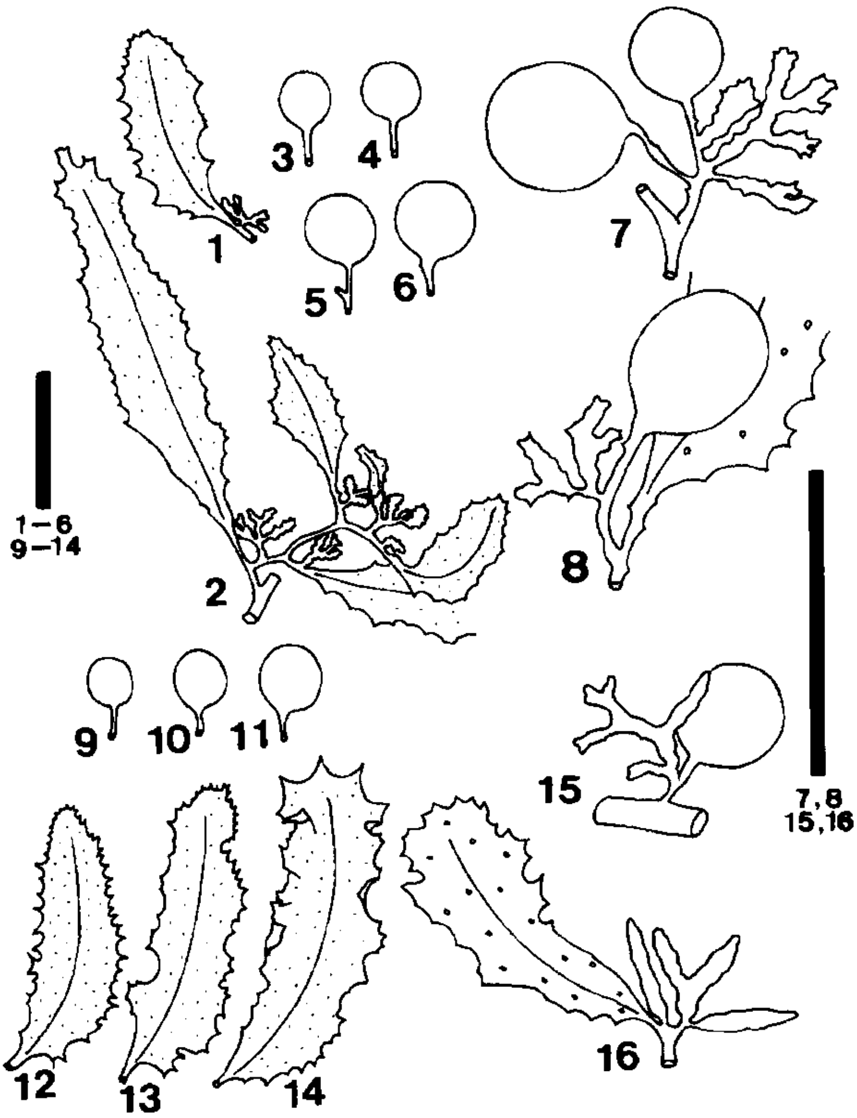

Fig. 7. *Sargassum glaucescens* J. G. Agardh from Shimaura Island, Miyazaki Prefecture. 1 and 2, Leaves and receptacles on tertiary branch of female plant. 3–6, Vesicles. 7 and 8, Pseudozygocarpic, compressed receptacles with dentate margins on female plant. 9–11, Vesicles on male plant. 12–14, Leaves on secondary branches of male plant. 15 and 16, Pseudozygocarpic, cylindrical to fusiform receptacles on male plant. Scale bars = 1 cm.

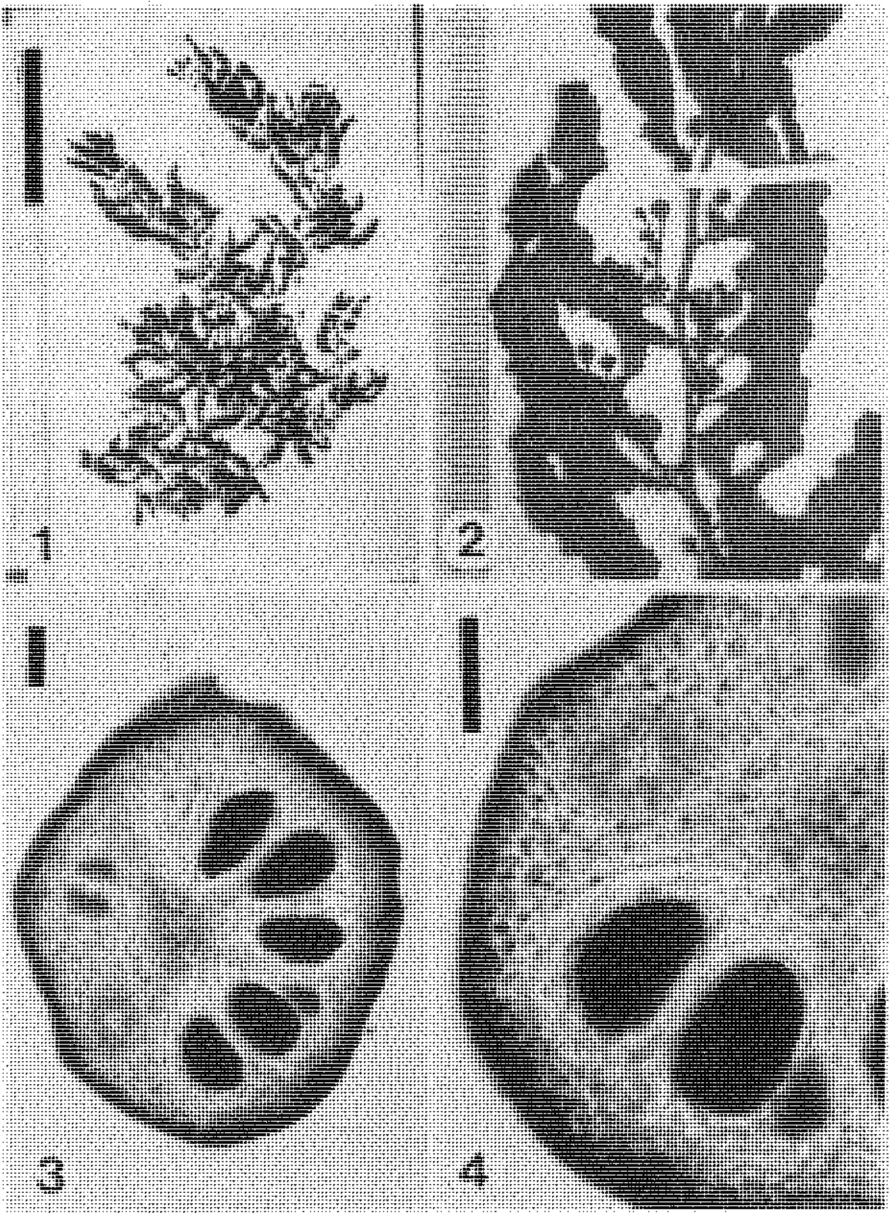

Fig. 8. *Sargassum incanum* Grunow from Shimaura Island, Miyazaki Prefecture. 1, Whole plant of dried specimen. 2, Pseudozygocarpic, cylindrical to fusiform receptacles. 3 and 4, Transverse section of androgynous receptacle showing an antheridium among four oogonia. Scale bars: 1, 10 cm; 3 and 4, 100 μm.

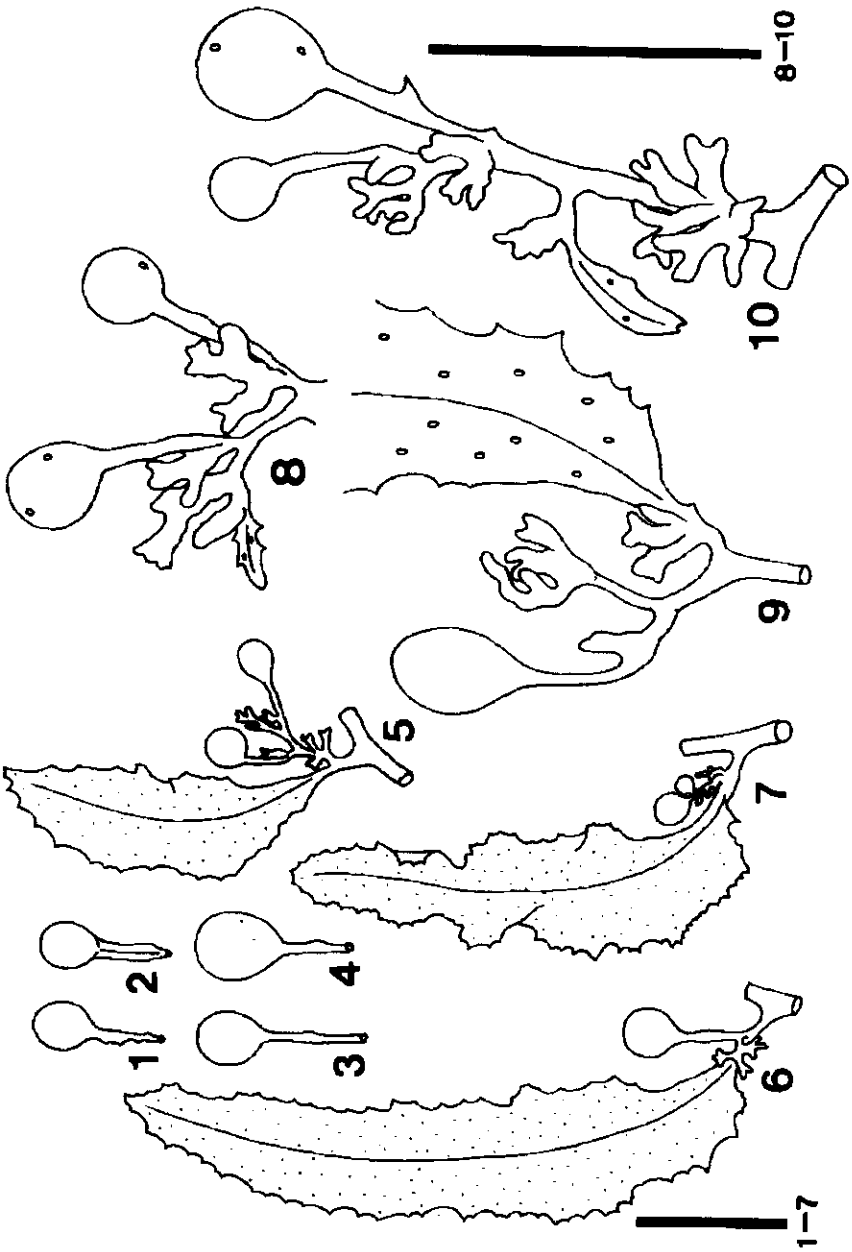

Fig. 9. *Sargassum incanum* Grunow from Shimaura Island, Miyazaki Prefecture. 1–4, Vesicles. 5–7, Leaves and cylindrical to fusiform receptacles. 8–10, Pseudozygocarpic receptacles with small leaves and vesicles. Scale bars = 1 cm.

branching, with an asymmetric to cuneate base, 10.5–50.0 (average, 31.2) mm long, 3.0–10.5 (average, 6.7) mm wide, 2.7–8.2 (average, 4.7) in length-to-width ratio (50 leaves), with round or acute apices, margin dentate with sharp teeth or duplicated teeth, midrib distinct, reaching near the apex, small cryptostomata scattered. Vesicles nearly spherical to elongated, 1.5–6.5 (average, 3.7) mm in long axis, 1.5–5.0 (average, 3.3) mm in short axis, entire at apex (50 vesicles); stalks terete (87%) or slender leafy (13%), 2.5–6.5 (average, 4.3) mm long, stalks longer than vesicles themselves (75%) or shorter than vesicles (15%).

Plants monoecious. Receptacles androgynous, cylindrical to fusiform, up to 4 mm long, up to 1.0 mm in diameter, solitary or forked two to three times, smooth on the surface, racemosely arranged, pseudozygocarpic.

Remarks: Materials of this species were collected by S. Ui, from Shimaura Island, Nobeoka City, Miyazaki Prefecture, on June 30, 1991, for the first time in Japan. Setchell (1935) and Tseng and Lu (1988) reported this species from Hong Kong and Shanghai in southern and central China. However, after examination of Setchell's specimens in SAP, those materials cannot be distinguished from *S. carpophyllum* J. G. Agardh. C. K. Tseng and Lu Baoren also realized this in the fifth workshop in Honolulu in June 1993.

Terawaki et al. (1983) reported the specimen with androgynous receptacles and identified it as *S. crispifolium* Yamada from Shibushi Bay, Kagoshima Prefecture, in Japan. However, the isotype specimen of *S. crispifolium* deposited in SAP has female receptacles (Fig. 4:4–6), and other specimens (isotype) are dioecious, whereas our interpretation of *S. incanum* includes monoecious plants only. Plants reported or identified by previous authors as *S. crispifolium* have androgynous receptacles and are similar to specimens of *S. incanum* from Miyazaki Prefecture. We need to research the distribution of this species again. In the herbarium of Kyoto University, we have materials of this species collected from Shirahama and Kushimoto, Wakayama Prefecture. Some materials collected by M. Miyata from Okinoshima, Tateyama City, Chiba Prefecture, have been identified as the same species and are deposited in the Natural History Museum and Institute, Chiba Prefecture.

We question how closely related *S. incanum* and *S. crispifolium* are, if the main difference is monoecious vs. dioecious conditions.

*Sargassum longifructum* Tseng et Lu, Oceanol. Limnol. Sin. 18:516, fig. 2, pl. 1, fig. 2, 1987. (Figs. 10–15)

Holdfast discoid to scutellate, up to 3 cm in diameter. Stem terete, up to 2.7 cm tall, up to 3.0 mm in diameter, with a smooth surface, bearing up to seven primary branches. Primary branches up to 72 cm long, terete to somewhat compressed, 2.0–4.5 mm in diameter, usually with a smooth surface, sometimes muricate at the proximal portion, giving rise to spirally arranged secondary branches. Leaves linear-elliptical to linear-lanceolate, simple, with a slightly asymmetric base, 6.0–39.5 (average, 20.4) mm long, 1.8–12.5 (average, 6.3) mm wide, 1.1–7.9 (average, 3.4) in length-to-width ratio (300 leaves), with an obtuse

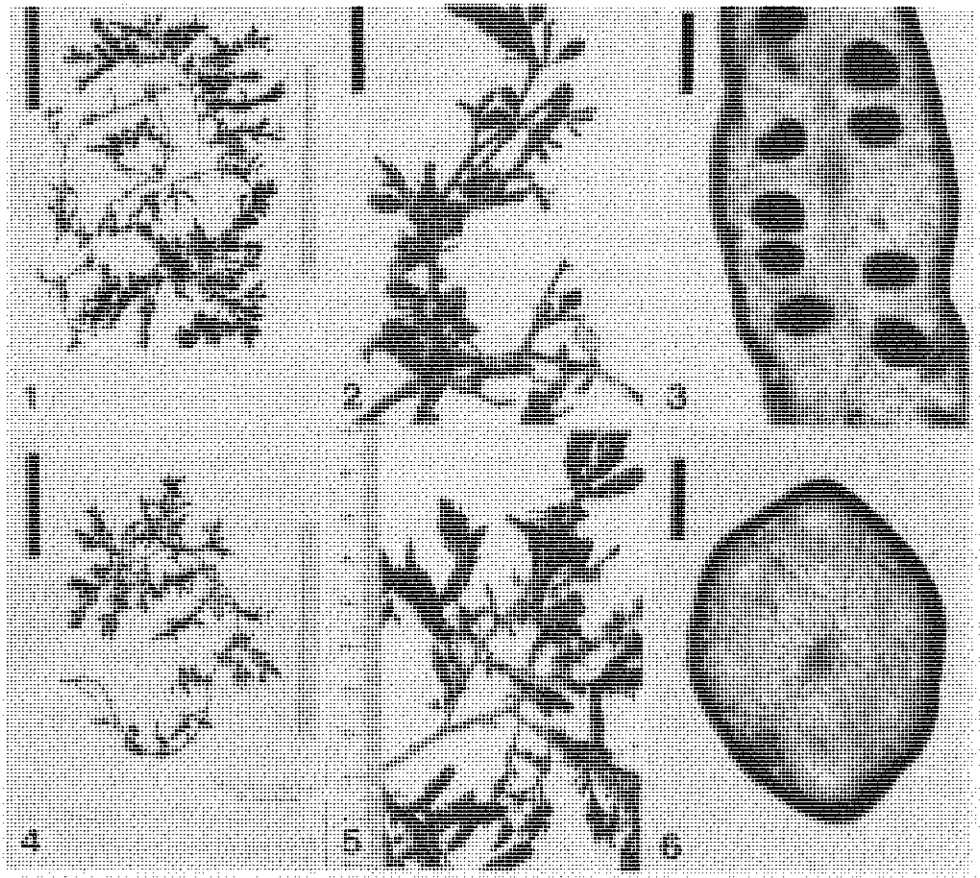

Fig. 10. *Sargassum longifructum* Tseng et Lu from Oura Bay, Okinawa Prefecture. 1, Whole plant of dried female specimen. 2, Flattened to triquetrous female receptacles with dentate margin. 3, Transverse section of female flattened receptacle. 4, Whole plant of dried male specimen. 5, Cylindrical male receptacles. 6, Transverse section of male receptacle. Scale bars: 1, 2, and 4, 10 cm; 3 and 6, 200 μm.

or acute apex, margin denticulate with coarse teeth (19%), dentate with small teeth (48%), or entire (33%), midrib somewhat immersed, percurrent; cryptostomata sometimes conspicuous, scattered on the surface. Vesicles spherical to elliptical, 3.5–6.8 (average, 4.9) mm long, 2.5–6.0 (average, 4.1) mm wide (100 vesicles), usually rounded at the apices, rarely with wings or crowned; cryptostomata scattered along the margin; stalks terete (65%), compressed above (32%), or foliaceous (3%), usually shorter than vesicles themselves (93%).

Plants dioecious. Wide ranges of the morphological variations observed among individuals; female receptacles flattened to triquetrous, 3–7 mm long, 1.0–1.5 mm wide, margin dentate with sharp teeth or spines, sometimes twisted,

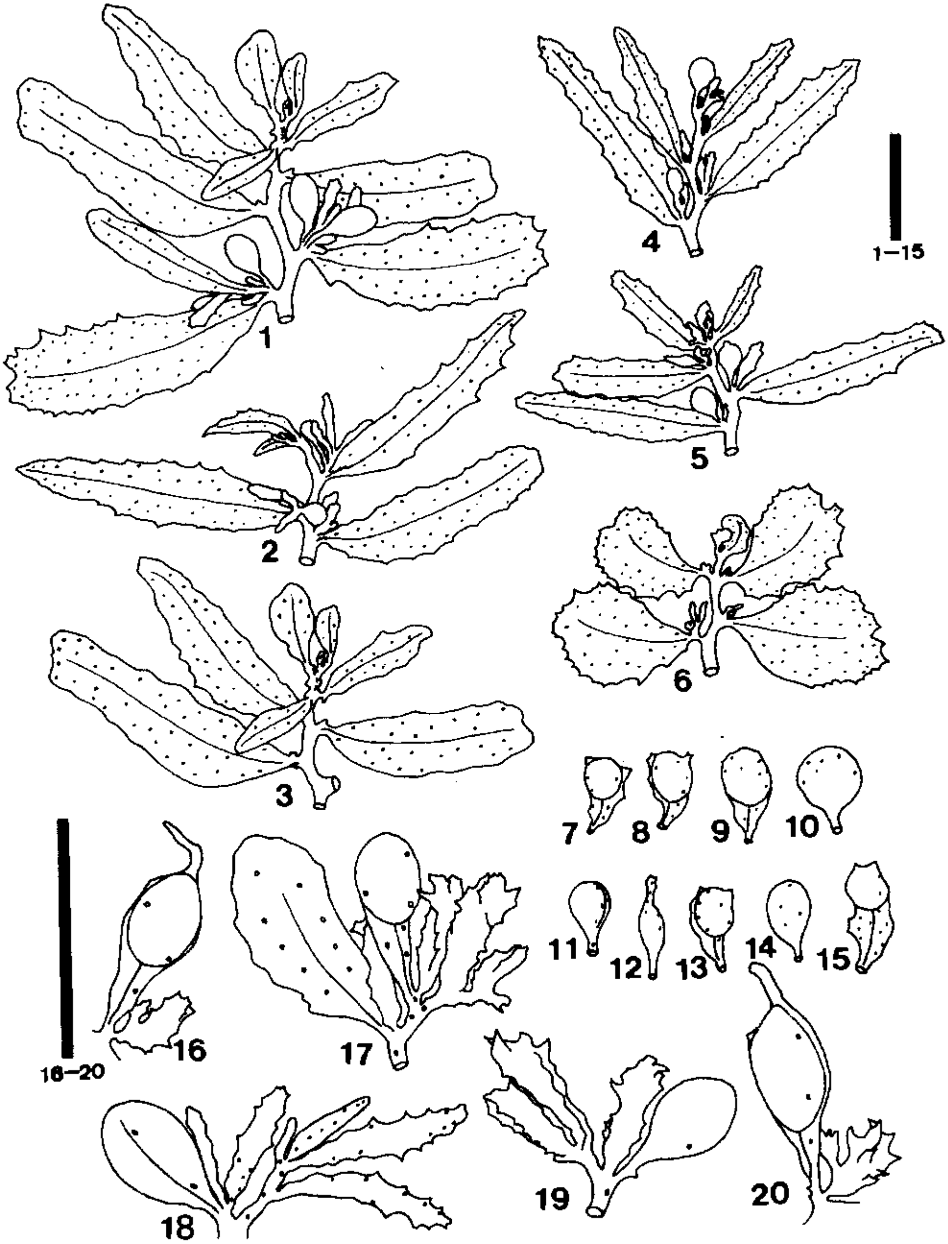

Fig. 11. Female plant of *Sargassum longifructum* Tseng et Lu from Oura Bay, Okinawa Prefecture. 1–6, Morphological variations of leaves on secondary branches. 7–15, Morphological variations of vesicles on secondary branches. 16–20, Flattened to triquetrous, pseudozygocarpic, female receptacles. Scale bars = 1 cm.

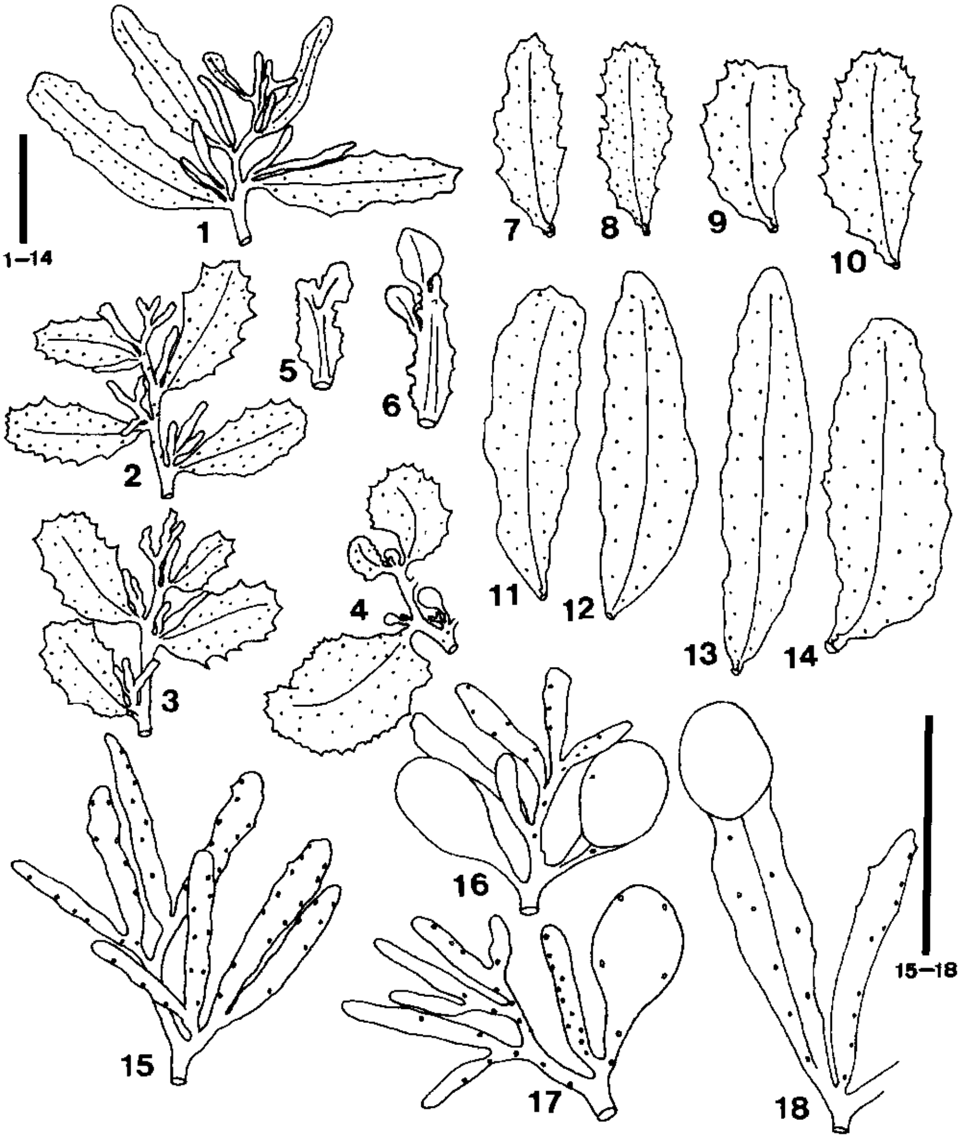

Fig. 12. Male plant of *Sargassum longifructum* Tseng et Lu from Oura Bay, Okinawa Prefecture. 1–4, Morphological variations of leaves on the secondary branches. 5 and 6, Juvenile primary branches. 7–14, Morphological variations of primary leaves. 15–18, Cylindrical to slightly compressed, pseudozygocarpic male receptacles, sometimes with a few spines. Scale bars = 1 cm.

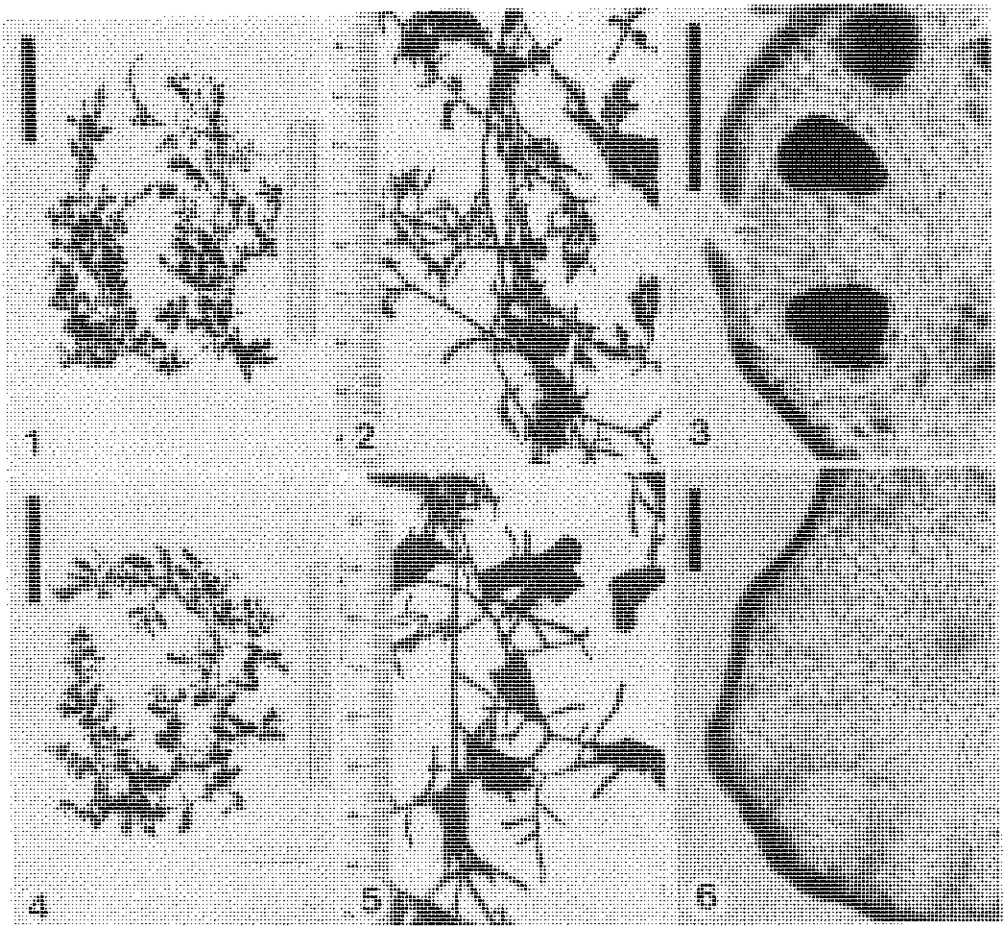

Fig. 13. *Sargassum longifructum* Tseng et Lu from Yagachi Island, Okinawa Prefecture. 1, Whole plant of dried female specimen. 2, Flattened to triquetrous female receptacles with dentate margins. 3, Transverse section of female receptacle. 4, Whole plant of dried male specimen. 5, Cylindrical to slightly compressed male receptacles. 6, Transverse section of male receptacle. Scale bars: 1 and 4, 10 cm; 3 and 6, 100 μm.

solitary or forked once to twice; male receptacles cylindrical to compressed at apex, 5–12 mm long, 1.0–1.5 mm in diameter, entire or with a few spines, solitary or forked three to four times, one row of cryptostomata arranged along the margin; both male and female receptacles pseudozygocarpic or holozygocarpic.

Remarks: This species was collected by T. Toma on September 25, 1989, from Oura Bay, Okinawa Prefecture (Figs. 10–12). In Okinawa Prefecture, T. Ajisaka also collected it from Yagachi Island (Figs. 13 and 14) on November 28, 1990, and from Nakagusuku Bay on June 6, 1991. The male plants were collected

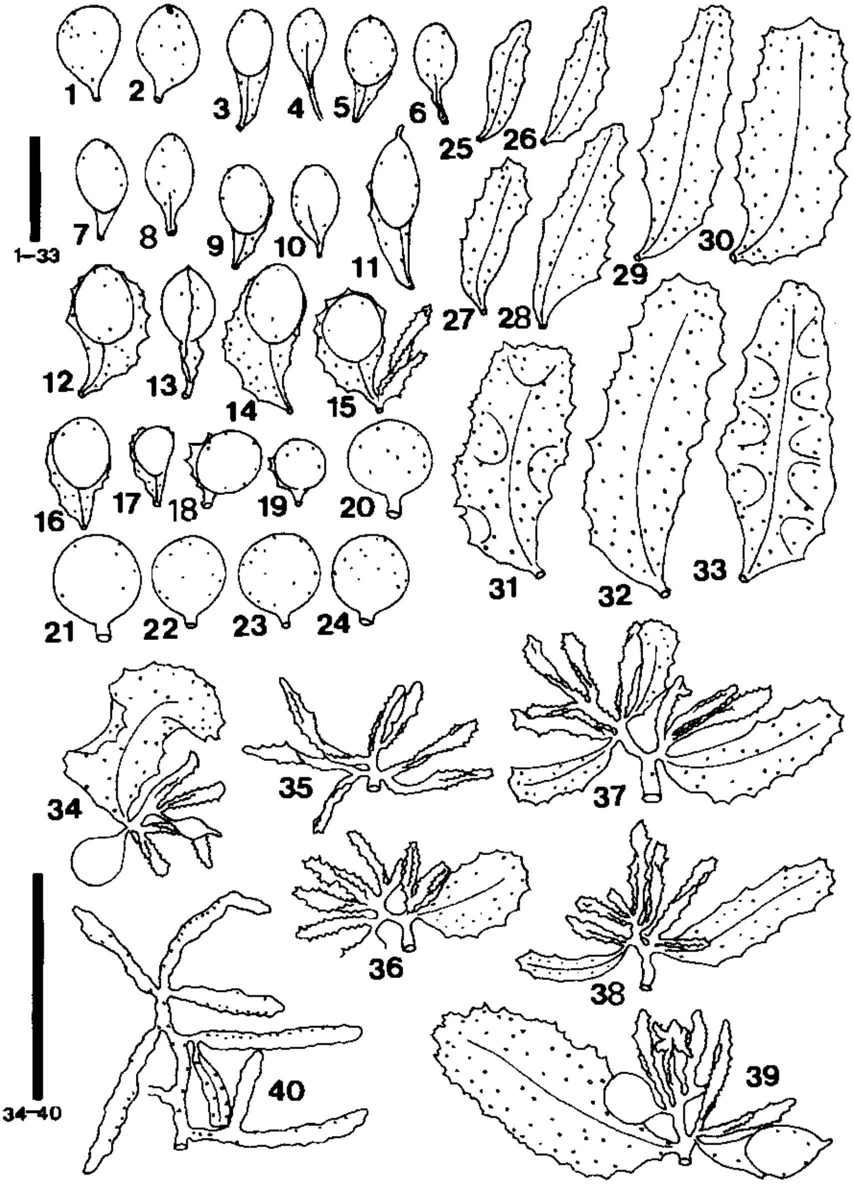

Fig. 14: *Sargassum longifructum* Tseng et Lu from Yagachi Island, Okinawa Prefecture. 1–24, Morphological variations of vesicles on secondary branches. 25–33, Morphological variations of leaves on secondary branches. 34–39, Pseudozygocarpic, compressed to triquetrous, female receptacles. 40, Pseudozygocarpic, cylindrical to slightly compressed male receptacles. Scale bars = 1 cm.

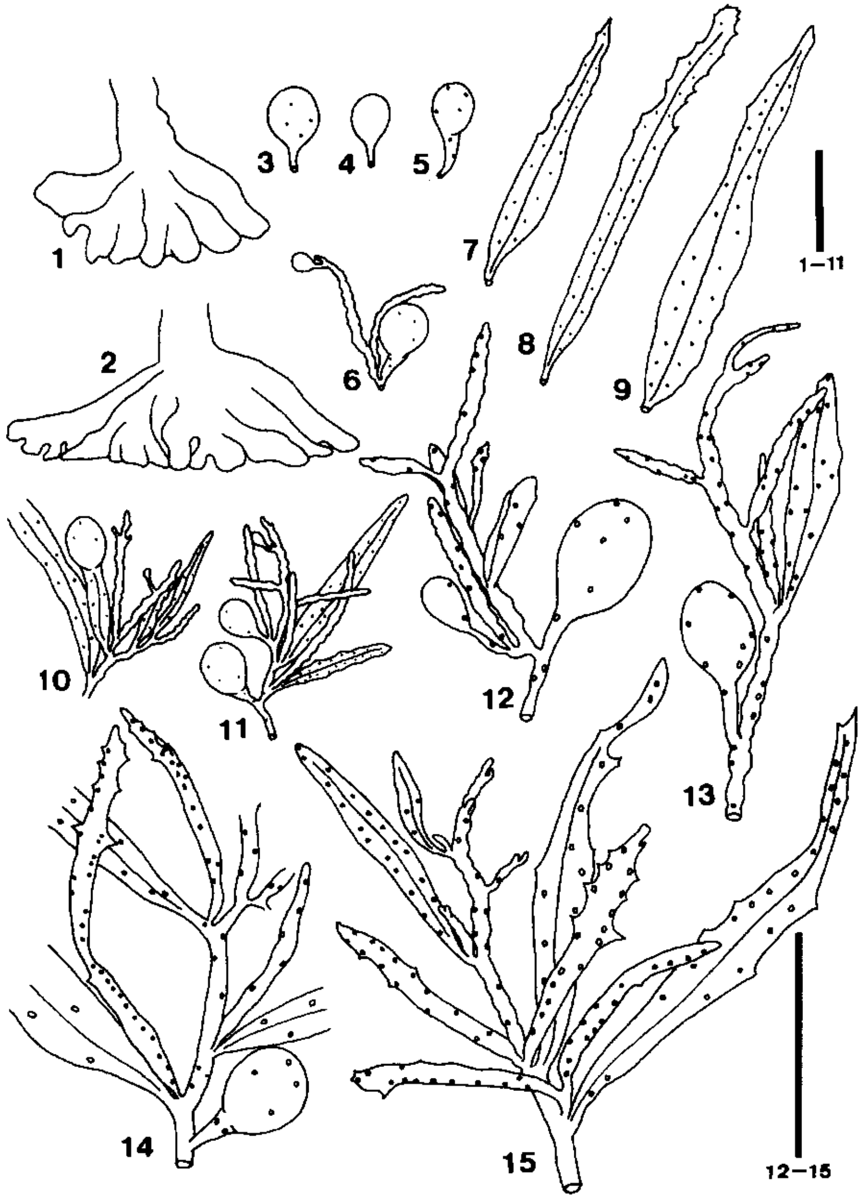

Fig. 15. *Sargassum longifructum* Tseng et Lu from Hamahiga Island, Okinawa Prefecture. 1 and 2, Scutellate holdfasts. 3–6, Vesicles. 7–9, Linear-lanceolate leaves. 10–13, Pseudozygocarpic, cylindrical, male receptacles. 14 and 15, Compressed male receptacles with dentate margins and holozygocarpic male receptacles. Scale bars = 1 cm.

by T. Tamaoki on October 28, 1993, from Hamahiga Island, Okinawa Prefecture (Fig. 15). A single male plant of this species was originally described from Naozhou Island, China (Tseng and Lu 1987). Ajisaka, Nang, and Dinh (1994) reported female and male plants from Ha Tien and Nhatrang in Vietnam. However, from Japan, we report male and female plants for the first time.

The Japanese and Vietnamese plants seem to have large morphological variations in leaves, vesicles, and receptacles. Leaves varied from elliptical to linear. Vesicles were entire at the apices or winged or crowned. Male receptacles were terete to compressed at the apices, sometimes spinous at the apices, and elongated, up to 2 mm long. Both male and female receptacles were sometimes holozygocarpic or pseudozygocarpic.

This species is sometimes difficult to distinguish from *S. siliquosum* J. G. Agardh previously reported from Japan (Yamada 1942) and China (Tseng and Lu 1992). We need to check on the holozygocarpic characters of Japanese and Chinese specimens of *S. siliquosum.*

*Sargassum myriocystum* J. G. Agardh, Sp. gen. ordines algarum, vol. 1, p. 314, 1848. Figs. 16–18)

Synonym: *S. opacum* J. G. Agardh, Kgl. Svenska. Vet.-Akad. Handl. 23:98, pl. 28, fig. 4, 1889. (Figs. 16–18).

Holdfast discoid, up to 1.2 cm in diameter. Stem terete, up to 6 mm tall, up to 3.0 mm in diameter, with a smooth surface, bearing up to seven primary branches. Primary branches up to 27 cm long, terete, 2–3 mm in diameter, usually muricate with crowded spines, producing spirally arranged secondary branches. Leaves spatulate to ovoid, simple, with an asymmetrical to cuneate base, 4.2–9.8 (average, 7.1) mm long, 2.8–6.7 (average, 4.9) mm wide, 1.1–2.3 (average, 1.5) in length-to-width ratio (100 leaves), with rounded apices, margin dentate with coarse teeth or entire, midrib indistinct, vanishing below the middle part of the leaf, cryptostomata scattered or arranged in rows on both sides of the midrib. Vesicles spherical to elliptical, 2–3 mm in diameter, with earlike wings on both sides of the vesicles or apiculate at apices, cryptostomata scattered; stalks terete, much shorter than vesicles themselves.

Plants dioecious. Wide ranges of morphological variations are observed among individuals; female receptacles flattened to triquetrous, 2–6 mm long, 2–3 mm wide, margin dentate with sharp teeth or spines, sometimes twisted, solitary or forked once; male receptacles cylindrical to flattened or triquetrous, cylindrical ones 2–15 mm long, up to 1 mm in diameter, entire or with a few spines, flattened or triquetrous ones 1.5–3.5 mm long, 0.8–1.8 mm wide, dentate with sharp teeth or spines, solitary or forked once; both male and female receptacles sometimes holozygocarpic or pseudozygocarpic.

Remarks: This species was originally described on the basis of Australian material (Agardh 1889). We observed cylindrical male receptacles on a specimen from northern Australia in Grunow's collection at the Vienna Natural Historical Museum (no. 1357) and flattened female receptacles with dentate margins in an

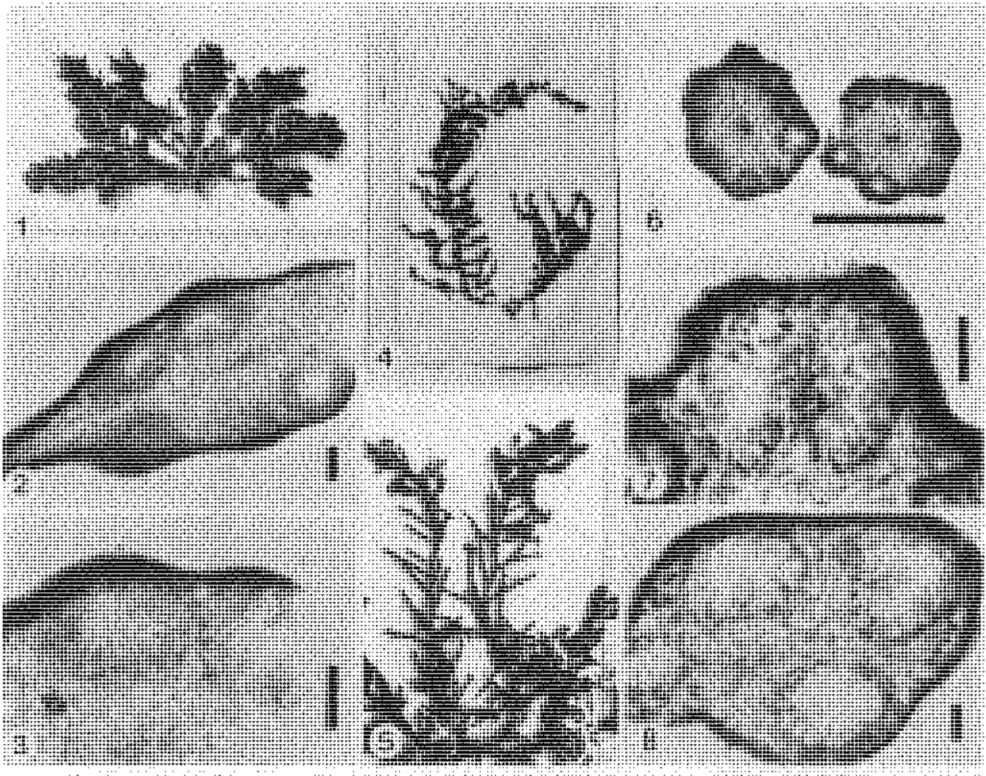

Fig. 18. *Sargassum myriocystum* J. G. Agardh from Okinawa Prefecture. 1–3, Male plant collected from Hedo Peninsula, Okinawa Prefecture: 1, Whole plant of wet male specimen. 2 and 3, Transverse sections of compressed male with dentate margins. 4–8, Male plant collected from Nakagusuku Bay, Okinawa Prefecture: 4, Whole plant of dried male specimen. 5, Long cylindrical, holozygocarpic male receptacles. 6 and 7, Transverse sections of long cylindrical, holozygocarpic, male receptacles. 8, Transverse section of compressed to triquetrous, pseudozygocarpic male receptacle. Scale bars: 2, 3, 7, and 8, 100 μm; 6, 1 mm.

Australian specimen in Vienna (no. 1361). On a specimen from Java in Reinbold's collection at Munich Botanical Garden (no. 619), female receptacles are triquetrous with dentate margins.

The male specimen (Fig. 18:1–21) was collected by T. Toma on September 29, 1989, from Hedo Peninsula, Okinawa Prefecture. The holozygocarpic male and female plants (Fig. 18:22–39) were collected by T. Ajisaka on June 6, 1991, from Nakagusuku Bay, Okinawa Prefecture. Female plants were collected by N. Miyamoto on October 25, 1992, from Taketomi Island, Okinawa Prefecture.

The species has two ecological habitats, a shallow one in the tidal zone (Taketomi Island and Hedo Peninsula) and one in the sublittoral zone (3- to 5-m depths; Nakagusuku Bay). Morphological variations in plants, leaves, vesicles,

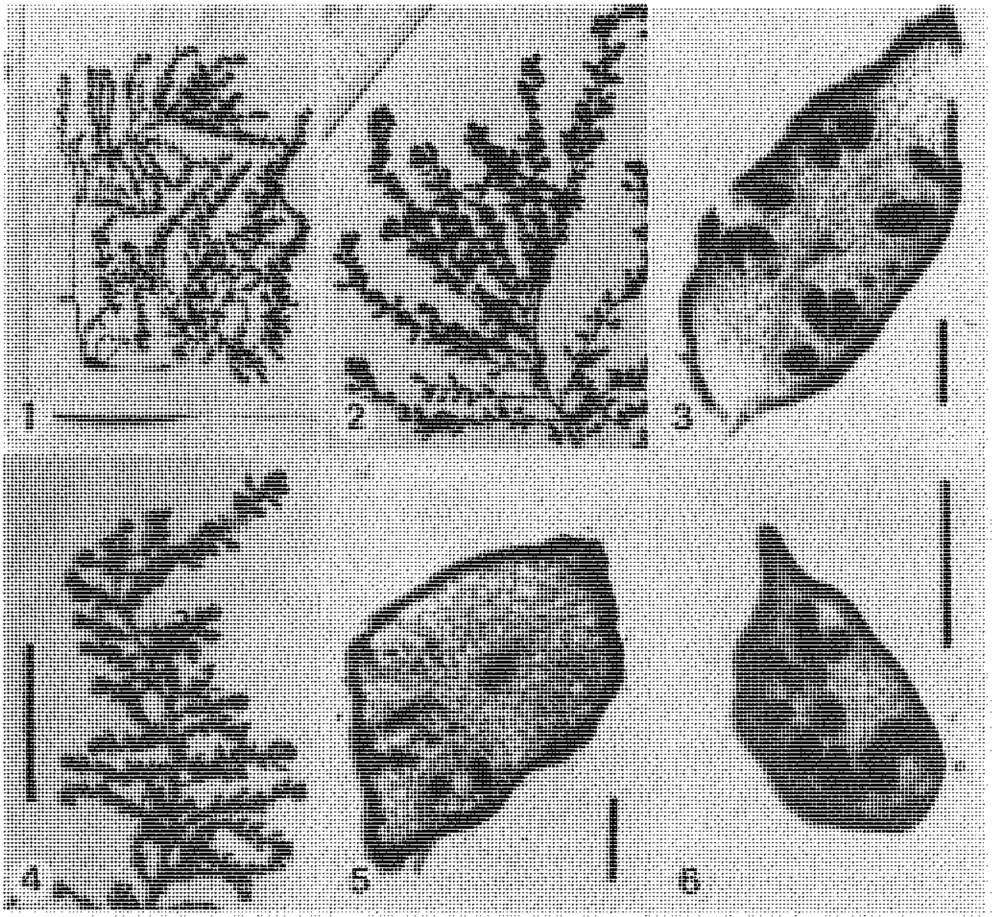

Fig. 17. *Sargassum myriocystum* J. G. Agardh from Okinawa Prefecture. 1–5, Female plants collected from Nakagusuku Bay, Okinawa Prefecture: 1, Whole plant of dried female specimen. 2, A part of a plant with compressed female receptacles. 3, Transverse section of compressed, pseudozygocarpic female receptacle. 4, A part of plant with triquetrous female receptacles. 5, Transverse section of triquetrous female receptacle with dentate margin. 6, Female plant collected from Taketomi Island: Transverse section of slightly compressed female receptacles with dentate margins. Scale bars: 3, 5, and 6, 100 μm; 4, 5 cm.

and receptacles between specimens from the two habitats have been observed. This species is similar to *S. polycystum* in its heavily muricated branches, but it has no rhizoidal branches. As we found holozygocarpic characters on both reproductive organs, it seems to be closely related to *S. polycystum* in the section *Zygocarpicae* of subgenus *Sargassum*.

This species is distributed widely on the coasts of Okinawa Prefecture in Japan. We have examined specimens from Cebu Island, the Philippines, and northern Australia (type locality) also.

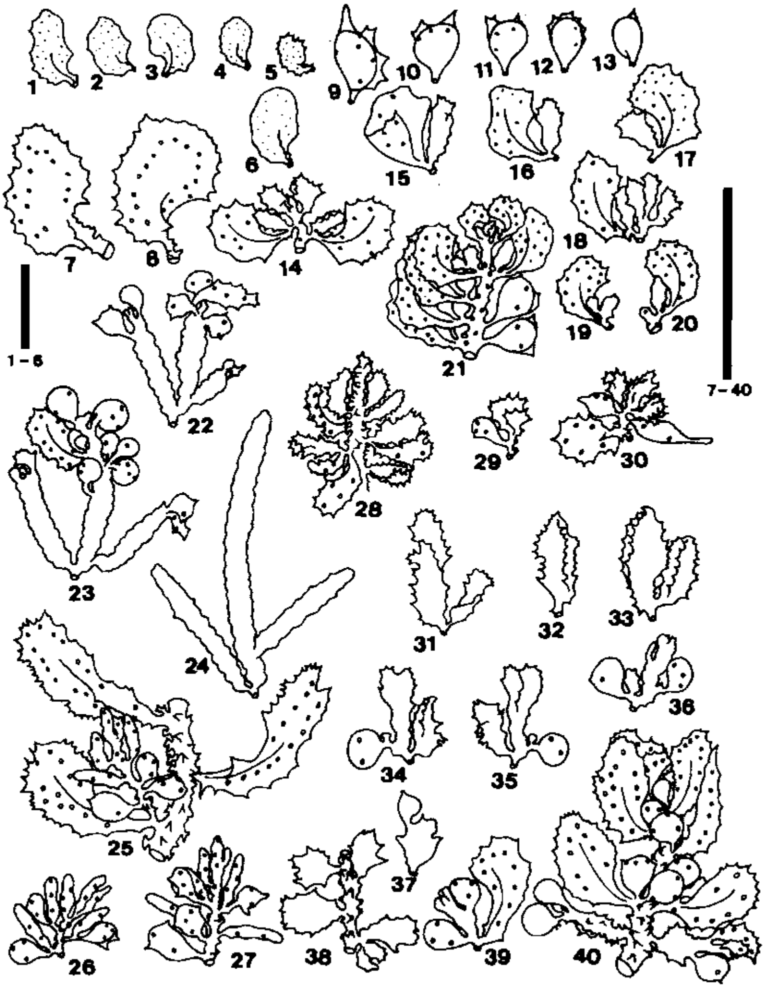

Fig. 18. *Sargassum myriocystum* J. G. Agardh from Okinawa Prefecture. 1–21, Male plant collected from Hedo Peninsula, Okinawa Prefecture: 1–13, Morphological variations of secondary branches.14–21, Compressed male receptacles. 22–39, Male plant collected from Nakagusuku Bay, Okinawa Prefecture: 22–24, Long, cylindrical, holozygocarpic male receptacles. 25–27, Short cylindrical, pseudozygocarpic male receptacles. 28, Compressed to triquetrous, pseudozygocarpic male receptacles. 29–40: Female plant collected from Nakagusuku Bay, Okinawa Prefecture. Compressed to triquetrous, pseudozygocarpic to holozygocarpic female receptacles. Scale bars = 1 cm.

*Sargassum polycystum* C. A. Agardh, Syst. algarum, p. 304, 1824.
(Figs. 19, 20)

Holdfast small, discoid, up to 6 mm in diameter. Stem terete to slightly compressed, 7.5–12.0 mm tall, 2.0–3.5 mm in diameter, with a warty surface, bearing three to seven rhizoidal branches and one to five primary branches. Rhizoidal branches terete or slightly compressed at their proximal portions, irregularly alternately branched, muricate with spines, 3.5–7.0 cm long, 2.0–2.5 mm in diameter; primary branches up to 50 cm or more long, terete, 1.5–2.2 mm in diameter, usually muricate with highly branched spines, giving rise to alternately arranged secondary branches; spines up to 1 mm tall, sometimes forked in Y-shape at apical portion; secondary branches up to 4 cm long, terete, crowded with spines. Primary leaves of juvenile plants wider, elliptical to lanceolate, leaves on secondary and tertiary branches slender, spatulate to linear-lanceolate, simple, with an asymmetrical base, 7.0–34.0 (average, 17.8) mm long, 1.0–10.5 (average, 3.8) mm wide, 2.4–13.0 (average, 5.4) in length-to-width ratio (200 leaves), with an acute apex, margin dentate with small teeth or entire, midrib distinct, reaching near apex, cryptostomata prominently raised all over surface, juvenile plants scattered or arranged in rows on both sides of the midrib at the slender leaves. Vesicles spherical to obovate, 2.0–5.0 (average, 3.2) mm in long axis, 1.8–3.8 (average, 2.8) mm in short axis, entire at the apex, cryptostomata prominently raised throughout the surface (100 vesicles); stalks terete, 1.0–2.2 (average, 1.5) mm long, shorter than the vesicles themselves.

Plants dioecious. Female receptacles cylindrical to fusiform, slightly compressed, up to 3 mm long, up to 1 mm in diameter, solitary or forked once, with a strongly warty surface, rarely with a few spines; male receptacles cylindrical, up to 8 mm long, up to 1 mm in diameter, solitary or forked once, with a warty surface; both female and male receptacles holozygocarpic.

Remarks: The immature plants (Fig. 20:1–12) were collected by T. Ajisaka on November 27, 1990, from Awase, Okinawa Prefecture. Mature male plants (Figs19:1–3 and 20:13) were collected by T. Ajisaka on June 2, 1991, from Taketomi Island, and a mature male plant (Figs. 19:4–6, and 20:14) was collected by Y. Yokochi in August 1982 from Sono, Iriomote Island, Okinawa Prefecture. Holozygocarpic female receptacles have been reported from Hainan Island and Xisha Island, southern China (Tseng and Lu 1988). This is the first report for the holozygocarpic male receptacles on this species.

This species is common in the Okinawa area and along the Pacific Ocean. Its small leaves, holozygocarpic dioecious receptacles, and heavily muricated branches look like those of *S. myriocystum*. However, *S. polycystum* is easily identified on the basis of its rhizoidal branches.

*Sargassum* sp. 1. (Figs. 21, 22)

Holdfast discoid, up to 1.3 cm in diameter. Stem terete up to 1.8 cm tall, with a warty surface, bearing six to eight primary branches. Primary branches up to 1 m or more long, distinctly compressed, 5.0–7.5 mm wide, 1.5–2.3 mm thick, with

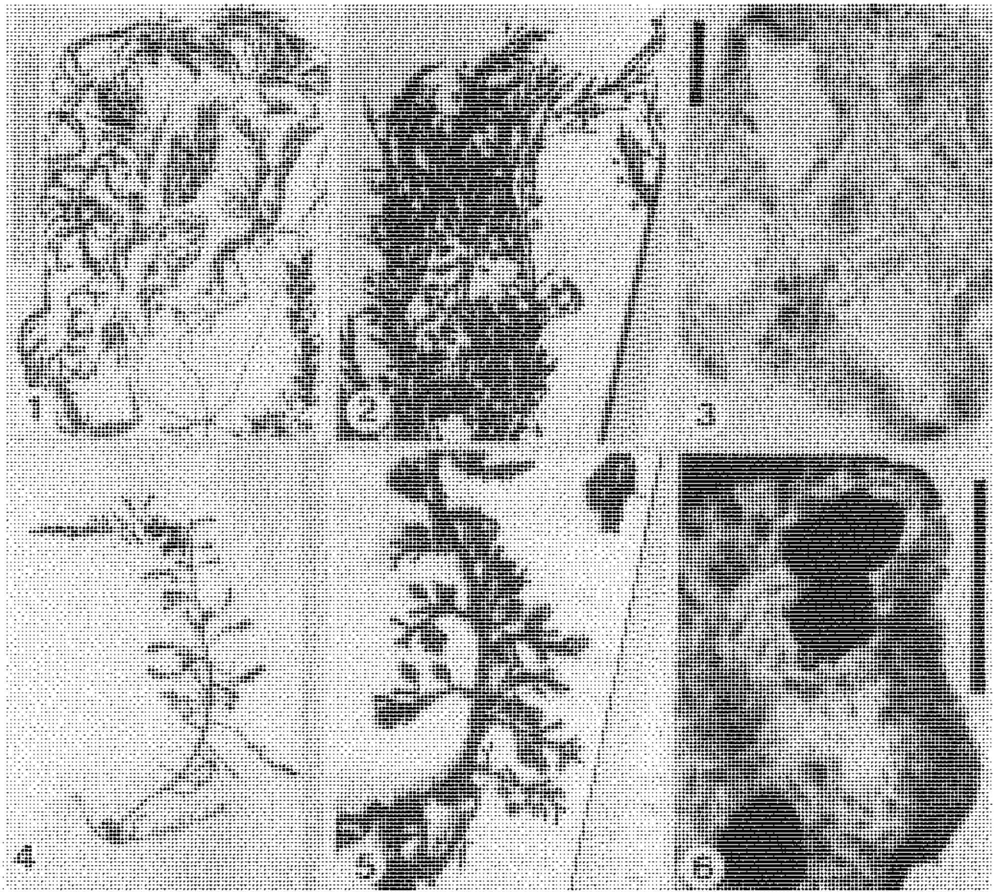

**Fig. 19.** ***Sargassum polycystum*** **C. A. Agardh from Okinawa Prefecture. 1, Whole plant of dried male specimen from Iriomote Island. 2, Holozygocarpic, cylindrical male receptacles. 3, Transverse section of male receptacle. 4, Whole plant of dried male specimen from Taketomi Island. 5, Holozygocarpic, cylindrical to fusiform female receptacles. 6, Transverse section of female receptacle. Scale bars: 3 and 6, 100 μm.**

a smooth surface, but sometimes with small spines on the margin, giving off regularly alternately arranged secondary branches. Secondary branches up to 76 cm long, compressed, producing lateral branches alternately. Leaves linear-lanceolate to lanceolate or spatulate, simple, 5.2–51.0 (average, 28.2) mm long, 2.5–13.5 (average, 8.2) mm wide, 1.5–5.2 (average, 3.4) in length-to-width ratio (450 leaves), with an acute apex, margin dentate with teeth or entire, midrib distinct, reaching near apex, cryptostomata scattered or arranged in rows on both sides of midrib. Vesicles spherical or elliptical, 3.8–9.9 (average, 6.6) mm in long axis, 3.5–8.5 (average, 5.8) mm in short axis (200 vesicles), entire at apex,

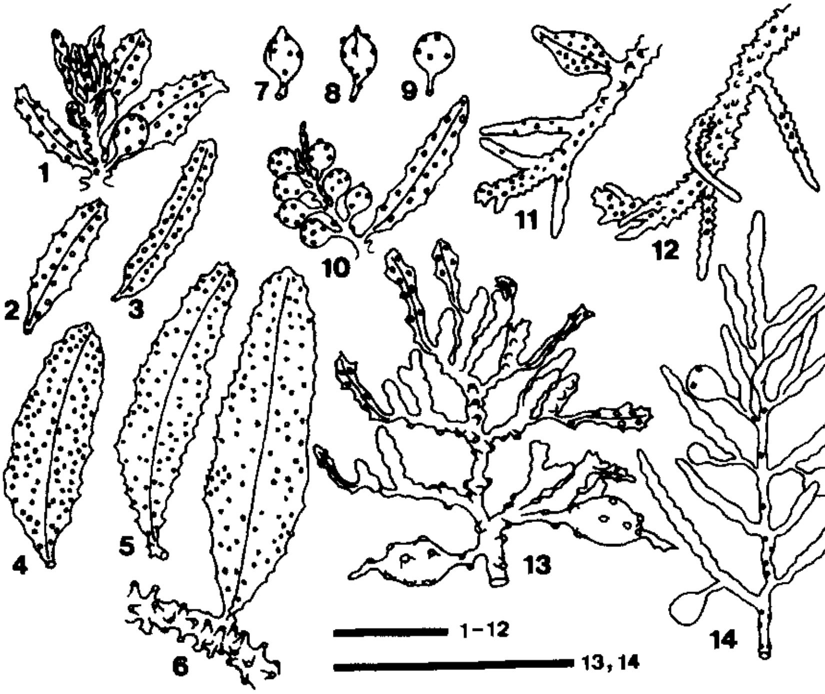

Fig. 20. *Sargassum polycystum* C. A. Agardh from Okinawa Prefecture. 1–12, Plant collected from Awase, Okinawa Prefecture: 1, Apical portion of secondary branches. 2–6, Morphological variations of primary leaves. 7–10, Vesicles. 11 and 12, Rhizoidal branches. 13, Apical portion of tertiary branches with holozygocarpic, cylindrical to fusiform female receptacles of the plant collected from Taketomi Island. 14, Apical portion of tertiary branches with holozygocarpic, cylindrical male receptacles of the plant collected from Iriomote Island. Scale bars = 1 cm.

cryptostomata scattered; stalks terete, 0.8–2.0 (average, 1.1) mm long, shorter than the vesicles themselves.

Plants monoecious. Receptacles androgynous, terete to slightly compressed at upper portion, 3–6 mm long, 0.8–1.5 mm in diameter, solitary or forked two to three times, warty, without spines or with a few spines, usually pseudozygocarpic.

Remarks: This species could be identified as *S. oligocystum* Montagne. However, it is better now to place it in the section *Zygocarpicae* because of its pseudozygocarpic receptacles. The drifted specimen (Figs. 21:1–4 and 22) was collected by T. Toma on October 23, 1981, from Yonaha Bay, Miyako Island, Okinawa Prefecture. The same species has been collected by T. Ajisaka from Bolinao, the Philippines, January 13–15, 1990. Similar morphological characteristics and pseudozygocapic receptacles have been observed in both collections. The juvenile plants (Fig. 21:5–6) were also collected by T. Ajisaka from Taketomi

Island and Iriomote Island, Okinawa Prefecture, on June 7 and 8, 1990. They were growing in the sublittoral zone (depth, about 1 m).

*Sargassum* sp. 2. (Figs. 23, 24)

Holdfast discoid, up to 6 mm in diameter. Stem erect, terete, up to 4 mm long, up to 1.5 mm in diameter, with a smooth surface, bearing up to four primary branches. Primary branches very slender, terete to slightly compressed, up to 50 cm long, 1–2 mm wide, with a smooth surface, without cryptostomata; secondary branches terete to slightly compressed, with a smooth surface, without cryptostomata. Leaves very thin, membranous, sometimes glaucescent with heavily attached diatoms; leaves of primary branches deciduous, up to 2.7 cm long, up to 6 mm wide; leaves of secondary branches up to 2.2 cm long, up to 4 mm wide; all leaves lanceolate, with a cuneate base, sometimes with a few spines at the base, margin with small denticulation, with a sharp apex, midrib conspicuous, vanishing near the apex; cryptostomata small, conspicuous, scattered throughout the surface. Vesicles spherical, up to 4 mm in diameter, usually rounded at the apex, but sometimes with an apiculate or small earlike appendage, with a few cryptostomata; stalk terete and nearly as long as vesicles, but sometimes compressed like leaves and longer than vesicles.

Plants monoecious. Receptacles androgynous, terete to fusiform, sometimes slightly compressed, up to 5 mm long, up to 1 mm wide, solitary or furcately branched once to twice, without spines or sometimes with a few spines, holozygocarpic.

Remarks: The specimens (Figs. 23 and 24) were collected by T. Noro from Natui, Shibushi, Kagoshima Prefecture, on May 2, 1988, and June 1, 1988, and deposited in the herbarium of Marine Botany, Faculty of Fisheries, Kagoshima University (KF 880391 and KF 880452). They were identified as *S. crispifolium* by Noro. However, the specimens are different from the type specimen of *S. crispifolium* in Hokkaido University. The holotype specimen is a female plant, and *S. crispifolium* is dioecious. The specimens collected at Natui have very small leaves and are monoecious, with androgynous receptacles, which are holozygocarpic, with a few spines. From the key of zygocarpic species from China (Tseng and Lu 1988), it can be identified as *S. tenerrimum.* However *S. tenerrimum* from China has compressed receptacles with a few spines, and the specimens from Japan have terete and/or fusiform or slightly compressed receptacles with or without a few spines.

## Systematic Arrangement for the Species of *Zygocarpicae*

Tseng and Lu (1988) reported 17 species of Chinese zygocarpic *Sargassum.* Nguyen (1986) reported 1 new species, and Ajisaka, Huynh, and Nguyen (1994) reported 2 Vietnamese species. Here, we report 10 Japanese zygocarpic species. Altogether 23 species of zygocarpic *Sargassum* have been reported so far from the western Pacific area. Tseng and Lu (1988) have already proposed the

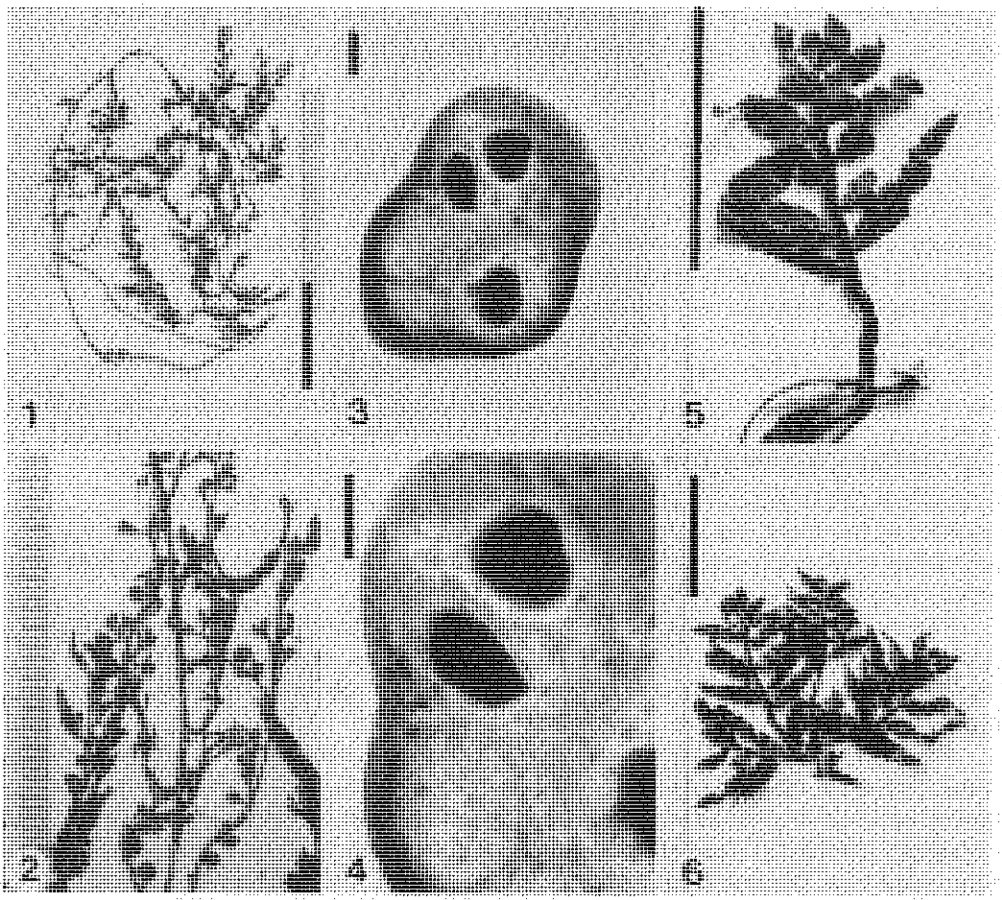

**Fig. 21.** ***Sargassum*** **sp. 1 from Okinawa Prefecture. 1–4, Plant collected from Miyako Island: 1, Whole plant of dried specimen. 2, Terete to slightly compressed receptacles and flattened primary branches. 3 and 4, Transverse section of androgynous receptacle showing three antheridia and two oogonia. 5 and 6, Plants collected from Taketomi Island: 5, Juvenile primary branches on wet specimen. 6, Immature wet specimen. Scale bars: 1, 5, and 6, 10 cm; 3 and 4, 100 μm.**

systematic arrangement of Chinese species of section *Zygocarpicae*. We follow their proposal of making a small modification of Setchell's system for the arrangement of the species. However, we would make another modification in the arrangement: (1) Nguyen (1986) reported from Vietnam a new species, *S. vietnamense* Zinova et Dinh subsection *Holozygocarpicae*. Receptacles are dioecious. Female receptacles are terete or compressed or triquetrous, and male receptacles are compressed; both have spines. These characteristics indicate a new species group: *Vietnamensa* Ajisaka. (2) Ajisaka, Nang, and Dinh (1994) reported from Vietnam a new species, *S. denticarpum* Ajisaka, which was assigned to subsection

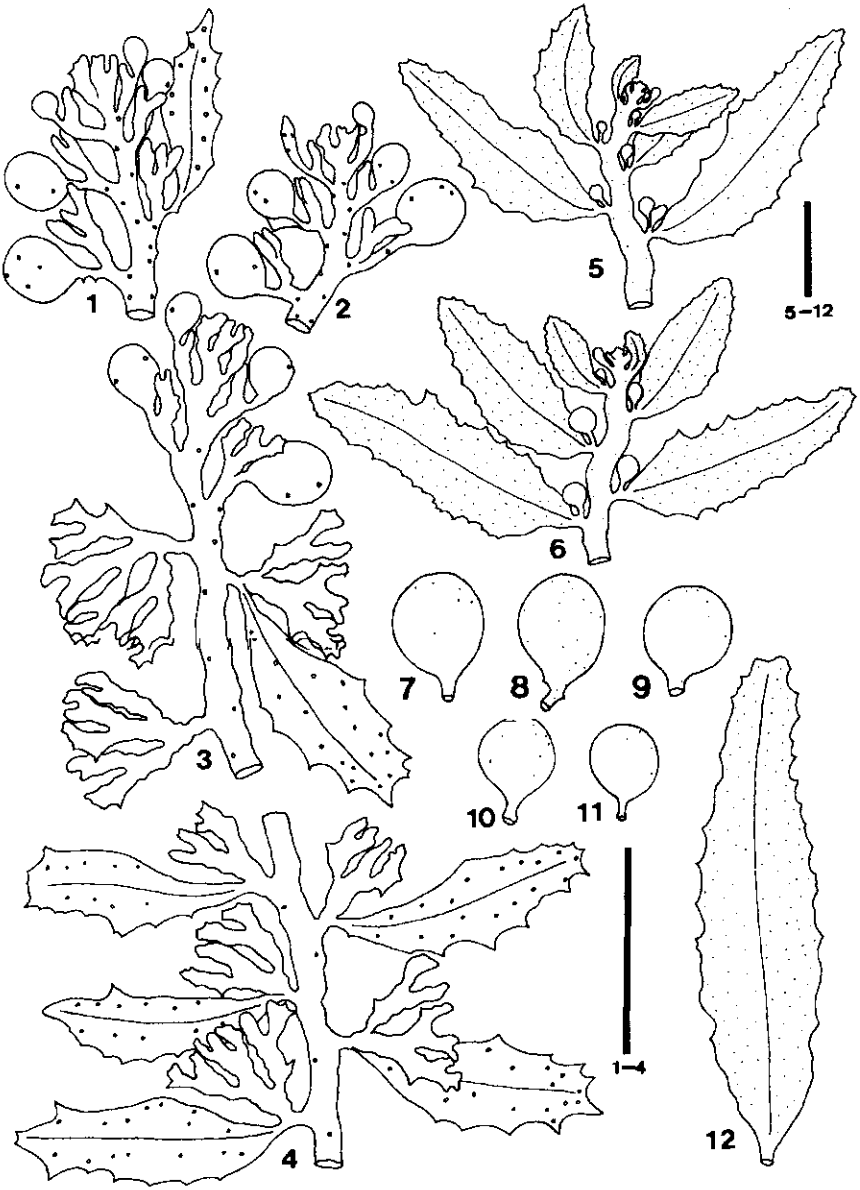

Fig. 22. *Sargassum* sp. 1 from Miyako Island, Okinawa Prefecture. 1–4, Pseudozygocarpic, terete to slightly compressed receptacles. 5 and 6, Apical portion of secondary branches. 7–11, Vesicles. 12, A primary leaf. Scale bars = 1 cm.

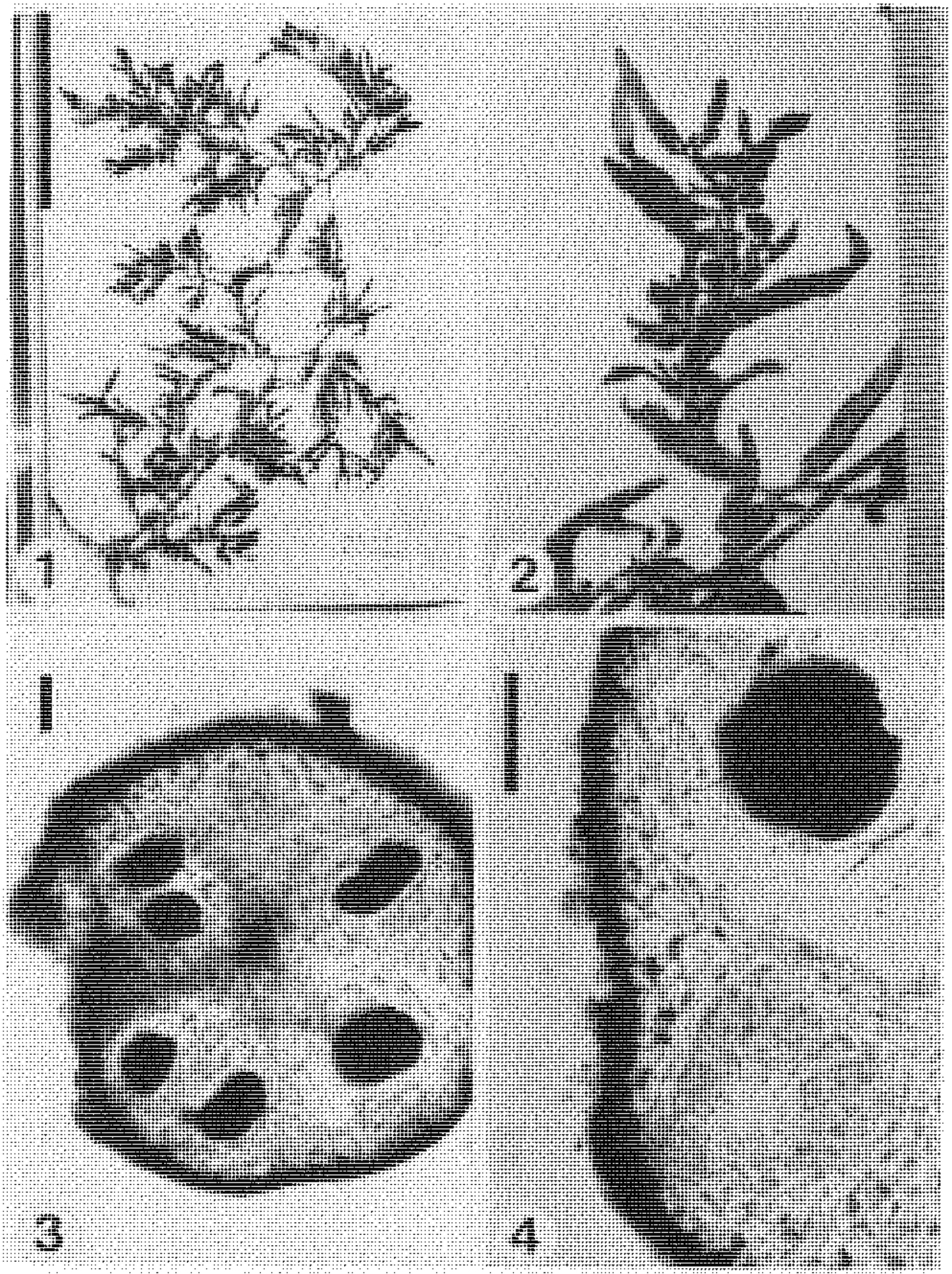

Fig. 23. *Sargassum* sp. 2 from Shibushi, Kagoshima Prefecture. 1, Whole plant of dried specimen. 2, Apical portion of the secondary branches, with receptacles. 3 and 4, Transverse section of androgynous receptacles showing antheridia and three oogonia. Scale bars: 1, 10 cm; 3 and 4, 100 μm.

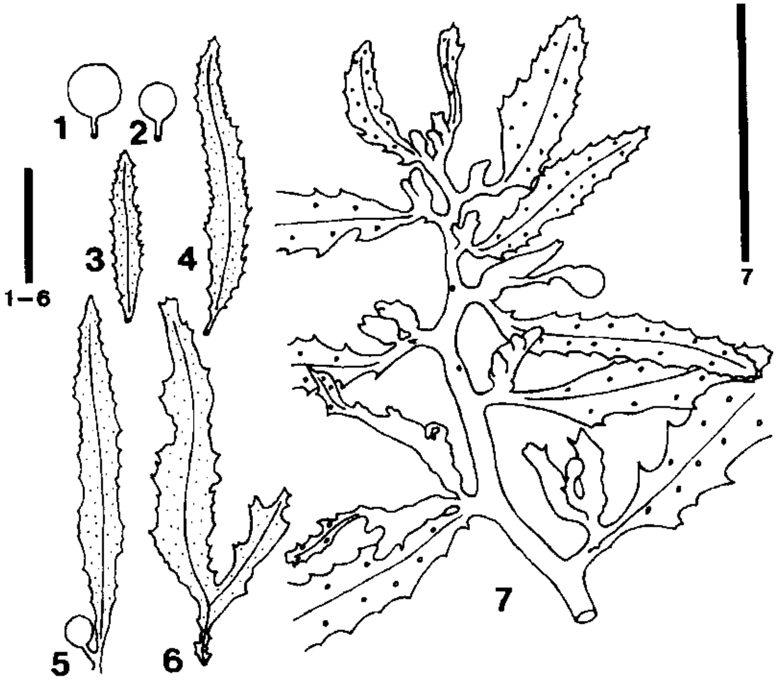

**Fig. 24.** ***Sargassum*** **sp. 2 from Shibushi, Kagoshima Prefecture. 1 and 2, Vesicles. 3–6, Morphological variations of the secondary leaves. 7, Apical portion of the secondary branch, showing holozygocarpic, cylindrical receptacles with a few spines. Scale bars = 1 cm.**

*Pseudozygocarpicae.* The receptacles are androgynous, compressed to triquetrous, with spines. These characteristics indicate a new species group: *Denticarpa* Ajisaka. (3) The species group *Vachelliana* Setchell includes members that have heterogeneous characteristics, androgynous, and dioecious. It should be separated as in the subsection *Holozygocarpicae* to two species groups, a new species group, *Incana* Ajisaka, and *Vachelliana* Setchell. The species group *Incana* includes *S. incanum*, *S. bulbiferum* , and *S.* sp. 1. The species group *Vachelliana* includes *S. graminifolium*, *S. vachellianum*, and *S. crispifolium.* (4) *Sargassum* sp. 2 belongs to the species group *Carpophylleae,* and *S. myriocystum* belongs to the species group *Tenuia.*

With these changes, the systematic arrangement of the section *Zygocarpicae* is as follows:

1. *Sargassum* subgenus *Sargassum* subsection *Holozygocarpicae* Setchell
  - Series 1. *Carpophylleae* J. G. Agardh
    - Species group 1: *Carpophylleae* J. G. Agardh (receptacles androgynous, terete to fusiform, without spine or with a few spines)
      1. *S. angustifolium* (Turner) J. G. Agardh
      2. *S. carpophyllum* J. G. Agardh
      3. *S.* sp. 2
    - Species group 2: *Tenerrima* Setchell (receptacles androgynous, compressed to triquetrous, with spines at apex)
      4. *S. tenerrimum* J. G. Agardh
      5. *S. assimile* Harvey
      6. *S. subtillissimum* Tseng et Lu
      7. *S. aemulum* Sonder
      8. *S. parvivesiculosum* Tseng et Lu
    - Species group 3: *Longifructa* Tseng et Lu (receptacles dioecious; male and female ones cylindrical, without spines or with a few spines)
      9. *S. naozhouense* Tseng et Lu
      10. *S. longifructum* Tseng et Lu
    - Species group 4: *Tenuia* Setchell (receptacles dioecious; male ones cylindrical, without spines; female ones compressed to triquetrous, with spines)
      11. *S. polycystum* C. A. Agardh
      12. *S. myriocystum* J. G. Agardh
      13. *S. tenue* J. G. Agardh
      14. *S. laxifolium* Tseng et Lu
    - Species group 5: *Vietnamensa* Ajisaka (receptacles dioecious; male and female ones compressed to triquetrous, with spines)*
      15. *S. vietnamense* Zinova et Dinh
2. *Sargassum* subsection *Pseudozygocarpicae* Setchell
  - Series 2. *Cinerea* Tseng et Lu
    - Species group 6: *Incana* Ajisaka (receptacles androgynous, terete to fusiform, without spines or with a few spines)*
      16. *S. incanum* Grunow
      17. *S. bulbiferum* Yoshida
      18. *S.* sp. 1
    - Species group 7: *Denticarpa* Ajisaka (receptacles androgynous, compressed to triquetrous, with spines)*
      19. *S. denticarpum* Ajisaka
    - Species group 8: *Vachelliana* Setchell (receptacles dioecious; male and female ones terete to fusiform, without spines or with a few spines)
      20. *S. graminifolium* (Turner) J. G. Agardh
      21. *S. vachellianum* Greville
      22. *S. crispifolium* Yamada
    - Species group 9: *Cinerea* Setchell (receptacles dioecious; male ones terete, with or without spines; female ones compressed, with spines)

23. *S. cinereum* J. G. Agardh
24. *S. glaucescens* J. G. Agardh

*Editor's note: Items with an asterisk (*) are new "Species Groups," proposed by Dr. Ajisaka. However, according to the International Code of Botanical Nomenclature (ICBN, 1994 edition, as well as previous editions), this category has *no standing*, i.e., it is not recognized under the Code. Species Groups were explained by Abbott et al. in Tax. Econ. Seaweeds 2 (1988) as being a "convenient" category for species that may be closely related. It is expected to be a harbinger of reorganization, in which after population studies, either characteristics will be reordered and given different emphasis, or only single species may emerge from these groups.

Greuter, W. 1994. In: International Code of Botanical Nomenclature (Tokyo Code). Regnum Vegetabile 131, pp. 389. Koeltz. Königstein, Germany.

## Acknowledgments

We thank Mr. Takeshi Toma, Mr. Teruo Tamaoki, Mrs. Naho Miyamoto, and Mr. Satoshi Namba for their kind help and contributions of the specimens. We also thank Dr. Abbott for her careful editing of this paper.

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# STUDIES OF TWO ZYGOCARPIC SPECIES OF *SARGASSUM* (SUBGENUS *SARGASSUM*) FROM VIETNAM

Tetsuro Ajisaka, Huynh Quang Nang, and Nguyen Huu Dinh

## Abstract

Two species of the section *Zygocarpicae* subgenus *Sargassum* (Phaeophyta, Fucales, genus *Sargassum*) from Vietnam are reported. *Sargassum denticarpum* Ajisaka has pseudozygocarpic androgynous receptacles, which are compressed and dentate at the margin. This species is endemic to Vietnam. *Sargassum longifructum* Tseng et Lu has holozygocarpic dioecious receptacles. Female receptacles are compressed and have a dentate margin; male receptacles are terete to slightly compressed at the apex, with an entire margin or a few marginal spines.

## Introduction

Pham (1967, 1969) reported 39 species of *Sargassum* from Vietnam, of which 31 belonged to the subgenus *Sargassum* and 6 to the section *Zygocarpicae* (J. G. Agardh) Setchell. However, Tseng and Lu (1988) thought that *S. carpophyllum* of Pham seemed to be *S. parvivesiculosum* Tseng et Lu.

For a critical resurvey of the marine flora of the Vietnamese coasts, we collected many species from central to southern Vietnam in January and February, 1993. Among the many species of *Sargassum*, some belonged to the subgenus *Bactrophycus* and others to the subgenus *Sargassum*.

We report two species in the section *Zygocarpicae* of subgenus *Sargassum*, *S. denticarpum* Ajisaka (Ajisaka et al. 1994) and *S. longifructum* Tseng et Lu, found in Vietnam. The original description of *S. longifructum* is based on material from Naozhou Island, southern China (Tseng and Lu 1987, 1988).

## Materials and Methods

Plants of both species were collected by snorkeling: *S. denticarpum* from station 3 (21 January, 1993) and *S. longifructum* from station 16 (5 February, 1993) in central to southern Vietnam (Fig. 1). They were growing at a depth of 1–5 m on the rocky substratum. Collected materials were immediately fixed with 10% formaldehyde. Later, in the laboratory, specimens were examined for vegetative traits. The length, width, and length-to-width ratio, and qualitative morphological characteristics were noted for 200 leaves. Quantitative characteristics such as long and short diameter and length of stalk and qualitative morphological characteristics were determined for 100 vesicles. The length, width, branching, and other morphological characteristics of 20 receptacles were noted, and their sex was confirmed by examining transverse sections. The type specimen (AST 551767) of *S. longifructum*, deposited in the herbarium of the Institute of Oceanology, Academia Sinica, Qingdao, was also examined.

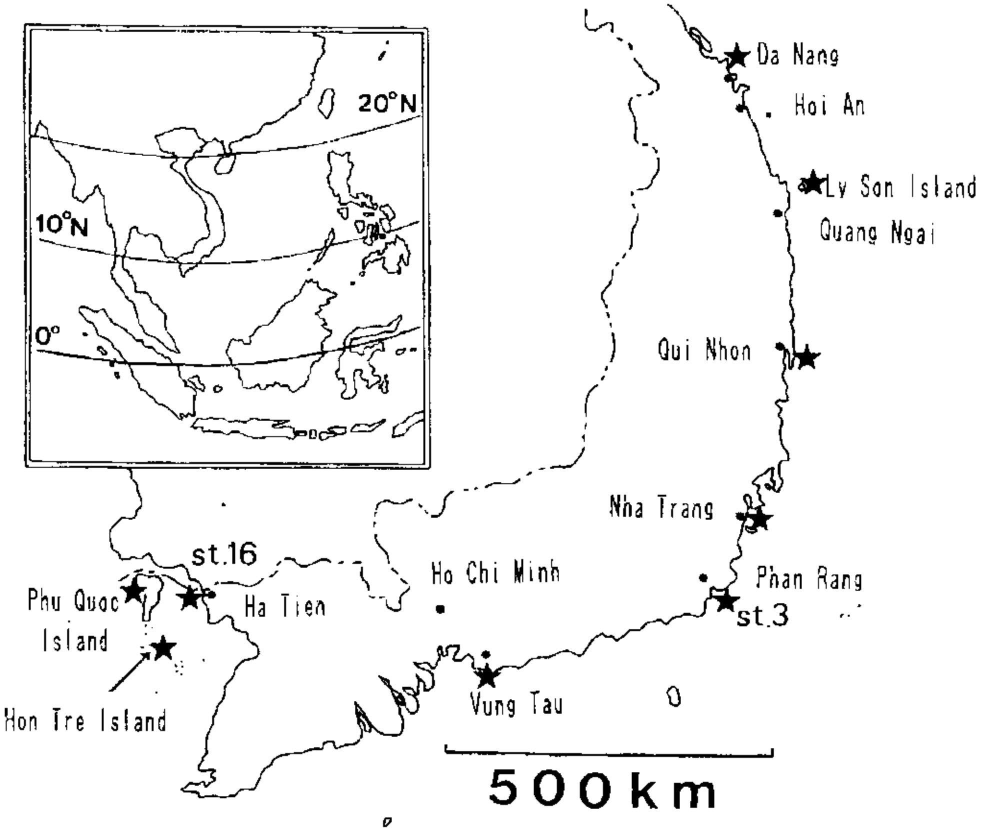


**Fig. 1. Collection sites (solid stars) in the scientific survey of southern Vietnam in January and February 1993.**

## Description of the Species

*Sargassum denticarpum* Ajisaka, Jpn. J. Phycol. 42:394–396, Figs. 2–10, 1994. (Figs. 2–5)

Specimens greenish-brown when dried. Holdfast discoid or conical, up to 14 mm in diameter. Stem erect, terete, up to 10 mm long, up to 5 mm in diameter, with a smooth surface, bearing up to five primary branches from the distal portion. Primary branches up to 50 cm long, compressed near the proximal portion, up to 5 mm wide, slightly compressed to angular at the distal portion, up to 3 mm wide, with a smooth surface. Secondary branches arising distichously at 5-cm intervals, each up to 50 cm long, with a smooth surface. Leaves with a short stalk, simple, elongate-elliptical or linear-lanceolate, up to 5 cm long, up to 2 cm wide, with an asymmetrical base and an acute apex; margin irregularly dentate; cryptostomata conspicuously developed but irregularly scattered throughout the leaf; midrib well-developed, distinct, evanescent, or percurrent, sometimes spinose. Vesicles

Fig. 2. Holotype specimen of *Sargassum denticarpum* Ajisaka. Scale bar = 10 cm.
Fig. 3. Apical portion of secondary branches of *Sargassum denticarpum* Ajisaka.

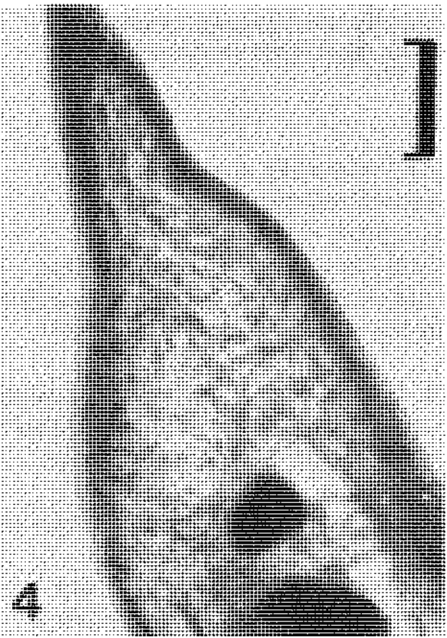


Fig. 4. Transverse section of androgynous receptacle of *S. denticarpum* Ajisaka shows antheridial and oogonial conceptacles. Scale bar = 100 µm.

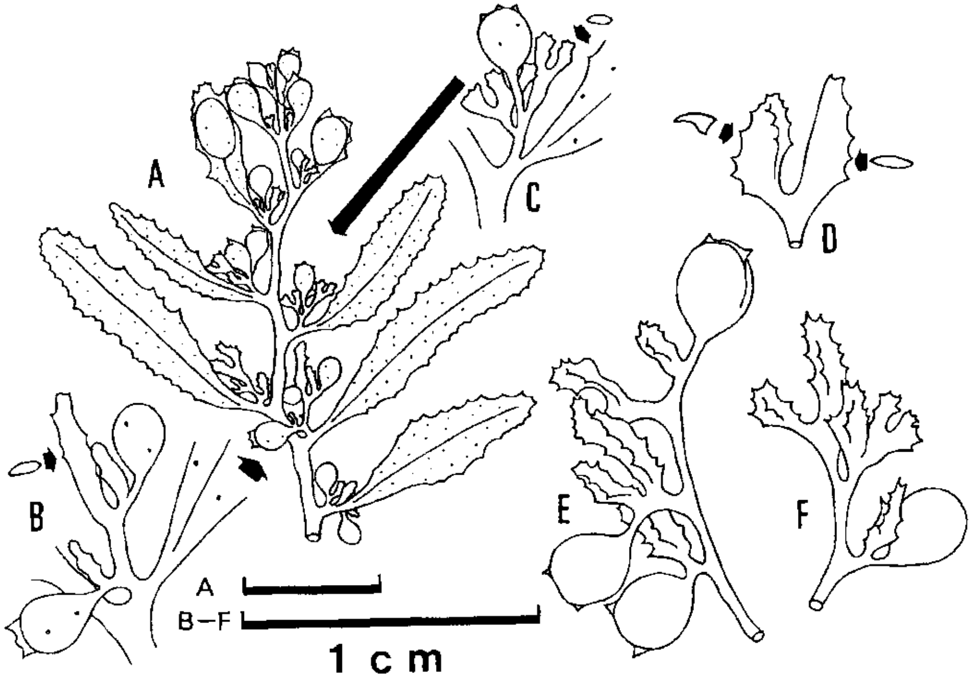


**Fig. 5. Leaves, vesicles, and receptacles of *Sargassum denticarpum* Ajisaka. A, Apical portion of secondary branch. B–F, Pseudozygocarpic receptacles compressed or triquetrous with dentate margins.**

spherical to ellipsoidal, up to 8.5 mm long, up to 7 mm wide, apiculate, with or without spinose or entire appendages at the apex or margin, with scattered cryptostomata; stalk short, terete or foliaceous, up to 3 mm long.

Plant monoecious. Receptacles androgynous (very few male conceptacles among female conceptacles), compressed to triquetrous, up to 4 mm long, up to 1 mm wide, simple or branched furcately once or twice, margin acutely dentate; pseudozygocarpic.

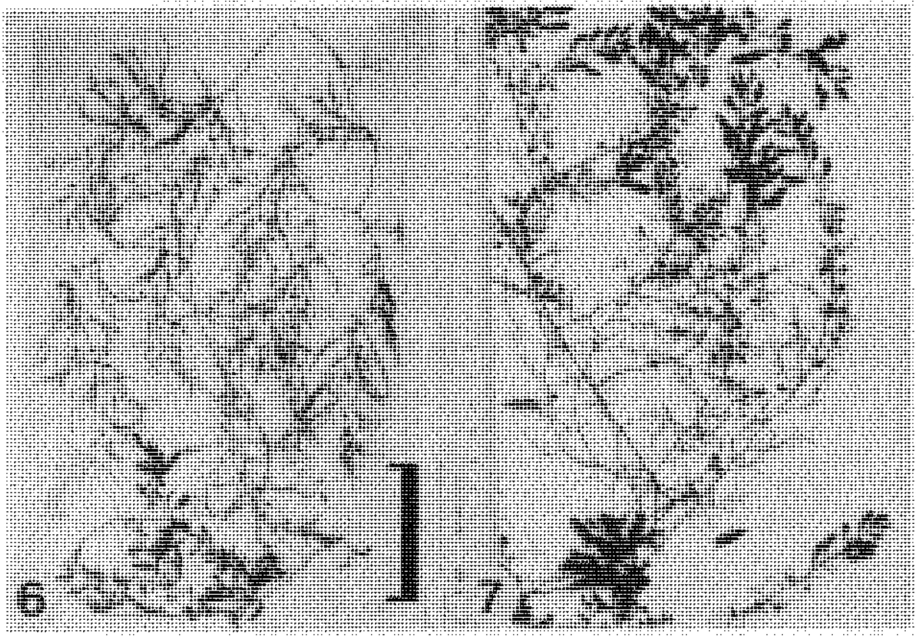
Sources of Specimens Examined: Son Hai, Ninh Phuoc, Ninh Thuan Province (type locality), and Nhatrang, Khanh Hoa Province, in central Vietnam, deposited in the herbarium of Fisheries Resources, Faculty of Agriculture, Kyoto University.

Distribution: Endemic to central Vietnam.

Remarks: The specimens examined have pseudozygocarpic and androgynous receptacles, which are compressed to triquetrous with a dentate margin. Pseudozygocarpic receptacles are paired with leaves or vesicles, or both, but pedicels of receptacles are usually constant (Tseng et Lu 1988). This species is thus separable to the subsection *Pseudozygocarpicae* Setchell.

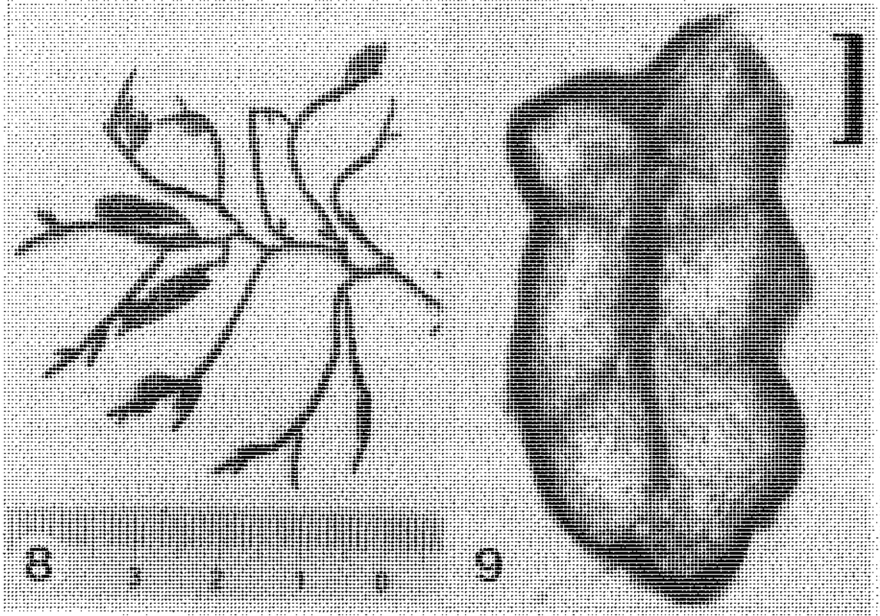
*Sargassum longifructum* Tseng et Lu, Oceanol. Limnol. Sin. 18:516, fig. 2, pl. 1, fig. 2, 1987. (Figs. 6–15)

Specimens greenish-brown when dried. Holdfast discoid to scutellate, up to 10 mm in diameter. Stem erect, terete, up to 2 cm high, up to 4 mm in diameter, with a warty surface, bearing up to eight primary branches from the distal portion. Primary branches slender, terete, up to 50 cm long, up to 2 mm in diameter, with a smooth surface. Secondary branches arising alternately at 5-cm intervals, up to 25 cm long, with a smooth surface. Leaves with a short petiole, simple or rarely once divided, elongate-lanceolate, up to 5 cm long, up to 13 mm wide, with a cuneate base and an acute apex; margin slightly to coarsely dentate; cryptostomata scattered or arranged in rows on both sides of the midrib in linear leaves; midrib distinct, percurrent, evanescent. Vesicles spherical to ellipsoidal, up to 7.5 mm long, up to 5 mm wide, with or without spinose or entire appendages at the apex, with inconspicuously scattered cryptostomata; stalk of vesicle terete, up to 3 mm long.

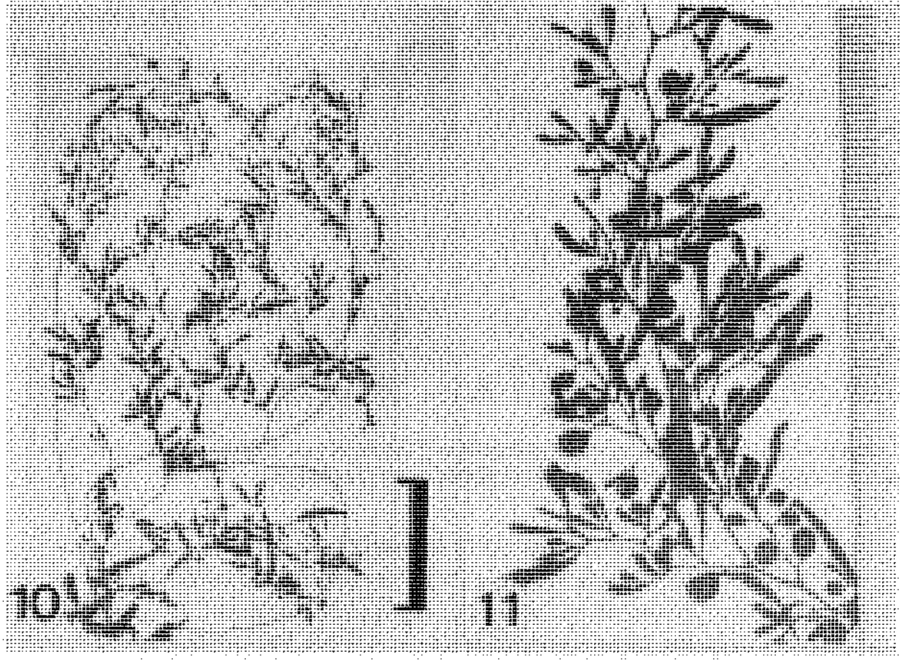


**Figs. 6–7. Male plant of *Sargassum longifructum* Tseng et Lu. Fig. 6, Whole plant. Scale bar = 10 cm. Fig. 7, Apical portion of secondary branches.**

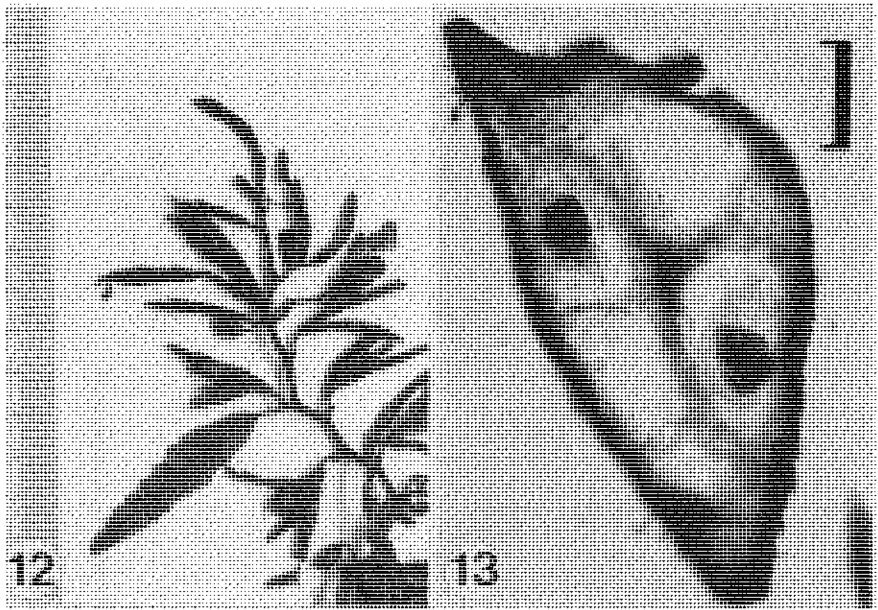
Plant dioecious. Female receptacles compressed to triquetrous, sometimes twisted, up to 6 mm long, up to 2 mm wide, simple or furcately divided, with a dentate margin, pseudozygocarpic to holozygocarpic; only oogonial conceptacles found in transverse sections. Male receptacles terete to slightly compressed, up to 30 mm long, up to 1 mm wide, simple or branched furcately once to several times,



Figs. 8–9. *Sargassum longifructum*. Fig. 8, Holozygocarpic male receptacles. Fig. 9, Transverse section of male receptacle with antheridial conceptacles. Scale bar = 200 µm.



Figs. 10–11. Female plant of *Sargassum longifructum* Tseng et Lu. Fig. 10, Whole plant. Scale bar = 10 cm. Fig. 11, Apical portion of secondary branches.



Figs. 12–13. *Sargassum longifructum*. Fig. 12, Holozygocarpic female receptacles. Fig. 13, Transverse section of female receptacle with oogonial conceptacles. Scale bar = 200 μm.

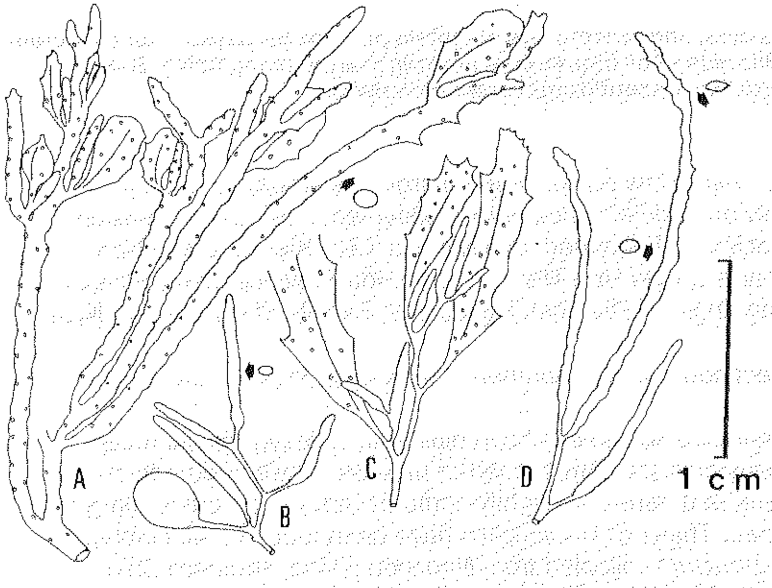


Fig. 14. Leaves, vesicles, and receptacles of male plant of *Sargassum longifructum* Tseng et Lu. A, Long, terete, holozygocarpic receptacles. B and C, Short, terete, pseudozygocarpic receptacles. D, Long, terete receptacles with apices slightly compressed and a few spines.

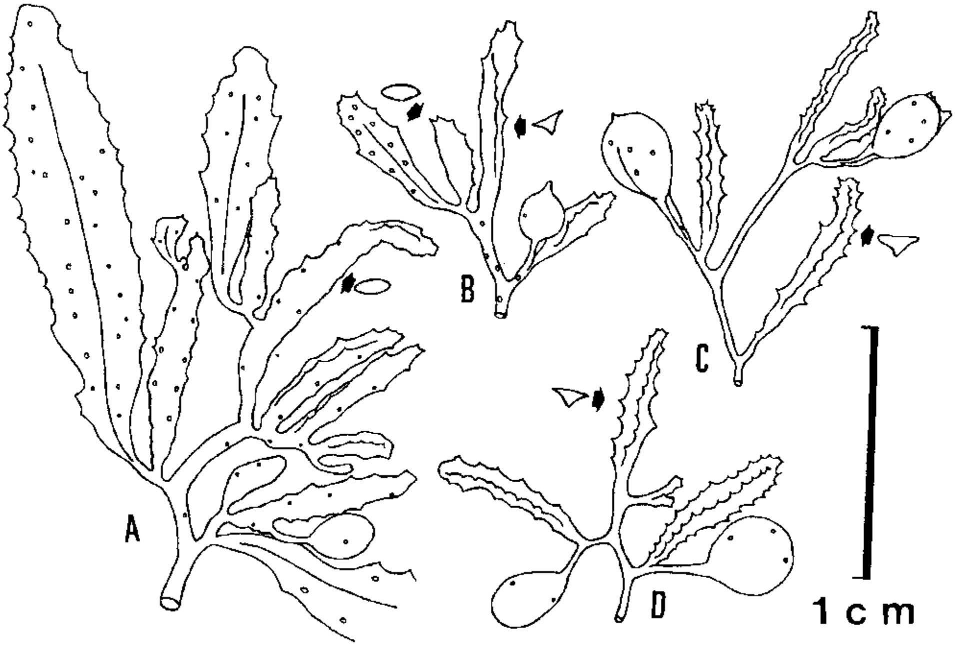


**Fig. 15. Leaves, vesicles, and receptacles of female plant of *Sargassum longifructum* Tseng et Lu. A, Compressed or triquetrous, holozygocarpic receptacles. B–D, Compressed or triquetrous pseudozygocarpic receptacles.**

entire or sometimes with a few spines at the margin, pseudozygocarpic to holozygocarpic; only antheridial conceptacles observed in transverse sections.

Sources of Specimens Examined: Mui Nia, Ha Tien, Kien Giang Province, southern Vietnam, and Cauda Nha Trang, Khanh Hoa Province, central Vietnam, deposited in the herbarium of Fisheries Resources, Faculty of Agriculture, Kyoto University.

Distribution: Naozhou Island in southern China (type locality), Japan, and Vietnam.

Remarks: Vietnamese specimens have dioecious holozygocarpic receptacles. Female receptacles are compressed or triquetrous with a dentate margin; male receptacles are long, terete or slightly compressed with an entire margin or a few marginal spines. These characteristics have been found in the holotype specimen of *S. longifructum* collected from Naozhou Island, southern China (Tseng and Lu 1987, 1988). However, as this species was described on the basis of male material only, the preceding description of female reproduction is the first for this species.

## Acknowledgments

We thank Dr. I. A. Abbott, University of Hawaii, for her kind advice on improving the manuscript.

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Tseng, C. K., and Lu Baoren. 1987. Three new species of *Sargassum* (Fucales, Phaeophyta) from South China Sea. Ocean. Limonol. Sin. 18:515–523, pl. I–II.

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# VARIATIONS IN *SARGASSUM SILIQUOSUM* J. AGARDH (FUCALES, PHAEOPHYTA) FOUND IN MALAYSIA AND SINGAPORE

Siew-Moi Phang, Tadahide Noro, and Tadao Yoshida

## Abstract

Twenty-seven specimens of *Sargassum siliquosum* J. Agardh, including 7 from the herbarium of Grunow, collected near Singapore, the type locality of the species, were examined and compared. Most characteristics of the species, such as holdfast, stem, branches, the shapes of leaves and vesicles, and overall form and branching, are relatively constant. The most variable characteristic is the size of the leaves, which are generally longer and larger on young sterile plants and smaller and narrower on fertile plants.

## Introduction

*Sargassum* (subgenus *Sargassum*) species dominate the coral reefs around peninsular Malaysia and Singapore (Phang and Wee 1991). Of the species reported in Malaysia and Singapore (Phang and Wee 1991), *S. siliquosum* J. Agardh appears to be one of the more widely distributed species in the waters.

All specimens with terete, smooth stems; almost alternately arranged secondary branches; elliptical, lanceolate to obovate leaves; and long terete male receptacles and much shorter female receptacles, both racemosely branched, often with vesicles subspherical to obovoid and stalked, are designated as *S. siliquosum* for this paper. Nineteen herbarium specimens were studied: 4 from coral reefs, 3 from rocky shores, and 12 drift specimens. In addition, 7 herbarium specimens from the Grunow Collection deposited at the Herbarium, Natural History Museum at Vienna, examined during a short visit by Phang in September 1994, are included for discussion. The Grunow specimens were collected from Singapore (6 specimens) and the China Sea (1 specimen). One specimen collected from Palawan, Philippines, was provided by Tadahide Noro.

*Sargassum* is a large genus with a polymorphic nature that has led to much “confusion and proliferation of names in the literature” (Ang and Trono 1987). The delineation of a species should consider variation in the traditionally used morphological characteristics that are due to phenotypic plasticity, ontogenetic differences, polymorphism, hybridization, and polyploidy (Kilar et al. 1992). Studies on seasonal variations, different phenotypes from a single genotype (“reaction norm”), interlocality differences, numerical taxonomy analysis, natural products and genetics have been recommended as research areas for determination of a species.

Often type specimens do not contain all the important features for delineation of a species, especially when reproductive structures are absent (Kilar et al. 1992). *Sargassum siliquosum* has been described by J. Agardh (1848), Yendo

(1907), Reinbold (1913), Grunow (1916), Yamada (1942), Chou and Chiang (1981), Ang and Trono (1987), Yoshida (1988), Tseng and Lu (1992), and Trono (1992).

The holotype specimen from Singapore as described by Agardh (1848) cannot be located. Agardh did not state the sex of the type specimen, but Ang and Trono (1987) reported that the material in the Agardh Herbarium (LD, Herbarium Agardh No. 3260, lectotype) is male. Yamada (1942) mentioned male and female receptacles, and Ang and Trono (1987) and Trono (1992) emphasized the "strongly triquetrous and twisted female receptacles" as the distinguishing feature of *S. siliquosum.*

Tadao Yoshida, at the fifth Sea Grant taxonomy workshop in Honolulu, suggested that we produce a detailed description of the Malaysian and Singaporean specimens of *S. siliquosum* and the variations as an attempt to delineate the species and to establish the morphological variations. We hope that these specimens collected from the vicinity of Singapore, the type locality, give the closest description of the species.

## Materials and Methods

The materials examined are listed in Table 1. All materials were herbarium specimens. Of the 27 specimens examined, 13 were fertile. Receptacles of 12 specimens were dissected. The receptacles were cut from the tip to the base, and the cross-sections were stained with methylene blue, mounted in glycerine, and examined sequentially to verify the unisexual or bisexual condition.

## Results

Most of the fertile specimens were collected from March to October, indicating that *S. siliquosum* is probably fertile throughout the year. Largo et al. (1994) observed that the subtidal population of *S. siliquosum* in Cebu, Philippines, had reproductive branches throughout the year although the plants matured from September to December. Of the 12 specimens we dissected, 6 were males, and 5 were females. All plants were dioecious; that is all had single receptacles, all male or all female.

## Description of the Species

*Sargassum siliquosum* J. Agardh, Sp. gen. ordines algarum, vol. 1, p. 316, 1848.
(Figs. 1–18)

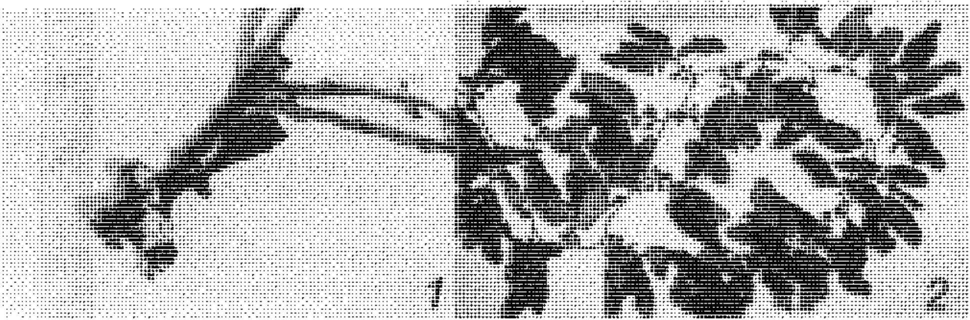
Other literature: Agardh 1889, p. 121, pl. 10; Grunow 1916, p. 173; Ang and Trono 1987, p. 395; Yoshida 1988, p. 18, fig. 17; Tseng and Lu 1992, p. 20, fig. 20; Trono 1992, p. 65, fig. 97.

Plants are yellowish-brown to dark brown when dried. Fertile plants reach 100 cm in height, whereas nonfertile plants reach 75 cm. Holdfasts are discoid, reaching a maximum diameter of 15 mm and giving rise to short, cylindrical to

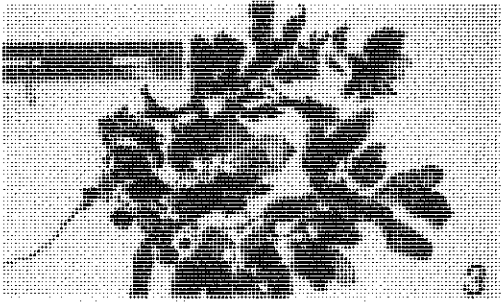
**Table 1. Herbarium Specimens of *Sargassum siliquosum***

| Locality | Habitat | Sex | Date of Collection | Source (Collection No.) |
|---|---|---|---|---|
| Singapore | | | | |
| Raffles Lighthouse | Drift | Y | 15.7.79 | UM (WYC 545) |
| Punggol Beach | Drift | Y | 26.5.93 | UM (PSM 1290) |
| Pulau Hantu Besar | Intertidal rocks | Y | 27.5.93 | UM (PSM 1291) |
| | | Y | 27.5.93 | UM (PSM 1292) |
| Pulau Biola | Drift | Y | 27.5.93 | UM (PSM 1295) |
| Pulau Malaysia | | | | |
| Cape Rachado, Port Dickson | Intertidal corals | M | 15.4.91 | UM (PSM 1113) |
| | | F | 16.5.91 | UM (PSM 1140) |
| | | M | 23.6.93 | UM (PSM 1324) |
| Telok Kemang, Port Dickson | Intertidal corals | Y | 4.7.93 | UM (PSM 1327) |
| Pulau Kukup, Johor | Drift | Y | 23.5.93 | UM (PSM 1266) |
| | | M | 26.6.94 | UM (PSM 1340) |
| | | F | 26.6.94 | UM (PSM 1341) |
| Pulau Besar, Melaka | Drift | M | 5.8.94 | UM (PSM 1359) |
| | | Y | 5.8.94 | UM (PSM 1360) |
| | | M | 5.8.94 | UM (PSM 1361) |
| | | F | 5.8.94 | UM (PSM 1362) |
| | | F | 5.8.94 | UM (PSM 1363) |
| | | F | 5.8.94 | UM (PSM 1364) |
| Pulau Sibu, Johor | Intertidal rocks | M | 6.3.92 | UM (PSM 1231) |
| Singapore | ? | MF | ? | Grunow 789 (W) |
| | ? | ? | ? | Grunow 795 (W) |
| | ? | ? | October 1861 | Grunow 796 (W) |
| | ? | ? | ? | Grunow 798 (W) |
| | ? | ? | ? | Grunow 799 (W) |
| | ? | ? | ? | Grunow 802 (W) |
| China Sea | ? | ? | ? | Grunow 800 (W) |
| Philippines, Palawan Island | | F | 25.1.84 | UM (Noro) |

Note—Y = young, sterile, M = male, F = female. WYC = collection of Wee Yeow Chin, PSM = collection of Phang Siew Moi. UM = Herbarium at the Institute of Advanced Studies, University of Malaya, Kuala Lumpur, Malaysia; W = Natural History Museum, Vienna, Austria.



**Figs. 1–18. Specimens of *Sargassum siliquosum* collected in Malaysia and Singapore. Fig. 1, Discoid holdfast and stem of specimen PSM 1327 shows primary branches arising at the distal end of a 2-cm-long scarred stem. Fig. 2, Specimen PSM 1360 shows an almost alternate arrangement of a secondary branch giving rise to a zig-zag form of the primary branch.**



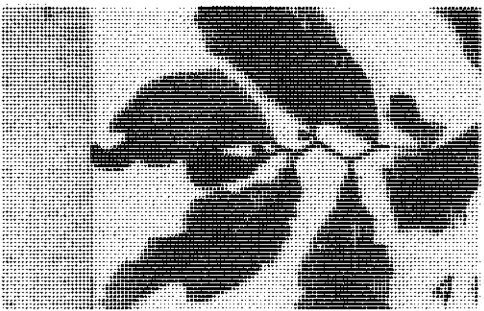


Fig. 3, Specimen WYC 545 shows leaves arranged alternately on secondary branches giving rise to a zig-zag form in the branch. Fig. 4, Leaves of specimen PSM 1292 show typical cuneate base and unequal leaf blades on either side of the midrib.

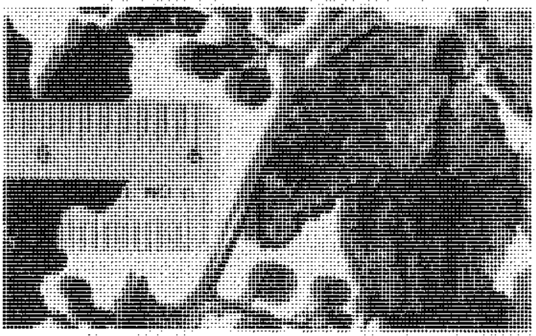


Fig. 5, Specimen PSM 1360 shows single and paired subspherical vesicles, subtended by a leaf.

Fig. 6, Female receptacular branch of specimen PSM 1364 shows subspherical vesicles with flattened stalks and irregular dentations on the vesicle surface.

terete main stems. The main stems are generally scarred by deciduous cauline leaves, with diameters up to 5 mm; primary branches arise from almost at the holdfast to 2 cm (specimen PSM 1327) up the stem (Fig. 1). Cauline leaves were not available. The primary branches generally arise close together, about 1–2 mm apart, in an almost radial arrangement, whether near the distal end of a longer stem or on a short stem; primary branches are terete, more obvious in young plants, and smooth, with diameters up to 2 mm. Secondary branches are terete,

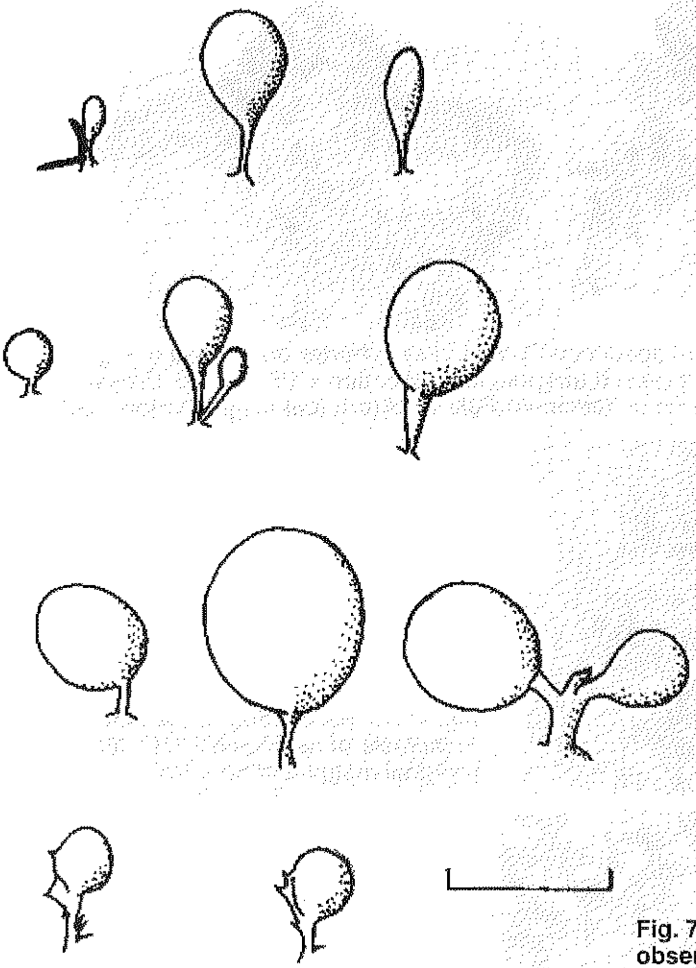


Fig. 7, Variations of vesicles observed in the specimens. Scale bar = 1 cm.

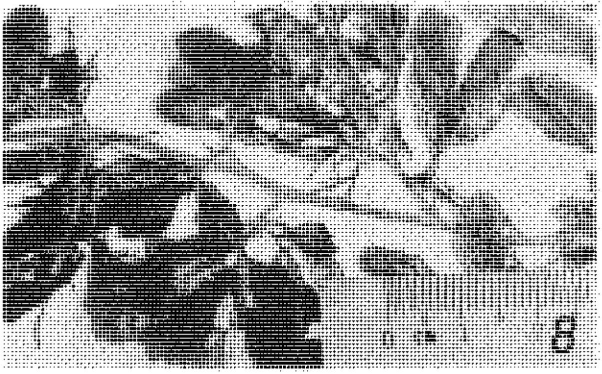
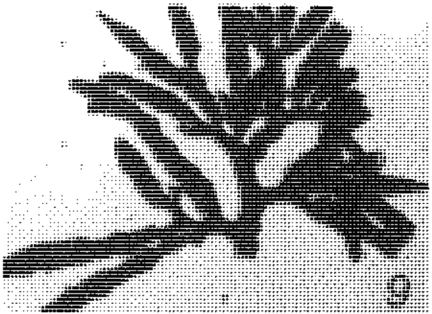


Fig. 8, Male receptacular branch of specimen PSM 1113 shows racemosely arranged, long, terete male receptacles.



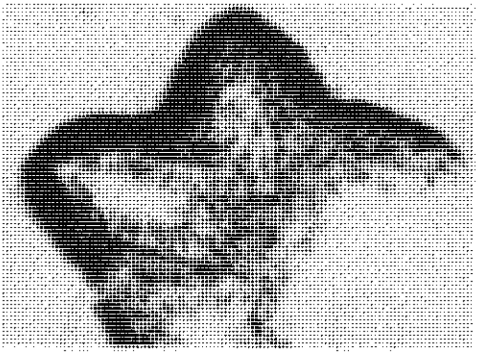


Fig. 9, Female receptacles of specimen PSM 1140 are shorter than those of Fig. 8, branched, and slightly compressed (original magnification × 10). Fig. 10, Cross-section of the male receptacle of specimen PSM 1324 (original magnification × 50).

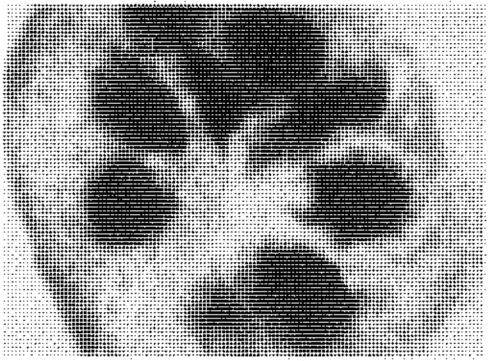
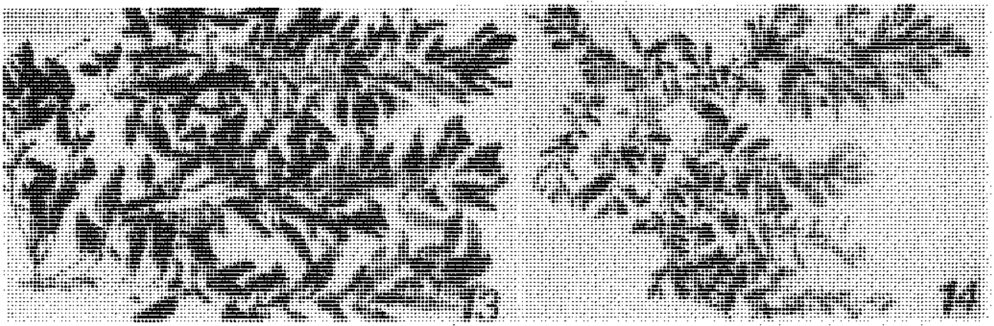


Fig. 11, Cross-section of the female receptacle of specimen PSM 1362 (original magnification × 50).

Fig. 12, Specimen from Palawan, Cebu Island, Philippines, shows atypical long, terete female receptacles.

smooth, and arranged almost alternately on the primary branches, at times resulting in a zig-zag form in the primary branches (Figs. 2 and 3; specimens WYC 545 and PSM 1113, 1140, 1231, 1266, 1290, 1292, 1324, 1327, and 1360); the diameter of the secondary branches is up to 0.5 mm. Leaves are lanceolate, narrowed, almost cuneate at the base, broadening toward the middle, and narrowing toward a generally rounded blunt tip; midrib is distinct but disappearing near the tip; leaf edge is irregularly dentate. Cryptostomata are randomly distributed



Figs. 13 and 14, Specimens PSM 1324 and PSM 1231 shows typical forms of *S. siliquosum.*

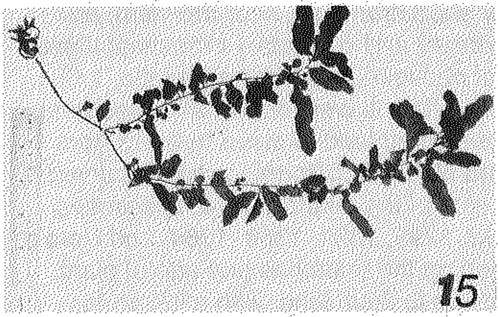
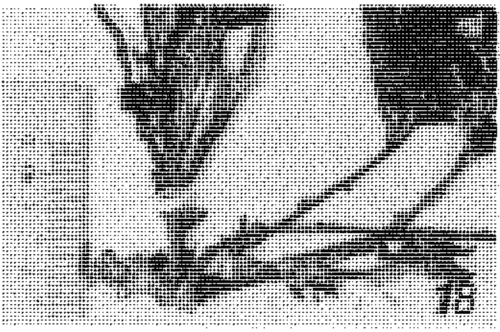


Fig. 15, A young plant belonging to specimen PSM 1295 shows large leaves and vesicles.

Fig. 16, Specimen PSM 1113 shows larger broader leaves on young sterile branches and narrower leaves on the branch bearing male receptacles.

Fig. 17, Fertile branches of specimen PSM 1364 bear narrow lanceolate leaves together with female receptacles.



18. Holdfast of specimen PSM 1324 is multistiped, suggesting that the intertidal Malaysian species may also be an annual.

over the leaf surface. In specimen PSM 1140, found growing near the edge of an intertidal coral reef, the leaves on the lower short branches, near the stem, are much broader than leaves farther up the primary and secondary branches; these lower leaves are larger and broader, almost obovoid (length-to-width ratio, 1.6) compared with more linear (2.7) upper leaves. The leaves, especially those near the distal ends of primary and secondary branches, tend to curve outward from the point of insertion and then inward toward the branch, forming slightly curved leaves with asymmetrical blades on either side of the midrib (Fig. 4; specimens WYC 545 and PSM 1140, 1231, 1266, 1292, 1295, 1324, 1360, 1364, and Noro's specimen). Sizes of leaves vary with position on the branches and age of plant. Young and sterile plants have larger leaves, up to 8 cm long, with a length-to-width ratio of 2.7; leaves of female plants are up to 7 cm long, with a length-to-width ratio of 3.1; and leaves of male plants are up to 5 cm long, with length-to-width ratio of 3.2. Vesicles are solitary or paired (Figs. 5 and 7), usually subtended by a leaf, obovoid to subspherical, with stalks as long as the vesicles supporting an often narrowed base of the vesicle, which broadens to a rounded top; smaller vesicles tend to be more elliptical; larger vesicles are almost spherical. In two specimens (PSM 1363 and PSM 1364) obovate vesicles (Fig. 6) with slightly thickened stalks and dentations on the vesicle surface are present on fertile branches bearing female receptacles. Vesicles (largest on individual specimens) on young sterile plants are generally larger (0.5–1.0 cm in diameter) than those on female plants (0.3–0.6 cm in diameter) and male plants (0.2–0.7 cm in diameter).

Plants are dioecious. Receptacles are generally racemosely arranged on the much branched receptacular branches, which may be up to 3 cm long. The receptacular branches may or may not be subtended on the leaf bearing solitary or paired vesicles. Male receptacles (Figs. 8 and 10) are generally long, up to 1 cm, terete with straight to wavy outlines, sometimes slightly flattened and, in one specimen (PSM 1359), bifurcate. Female receptacular branches are much branched, ranging from short (1.0 cm) to longer (2.7 cm), with slightly compressed receptacles ending in pointed tips and with wavy to serrated outlines (Figs. 9 and 11). Most of the female receptacles are short except for Noro's specimen from the Philippines on which female receptacles resemble male receptacles (Fig. 12).

Habitat: Common in intertidal coral reefs and rocky shores. Although found throughout the year in most habitats, the biomass peaked around February to March and July to August, after the monsoons in the Cape Rachado coral reefs, Port Dickson, Negeri Sembilan, Malaysia (Phang 1989).

Distribution: Singapore (type locality), Malaysia, Vietnam, China, Japan, Philippines, and Indonesia.

## Discussion

Table 2 compares the important characteristics used in the various descriptions of *S. siliquosum.* These characteristics are common to those found amongst the Malaysian and Singaporean specimens examined for this paper and can be taken as representative of the species.

The closest species related to *S. siliquosum,* as described by Yoshida (1988), appears to be *S. assimile,* which can be separated on the basis of the much furcated female receptacle and sparingly dentate leaf margin of *S. assimile.* In Tseng and Lu's (1992) studies on the Chinese *Racemosae,* the distinguising characteristics of their specimens identified as *S. siliquosum* were the "lanceolate leaves"... with strongly asymmetrical oblique bases and obtuse apices" and smooth, terete, racemose male receptacles. As pointed out by Tseng and Lu, the specimen of Chou and Chiang (1981), which has elliptical, duplicated leaves, may not be *S. siliquosum.* Duplicated leaves have not been reported, and we did not observe any in the Malaysian and Singaporean specimens. The specimen described by Trono (1992) as *S. siliquosum* is female and is characterised by "female receptacular branch compressed, triquetrous and twisted when mature, with serrate or dentate margin." Grunow (1916) described a semiclavate female receptacle, and among the Malaysian and Singaporean specimens, some are slightly compressed with wavy outlines, approaching the "triquetrous twisted" nature. The specimen from Palawan Island, Philippines (supplied by Noro), has long terete racemose receptacles that dissection showed contain oogonia. This is the only female specimen with relatively long receptacles. Although all previous descriptions of the male receptacle report it as long and terete, one Malaysian specimen has a few bifurcated male receptacles.

Examination of the 27 herbarium specimens showed that the nature of the holdfast, stem, branches, the shape of the leaves and vesicles, and overall form and branching (Figs. 13 and 14) are relatively constant regardless of habitat (although most specimens were from intertidal coral reefs and rocky areas, many were drift specimens and their habitat unknown), age of plant, and time of year of collection. However, the most variable characteristic is the size of the leaves, which are generally longer and larger on young sterile plants (Fig. 15) and smaller and narrower on fertile plants (Figs. 16 and 17). Vesicles are also generally larger on young sterile plants. In three specimens, the vesicles on the female

## Table 2. Comparison of Important Characterisitics from Selected Descriptions of *Sargassum siliquosum*

| | Reference | | | | | |
|---|---|---|---|---|---|---|
| **Characteristic** | **Agardh 1889** | **Grunow 1916** | **Yoshida 1988** | **Tseng and Lu 1992** | **Trono 1992** | **Specimens Examined for this Chapter** |
| Holdfast | | | | | | |
| Plate/disc/shield | – | – | + | + | + | + |
| Stem | | | | | | |
| Terete | + | + | + | + | + | + |
| Smooth | – | – | + | + | – | – |
| Warty | + | – | – | – | + | + |
| Branches | | | | | | |
| Terete | + | + | – | + | + | + |
| Slightly compressed | – | – | + | – | + | – |
| Smooth | + | + | + | + | + | + |
| Leaves | | | | | | |
| Lanceolate/elliptical/obovate | + | + | + | + | + | + |
| Dentate margin | + | + | + | + | + | + |
| Midrib disappears near apex | – | + | + | + | + | + |
| Asymmetrical | + | + | + | + | + | + |
| Cryptostomata scattered | + | + | + | + | + | + |
| Vesicles | | | | | | |
| Obovoid to subspherical | + | + | + | + | + | + |
| Stalked | + | + | + | + | + | + |
| Solitary/paired | + | + | + | + | + | + |
| Dioecious receptacles | + | + | + | + | + | + |
| Racemose | + | + | + | + | + | + |
| Subtended by vesicle and leaf | + | + | + | + | + | + |
| Male receptacles | | | | | | |
| Long, terete | + | + | + | + | + | + |
| Female receptacles | | | | | | |
| Shorter, stouter, terete | + | – | – | – | – | + |
| Flat/semiclavate | – | + | – | – | + | |
| Triquetrous/twisted | – | – | – | – | + | + |
| Serrate/wavy margin | – | – | – | – | + | + |

receptacular branch have slightly thickened petioles and infrequent dentations on the surface of the vesicles.

"Multi-stiped holdfasts" were observed in the *S. siliquosum* specimens studied at Cebu, Philippines (Largo et al. 1994), where the subtidal plants were observed to be annuals. In some specimens (PSM 1113 and PSM 1324), the holdfast appears to support two to three main branches arising close together (Fig. 18), indicating that the intertidal species in Malaysia are also annual. Similar studies to determine seasonal variations in the morphology and reproduction in the species found in the intertidal coral reefs could add to the delineation of this species.

## Acknowledgments

We thank Professor Isabella Abbott and the California Sea Grant Program for providing the opportunity to work together on the specimens. The first author thanks Miss Ho Chai Ling for help in collecting some of the specimens and in preparing some of the dissections. The research grant R&D 4/180 provided funds for the collecting trips.

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# STUDIES ON THE GLOMERULATE *SARGASSUM* OF CHINA:
# I. THE SERIES *BINDERIANA*

C. K. Tseng and Lu Baoren

## Abstract

In the *Acanthocarpicae,* two subsections, the *Glomerulatae* and the *Biserrulae,* are recognized. The *Glomerulatae,* or the glomerulate *Sargassum,* are divided into two series: the *Binderiana* and the *Platycarpae.* The series *Binderiana* is again divided into two species groups, the *Swartzia* and the *Binderia,* on the basis of vesicle characteristics. The status of *S. swartzii* as the typical species of the species group is discussed.

## Introduction

The subgenus *Sargassum* was divided by J. Agardh (1889) into three series: *Zygocarpicae, Acanthocarpicae,* and *Malacocarpicae.* The series *Zygocarpicae* was raised to section rank by Setchell (1935) and the *Acanthocarpicae* and *Malacocarpicae* by Abbott et al. (1988).

Agardh divided the *Acanthocarpicae* into two tribes, Glomerulatae and Biserrulae, the former with 16 species and the latter with 20 species. In Grunow's treatment (1915), the same system was followed: in the tribe Glomerulatae, 22 species were recorded, and in the tribe Biserrulae, 59 species. In accordance with the International Code of Botanical Nomenclature (Voss et al. 1983), tribes are not recognized except at the family level. Both tribes Glomerulatae J. Agardh and Biserrulae J. Agardh are therefore assigned subsection status:

*Sargassum* section *Acanthocarpicae* (J. Agardh) Abbott, Tseng et Lu (1988).
  Subsection *Glomerulatae* (J. Agardh) Tseng et Lu, stat. nov.
    Basionym: Tribe Glomerulatae J. Agardh (1889, pp. 37, 85).
    Synonym: Tribe Glomerulatae J. Agardh (sensu Grunow, 1915, p. 381, sensu Setchell, 1936, p. 18).
  Subsection *Biserrulae* (J. Agardh) Tseng et Lu, stat. nov.
    Basionym: Tribe Biserrulae J. Agardh (1889, pp. 37, 91).
    Synonym: Tribe Biserrulae J. Agardh (sensu Grunow, 1915, p. 400; sensu Setchell, 1936, pp. 6, 18).

The subsection *Glomerulatae,* that is, the glomerulate *Sargassum,* consists of a group of *Sargassum* in which the receptacles form cymose or short subracemose glomerules with nondiscrete receptacular branches and spinulous or at least dentate receptacles. Grunow (1915) divided the group into two subtribes: the Binderiana, with distichous, complanate to compressed main branches, and the Platycarpae, with multifarious filiform main branches. In accordance with current practice, we suggest recognition of the two subtribes as series:

Series *Binderiana* (Grunow) Tseng et Lu, stat. nov.
  Basionym: Subtribe *Binderiana* Grunow (1915, p. 381).
Series *Platycarpae* (Grunow) Tseng et Lu, stat. nov.
  Basionym: Subtribe *Platycarpae* Grunow 1915, p. 388.

J. Agardh in 1889 listed the following 7 species that were included in Binderiana by Grunow (1915): *S. swartzii* (Turner) C. Agardh, *S. wightii* Greville, *S. cervicorne* Greville, *S. echinocarpum* J. Agardh, S. *binderi* Sonder ex J. Agardh, *S. ligulatum C.* Agardh, and *S. subalatum* Sonder ex J. Agardh. However, Grunow (1915) recognized only 6 of these 7 species and placed *S. cervicorne* as a variety of *S. binderi.* Grunow (1915) listed 4 species not recognized by J. Agardh: *S. acutifolium* Greville, *S. dumosum* Greville, *S. arnaudianum* Montagne, and *S. oligocystum* Montagne. Thus, 10 species were included by him in the series *Binderiana.*

In the series *Binderiana,* two species groups are recognized: the *Swartzia* group and the *Binderia* group. These two groups differ from each other in the form of their vesicles, which are ellipsoidal to subellipsoidal with generally longer stipes in the first and spherical to subspherical when mature with generally shorter stipes in the second.

The first species listed by both J. Agardh and Grunow in the series *Binderiana* is *S. swartzii,* which is broadly distributed in the Indo-West Pacific region, from Taiwan in the east through Guangdong, Hong Kong, Hainan, Vietnam, and the Indian Ocean to the Persian Gulf. It shows a great variation in morphology. The species was first described as *Fucus swartzii* by Turner (1819) and was transferred to the genus *Sargassum* by C. Agardh (1820). It is the species on which the *Swartzia* species group was founded, and therefore its history and characteristics should be better understood.

When one of us (Tseng) began studying Chinese seaweeds more than 60 years ago, many kinds of *Sargassum* were found near the city of Xiamen (Amoy). Collection of more specimens from the southern China coastal regions of Guangdong, Hainan, and Hong Kong included many more of the genus. A few specimens were sent to Professor W. A. Setchell, the leading scholar of Pacific *Sargassum* taxonomy. Among the returned specimens, quite a few were named "*S. swartzii.*" Thereafter, specimens of *Sargassum* with glomerules of spinulose receptacles were grouped under species related to *S. swartzii.*

A recent analysis of the hundreds of specimens in the group shows that actually many species are included. What is the real *S. swartzii* then? We have not been able to refer to the type specimen, but we have sufficient literature for our reference. According to the original description of *F. swartzii* of Turner (1819), the species has a "flat filiform stem beset with branches similar to itself,...leaves alternate ... furnished with a thin black midrib, rather blunt at the point, and at their margin serrulated with exceedingly minute scattered teeth, at their bases losing themselves in a short petiole; in every branch the lowest leaf considerably exceeds the rest ... and the uppermost not uncommonly quite entire at the margin." The "vesicles [are] elliptical, so pointed as almost to appear apiculate." The "receptacles [are] collected into a sort of racemus." The imperfect specimen was collected by Dr. Olof Swartz, but the location is unknown.

The species was transferred to *Sargassum* by C. Agardh (1820), who described it as "caulo plano, foliis linearibus serratis, vesiculis ellipticis mucronulatis, petiolis planis foliaceis uninervibus suffultis, receptaculis oblongis subracemosis." He added that it was collected "in maris forsan indico." While establishing the tribe Glomerulatae, in his description of *S. swartzii*, J. Agardh (1889) mentioned "receptaculis fere in axilla aggregatis, plurimis, obovato-oblongis, inferne teretiusculis, apice marginatis parce dentatis." Grunow (1915) placed *S. swartzii* as the first species in a group with subellipsoidal vesicles on an elongated stipe in Binderiana of Glomerulatae with distichously arranged complanate stems.

Setchell (1936) In the last installment of his treatise on Hong Kong seaweeds, included a long discussion on S. *swartzii* and enumerated some characteristics: (1) flattened stem; (2) pronouncedly distichous arrangement of leaves and branches; (3) elongated, rather fleshy leaves, flat and costate below, cylindrical and ecostate above; (4) vesicles ellipsoidal and apiculate, with stout, flattened pedicels longer than themselves; and (5) closely grouped receptacular branches in glomerules. Generally speaking, these characterize *S. swartzii* well enough. However, of the last characteristic, he wrote, "the rather closely grouped receptacular branches, shorter or longer, stouter or thinner, ancipitate to cylindrical, toothed or smooth." Apparently he had been bothered by the wide variation in the receptacular branches as well as that in the other parts of the plant. He mentioned 20 species "reasonably suspicioned, not only as closely related but as ultimately to be reduced to a single or at most a very few species." He had not, however, realized that despite the big range of variation, each species must still have a limit to each characteristic, especially the fruiting bodies.

Studying the hundreds of specimens available on hand, we were at first struck by widely varied yet similar characteristics of these *S. swartzii*-related species. However, we managed to arrange them into eight species, among which we have differentiated *S. swartzii* (Turner) C. Agardh from the Grevillean species *S. acutifolium* and *S. wightii.* We have also recovered the species status of *S. cervicorne* Greville. This species had been reduced to a variety of *S. binderi* Sonder by Grunow (1915), but it has ellipsoidal vesicles and vesicles with longer pedicels and also differences in receptacles. We are therefore tempted to recover its species status. Thus, we have found four old species and have added four new species, making a total of eight. These, we think, form a more or less natural species group typified by *S. swartzii.* They are discussed in the next chapter. In one of the undescribed species, namely, *S. primitivum,* the receptacles are cylindrical and cymosely arranged, like those of a typical member of *the Malacocarpicae-Fruticuliferae*, but some of the receptacles have spinulose apices

(Fig. 1); hence the species can be only a member of the *Acanthocarpicae-Glomerulatae*, despite its cylindrical receptacles. It is considered a primitive member of the *Glomerulatae*, evolved from a certain *Malacocarpicae* member.

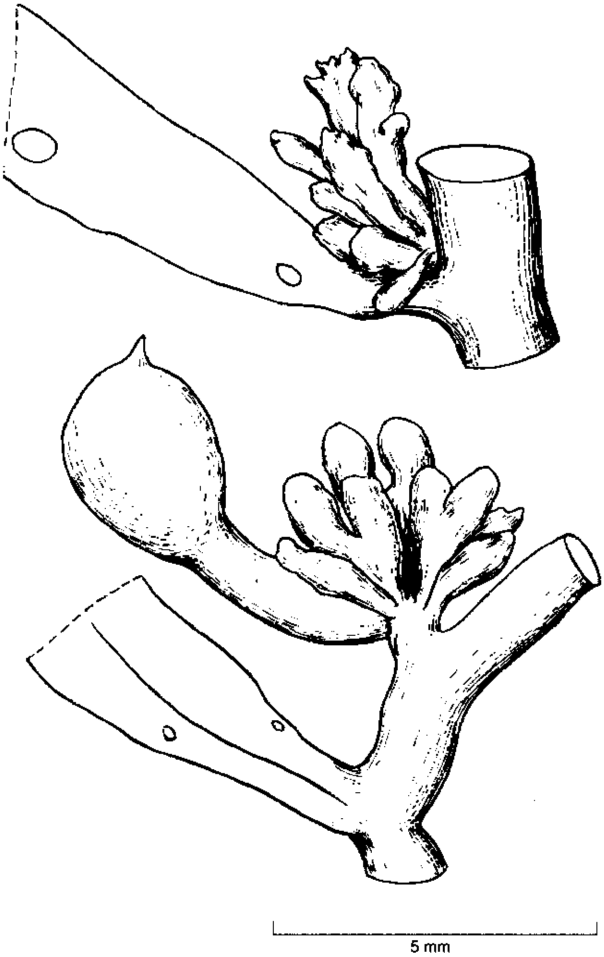

**Fig. 1. Slight apical spinulation in an older (top) and a younger (bottom) receptacle of *Sargassum primitivum* (AST 92–0296).**

The most important characteristic in the delineation of the species of *Sargassum,* we think, must be that of the receptacles. The subsection *Glomerulatae*, as a group of *Sargassum,* has most probably evolved from malacocarpic forms through dentation and spinulation on the apices in the simpler species, such as *S. swartzii.* Then gradually the receptacular spinules spread down to the sides of the receptacles, such as seen in *S. hainanensis.* In *S. swartzii,* for instance, the receptacles are cymosely or subracemosely arranged, somewhat flattened, furcate, slightly spinulose at the apices, and dioecious (Figs. 2 and 3). The second important characteristic is the shape and size of the vesicles and the form and length of the pedicel; the vesicles vary greatly but within limits. For instance, *S. swartzii* has ellipsoidal vesicles that may occasionally be somewhat oval, but never spherical (Fig. 4). The third important characteristic is the flattened main branch with distichous branchlets. The fourth important characteristic is the shape and costation of the leaves: broader and thinner, lanceolate with percurrent midrib and scattered cryptostomata below and ecostate elongated narrow cylindrical with a series of cryptostomata on both sides in the upper ones (Fig. 5). In specimens of some of the species (e.g., *S. swartzii*), after being dried and later soaked in water, certain parts become soft and tend to drop off, thus damaging the appearance of the specimens.

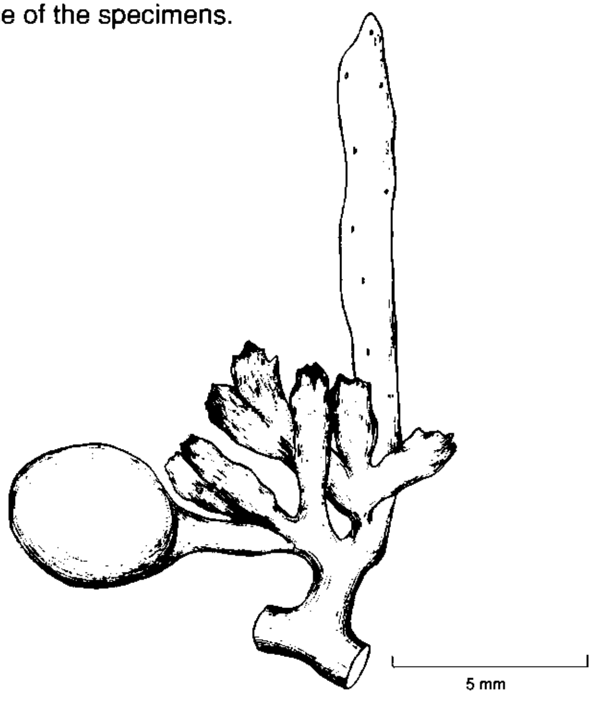

**Fig. 2. Apical spinulations in a receptacle of *Sargassum swartzii* from Hong Kong (Taam 106).**

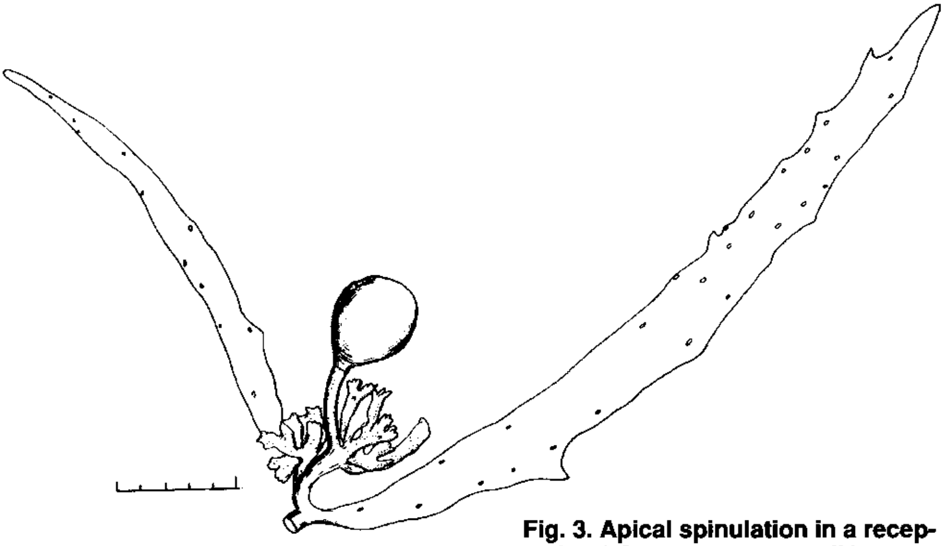

Fig. 3. Apical spinulation in a receptacle of *Sargassum swartzii* from Hainan (Tseng 757).

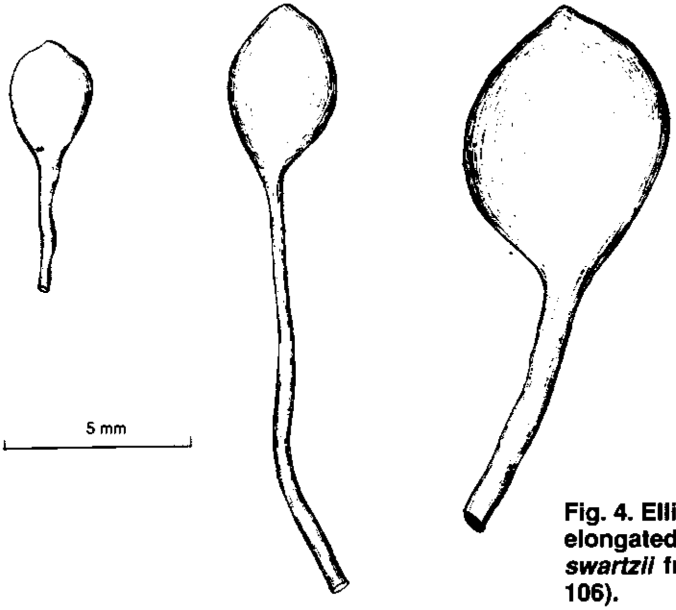

Fig. 4. Ellipsoidal vesicles with elongated stipes of *Sargassum swartzii* from Hong Kong (Taam 106).

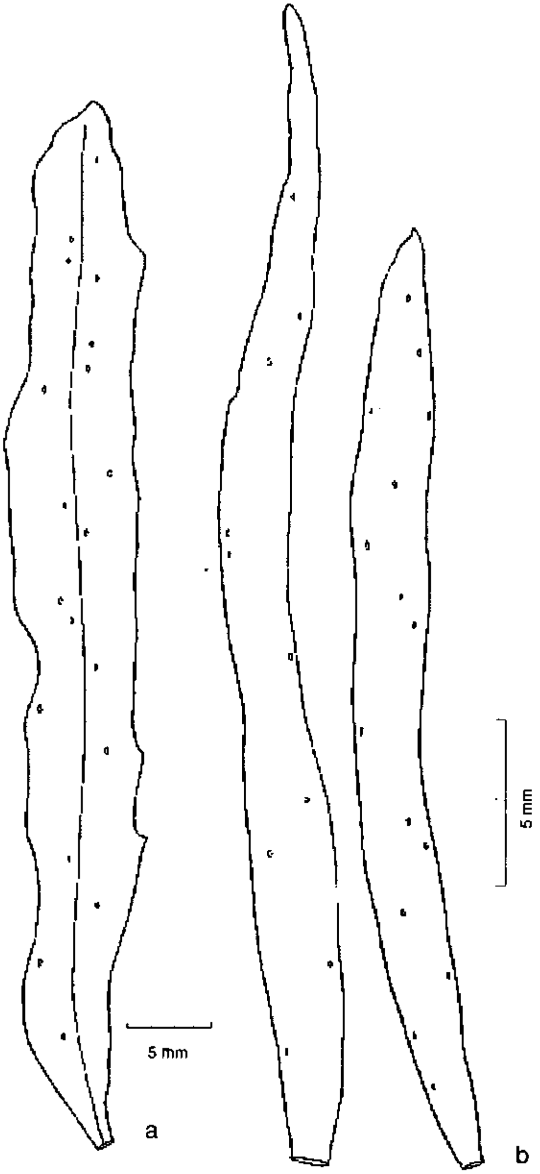

Fig. 5. Leaves of *Sargassum swartzii* from Hong Kong (Taam 106). a, A lower leaf. b, Two leaves near the apex.

Therefore, the *Swartzia* species group of the *Binderiana* series can be characterized by the following: (1) flattened main branches; (2) pronouncedly distichous arrangement of leaves and branches; (3) generally two kinds of leaves: a few broader, lanceolate, and costate near the base of the plant; the majority narrower to linear, elongated, and mostly ecostate; (4) vesicles ellipsoidal and generally apiculate, with generally stout, flattened pedicels longer than themselves; and (5) closely grouped flattened and dentate to spinulose receptacular branches in glomerules.

## Acknowledgments

The paper is contribution No. 2275 from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. We thank Dr. Isabella Abbott for reading and editing our manuscript. Thanks are also due Mr. Leng Zengfu for inking our drawings.

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# STUDIES ON THE GLOMERULATE *SARGASSUM* OF CHINA: II. THE SPECIES GROUP *SWARTZIA*

C. K. Tseng and Lu Baoren

## Abstract

The Chinese species of the species group *Swartzia* of the series *Binderiana* of the subsection *Glomerulatae* of the section *Acanthocarpicae Sargassum* were studied. This group now consists of 10 species: the Hawaiian *S. echinocarpum* J. Agardh, the Indian *S. dumosum* Greville, and the 8 Chinese species: *S. primitivum* Tseng et Lu, *S. swartzii* (Turner) C. Agardh, *S. wightii* Greville, *S. acutifolium* Greville, *S. hainanense* Tseng et Lu, *S. cervicorne* Greville, *S. wenchangense* Tseng et Lu, and *S. pusillum* Tseng et Lu. This species group is characterized by (1) flattened main branches; (2) markedly distichous arrangement of leaves and branches; (3) generally two kinds of leaves: a few broader, lanceolate, and costate in the lower part of the plant and most narrower to linear, elongated, and mostly ecostate; (4) ellipsoidal and generally apiculate vesicles with generally stout, flattened pedicels that are longer than the vesicles; and (5) closely grouped, generally flattened, and dentate to spinulose receptacular branches in glomerules.

## Introduction

As mentioned in the preceding chapter, the series *Binderiana* is divided into two subseries: the *Swartzia* and the *Binderia*. The *Swartzia* group now consists of 10 species, 8 of these from China. The two species not yet found in China are *S. dumosum* Greville and *S. echinocarpum* J. Agardh. The Hawaiian species *S. echinocarpum* J. Agardh was also reported from Taiwan by Yamada (1950), who referred some sterile Taiwanese specimens to this species. Until we observe specimens with receptacles, we cannot support the report by Yamada. The *Swartzia* group is characterized by subellipsoidal to oval vesicles, stipes longer than they are in diameter, flat or flattened main branches, and spinulose or dentate receptacles in glomerules. Generally, two kinds of leaves are observed. Those growing near the axis are generally broader and have distinct midribs; those at the tip are linear and lack midribs.

Receptacles are generally flattened or compressed. They may have spinules at the tips only or at the tips and extending laterally to the sides. We think that the *Swartzia* group evolved from the *Fruticuliferae* of the section *Malacocarpicae* through such plants as *S. primitivum*.

### Key to the Chinese species of the *Swartzia* Species Group

1. Receptacles cylindrical with few apical spinules ........................................ *S. primitivum*
1. Receptacles flattened or compressed, with apical and lateral spinules ........................ 2
  2. Receptacles with spinules at the apices, sometimes extending to the upper lateral parts ........................ 3
  2. Receptacles with apical and lateral spinules ........................ 4
3. With two kinds of leaves; upper leaves linear, cylindrical, ecostate, entire on the margins ........................ *S. swartzii*
3. With only one kind of leaf; thin and lanceolate. ........................ *S. wightii*
  4. Upper parts of receptacles when mature dilated and fanlike ........................ 5
  4. Upper parts of receptacles not so ........................ 7
5. Pedicels of vesicles cylindrical ........................ *S. wenchangense*
5. Pedicels of vesicles flat, leaflike ........................ 6
  6. Plants small, up only 11 cm tall, upper leaves irregular, oblanceolate ....... *S. pusillum*
  6. Plants large, up to 60 cm tall, leaves lanceolate ........................ *S. cervicorne*
7. Leaves acute at apices ........................ *S. acutifolium*
7. Leaves generally obtuse at apices ........................ *S. hainanense*

### Description of the species

*Sargassum primitivum* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press).
(Figs. 1, 9)

Frond dark brown, about 40 cm high. Primary branches flattened, smooth, about 40 cm long, 3 mm wide, giving rise to distichous secondary branches from both sides of the primary branches. Secondary branches flattened, 20–28 cm long, 2 mm wide, smooth at the surface, beset with many branchlets from both sides of the secondary branches. Branchlets subcylindrical, usually 10–12 cm long, 1 mm wide, with some slightly raised glands at the surface. Leaves on the primary branches lanceolate, usually 4.0–4.5 cm long, 10–12 mm wide, with some irregular large teeth at the margins, generally sharp or obtuse at the apex and oblique, asymmetrical at the base. Leaves on the secondary branches lanceolate, 4.5–5.0 cm long, 3–5 mm wide, with serrate margins and cuneate or slightly oblique at the base. Midrib on the primary and secondary leaves present on the upper thirds of the leaves. Cryptostomata not prominently raised, irregularly scattered on both sides of midribs. Vesicles ellipsoidal, usually 7–8 mm long 4–5 mm wide, the largest one up to 11 mm long, 6 mm wide with sharp apices; pedicels flattened, leaflike, and up to 16 mm long, 2 mm wide.

Plant androgynous. Receptacles cylindrical with a few spinules or teeth limited to the apices, usually forked once or twice, 4 mm long, 1.0–1.5 mm in diameter, several forming close cymosely-arranged glomerules.

Chinese Distribution: Growing on lower intertidal to subtidal rocks. Hainan Province: Wenchang in April (AST 92-0296).

Remarks: *Sargassum primitivum* is regarded as a primitive member of the *Swartzia* group. It is related to *S. swartzii* on the one hand and to *S. virgatum* of

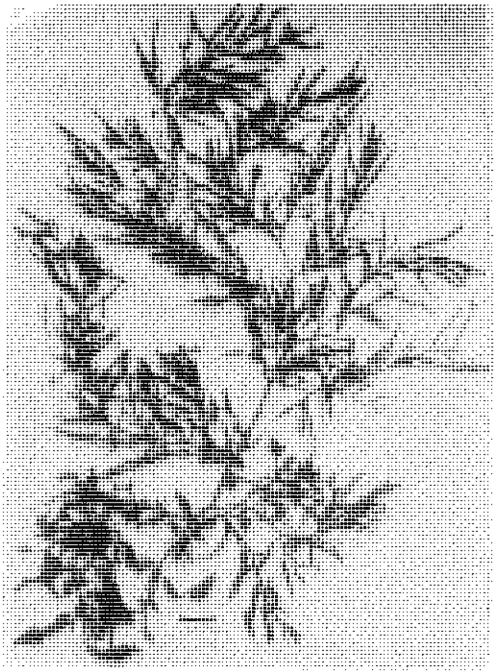


Fig. 1. *Sargassum primitivum* Tseng et Lu (AST 92-0296).

Fig. 2. *Sargassum swartzii* (Turner) C. Agardh (Taam 105).

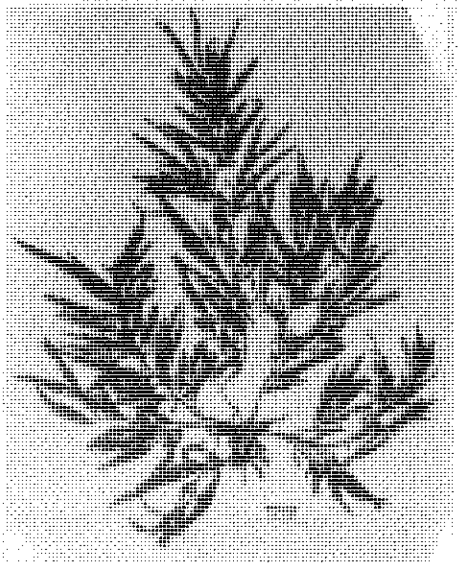


Fig. 3. *Sargassum wightii* Greville (AST 60-8097).

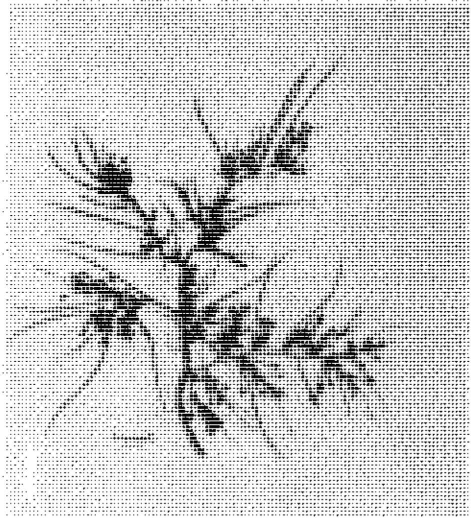


Fig. 4. *Sargassum acutifolium* Greville (AST 80-2034).

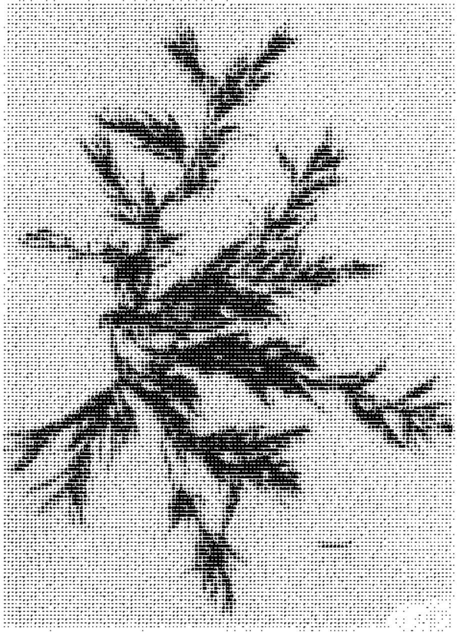


Fig. 5 *Sargassum hainanense* Tseng et Lu (AST 55-0714).

Fig. 6. *Sargassum cervicorne* Greville (AST 86-0952).

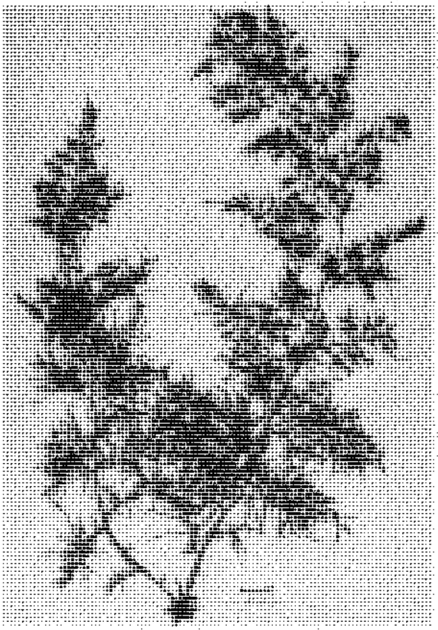


Fig. 7. *Sargassum wenchangense* Tseng et Lu (AST 58-6059).

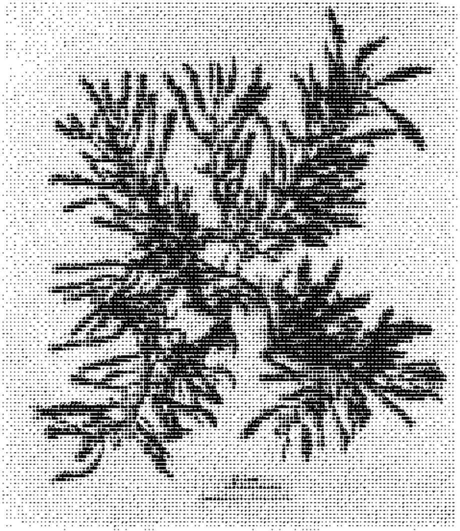


Fig. 8. *Sargassum pusillum* Tseng et Lu (AST 55-2113A).

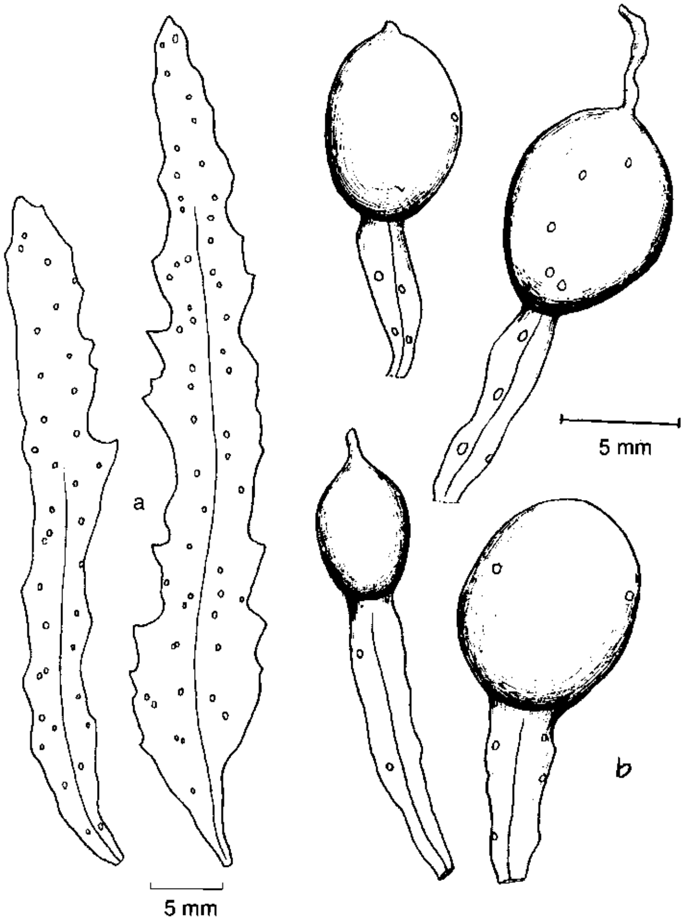


**Fig. 9 *Sargassum primitivum* Tseng et Lu. a, Leaves. b, Vesicles.**

*Fruticuliferae* on the other. Unlike *S. swartzii*, it has cylindrical receptacles and leaves with some sharp teeth, and unlike *S. virgatum*, it has toothed receptacles and broader toothed leaves. The specimen of *S.virgatum* we examined had receptacles with bifid apices, compressed stems, and ellipsoidal vesicles with elongated pedicels. We would not be surprised if examination of the type specimen showed some toothed receptacles, which would bring it to the *Swartzia* group.

*Sargassum swartzii* (Turner) C. Agardh, Species algarum 1:11, 1820.
(Figs. 2, 10)
Basionym: *Fucus swartzii* Turner, Fuci vol. 4, p. 120, pl. 248, 1819.

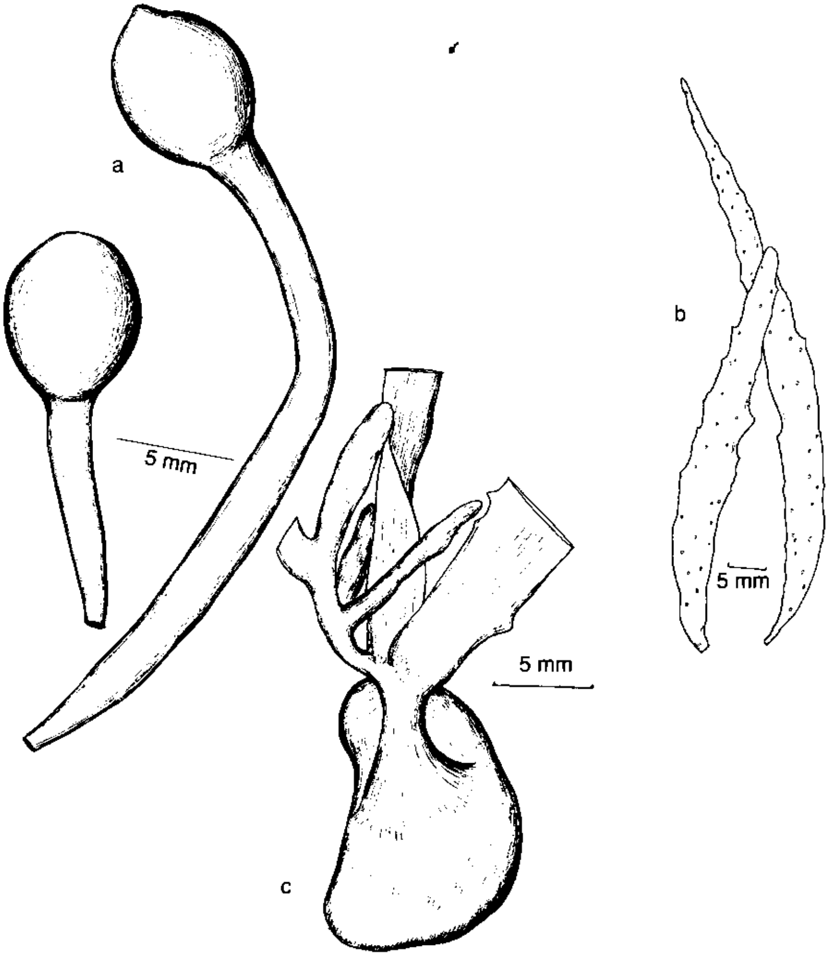


**Fig. 10.** ***Sargassum swartzii*** **(Turner) C. Agardh. a, Vesicles. b, Upper leaves. c, Holdfast.**

Fronds dark brown, reaching a height of 80 cm or more. Main axes arising from discoid holdfast, very short, about 10 mm long, 1–2 mm in diameter, cylindrical, giving rise to several primary branches from their upper portions. Primary branches flattened, broader below, narrower above, 50–80 cm or more long, 4 mm wide. Secondary branches distichous from both sides of the primary branches, flattened, short, glandular, alternate, at intervals of 3–4 cm. Leaves on primary branches thick and broad, lanceolate, 6–9 cm long, 5–7 mm wide, with percurrent midrib, a few shallow teeth at the margins, and cryptostomata scattered on both sides of the midrib. Leaves on secondary branches linear-lanceolate, 3–5 cm long, 2–3 mm wide, usually with percurrent midrib. Upper leaves cylindrical ecostate, entire at the margins, with cryptostomata forming two rows on both sides of midrib. Vesicles 7 mm long, 5 mm wide, with round apex, varying in well-developed plants from large below to small or even minute above, usually subellipsoidal to ellipsoidal, with long pedicels, young vesicles with sharp points, 2 mm long or more, 1 mm wide; both vesicles and pedicels with a few cryptostomata.

Plant androgynous. Receptacles compressed, furcate, 3–4 mm long, 0.8–1.0 mm wide, with small spines at the apices, very short, closely packed, in cymosely to subracemosely arranged glomerules.

Chinese Distribution: Hong Kong; washed ashore in February (McClure 70, 75a); on intertidal rocks in May (Tseng 2809, Taam 106). Guangdong Province: Naozhou in May (AST 73-0589, 73-0628). Hainan Province: Wenchung in March (Tseng 707) and April (Tseng 757, AST 92-0101) and Sanya in March (AST 92-0235).

Other Distribution: Widely distributed in the Indo-West Pacific region.

Remarks: This species is characterized by (1) flattened, distichous primary branches; (2) two kinds of leaves, those on the primary and secondary branches lanceolate, costate, and cryptostomatic and those near the apex narrowly cylindrical, ecostate, and cryptostomatic; (3) variations in vesicles in well-developed plants, from large below to small or even to minute above, subellipsoidal with long pedicels, both vesicles and pedicels with a few cryptostomata; (4) glomerulate receptacles, with very short spinules or teeth at the apices, cymosely or subracemosely arranged; and (5) softening and dropping off of some parts when dried specimens are soaked in water, thus damaging the appearance of the specimen.

*S. swartzii* has been studied by C. Agardh (1820, p. 11), J. Agardh (1848, p. 328; 1889, p. 85), Grunow (1916, p. 381), Setchell (1931, p. 250; 1936, p. 3, pl. 1), and Yoshida (1988, p. 19, fig. 18).

*Sargassum wightii* Greville, Algae orientales, p. 95, pl. 10, 1848.
(Figs. 3, 11)

Fronds yellow-brown, about 30 cm high. Main axes arising from a small conical to discoid holdfast, very short, terete, about 5 mm long, 3 mm in diameter, giving rise to several primary branches from the upper portions. Primary branches distinctly flattened or compressed, 25–27 cm long, 2–3 mm wide. Secondary branches usually compressed, distichous from both sides of primary branches, narrow, short, 10–12 cm long, 2 mm wide, alternate, at intervals of 1–2 cm. Fruiting branchlets short, terete, glandular, usually 1–2 cm long, 1.0–1.5 mm wide, beset with leaves, vesicles and receptacles. Leaves on primary branches similar to the upper leaves of secondary branches in size and appearance, membranous, thin, yellow-brown, lanceolate, acute at apices, 5–7 cm long, sometimes up to 9 cm long, 6–10 mm wide, entire or irregularly shallowly denticulate at the

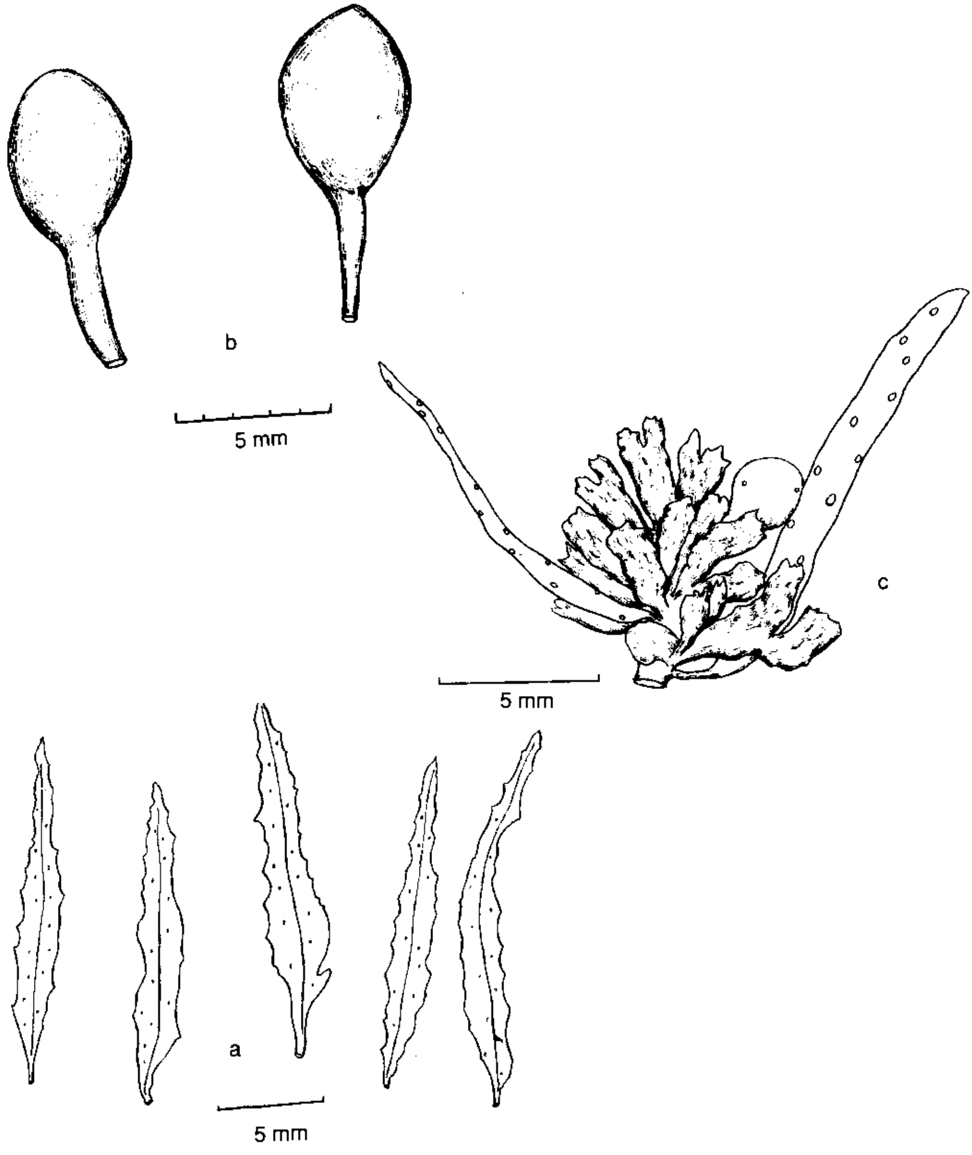


**Fig. 11.** ***Sargassum wightii*** **Greville. a, Leaves, b, Vesicles, c, Receptacles.**

margins, with percurrent midrib and inconspicuous cryptostomata scattered on both sides of midrib. Vesicles subellipsoidal, about 12 mm long, 7 mm wide, with some crytostomata on the surface, terete pedicels, 8 mm long 1 mm in diameter, mostly rounded on the apices, some apiculate.

Plant androgynous. Receptacles slightly compressed, particularly the upper portions, lightly flattened, furcate, spinules mainly at the apices, sometimes extending to upper lateral parts, very short, about 2.5 mm long, 0.5 mm wide, cymosely closely arranged in glomerules.

Chinese Distribution: Growing on lower intertidal and subtidal rocks. Guangdong Province: Xuwen in December (AST 621540). Hainan Province: Sanya in March to December (AST 57-6068, 62-2511, 62-2542, 60-7699, 60-7953, 60-7997, 60-8017, 60-8091, 60-8092, 60-8097, 60-8101, 60-8154, 60-8156, 81-0710).

Other Distribution: Peninsula of India and Ceylon.

Remarks: *Sargassum wightii* is an elegant species that resembles *S. swartzii* in its flattened or compressed receptacles with spinules limited mostly to the tips, extending only to the upper parts. It differs prominently by having only one kind of lanceolate leaf with comparatively more teeth. This species is recorded for the first time from China.

*S. wightii* has been studied by J. Agardh (1889, p. 86) and Grunow (1916, p. 328).

*Sargassum acutifolium* Greville, Algae orientales, p. 98, pl. 11, 1849.

(Figs. 4, 12)

Frond dark brown, arising from a small discoid holdfast. Main axes small, cylindrical, up to 5 mm high, 2 mm in diameter. Primary branches flattened, about 50 cm long, 2–3 mm wide. Secondary branches distichous from both sides of the primary branches glandular, alternate, at intervals of 4 cm. Leaves linear, long and narrow, 6–7 cm long, 1.0–1.5 mm wide, entire at the margins, sometimes slightly wavy, acuminate at the apices, percurrent with conspicuous midrib, with uniseriate cryptostomata on both sides of midrib. Vesicles vary in well-developed plants from large below to small above, elliptical to oblong, usually 3–4 mm wide, 4–8 mm long, and apiculate or crowned with leaflets, sometime up to 12 mm long, with flattened, long pedicels, 0.8–1.0 mm wide, 15–21 mm long, with a few cryptostomata.

Plant androgynous. Receptacles small, compressed, usually forked several times, spinulose at the apices and on both sides, cymosely or subracemosely arranged, forming closely packed glomerules.

Chinese Distribution: Drifted ashore. Hainan Province: Sanya in April, June, and December (AST 80-2034, 57-6067, 55-0816) and Beili (Bakloi) in May (Tseng 999).

Other Distribution: Australia.

Remarks: This species is characterized by (1) flattened primary branches; (2) elongated and narrow leaves, entire or wavy at the margins; (3) ellipsoidal to

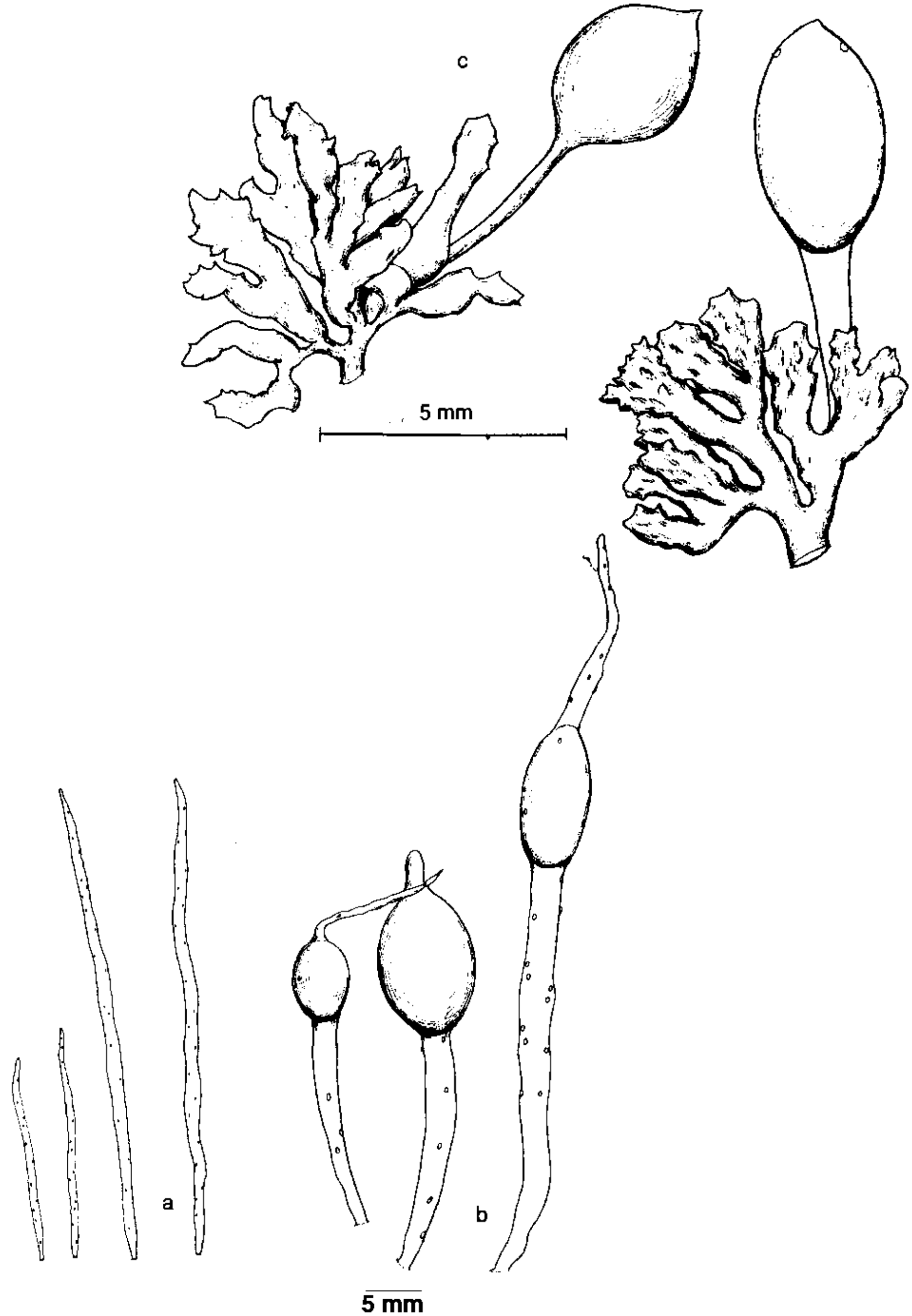


Fig. 12. *Sargassum acutifolium* Greville. a, Leaves, b, Vesicles, c, Receptacles.

oblong vesicles, crowned with long leaflets, and long flattened pedicels, usually three times as long as vesicles; and (4) small, compressed receptacles, forked with spinules at the apices and on both lateral sides, several receptacles forming in glomerules. This species is recorded for the first time from China.

*S. acutifolium* has been studied by (Grunow 1916, p. 381).

*Sargassum hainanense* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press).
(Figs. 5, 13)

Fronds dark brown, about 40 cm tall or more, arising from a discoid holdfast. Main axis short, cylindrical, about 2–3 mm in diameter, 4–5 mm long, giving rise to several primary branches from the upper portions. Primary branches flattened, broad, 3 mm wide, to about 40 cm long, upper parts narrow. Secondary branches flattened, distichous from both sides of primary branches, narrower and beset with many glandular branchlets, 1.5–2.0 mm wide, 9 cm long. Lower leaves lanceolate, 2.5–3.5 cm long, 5–7 mm wide, entire or wavy at the lower part of the leaves and shallowly toothed at the upper part. Upper leaves linear, narrow, 3.5–4.0 cm long,1–2 mm wide, with irregular short teeth on the upper parts only, the lower parts of the leaves entire or wavy, with inconspicuous midrib, vanishing below the apices, and small, prominently raised cryptostomata irregularly scattered on both sides of midrib. Vesicles ellipsoidal, from large below to small above, 2–4 mm wide, 3–7 mm long, with a few raised cryptostomata, apices often apiculate, with pedicels flattened, some leafy with midrib, entire at the margins, generally longer than the vesicle itself, 8–9 mm long and 1–2 mm wide.

Plant androgynous. Receptacles flattened, furcate, about 1.0–1.5 mm wide, 2–3 mm long, with conspicuous spines, mainly at the apex, some at the sides, forming cymose or subracemose glomerules.

Chinese Distribution: Endemic to China (Hainan). Growing on lower intertidal and subtidal rocks. In Hainan Province: Wenchang in March to May (AST 55-0714, 60-4270, 92-0297, 58-5866, 58-5879, 58-5904), Qionghai in July (AST 83-0081), and Sanya (AST 54-4577) in August.

Remarks: This species is closely related to *S. dumosum*. Both have sparingly divided, toothed, compressed receptacles, lanceolate leaves toothed almost exclusively at the upper part, and elliptical vesicles supported by flat elongated foliaceous pedicels. However, unlike *S. dumosum*, *S. hainanense* has elongated linear leaves, usually only 1–2 mm wide, and vesicles with a leaflike stalk without teeth at the margins.

*Sargassum cervicorne* Greville, Algae orientales, p. 96, pl. 10, figs. 1–6, 1849.
(Figs. 6, 14)

Frond yellow-brown, about 60 cm high, arising from a discoid holdfast. Main axes short, cylindrical, about 1 mm in diameter, 5 mm long, giving rise to several divided primary branches at the upper part. Primary branches flattened, about 60 cm long, 4–5 mm wide, giving rise to divided secondary branches from both sides.

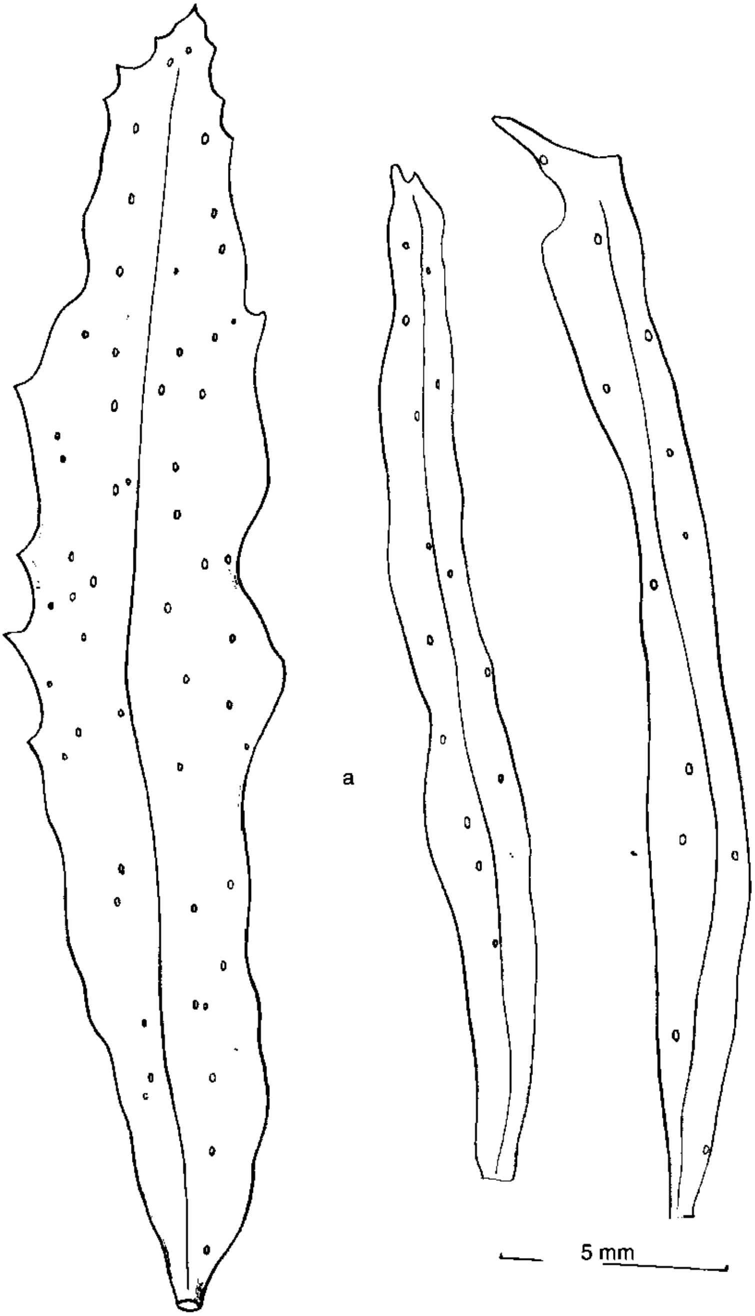
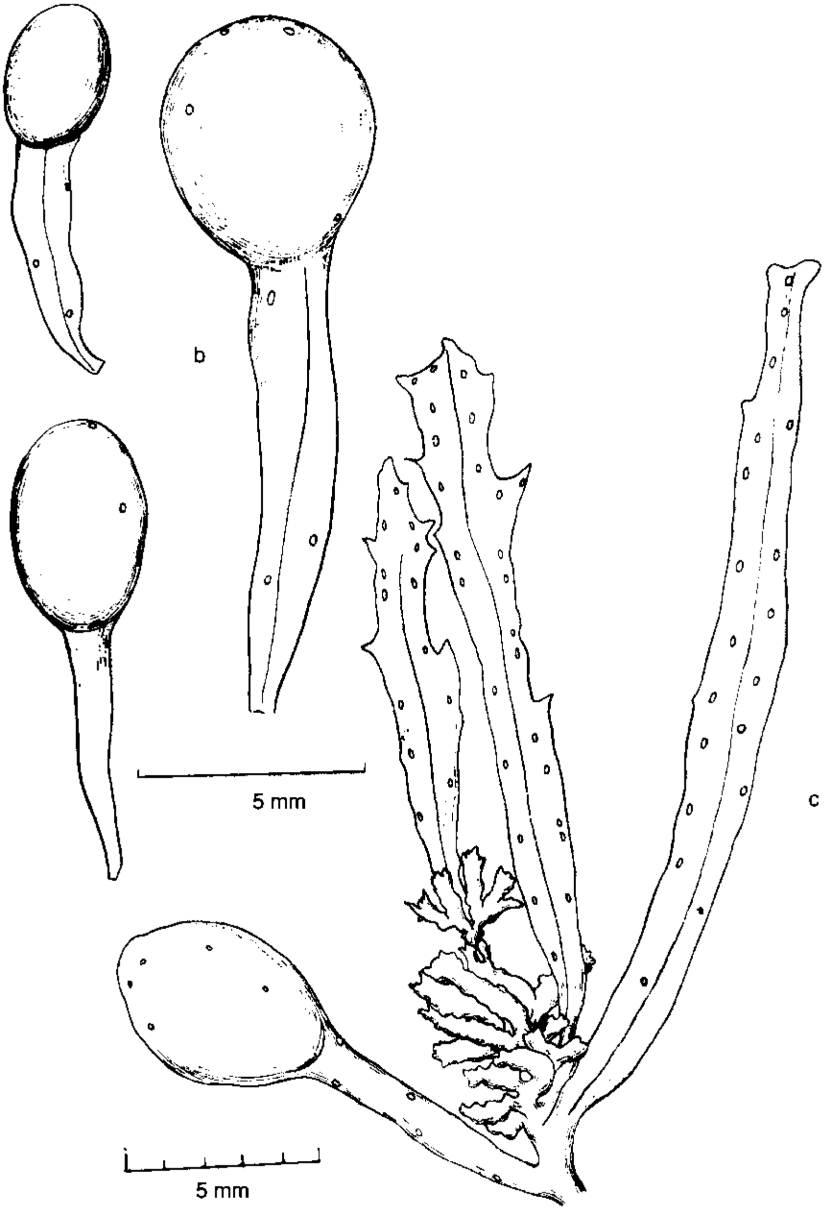


**Fig. 13.** *Sargassum hainanense* **Tseng et Lu. a, Leaves, b, Vesicles, c, Fertile branchlets with receptacles, vesicles, and leaves.**


b
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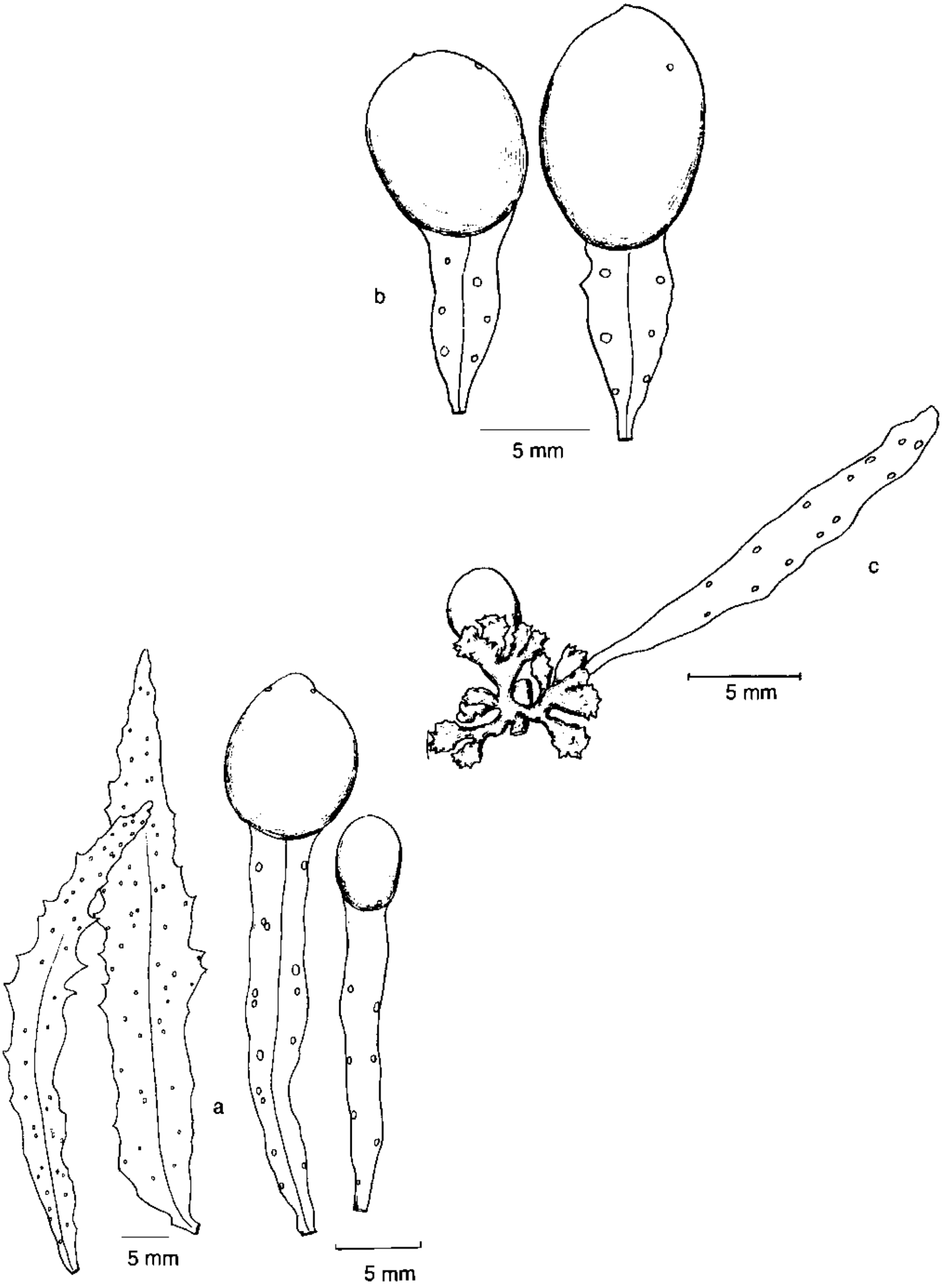

Fig. 14. *Sargassum cervicorne* Greville. a, Leaves, b, Vesicles, c, Receptacles.

Secondary branches flattened, at intervals of 1.5–6.0 cm, 8–22 cm long, 3 mm wide, beset with several short branchlets, glandular, generally 4–5 cm long, 1.0–1.5 mm wide. Leaves on primary branches elongate-lanceolate, 5–7 cm long or more, 12 mm wide, somewhat obtuse at the apices, and margins obscurely uneven-dentate, rarely with some sharp teeth at the margins, with conspicuous percurrent midrib, with scattered cryptostomata on both sides of midrib. Leaves on secondary branches lanceolate, 5–6 cm long, 6–8 mm wide, acute at the apex and somewhat sharply toothed at the margins, with conspicuous midrib, vanishing below the apex, and irregularly scattered cryptostomata on both sides of the midrib. Vesicles ellipsoidal, 10 mm long, 5–6 mm in diameter, often with a small sharp point at the apex, flattened with leaflike pedicels, entire or with one to two sharp teeth at the margins, about 7–8 mm long, 2–3 mm wide, and cryptostomata usually scattered on the surface.

Plant androgynous. Receptacles flattened or compressed, dilated in the upper parts, fanlike, about 2–3 mm long, 0.6–0.8 mm wide, usually forked two or three times, often with a few spines at the apices and sides, several in close cymose or subracemose glomerules.

Chinese Distribution: Growing on subtidal rocks, usually 4–6 m below low tides. Hainan Province: Sanya in April (AST 92-0132, CA 86-0952 [CA = China-America expedition, a cooperative collecting trip between the Chinese Academy of Science and the U.S. Smithsonian Institution]).

Other Distribution: Indian Peninsula.

Remarks: This species is related to *S. dumosum* but *S. cervicorne* has receptacles dilated in the upper parts, and lanceolate, irregularly toothed leaves, somewhat obtuse at the apices and with entire or obscurely uneven-dentate margins. This is the first record of *S. cervicorne* for China. It was reduced to a variety of *S. binderi* in Grunow's monograph (1916) and has been recovered to its species status here.

*Sargassum wenchangense* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press).
(Figs. 7, 15)

Fronds hard, dark brown, reaching a height of 50 cm, arising from a discoid holdfast. Main axes short, cylindrical, about 4–7 mm long, 2–3 mm in diameter, giving rise distally to several primary branches. Primary branches flattened, up to about 50 cm long, 2.0–2.5 mm wide. Secondary branches compressed, narrower and shorter, 9–10 cm long, 1.0–1.5 mm wide, distichous from both sides of primary branches. Fertile branchlets compressed or cylindrical, short, glandular, usually 2–3 cm long, 1 mm in diameter, beset with many leaves, vesicles and receptacles. Basal leaves small and variform, 1–4 cm long, 4–5 mm wide, midrib usually vanishing below the apices of the leaves; some toothed at the margins, obtuse at the apices, and asymmetrical, cuneate at the base, wavy or with a few shallow teeth at the margins; others elongated lanceolate, 2.5–3.0 cm long, 4 mm wide, midrib percurrent. In fruiting branchlets, leaves small, linear, usually 1.5–2.5 cm long, 1–2 mm wide, acuminate at the apices, and asymmetrical, cuneate at

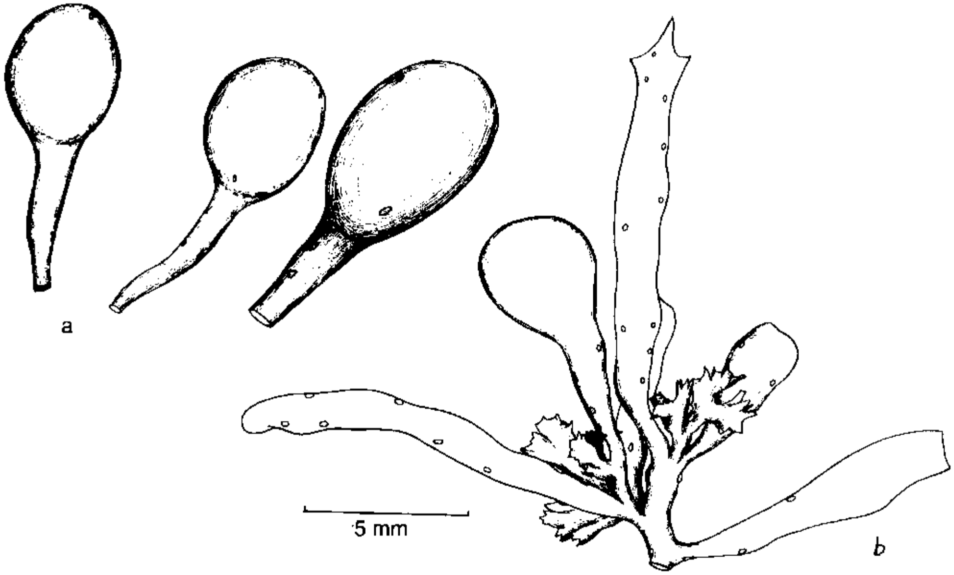

**Fig. 15.** ***Sargassum wenchangense*** **Tseng et Lu. a, Vesicles, b, Fertile branchlets with leaves and receptacles.**

the base, wavy or with a few teeth at the margins, midrib absent, or when present, vanishing below the middle parts or lower third of the leaves; cryptostomata conspicuous, scattered on the surfaces. Vesicles ellipsoidal, small, with a few cryptostomata, usually 3–4 mm long, 2–3 mm in diameter, the largest one 6 mm long, 4 mm wide, rounded at the apices, pedicels cylindrical, longer than vesicles, 5–7 mm long, 1.0–1.5 mm diameter.

Plants dioecious. Female receptacles flattened, dilated above, fanlike, usually forked, with spinules at the apices and the margins, 3–4 mm long, 1.5–2.0 mm wide, fairly closely racemosely arranged in glomerules. Male plants were not found.

Chinese Distribution: Endemic in China (Hainan). Growing on lower intertidal and subtidal rocks. Hainan Province: Wenchang in June to July (AST 58-5962, 58-5969, 58-6022, 57-6781).

Remarks: This species is cartilaginous to extremely firm (unusual for *Sargassum* ) and short. It is related to *S. hainanense* but differs by having short upper leaves, cylindrical vesicular pedicels and receptacles that are dilated in the upper parts, fanlike.

*Sargassum pusillum* Tseng et Lu, Oceanol. Linmol. Sin. 1995 (in press).
(Figs. 8, 16)

Frond short, yellow-brown, up to 11 cm high, arising from a small conical disc, 3 mm in diameter. Main axes cylindrical, 4 mm long, 1 mm in diameter,

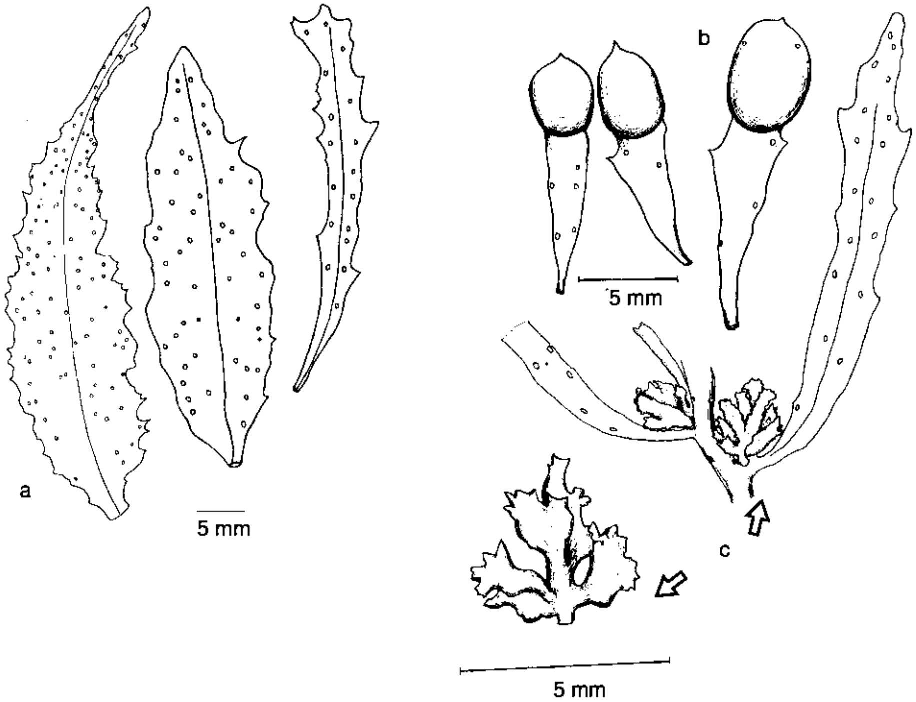

**Fig. 16.** ***Sargassum pusillum*** **Tseng et Lu. a, Different leaves. b, Vesicles. c, Fertile branchlets with leaves.**

giving rise to several primary branches from the upper parts. Primary branches flat, 10 cm long, 1.5–2.0 mm wide, glandular. Secondary branches distichous from both sides of primary branches and beset with several glandular short branchlets at intervals of 5 mm, usually 7 cm long. Leaves of two kinds: primary leaves lanceolate, 3 cm long, 10 mm wide, with percurrent midrib, symmetrical, irregularly serrate margins; secondary leaves oblanceolate, asymmetrical, 2–3 cm long, 2–3 mm wide, acuminate or obtuse at the apices, upper portions of the leaves usually wider than the lower portions, with irregular serrate margins, midrib inconspicuous, usually vanishing below the apices of leaves, cryptostomata scattered on both sides of the midrib. Vesicles subellipsoidal, 5 mm in diameter, with small sharp points at the apices, pedicels flat with some cryptostomata, 12 mm long, 2 mm wide.

Plant androgynous. Receptacles compressed, 3 mm long, 1 mm wide, usually forked, dilated above, with conspicuous spinules at the apices and margins, closely subracemosely arranged in glomerules.

Chinese Distribution: Endemic in China (Guangxi). Growing on lower intertidal rocks. Guangxi Province: Weizhou Island in April (AST 55-1973), and Fangcheng in May (AST 55-2113).

Remarks: This species is characterized by (1) its short frond, which is only about 11 cm high, flattened, and glandular; (2) two kinds of leaves, the primary ones lanceolate and symmetrical with irregular serrate margins and the secondary ones oblanceolate and asymmetrical; (3) subellipsoidal vesicles with flat pedicels; and (4) compressed receptacles, dilated above, fanlike, spinulose at the apices and lateral parts, closely subracemosely arranged in glomerules.

## Acknowledgements

The paper is contribution No. 2276 from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. We thank Dr. Isabella Abbott for reading and editing our manuscript. We also thank Mr. Leng Zengfu for inking our drawings.

## Postscript

We have carefully read the paper by Noro et al. (1994) that reports the results of studies of a large sample of specimens from various countries, and we have reduced the number of species in Binderiana from 10 to 5. We have also studied a large sample of specimens, but from Chinese sources only. We dealt with the systematics of *Sargassum* from an evolutionary point of view. We think that the glomerulate *Sargassum* evolved from the malacocarpic *Sargassum*, the receptacles evolving from cylindrical to flattened and the receptacular spinules from a few to many and from apical to lateral. We have thus arrived at conclusions different from those of Noro and others and have managed to describe four new species. Our perspective may be too narrow, and scholars may judge for themselves.

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# STUDIES ON THE GLOMERULATE *SARGASSUM* OF CHINA:
# III. THE SPECIES GROUP *BINDERIA*

C. K. Tseng and Lu Baoren

## Abstract

The Chinese species of *Sargassum* that belong to the species group *Binderia* of the series *Binderiana* of the subsection *Glomerulatae* of the section *Acanthocarpicae* were studied. The *Binderia* group now consists of nine species: the Australian species *S. ligulatum* C. Agardh and *S. subalatum* Sonder; the Red Sea species *S. arnaudianum* Montagne; and the six Chinese species, namely, *S. intermedium* Tseng et Lu, *S. binderi* Sonder ex J. Agardh, *S. oligocystum* Montagne, *S. qionghaiense* Tseng et Lu, *S. feldmannii* Pham, and *S. erumpens* Tseng et Lu. This species group is characterized by (1) glomerulate receptacular branches with flattened, compressed or terete, and dentate to spinulose receptacles; (2) flattened or compressed primary branches; (3) distichously arranged branches and leaves; and (4) vesicles that are spherical when mature and have pedicels that are generally as long as, or shorter than, the vesicles.

## Introduction

The series *Binderiana* of the glomerulate *Sargassum* is divided into two species groups, *Swartzia* and *Binderia*. The Chinese species of the *Swartzia* group are described in the preceding chapter. The *Binderia* group now consists of nine species, including the six Chinese species described here. The three species not yet found in China are *S. ligulatum* C. Agardh and *S. subalatum* Sonder, both from Australia, and *S. arnaudianum* Montagne, from the Red Sea near Hodeida. The *Binderia* group is characterized by (1) flattened, compressed or terete, dentate to spinulose receptacles closely arranged in glomerules; (2) flattened or compressed primary branches; (3) distichously arranged branches and leaves; and (4) vesicles that are spherical when mature and that have pedicels usually as long as or shorter than the vesicles.

### Key to the Chinese Species of the *Binderia* Species Group

| | |
|---|---|
| 1. Receptacles cylindrical and vesicles with phyllocysts[1] | *S. feldmannii* |
| 1. Receptacles flattened or compressed, without phyllocysts | 2 |
|     2. Leaves linear | *S. intermedium* |
|     2. Leaves lanceolate or oblong | 3 |
| 3. Leaves lanceolate, acute at the apex | *S. binderi* |
| 3. Leaves broad-lanceolate or oblong, obtuse or round at the apex | 4 |
|     4. Branchlets with raised, open glandules | *S. erumpens* |
|     4. Branchlets smooth, without raised, open glandules | 5 |
| 5. Leaves broad-lanceolate | *S. qionghaiense* |
| 5. Leaves oblong, sometimes lanceolate | *S. oligocystum* |

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[1] Phyllocyts are leaves that have inflated middle portions (see Figs. 12a and 12b).

*Sargassum intermedium* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press). (Figs. 1, 7, 8)

Fronds dark brown, small, about 20–25 cm high, arising from a conical holdfast, usually 1 cm high, 1.5 cm in diameter. Main axes short, cylindrical, 5–6 mm high, 2–3 mm in diameter, giving rise to several primary branches from the upper parts. Primary branches compressed, smooth, usually 20–25 cm long, 3–4 mm wide. Secondary branches alternate and distichous from both sides of primary branches, short and narrow, smooth, subcylindrical, 5–12 cm long, 2 mm in diameter, beset with many branchlets with leaves, vesicles, and receptacles, at intervals of 1.0–1.5 cm. Leaves on primary branches linear, coarsely dentate at the margin, 5–7 cm long, 3–4 mm wide, with midribs, with obscure slightly raised cryptostomata irregularly scattered on both sides of the midrib. Leaves on secondary branches and branchlets similar to those of the primary branches, linear, 4–5 cm long, 1.5–2.0 mm wide, entire or wavy, occasionally dentate at upper margin, acute at apex, oblique at base, midribs absent or obscure. Vesicles elliptical to subspherical when young, spherical when mature, generally 4–6 mm, sometimes to 8 mm in diameter, mucronate or round at the apex, with a few cryptostomata and cylindrical pedicels, usually 8–12 mm long, 0.8–1.0 mm in diameter.

Plants androgynous. Receptacles compressed at upper parts and slightly subcylindrical below, 2.5–3.0 mm long, 0.8–1.0 mm in diameter, spines mainly at the apex, a few on the sides, several receptacles closely subracemosely arranged in glomerules.

Distribution: Endemic in China (Guangdong, Guangxi, and Hainan provinces). Growing on intertidal and subtidal rocks. Guangdong Province: Xuwen in March (AST 55-1490A), Haikang in March (AST 55-1424), and Baoan in May (AST 56-1843). Guangxi Province: Weizhou in April to June (AST 87-1307, 55-1825, 55-1876, 55-0186, 55-1889, 55-1906, 55-1973, 75-0594, 78-0030). Hainan Province: Dongfang, in February (AST 60-4059, 60-4080).

Remarks: *S. intermedium* is characterized by slender and linear leaves that have entire or dentate margins and no midrib or an obscure midrib; vesicles that are elliptical to subspherical when young and spherical when mature; and receptacles that are compressed above and subcylindrical below, with elongated stipes spinulate at the apex, slightly so on the sides. It is related to *S. acutifolium* but differs in having leaves with no midrib or an obscure midrib and vesicles that are spherical when mature. A specimen from Haikang, Guangdong Province (AST 55-1424, was also referred to this species (Fig. 8); it differs from the others in that dried specimens disintegrate in water. This species differs from the others in the *Binderia* group in its usually elongated pedicels of the vesicles.

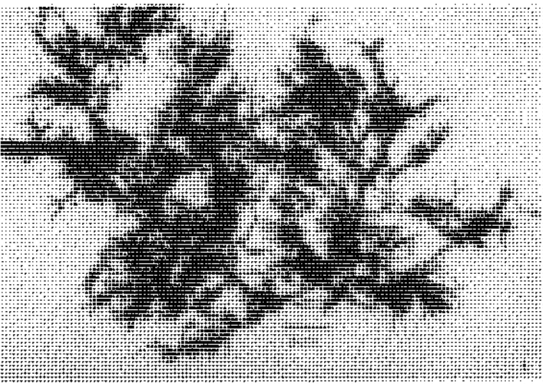
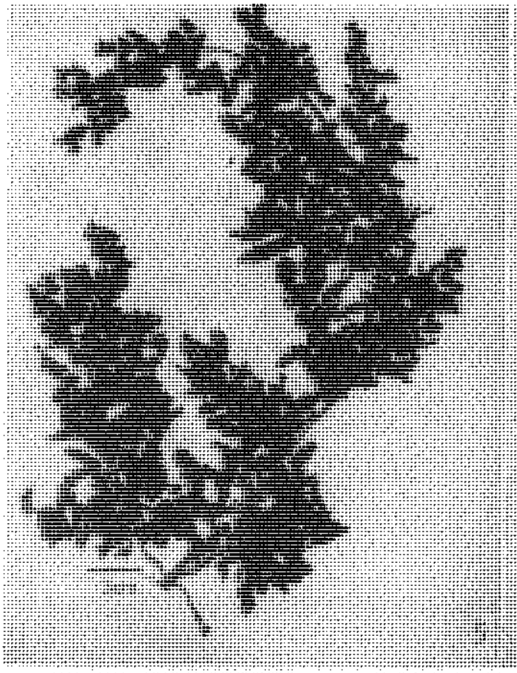


Fig. 1. *Sargassum intermedium* Tseng et Lu (AST 75-0594). Fig. 2. *Sargassum binderi* Sonder ex J. Agardh (CA 83-96).

Fig. 3. *Sargassum oligocystum* Montagne (AST 87-0057). Fig. 4. *Sargassum qionghaiense* Tseng et Lu (CA 83-16).



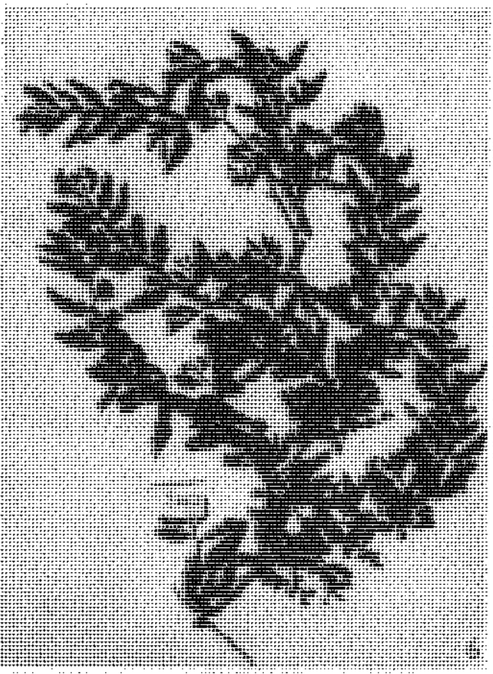


Fig. 5. *Sargassum feldmannii* Pham (AST 75-0885). Fig. 6. *Sargassum erumpens* Tseng et Lu (AST 82-0413).

*Sargassum binderi* Sonder ex J. Agardh Sp. gen. ordines algarum, vol. 1, p. 328, 1848. (Figs. 2, 9)

Fronds dark brown, to about 40 cm long, arising from a discoid holdfast. Main axes short, cylindrical, about 5–6 mm high, 2–3 mm in diameter. Primary branches arising from upper parts, flattened, smooth, usually 30–40 cm long, 4–5 mm wide. Secondary branches flattened, alternate and distichous, 4–5 cm long, 2.5–3.0 mm wide, smooth, beset with branchlets, vesicles, and receptacles. Lower leaves lanceolate, 4–5 cm long, 8–10 mm wide, acute at the apex, cuneate at the base, dentate at the margin, with conspicuous, percurrent midrib. Cryptostomata prominent, regularly scattered in two rows on both sides of the midrib. Upper leaves narrower lanceolate, about 3–5 cm long, 3–5 cm wide, dentate, very sharp at the margins, midrib conspicuous, usually vanishing below the apex. Vesicles elliptical to subspherical when young, subspherical to spherical when mature, usually 4–5 mm in diameter, mucronate or round at tip, cryptostomatic, the pedicels foliaceous, 3–4 mm long, 1.5–4.0 mm wide, with a few cryptostomata.

Plant androgynous. Receptacles compressed, spinulose at the margins, 4–5 mm long, 1–2 mm wide, glomerulate.

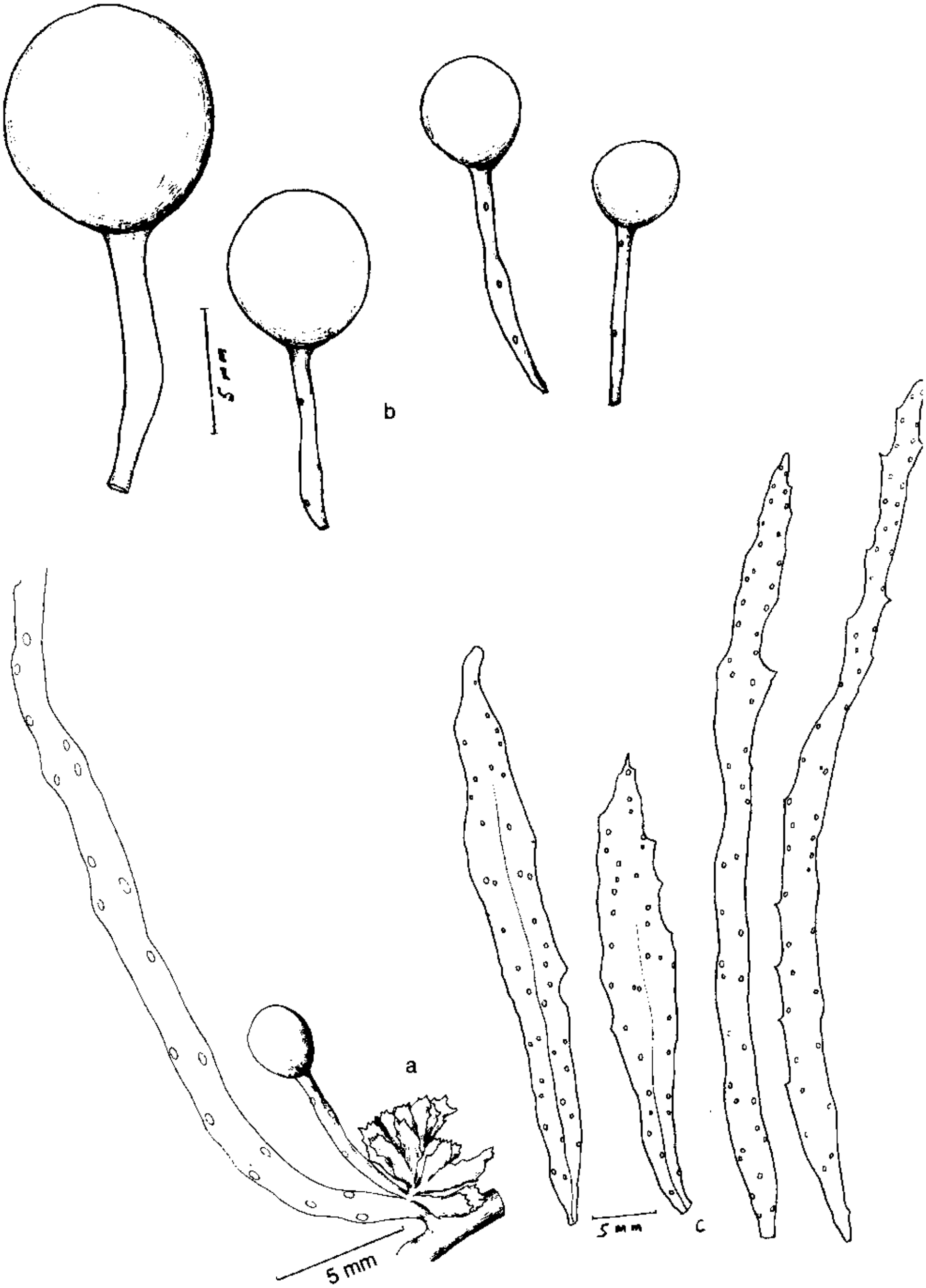


Fig. 7. *Sargassum intermedium* Tseng et Lu (AST 75-0594). a, Receptacles with leaf and vesicles. b, Forms of vesicles. c, Leaves from different branch orders.

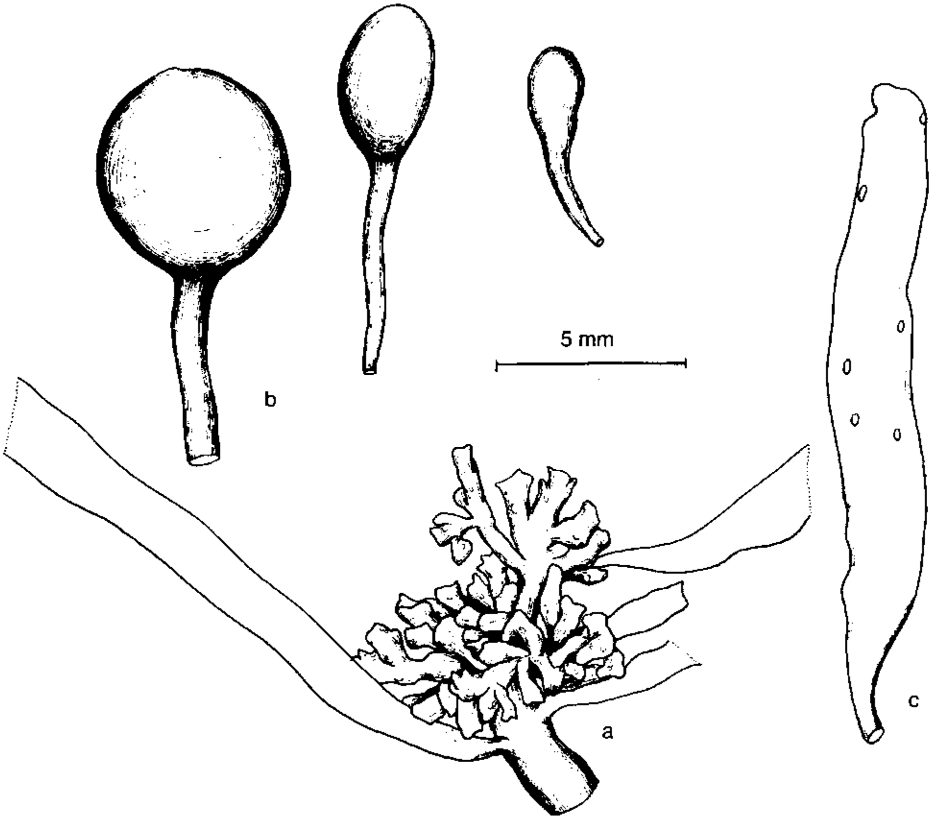


**Fig. 8.** ***Sargassum intermedium*** **Tseng et Lu (AST 55-1424). a, Receptacles. b, Forms of vesicles. c, Leaf.**

Chinese Distribution: Growing on intertidal to subtidal rocks. Hainan Province: Wenchang in April (Tseng 809), Qionghai in July (CA 83-998), Lingshui in April (AST 58-5386, 58-5470), and Sanya in March (PH 92-162, AST 73-0404, 92-0367, 92-0370, 92-0540).

Other Distribution: India, Sri Lanka, Malaya, Philippines, Japan, Taiwan, and Australia.

Remarks: *Sargassum binderi* Sonder was described by J. Agardh in 1848 and illustrated in 1889 when he also described the series *Binderiana* and separated the two species groups on the basis of their vesicular characteristics. Since then, the species has been reported from various places in the Indo-West Pacific region. In their studies of the marine algae of the Solomon Islands, Womersley and Bailey (1970) reduced the species to a synonym of the earlier published *S. oligocystum* Montagne (1845). They state that *S. oligocystum* Montagne is "almost certainly the same as the comparatively well known *S. binderi.*" They studied the type specimen of *S. oligocystum* but did not describe the shape of the leaves and did not notice

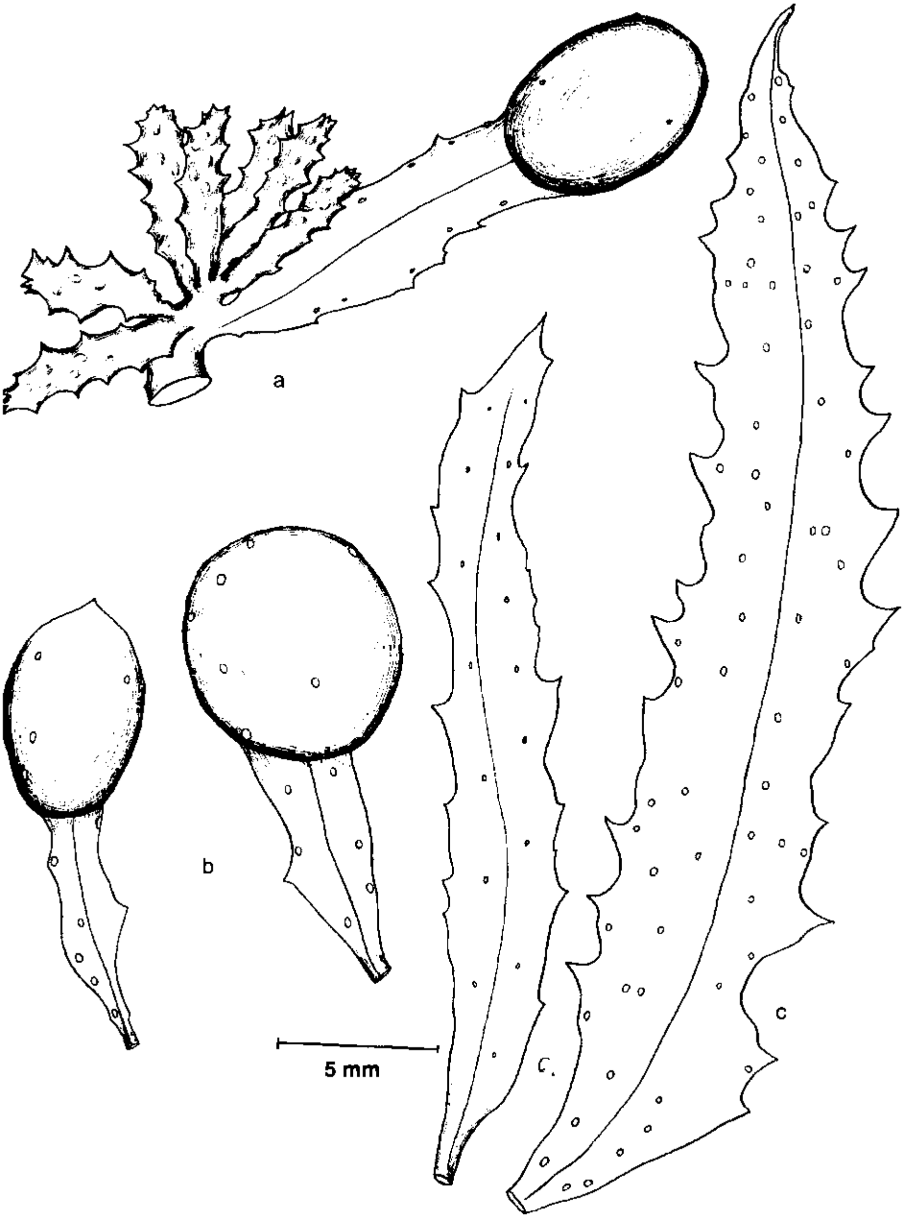


Fig. 9. *Sargassum binderi* Sonder ex J. Agardh (CA 83-98). a, Receptacles with vesicles. b, Forms of vesicles. c, Leaves from different branch orders.

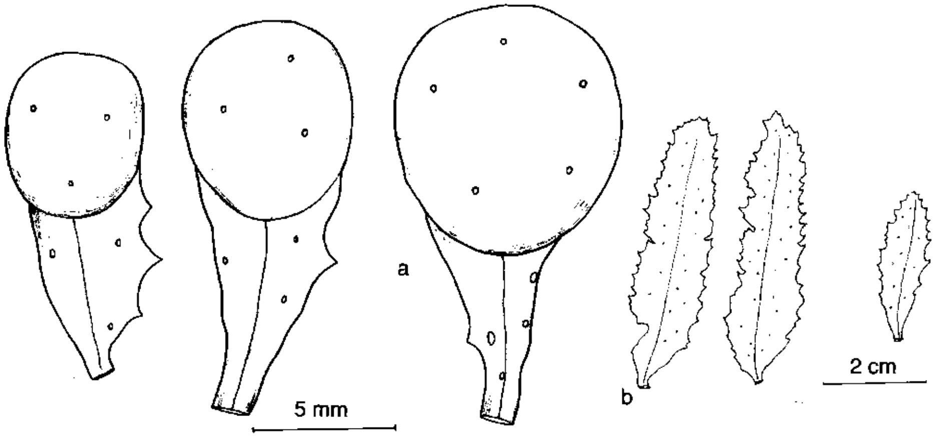


**Fig. 10.** ***Sargassum oligocystum*** **Montagne (AST 67-005). a, Forms of vesicles showing foliar pedicels. b, Leaves from different branch orders.**

any vesicles. Unfortunately we have not been able to study type specimens of these two species of *Sargassum* and must depend on the works of J. Agardh (1889) and Grunow (1915). *S. binderi* and *S. oligocystum* closely resemble each other, especially in the foliar pedicel of the vesicle and the dentate lanceolate leaves, but *S. binderi* has acute to subacute leaves and oval vesicles when young and suboval, subspherical to spherical vesicles when mature, whereas *S. oligocystum* has broader and obtuse, sometimes subacute, more rigid leaves and mostly spherical sometimes subovate vesicles even when young. We therefore tentatively separate the two species as mentioned here, hoping that some day we may be able to study the type specimens ourselves.

*Sargassum binderi* has been previously studied by J. Agardh (1889, p. 87, pl. 26(2), figs. 7-12), Grunow (1915, p. 383), Yamada (1925, p. 245, fig. 2), Durairatnam (1961, p. 45, pl. 9, figs. 11–15, pl. 10, figs. 1–2), Misra (1966, p. 178), and Yoshida (1988, p. 10).

*Sargassum oligocystum* Montagne, Voy. Pol. Sud. Bot. 1:67, 1845.
(Figs. 3, 9)

Fronds dark brown, to about 40 cm high, arising from discoid holdfasts. Main axes short, cylindrical, about 5 mm long, 2 mm in diameter, smooth, giving rise to several primary branches. Primary branches flattened, up to 40 cm long, 4 mm wide, smooth. Secondary branches alternate and distichous, flattened, up to 6–8 cm long, 2 mm wide. Leaves oblong to lanceolate, 3–5 cm long, 8–10 mm wide, obtuse at apices, slightly cuneate at base, distinctly dentate at margins, midrib percurrent or vanishing below apices, cryptostomata conspicuous, scattered on both sides of the midrib. Vesicles mostly subspherical and spherical, sometimes suboval, up to 7 mm in diameter, sometimes up to 10 mm in diameter, rounded at the apices, cryptostomata conspicuous, scattered on the surface of the vesicles, and pedicels foliaceous, 4–5 mm long, 2–3 mm wide, dentate at the margins with midrib and cryptostomata.

Chinese Distribution: Growing on intertidal and subtidal rocks. Hainan Province: Wenchang in February to May (AST 60-1480) and Sanya in March (AST 67-0057).

Other Distribution: Japan, Indonesia, and Philippines.

Remarks: The identification of this species is based entirely on sterile materials and is therefore tentative. The flattened main axis, the rigid broadly lanceolate leaves, and the characteristically foliaceous midribbed pedicels of the strongly spherical vesicles tempted us to place it in *Binderia* near *S. binderi*. As mentioned in the remarks on that species, the predominantly obtuse apex of the rigid leaves and the predominantly spherical vesicle led us to place it in *S. oligocystum*.

*Sargassum oligocystum* has been studied by Reinbold (1913, p. 156), Grunow (1915, p. 385), Setchell (1935, p. 266, pls. 11–15, figs. 1–9) and Tseng (1983, p. 234, pl. 118. fig. 1).

*Sargassum qionghaiense* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press). (Figs. 4, 11)

Frond dark brown, up to 50 cm high, arising from discoid holdfast. Main axis short, about 6 mm long, 3 mm in diameter, cylindrical, giving rise to two to three primary branches in upper portion. Primary branches flattened, broader below, narrower above, smooth, up to 50 cm long, 3–4 mm wide. Secondary branches shorter and narrower, compressed, about 6–12 cm long, 2–3 mm wide, alternately and distichously branched, beset with many branchlets at intervals of 2–4 cm. Leaves on the primary branches membranous, thin and broad-lanceolate, obtuse at apex, obliquely cuneate at base, about 2.0–3.5 cm long, 10–12 mm wide, denticulate at the margin, midrib percurrent, obscure, with conspicuous, slightly raised, irregularly scattered cryptostomata. Leaves on secondary branches similar to those on primary branches, slightly narrower and smaller, about 2–3 cm long, 4–6 mm wide, somewhat acute or obtuse at the apex. Vesicles subspherical when young, spherical when mature, mucronate or rounded at the apices, about 3–4 mm in diameter, sometimes up to 6 mm in diameter, with a few slightly raised cryptostomata and foliaceous pedicels with midribs, about 4–5 mm long, 2–3 mm wide, entire or dentate at the margins.

Plant androgynous. Receptacles flattened, usually forked several times, about 3–4 mm long, 0.8–1.0 mm wide, conspicuously spinulose at the apices and the sides, several in glomerules.

Chinese Distribution: Endemic in China (Qionghai, Hainan). Growing on subtidal rocks, usually 4-6 m in subtidal regions. Hainan Province: Qionghai in July (CA 83-0016, 83-0017).

Remarks: This species is related to *S. binderi*. However, *S. qionghaiense* has broad-lanceolate, thinner leaves, usually obtuse at the apex, with an obscure midrib, smaller vesicles, and smaller flattened receptacles.

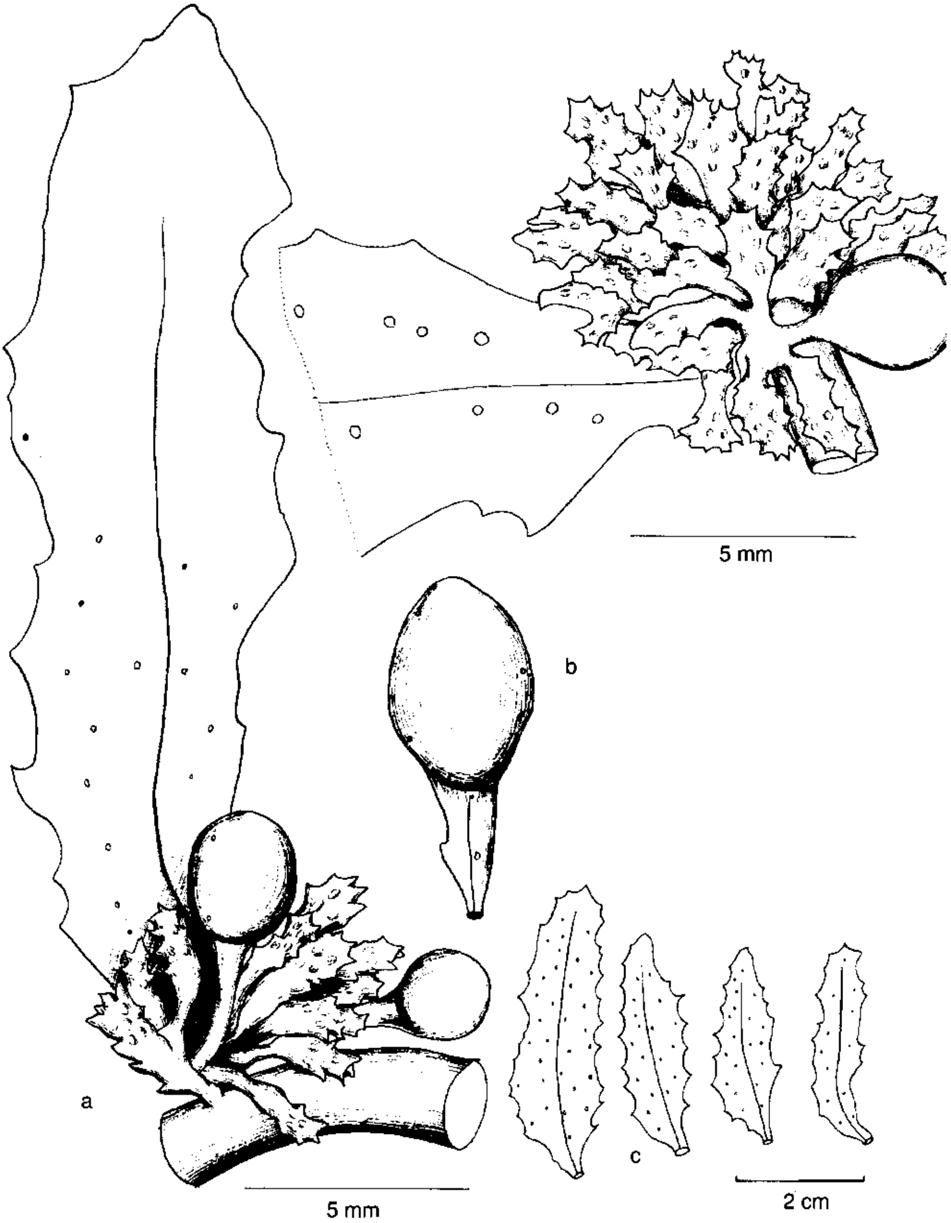


Fig. 11. *Sargassum qionghaienese* Tseng et Lu (CA 83-16). a, Fertile branchlets with leaves and receptacles. b, Forms of vesicles. c, Leaves.

*Sargassum feldmannii* Pham, Ann. Fac. Sci. Saigon, p. 297, fig. 15. 1967.
(Figs. 5, 12)

Synonym: *Sargassum echinocarpum* J. Agardh var. *phyllocysta* Grunow, Verh. Zool. Bot. 65:383, 1915.

Fronds dark brown, attaining a height of 40–50 cm, arising from discoid holdfasts. Main axes short, terete, smooth, up to 5 mm long, 2 mm in diameter. Primary branches compressed, smooth, to about 50 cm long, 2–3 mm wide. Secondary branches subcylindrical, narrower and shorter, smooth, usually 6–8 cm long, 1 mm in diameter, distichous alternate, at intervals of 1–3 cm. Ultimate branchlets short, terete, usually 1–2 cm long, 1 mm in diameter, beset with leaves, vesicles, and receptacles. Leaves on primary branches oblong to lanceolate, usually 2–3 cm long, 1.5 cm wide, slightly oblique or cuneate at base, and rounded or obtuse at apex, generally dentate, sometimes doubly dentate at the margin, obtuse at the apex, midrib inconspicuous, vanishing below the apex. Cryptostomata distinct, numerous, scattered on both sides of the midrib. Leaves on secondary and ultimate branches similar to those on primary branches, oblong or, lanceolate, usually duplicated at the apex, generally 2.5 cm long, 10 mm wide, cuneate at the base, midrib not apparent or vanishing at the middle parts of the leaves, sometimes not present. Vesicles leaflike with inflated center (Figs. 12a and 12b), oblong or subspherical when mature, 8–10 mm in diameter, margin of inflated vesicles sharply dentate, with some conspicuous cryptostomata.

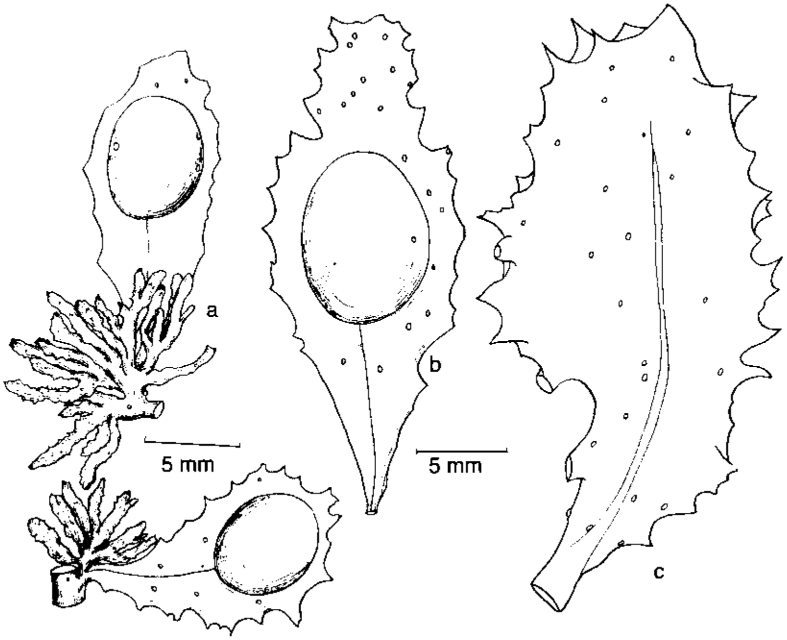


**Fig. 12. *Sargassum feldmannii* Pham (AST 75-0855). a, Receptacles with phyllocysts. b, Phyllocyst. c, Leaf.**

Plants androgynous. Receptacles terete, slightly warty, usually forked, conspicuously spinulose at apex and margin, about 5–6 mm long, 1.0–1.5 mm in diameter, several closely arranged in glomerules.

Chinese Distribution: Growing on lower intertideal and subtidal rocks. Hainan Province: Wenchang in April (AST 73-0501) and Sanya in March to June (Tseng 821, 982; AST 80-2707, 58-5040, 62-2557, 58-5117, 80-2042, 75-0821, 75-0855, 75-1313, 73-0403, 80-2071, 76-1973, 76-1974, 76-2043, 92-0372, 92-0497, 58-5515, 57-5620, 57-6180, CA 86-844).

Other Distribution: Vietnam and Philippines.

Remarks: One of the specimens (Tseng 821) was identified as *S. echinocarpum* J. Agardh var. *phyllocysta* Grunow by Setchell in the 1930s. In the 1950s, we collected many more specimens from Hainan, which we referred to that variety. In the 1970s, when we resumed work after the Cultural Revolution, we came across the publication of Pham (1967) and comparing our specimens with Pham's description, we have no doubt that our specimens belong to the Vietnamese species. Grunow's variety *phyllocysta* of *S. echinocarpum* (Grunow 1915, p. 383) is the same species.

*S. feldmannii* has been previously studied by Trono (1992, p. 53, figs. 16–22, 94).

*Sargassum erumpens* Tseng et Lu, Oceanol. Limnol. Sin. 1995 (in press).
(Figs. 6, 13)

Frond dark brown, up to 48 cm high, arising from small discoid holdfast. Main axes short, cylindrical, about 5 mm high, 2 mm in diameter, giving rise to several flattened primary branches, up to 47.5 cm long, 3–4 mm wide. Secondary branches flattened, arising alternately and distichously, usually about 20 cm long, 3 mm wide, with a few raised open glandules. Branchlets shorter, usually cylindrical, about 3 cm long, 1 mm in diameter, with raised open glandules. Leaves oblong to lanceolate, about 3–4 cm long, 10–12 mm wide, obtuse at apex, slightly cuneate at base, dentate at margin, with midrib percurrent or vanishing below the apex, and many open cryptostomata conspicuously raised at the surface, irregularly scattered on both sides of the midrib. Vesicles spherical, about 7 mm in diameter, with a few conspicuously raised open cryptostomata, usually apiculate or rounded at the apex, pedicels foliaceous with midrib and raised open cryptostomata, dentate at the margins, 3–4 mm long, 2–3 mm wide.

Plants androgynous. Receptacles subcylindrical to slightly compressed, furcate, spinulose, 4–5 mm long, 05–1.0 mm wide, cymosely arranged in glomerules.

Distribution: Endemic in China (Hainan Province). Growing on intertidal to subtidal rocks. Hainan Province: Lingao in February to May (AST 60-4113, 63-2380, 58-5612, 58-5717), Wenchang in May (AST 58-5932), Qionghai in July (CA 83-50), Sanya in March to April ( AST 62-2018, 58-5365, 55-0608, 58-5018, 58-5059, 92-0143, 58-5172, 92-0166, 92-0233, 58-5316, 55-0669, 75-1314, 80-2062,

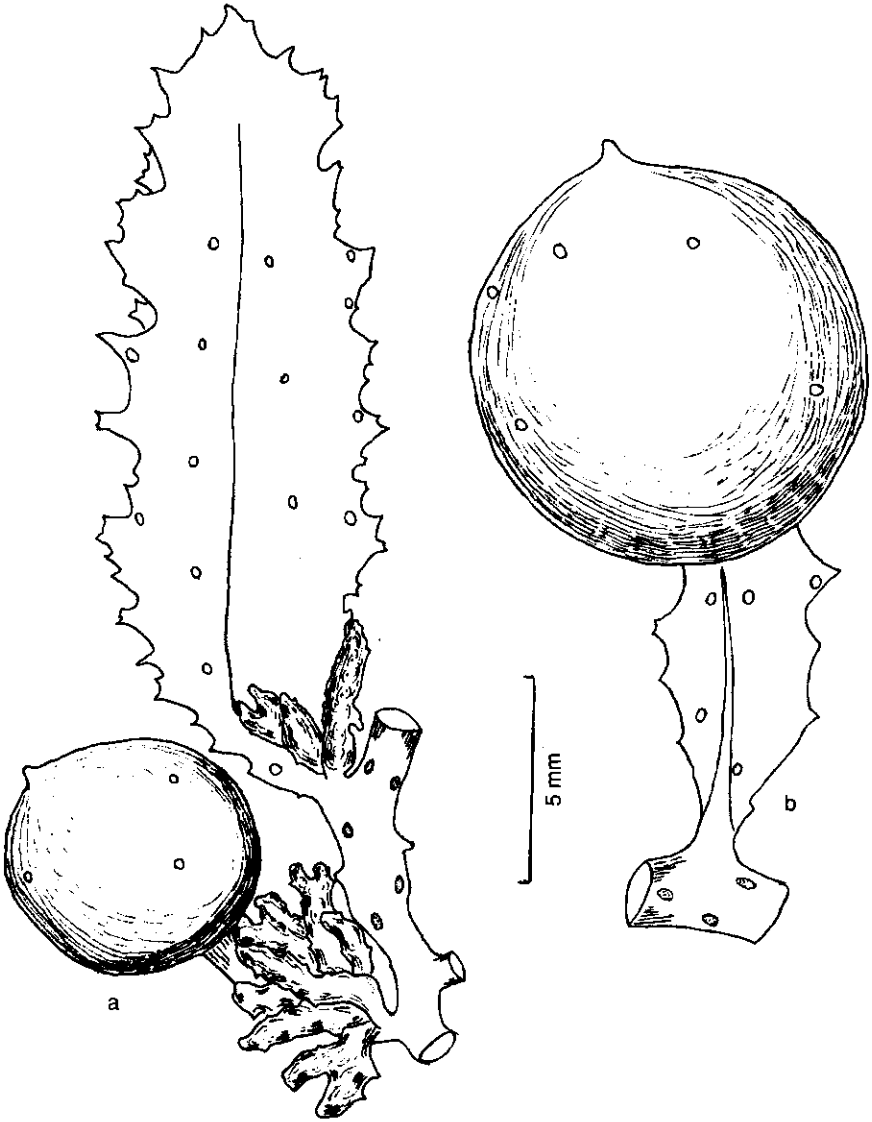


Fig. 13. *Sargassum erumpens* Tseng et Lu (AST 82-0413). a, Receptacles with vesicle and leaf. b, Vesicle.

73-0369, 80-2056, 63-2397, 92-0530, 92-0588, 82-0413, 86-1096, 86-1200), and Yingehai in April ( AST 55-0629, 57-5827.

Remarks: This species is characterized by (1) branches with raised open glandules; (2) oblong to lanceolate leaves, with a few raised open conspicuous cryptostomata; (3) spherical vesicles, with conspicuous raised open cryptostomata; and (4) subcylindrical to slightly compressed receptacles, cymosely arranged in glomerules. It is closely related to *S. xishaense* but differs in having oblong leaves and furcate receptacles, cymosely arranged in glomerules. *Sargassum xishaense* has large lanceolate leaves and biserrulate receptacles.

## Acknowledgments

The paper is contribution No. 2399 from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. We thank Dr. Isabella Abbott for reading and editing our manuscript. We also thank Mr. Leng Zengfu for inking our drawings.

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# BIOGEOGRAPHY OF *SARGASSUM* (PHAEOPHYTA) IN THE PACIFIC BASIN

Naomi Phillips

## Abstract

*Sargassum* is a large, economically important brown alga common to all the world's oceans except the Antarctic. It is an ecologically dominant alga in much of the tropics. However, despite its importance, not much is understood about its biogeography or evolutionary history. This chapter builds a foundation for the Pacific basin from which questions of this nature can be addressed.

The chapter has three basic objectives: (1) presentation of the current taxonomy of *Sargassum* ; (2) presentation of comprehensive distribution tables and a map, including pertinent literature listings for Pacific basin subgenera and species; and (3) use of biogeographical models to interpret distribution, endemism, and patterns of diversity for the various subgenera and species in the Pacific basin.

## Introduction

*Sargassum* is one of the most ecologically abundant, economically, culturally, and taxonomically important brown algal genera. It is the largest genus in the Phaeophyta (Yoshida 1983), with over 400 species distributed in most of the world's ocean basins, with the exception of the waters around the Antarctic (Nizamuddin1961). *Sargassum* is also one of the few brown algal genera that spans temperate to tropical environments. In some areas, such as the temperate Pacific northwestern coast of America, species in this genus are minor components of the local flora, whereas in other areas, such as Australia or Hawaii, certain species are ecological dominants, contributing not only considerable biomass to local systems, but also playing an overstory role similar to that of kelps in temperate coasts (Glenn et al. 1990, Kilar et al. 1992).

*Sargassum* researchers face many challenges: the genus is notoriously plastic morphologically, comprehensive taxonomic treatments are difficult, and appropriate and pertinent literature is patchy and often difficult to locate. To help remedy this situation, this chapter explores the current taxonomy of *Sargassum*; provides a comprehensive distribution and literature base for the Pacific basin; and synthesizes data on the distribution of subgenera and species in the Pacific basin, emphasizing diversity and endemism when possible. The creation of a comprehensive picture of the biogeography of *Sargassum* makes it possible to ask more refined questions about the evolution and biogeography of this large complex genus. In the compilation given here, the most contemporary species list for a location is used in distribution tables. However, for a given species, historical locations are included in the text that are not currently considered part of its distribution limit. These locations are included to provide complete collection records for the genus, with herbarium sources and literature cited. For example, a researcher writing a monograph on a certain species may need to review all the distribution records (correct or not) reported for that species. This table provides the necessary information.

## Current Taxonomy of *Sargassum*

*Sargassum* is one of seven genera in the family Sargassaceae (Kuetzing), in the order Fucales. Of the six families currently recognized for the order, the Sargassaceae is one of the more primitive (Clayton 1984). This family is characterized by specialized branch systems, a single egg per oogonium and a three sided apical cell (Womersley 1987, Bold and Wynne 1985, Lee 1989). As might be imagined with more than 400 species, *Sargassum* taxonomy is complex. J. Agardh (1889), author of the genus, created a system of classification for it. With modifications by Grunow (1915, 1916) and Setchell (1933b, 1935, 1936), this system is still largely followed today.

Agardh divided the genus into five subgenera: *Phyllotricha*, *Schizophycus*, *Bactrophycus*, *Arthrophycus*, and *Eusargassum* (=*Sargassum*) based on morphogenic relations between stem and blade (Agardh 1889, Yoshida 1983). These subgenera were further subdivided, but the divisions did not always follow the Botanical code, as Abbott et al. (1988) indicate in a recent revision of the subgenus *Sargassum*. (Appropriate subdivisions are secto [section], subsecto [subsection], series, subseries, and species.) In addition to this nomenclatural confusion, placement of species within these subgenera and subsequent subdivisions has proved difficult (Womersley 1954, Yoshida 1983). To deal with these apparent taxonomic ambiguities, Yoshida (1983) has suggested dividing *Sargassum* subgenera into two groups: those with lamina perpendicular to the axis (horizontal) and those with lamina parallel to the main axis (vertical) (Fig. 1). *Arthrophycus* and *Bactrophycus* are in the horizontal-lamina category; the other three subgenera are in the vertical-lamina category.

Yoshida (1983) further distinguished between *Arthrophycus* and *Bactrophycus* on the basis of geographical occurrence. Species found in the Northern Hemisphere are assigned to *Bactrophycus*; those in the Southern Hemisphere to *Arthrophycus*. *Bactrophycus* is further divided into five sections: *Repentia*, *Spongocarpus*, *Teretia*, *Halochloa*, and *Phyllocystae* (Yoshida 1983, Tseng 1985, Tseng et al. 1985).

For the vertical-leaf category, subgenera are distinguished largely on the basis of morphological characteristics. The *Sargassum* subgenus has decompound axillary fronds, simple lamina, and vesicles arising from distal portions of the lamina. Receptacles are compound, forming on modified axillary branches, and are either smooth or armed. The subgenus is divided into three sections: *Zygocarpicae*, *Malacocarpicae* and *Acanthocarpicae*. *Zygocarpicae* is divided into two subsections: *Holozygocarpicae,* series *Carpophylleae* and *Pseudozygocarpicae,* series *Cinerea*. *Malacocarpicae* has three subsections:

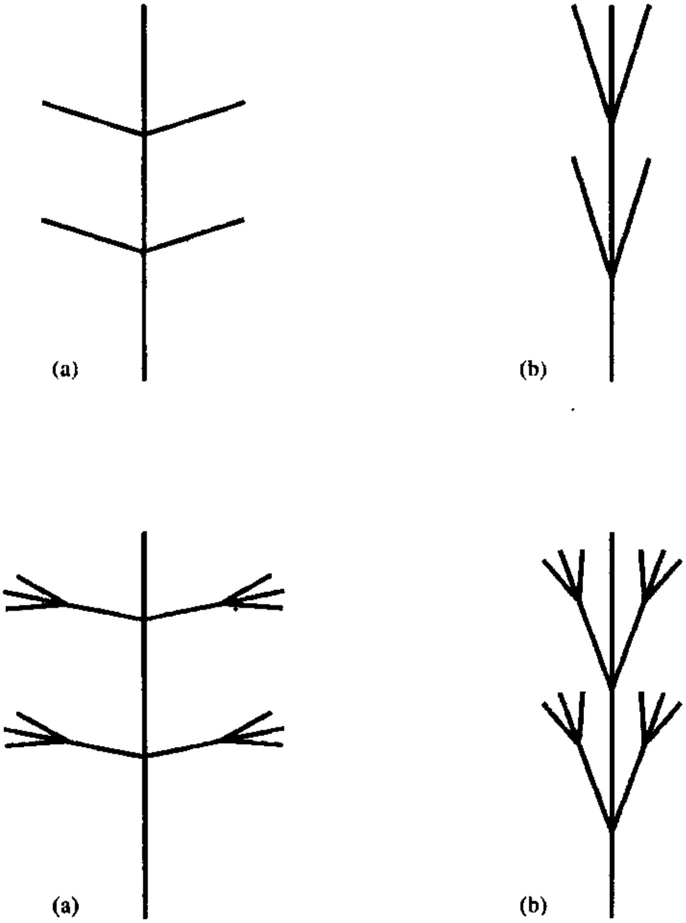


**Fig. 1. Horizontal (a) and vertical (b) groups of *Sargassum* as described by Yoshida (1983).**

*Fruticuliferae*, *Cymosae*, and *Racemosae*. Subsection *Racemosae* is further divided into three series: *Acinariae*, *Glandulariae*, and *Siliquosae*. Section *Acanthocarpicae* is divided into two subsections: *Glomerulatae* and *Biserrulae* (Abbott et al. 1988, Yoshida 1988, Tseng and Lu 1992a, 1992b). The subgenus *Phyllotricha* is very distinct. It is characterized by lower "pinnatifed" laterals, compressed to terete primary branches, and simple receptacles in racemose clusters. Agardh (1889) divided *Phyllotricha* into five tribes. Womersley (1954) thought that further subdivision of the subgenus caused more confusion and should be avoided. However, if tribes are to be maintained, they should be converted to sections according to the International Botanical Code (Abbott et al. 1988). Womersley

(1954) questioned the status of subgenus *Schizophycus* and suggested its collapse into *Phyllotricha,* which has since been supported (Yoshida 1983). To date, much of the higher level framework for *Sargassum* taxonomy is in hand (Fig. 2). However, placement of species within these groups is still controversial and an area of active research. In conclusion, slowly, through detailed work, our understanding of *Sargassum* taxonomy is increasing. However, we are still far from a comprehensive understanding, and much work is needed. The following text focuses on the subgenera and the species therein, without a detailed treatment of sections, subsections, or series.

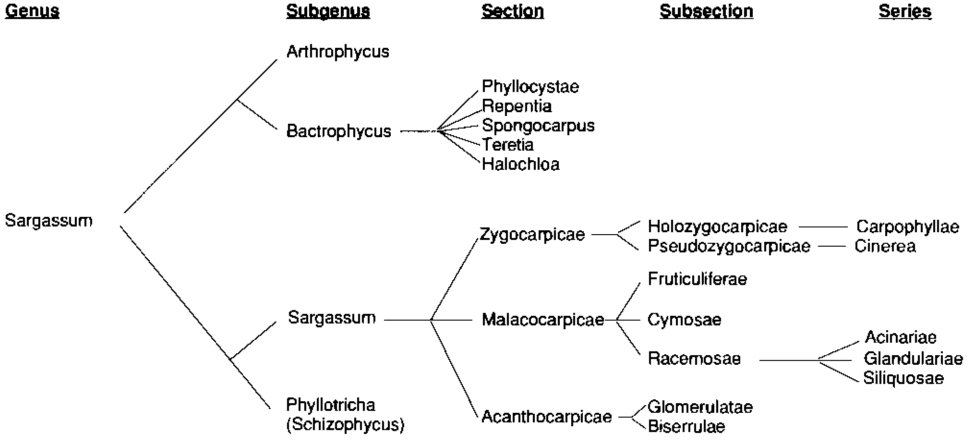
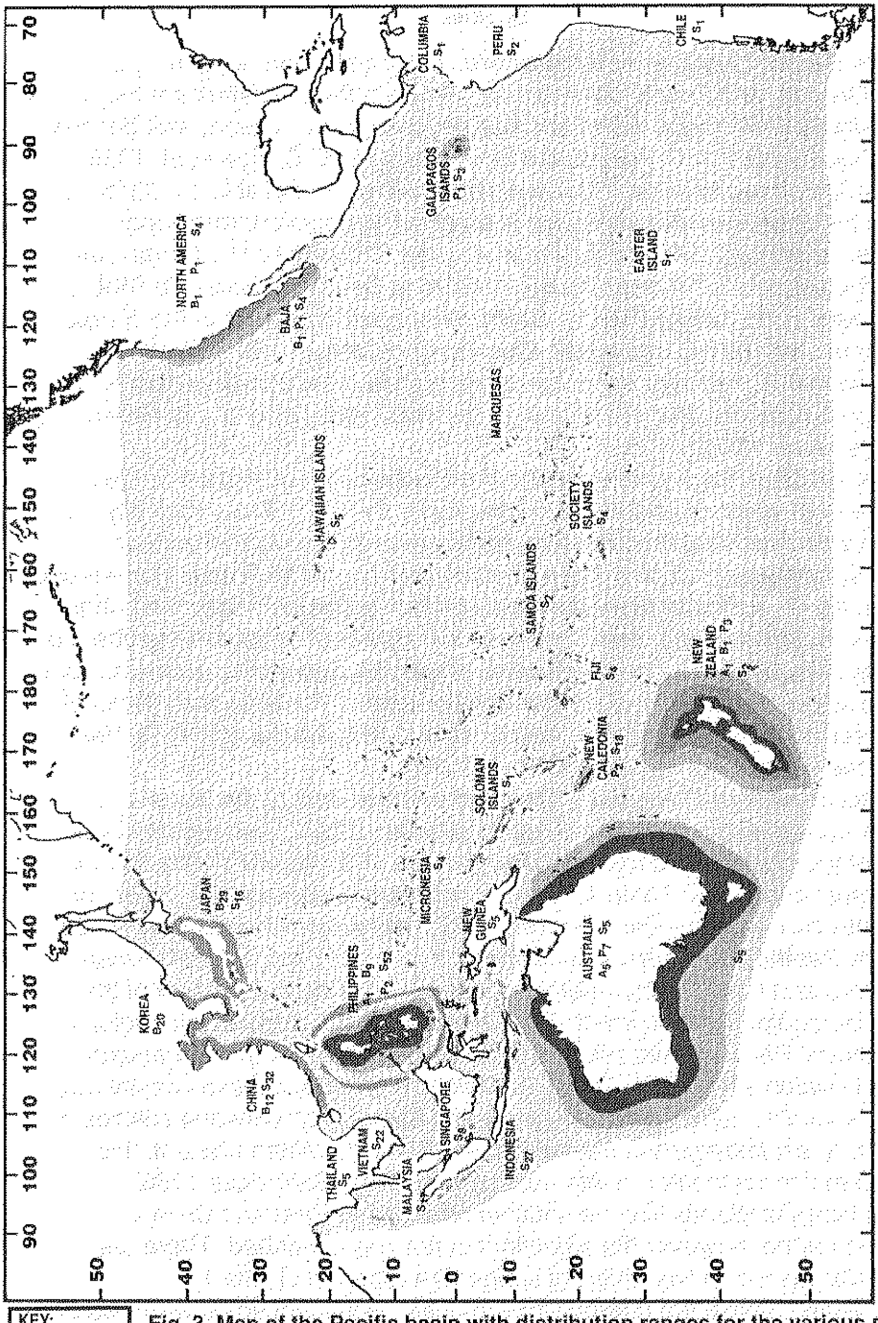


**Fig. 2. Current taxonomic associations among subgenera in the genus *Sargassum* (J. Agardh 1889; Grunow 1915, 1916; Setchell 1933a, 1936; Womersley 1954; Yoshida 1983, 1988; Abbott et al. 1988; Tseng and Lu 1992a, 1992b).**

## Distribution and Literature for Subgenera and Species

### Subgenera

*Phyllotricha* has 16 species worldwide: 15 restricted to the Pacific basin and one in the Atlantic basin. Of the 15 Pacific species, 10 are found in Australia and New Zealand, one in New Caledonia, and two in the Philippines (Tables 2 and 3, Fig. 3). For *Arthrophycus,* seven species currently are recognized for the Pacific basin: five in Australia, one in New Zealand, and one in the Philippines (Tables 2 and 3, Fig. 3). *Bactrophycus* has 32 Pacific basin species: 22 concentrated in eastern Asia, nine in the Philippines, and one in the northeastern Pacific (Tables 1–3, Fig. 3). *Sargassum* is by far the most widely distributed and specious subgenus in the Pacific basin. A total of 110 species are recognized for the Pacific basin. The highest concentration of species, overall, is found in tropical to subtropical areas: New Caledonia, southern Japan and China, Malaysia/Singapore, and the Philippines (Tables 1–3, Fig. 3).



KEY:
A= ▩
B= ▨
P= ▧
S= ░

Fig. 3. Map of the Pacific basin with distribution ranges for the various subgenera of *Sargassum*. Numbers represent species numbers within specific geographical areas; letters represent the various subgenera: A = *Arthrophycus*, B =*Bactrophycus*, P = *Phyllotricha*, S = *Sargassum*.

## Species

**Eastern Pacific: Northern Hemisphere.** The Pacific northeast including California, Oregon, and British Columbia, is linked via the persistent southerly flow of the cold-water California Current and has phycologically diverse, well-described temperate habitats (9–13°C; Abbott and Hollenberg 1976, Scagel et al. 1986). This area shares three species in three different subgenera (Table 1). *Sargassum muticum* in the subgenus *Bactrophycus* is an alien introduction from Japan (Abbott and Hollenburg 1976, Critchley et al. 1983, Stewart 1991). *Sargassum palmeri* in the subgenus *Phyllotricha* is restricted to Southern California (Abbott and Hollenberg 1976, Stewart 1991). *Sargassum agardhianum* is in the *Sargassum* subgenus, with San Diego as the type locality (Stewart 1991). Both *S. agardhianum* and *S. muticum* can form dense stands, whereas *S. palmeri* is a minor component in intertidal communities (Setchell 1937, Abbott and Hollenberg 1976, Scagel et al. 1986).

Coastal waters of Baja California and the Pacific coast of Mexico range in temperature from warm temperate to subtropical (10–18°C). Phycologically, this area is less well described than the temperate areas to the north. Fourteen species of *Sargassum*, including three species from the north (Table 1) are found in this area. Again, as in the more northern areas, species belong to the subgenera *Sargassum*, *Phyllotricha*, and *Bactrophycus*. However, most are members of the *Sargassum* subgenus. The dominance of species also varies. Some species form dense stands and others are minor components of the local flora (Setchell 1937, Dawson 1946, Dawson 1966, Aquilar et al. 1984, Aquilar and Ruiz 1985, Aquilar Rosas, R. and Aquilar Rosas, M. A. 1986).

The Pacific coast of Colombia is the southernmost limit of the warm-water zone and is considered a subtropical region (Ekman 1953). This region is well described phycologically and has only one species of *Sargassum*: *S. liebmanii* in the *Sargassum* subgenus (Table 1). When present, this species is a major component of intertidal communities (Setchell 1937, Schnetter and Bula Meyer 1982).

**Eastern Pacific: Southern Hemisphere.** Waters of coastal South America, including Peru and Chile, are temperate because of the northward flow of the cold-water Humboldt (Peru) current. The taxonomy of the algae in this region is well understood. Peru has two species of *Sargassum*, both in the *Sargassum* subgenus (Dawson et al. 1964; Table 1). Chile has a large, diverse coastal range. However, despite its geographical expanse and complexity, only one species of *Sargassum, S. skottsbergii* has been reported (Table 1). When present, this species is a major contributor to intertidal communities (Santelices 1988).

The Galapagos islands like the continental areas of Peru and Chile are temperate in nature, however the algal flora is not well described. There are five species of *Sargassum* in two different subgenera reported (Table 1).

Easter Island, unlike the nearby Chilean coast, is influenced by warm water currents and is subtropical. Many researchers (Børgesen 1924, Sjoestedt 1924, Petersen 1928, Levring 1960, Etcheverry 1964) have studied the algal flora of

Easter Island, but the first synthesis was not published until 1987 (Santelices and Abbott 1987). Only one species of *Sargassum*, *S. skottsbergii*, is recognized. It tends to be an ecological dominant in low intertidal to subtidal areas (Table 1).

**Central Pacific Region: Northern Hemisphere.** Most island groups in the central Pacific region are isolated, are of volcanic origin, and have tropical seawater temperatures (24–30°C). The Hawaiian archipelago is no exception. This island group spans 3000 km and includes high islands, low islands, atolls and seamounts. *Sargassum* taxonomy in Hawaii is well known. The island archipelago has five species in the *Sargassum* subgenus; four of these are described at the species level and are considered endemic (Magruder 1988; Table 2). The three most common species, *S. echinocarpum*, *S. obtusifolium*, and *S. polyphyllum*, are reef flat components and form dense stands that create overstory canopies in local communities (De Wreede 1973, Magruder 1988, Glenn et al. 1990). *Sargassum hawaiiensis* is a subtidal species and has the deepest recorded distribution (200 m) for a phaeophyte (Doty and Newhouse 1966, DeWreede and Jones 1974).

Micronesia includes several island groups: the Gilbert, Marshall, Caroline, and Mariana islands and Guam. Thanks to work by Tsuda and colleagues, the marine intertidal flora of these island groups is phycologically well described. The diversity of *Sargassum* in these islands is limited. Only four species are found and none of these are endemic (Tsuda 1965, 1966, 1968, 1972a, 1972b, 1976, 1981, 1988; Tsuda and Trono 1968; Tsuda and Belk 1972; Tsuda and Tobias 1977; Tsuda and Wray 1977; Table 2). However, when present, species of *Sargassum* tend to be ecologically dominant and make large contributions to the biomass.

For unknown reasons, as noted by Doty (1954), many of the central Pacific atolls or low islands (Johnson, Howland, and Baker) are devoid of *Sargassum*. However, two recently discovered atolls are the exception to this trend: Ulithi and Kayangel in the western Carolines (Tsuda 1976; Table 2). Although the reasons for these differences in distribution remain unclear, it may be differences in nutrient supply that favor growth of *Sargassum* (Glenn et al. 1990).

**Southern Hemisphere.** The most comprehensive distribution list for Indonesia and New Guinea comes from the Siboga expeditions (Reinbold 1913). For Indonesia, 27 species of *Sargassum* are listed, all of which belong to the *Sargassum* subgenus. For New Guinea, only two species are listed, also both in the *Sargassum* subgenus (Table 2).

The Solomon Islands are between New Guinea and Fiji. Several contributions (Reinbold 1913, Setchell 1935, Levring 1960, Womersley and Bailey 1969) have greatly increased our phycological knowledge of this region overall. Four species of *Sargassum* subgenus *Sargassum* have been reported for the islands. *Sargassum cristaefolium* is the most common and the only one described at the species level (Table 2).

New Caledonia, a large, phycologically rich island has 24 species of *Sargassum*, including 12 endemic species (Garrigue and Tsuda 1988; Table 2). Most of the species are in the *Sargassum* subgenus; two are in *Phyllotricha*. As in other

Pacific regions with large island masses and presumed high nutrient loading in coastal areas, *Sargassum* is one of the ecologically dominant genera.

Fiji is an immense archipelago consisting of 332 islands of different sizes surrounded by barrier reefs interspersed with patch reefs. Our understanding of Fijian algae is developing rapidly via efforts by Garbary et al. (1991) and South and Kasahara (1992). According to these reports, four species of *Sargassum* are found in Fiji including the widespread *S. cristaefolium* and *S. polycystum* and two endemic species (Table 2). All four taxa are in the *Sargassum* subgenus.

The Samoan islands are between Fiji and the Society Islands. Aside from early contributions by Setchell in 1924 and some more recent benthic monitoring work (Hunter et al. 1993), little phycological information is available. According to Setchell (1924), two species of *Sargassum* are common on reef habitats (Table 2).

The Society Islands (French Polynesia) are a large, diverse group of high and low islands. Through the contributions of Setchell and Parks (1926), Taylor (1973), Payri and Naim (1982) and Payri (1987), we are approaching a comprehensive understanding of the marine flora in these islands. Four species of *Sargassum*, all in the *Sargassum* subgenus, are found here (Table 2). As in other tropical areas of the Pacific basin, when it is present, *Sargassum* tends to be an ecological dominant.

Australia is an ecologically and geographically diverse continent. Its coastlines span temperate, subtropical, and tropical climates which consequently have a diverse and complex algal flora. In his 1889 treatment of Australian *Sargassum*, J. Agardh lists 143 species distributed among all five subgenera and across all three thermal zones. Subsequent research in the different regions of Australia has led to substantial revisions. In general, the current flora of southern Australia is the best described, with 16 species of *Sargassum*, 13 species of which are endemic. Four species are in the *Sargassum* subgenus, six in the *Phyllotricha* subgenus, and five in the *Arthrophycus* subgenus (Womersley 1987; Table 2). Detailed and separate information on distributions or abundances of *Sargassum* subgenera for eastern and western Australia is patchy. The best described subgenus for these regions is *Phyllotricha*. Western Australia has seven species (Table 2): one endemic to Lord Howe Island and five also found in southern Australia. Eastern Australia has three species, two also found in western Australia and one also present in southern Australia (Womersley 1954). With these areas included, the total number of *Sargassum* species for the whole of Australia is 18, of which 15 are endemic. However, as Womersley (1987) indicates, detailed information on species distributions for eastern and western regions for the *Sargassum* subgenus is incomplete and needs critical review.

The main New Zealand land mass is primarily temperate, but some of the outer islands are subtropical. The algal flora is quite diverse and well described and includes many Australian elements (Lindauer et al. 1961, Hay et al. 1985). New Zealand has six species of *Sargassum* in three subgenera: three species in *Phyllotricha*, one species in *Arthrophycus*, and two in *Sargassum*. All except one *Phyllotricha* species are endemic (Table 2).

**Western Pacific.** The Japanese islands have diverse coasts and are surrounded by waters that range from temperate to subtropical in temperature. These islands are bounded by different water masses, the Japan and East China seas and the Pacific Ocean. The algal flora is well described. Numerous species of *Sargassum* are recognized, many of which are considered endemic (Table 3). *Bactrophycus* appears to be the dominant subgenus in temperate to subtropical areas, at least in the number of species found (Tseng et al. 1985). Twenty-nine species are recognized for *Bactrophycus*, with 10 species considered endemic. In the subgenus *Sargassum*, 16 species are recognized (Yendo 1907, Yamada 1942, Yoshida 1983, Yoshida 1988, Noro et al. 1994). Three of these are considered endemic. Many of these species are components of offshore floating algal beds. The Ryukyu Islands, a southern subtropical island group, have 27 species of *Sargassum* (Tsuda 1991; Table 2): 13 in *Sargassum*, eight in *Bactrophycus*, and two in *Phyllotricha*. Many of these species are also common in other parts of Japan (Table 3).

Temperatures in Korea's marine habitats range from temperate to subtropical. Historical and recent studies on Korean *Sargassum* greatly increased our understanding (Kang 1966, Lee and Kang 1986, Lee and Yoo 1992). For *Bactrophycus*, 20 species are now recognized. Several of the species are also found in Japan (Table 3). Current floristic lists include species within the subgenus *Bactrophycus* only; however, it is unclear if the *Sargassum* subgenus is just omitted or if it does not occur along these shores. Regardless of the subgenera present, *Sargassum* is a dominant component of the overall marine flora.

Mainland China has an extensive distance of coastline spanning ecologically, geologically, and oceanographically diverse regions with waters ranging from warm temperate to tropical. In general, the algal flora and *Sargassum* are well known. China (including Taiwan) has 12 species of *Bactrophycus*, two of which are endemic. For *Sargassum*, 32 species have been reported, 16 of which are considered endemic (Setchell 1933b, 1935, 1936; Tseng et al. 1985; Tseng and Lu 1992a, 1992b; Table 3). As in many regions, when present, *Sargassum* species are major contributors to the biomass of local marine ecosystems.

Vietnam, Thailand, and Cambodia are parts of a peninsula bounded by the South China Sea. Unfortunately, phycologically, much of this peninsula is in an early descriptive state. To date, the marine algae of Vietnam are the best described of the floras of these countries. Dawson's 1954 account lists eight species of *Sargassum*, with only four assigned an epithet. These species include the widespread *S. crassifolium* and *S. polycystum* of the subgenus *Sargassum*. More recently, Dinh et al. (1993) assigned 22 species: 19 listed for the *Sargassum* subgenus and three for *Bactrophycus* (Table 3). Because this publication was so recent, endemic numbers and species lists were not adjusted in diversity and distribution accounts reported here. *Sargassum* numbers in Thailand are much smaller; only two species have been reported (Table 3).

Malaysia and Singapore are at the southernmost end of the peninsula formed by Vietnam, Thailand, and Cambodia. Our understanding of the marine algal resources of Malaysia and Singapore is somewhat more advanced than that of the more northern countries. Malaysia includes both island and mainland regions and has coastlines bounded by four seas: South China, Andaman, Sulu, and Celebes. Recent research (Phang 1986), has made great progress in putting togther a comprehensive understanding of this rich and diverse algal flora. Phang (1986) lists 17 species of *Sargassum*, all in the *Sargassum* subgenus (Table 3); seven are considered endemic. Because of their geographical proximity, Singapore and Malaysia share many algal components and endemic species. Wei and Chin (1983) list eight species of *Sargassum*, all in the *Sargassum* subgenus, in their treatment of Malaysian algae. *Sargassum* is a major component of the regions marine algal flora.

The Philippines are a large diverse island group under the influence of the warm North Equatorial Current. The islands are one of the most phycologically rich and challenging regions of the tropics. Silva et al. (1987) reported 70 species of *Sargassum* for the Philippines: 35 in the subgenus *Sargassum*, one in *Arthrophycus*, six in *Bactrophycus*, and one in *Phyllotricha* (Table 3). Trono (1992, 1994) recently published a detailed account of 28 taxa of the *Sargassum* subgenus, and described five new species (Table 3). According to Trono, much of the herbarium material available for *Sargassum* is fragmentary and of limited use. Consequently, Silva's earlier list for *Sargassum* is best treated as preliminary. Clearly, more detailed work such as Trono's is needed for the other subgenera before we fully understand this complicated genus in the Philippines.

## Synthesis of Subgenera and Species

As evident from the descriptions of subgenera and species, several regional floras and some species of *Sargassum* are well known in the Pacific basin. North and South America, much of Korea, China, Japan, southern Australia, New Zealand, Micronesia, Hawaii, New Caledonia, the Solomons, Fiji, the Society Islands, Malaysia, Singapore, and Vietnam are among the best described regions. However, few specimens have been collected from northern, eastern, and western Australia; the Philippines; Indonesia; New Guinea; Thailand; Cambodia; and the Samoan islands, resulting in little descriptive information for these areas. Despite this incomplete knowledge of Pacific flora as a whole, we can still make some general statements about the floras and perhaps gain some insights into possible centers of origin and diversity, patterns of endemism, and dispersal routes for Pacific subgenera and species of *Sargassum*.

### Patterns of Oceanic Current and Models of Biogeography

A short description of the basic patterns of oceanic currents in the Pacific basin and the relevant models of biogeography used for other marine organisms may be useful for the following syntheses. Patterns of ocean currents develop in ocean basins in response to the rotation of the earth and the patterns of prevailing

**Table 1: Distribution of Species of *Sargassum* in the Eastern Pacific**

| Hemisphere | State/Country | Subgenus | Species | Distribution |
|---|---|---|---|---|
| Northern | British Columbia | *Bactrophycus* | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |

Literature: Abbott and Hollenburg 1976, Critchley et al. 1983, Scagel et al. 1986.

| | | | | |
|---|---|---|---|---|
| | Washington | *Bactrophycus* | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |

Literature: Setchell 1937, Abbott and Hollenburg 1976, Critchley et al. 1983, Stewart 1991.

| | | | | |
|---|---|---|---|---|
| | California | *Bactrophycus* | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |
| | | *Phyllotricha* | *S. palmeri* | Mid to southern California, Baja California, Mexico |
| | | *Sargassum* | *S. agardhianum* | Southern California |

Literature: Setchell 1937, Abbott and Hollenburg 1976, Critchley et al. 1983, Stewart 1991.

| | | | | |
|---|---|---|---|---|
| | Baja/Mexico | *Bactrophycus* | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |
| | | *Phyllotricha* | *S. palmeri* | Mid to southern California, Baja California, Mexico |
| | | *Sargassum* | *S. agardhianum* | Southern California, Baja, Philippines |
| | | | *S. howellii* | Southern California, Baja |
| | | | *S. liebmannii* | Southern California, Baja, Columbia, Peru |
| | | | *S. pacificum* | Peru, Chile* |

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*Location is not currently considered part of the particular species distribution bounds.

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|---|---|---|---|---|
| | Baja Mexico (continued) | Unknown | *S. brandegeei* | Baja |
| | | | *S. herporhizum* | Baja |
| | | | *S. horridum* | Baja |
| | | | *S. johnstonii* | Baja |
| | | | *S. lapazeanum* | Baja |
| | | | *S. macdougalii* | Baja |
| | | | *S. sinicola* | Baja |
| | | | *S. sonorense* | Baja |

Literature: Setchell 1937, Dawson 1944, Dawson 1945a–c 1946, Taylor 1945, Ekman 1953, Dawson 1958, Dawson et al. 1960, Dawson 1966, Abbott and Hollenburg 1976, Aquilar and Ruiz 1985, Aquilar Rosas, R. and Aquilar Rosas, M. A. 1986, Stewart 1991.

| | | | | |
|---|---|---|---|---|
| | Columbia | *Sargassum* | *S. liebmanii* | Southern California, Baja, Columbia |

Literature: Schnetter and Bula Meyer 1982.

| | | | | |
|---|---|---|---|---|
| Southern | Galapagos | *Phyllotricha* | *S. zacae* | Galapagos |
| | | *Sargassum* | *S. galapagense* | Galapagos |
| | | | *S. setifolium* | Galapagos |
| | | | *S. temletonii* | Galapagos |
| | | Unknown | *S. rigidiusculum* | Galapagos |

Literature: Taylor 1945.

| | | | | |
|---|---|---|---|---|
| | Peru | *Sargassum* | *S. ecuadoreanum* | Peru |
| | | | *S. pacificum* | Chile*, Peru, Baja, Mexico |

Literature: Dawson et al. 1964.

| | | | | |
|---|---|---|---|---|
| | Chile | *Sargassum* | *S. skottsbergii* | Chile, Easter Island |

Literature: Levring 1960, Santelices and Abbott 1978, Santelices 1988.

| | | | | |
|---|---|---|---|---|
| | Easter Island | *Sargassum* | *S. skottsbergii* | Chile, Easter Island |

Literature: Børgesen 1924, Sjoestedt 1924, Levring 1960, Etcheverry 1964, Santelices and Abbott 1987.

**Table 2: Distribution of *Sargassum* in the Central Pacific**

| Hemisphere | State/Country | Subgenus | Species | Distribution |
|---|---|---|---|---|
| Northern | Hawaii | *Sargassum* | *S. echinocarpum* | Taiwan*, Solomons*, Indonesia*, Fiji*, New Caledonia*, Tonga*, Saudi Arabia*, Ethiopia*, Kenya*, Hawaii |
| | | | *S. hawaiiensis* | Hawaii |
| | | | *S. obtusifolium* | Society Islands*, Singapore*, Guam*, Hawaii |
| | | | *S. polyphyllum* | Fiji*, New Caledonia*, Hawaii, South China* |
| | | | *S.* species | Hawaii |

Literature: Doty and Newhouse 1966, Tsuda 1966, De Wreede and Jones 1973, Magruder 1988, Abbott 1989, Noro et al. 1994.

| | | | | |
|---|---|---|---|---|
| | Micronesia | *Sargassum* | *S. crassifolium* | Micronesia, New Caledonia, Japan, Taiwan, Vietnam Indonesia, East Africa, Sri Lanka, India, Philippines |
| | | | *S. cristaefolium* (=*S. ilicifolium*) | Micronesia, Fiji, Indian Ocean, Japan Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Okinawa, Kermadec Islands |
| | | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |
| | | | *S. tenerrimum* | India, Ceylon China, Vietnam |

Literature: Tsuda 1965, 1968, 1972b, 1981, 1988; Tsuda and Belk 1972; Tsuda and Wray 1977; Tsuda and Tobias 1977; Noro et al. 1994.

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*Location is not currently considered part of the particular species distribution bounds.

| | | | | |
|---|---|---|---|---|
| Southern | Indonesia | *Sargassum* | *S. bacciferum* | New Zealand*, Indonesia, Tahiti*, Australia* |
| | | | *S. baccularia* | Singapore, China, Indonesia, Vietnam, Philippines |
| | | | *S. biserrula* | Indonesia, Philippines, Australia*, Singapore, New Guinea |
| | | | *S. carpophyllum* | Ceylon, Hong Kong, Australia, Indonesia, New Caledonia |
| | | | *S. cristaefolium* | Micronesia, Fiji, Indian Ocean, Japan Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Taiwan, Guam, Okinawa, Kermadec Islands |
| | | | *S. decaisnei* | Indonesia |
| | | | *S. duplicatum* | New Caledonia, Singapore, Malaysia, Philippines, Indonesia |
| | | | *S. echinocarpum* | Taiwan*, Solomons*, Indonesia*, Fiji*, New Caledonia*, Tonga*, Saudi Arabia*, Ethiopia*, Kenya*, Hawaii |
| | | | *S. gracile* | Indian Ocean, Indonesia, Philippines |
| | | | *S. granuliferum* | India, Indonesia, Malaysia, Philippines, New Guinea |

| | | | | |
|---|---|---|---|---|
| Southern | Indonesia (continued) | *Sargassum* | *S. grevillei* | Indonesia, Malaysia |
| | | | *S. hemiphylloides* | Indonesia |
| | | | *S. heterocystum* | Philippines, Indonesia*, New Guinea* |
| | | | *S. ilicifolium*<br>(= *S. sandei)* | Philippines, Indonesia, New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka |
| | | | *S. microcystum* | China*, Singapore, Philippines, Australia*, Indonesia |
| | | | *S. microphyllum* | Indonesia, Australia*, China* |
| | | | *S. myriocystum* | Indonesia, Philippines, New Caledonia |
| | | | *S. oligocystum*<br>(=*S. binderi)* | Japan, Taiwan, Vietnam, Malaysia, Indonesia, Sri Lanka, Indian Ocean, western Pacific, Philippines |
| | | | *S. paniculatum* | Indian Ocean, China, Pacific coast, Indonesia |
| | | | *S. plagiophylloides* | Indonesia, Philippines |
| | | | *S. parvifolium* | Singapore, China, Australia*, Indonesia, Philippines |
| | | | *S. polycystum* | Indonesia, Micronesia, Singapore, Australia, Japan, China, Sri Lanka, India, Philippines, Thailand |
| | | | *S. spinifex* | China Sea, Philippines, Indonesia |

| | | | | |
|---|---|---|---|---|
| Southern | Indonesia (continued) | *Sargassum* | *S. siliquosum* | Taiwan, Indonesia, Japan, Singapore, Philippines, Vietnam, China, New Guinea |
| | | | *S. swartzii* | Western Pacific, Tahiti*, Indonesia, New Guinea |
| | New Guinea | *Sargassum* | *S. baccularia* | Singapore, China, Indonesia, Vietnam, Philippines |
| | | | *S. biserrula* | Indonesia, Philippines, Australia*, Singapore, New Guinea |
| | | | *S. granuliferum* | India, Indonesia, Malaysia, Philippines, New Guinea |
| | | | *S. hetrocystum* | Philippines, Indonesia*, New Guinea* |
| | | | *S. pulchellum* | New Guinea, Singapore, Philippines |
| | | | *S. siliquosum* | Taiwan, Indonesia, Japan, Singapore, Philippines, Vietnam, China, New Guinea |
| | | | *S. tenue* | India, China, New Guinea |
| | Solomon Islands | *Sargassum* | *S. cristaefoliuim* | Micronesia, Fiji, Indian Ocean, Japan, Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Okinawa, Kermadec Islands |

Literature: Reinbold 1913, Setchell 1935, Levring 1960, Womersley and Bailey 1969.

| | | | | |
|---|---|---|---|---|
| | New Caledonia | *Phyllotricha* | *S. boryii* | New Caledonia |
| | | | *S. verruculosum* | New Caledonia |
| | | *Sargassum* | *S. carpophyllum* | Ceylon, Hong Kong, Australia, Indonesia, New Caledonia |

|  |  |  |  |
|---|---|---|---|
| New Caledonia (continued) | *Sargassum* | *S. cinctum* | New Caledonia, Japan, Indonesia, Indian Ocean, Philippines |
|  |  | *S. coriifolium* | Taiwan, Solomons, western Australia, Pakistan, New Caledonia |
|  |  | *S. crassifolium* | Micronesia, New Caledonia, Japan, Taiwan, Vietnam, Indonesia, East Africa, Sri Lanka, India, Philippines |
|  |  | *S. desvauxii* | New Caledonia |
|  |  | *S. duplicatum* | New Caledonia, Singapore, Malaysia, Philippines, Indonesia |
|  |  | *S. echinocarpum* | Taiwan*, Solomons*, Indonesia*, Fiji*, New Caledonia*, Tonga*, Saudi Arabia*, Ethiopia*, Kenya*, Hawaii |
|  |  | *S. filifolium* | Australia, New Caledonia, Philippines |
|  |  | *S. fissifolium* | New Caledonia |
|  |  | *S. flavicans* | New Caledonia |
|  |  | *S. ilicifolium* | Philippines, Indonesia, New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka |
|  |  | *S. lophocarpum* | New Caledonia |
|  |  | *S. myriocystum* | New Caledonia, Malaysia, Singapore, Philippines |
|  |  | *S. oligocystum* | Indonesia, Philippines, New Caledonia |
|  |  | *S. polycanthum* | New Caledonia |
|  |  | *S. spathulaefolium* | New Caledonia, Singapore, Malaysia |

| | | | |
|---|---|---|---|
| New Caledonia (continued) | *Sargassum* | *S. stenophyllum* | New Caledonia |
| | | *S. torvum* | New Caledonia |
| | | *S. turbinarioides* | New Caledonia, Philippines |
| | Unknown | *S. albermarlense* | New Caledonia |
| | | *S. scabripes* | New Caledonia |
| | | *S. spinuligerum* | New Caledonia |

Literature: Garrigue and Tsuda 1988.

| | | | |
|---|---|---|---|
| Fiji | *Sargassum* | *S. cristaefolium* | Micronesia, Fiji, Indian Ocean, Japan, Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Okinawa, Kermadec Islands |
| | | *S. horridulum* | Fiji |
| | | *S. obovatum* | Fiji |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Fiji, Thailand |

Literature: Garbary et al. 1991, South and Kasahara1992.

| | | | |
|---|---|---|---|
| Samoan islands | *Sargassum* | *S. anapense* | Samoa |
| | | *S. fonanonense* | Samoa |

Literature: Setchell 1924, Hunter et al. 1993.

| | | | |
|---|---|---|---|
| Society Islands | *Sargassum* | *S. boraborense* | Society Islands |
| | | *S. magarevense* | Society Islands |
| | | *S. sociale* | Society Islands |
| | | *S. tahitense* | Society Islands |

Literature: Setchell and Parks 1926, Taylor 1973, Payri and Naim 1982, Payri 1987.

| | | | |
|---|---|---|---|
| Australia | *Arthrophycus* | *S. fallax* | Australia |
| | | *S. lacerfolium* | Australia |
| | | *S. paradoxum* | Australia |
| | | *S. tristichum* | Australia |
| | | *S. vestitum* | Australia |
| | *Phyllotricha* | *S. decipiens* | Australia |
| | | *S. decurrens* | Australia |

|  |  |  |  |
|---|---|---|---|
| Australia (continued) | *Phyllotricha* | *S. heteromorphum* | Australia |
|  |  | *S. howeanum* | Australia |
|  |  | *S. sonderi* | Australia |
|  |  | *S. varians* | Australia |
|  |  | *S. verruculosum* | Australia, New Zealand, New Caledonia |
|  | *Sargassum* | *S. distichum* | Australia |
|  |  | *S. filifolium* | Australia, New Caledonia, Philippines |
|  |  | *S. linearifolium* | Australia |
|  |  | *S. peronii* | Australia, New Caledonia* |
|  |  | *S. podacanthum* | Australia |
|  |  | *S. spinuligerum* | Australia |

Literature: Agardh 1889; Lucas 1935; Womersley 1954, 1959, 1966, 1967, 1987; Shepherd and Womersley 1971; Clayton and King 1981.

|  |  |  |  |
|---|---|---|---|
| New Zealand | *Arthrophycus* | *S. sinclairii* | New Zealand |
|  | *Bactrophycus* | *S. serratifolium* | New Zealand, Japan, Korea, Philippines |
|  | *Phyllotricha* | *S. johnstoni* | New Zealand |
|  | *Phyllotricha* | *S. undulatum* | Australia*, New Zealand |
|  |  | *S. verrculosum* | New Zealand |
|  | *Sargassum* | *S. fissifolium* | Australia*, New Zealand |
|  |  | *S. spinuligerum* var. *novae-zealandiae* | New Zealand |

Literature: Lindauer et al. 1961, Hay et al. 1985, Nelson et al. 1992.

**Table 3: Distribution of *Sargassum* in the Western Pacific**

| State/Country | Subgenus | Species | Distribution |
|---|---|---|---|
| Japan | *Bactrophycus* | *S. ammophilum* | Japan |
| | | *S. autumnale* | Japan, Korea |
| | | *S. confusum* | Japan, China, Korea |
| | | *S. coreanum* | Japan |
| | | *S. filicinum* | Japan, Korea, Philippines |
| | | *S. fulvellum* | Japan, Hong Kong, Korea, China, Philippines |
| | | *S. giganteifolium* | Japan |
| | | *S. hemiphyllum* | Japan, Hong Kong, Vietnam, Taiwan, China |
| | | *S. horneri* | Japan, China, Taiwan, Hong Kong, Korea |
| | | *S. macrocarpum* | Japan, Korea |
| | | *S. microceratium* | Japan, Korea |
| | | *S. micracanthum* | Japan, Korea |
| | | *S. miyabei* | Japan, Korea |
| | | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |
| | | *S. nipponicum* | Japan, Korea |
| | | *S. nigrifolium* | Japan |
| | | *S. okamurae* | Japan |
| | | *S. pallidum* | Japan, Korea |
| | | *S. ringgoldianum* | Japan |
| | | *S. sagamianum* | Japan, Korea |
| | | *S. segii* | Japan |
| | | *S. serratifolium* | Japan, Korea, New Zealand, Philippines |
| | | *S. siliquastrum* | Japan, China, Hong Kong, Korea |
| | | *S. tennuifolium* | Japan |
| | | *S. thumbergii* | Japan, China, Hong Kong, Korea |
| | | *S. trichophyllum* | Japan |
| | | *S. yamadae* | Japan, Korea |
| | | *S. yamamotoi* | Japan |
| | | *S. yezoense* | Japan, Korea |
| | *Sargassum* | *S. alternato-pinatum* | Japan |
| | | *S. angustifolium* | Japan, China, Indian Ocean |
| | | *S. assimle* | Indowestern Pacific, Japan, China, Vietnam, Ceylon |
| | | *S. coriifolium* | Taiwan, Solomons, western Australia, Pakistan, New Caledonia |
| | | *S. crassifolium* | Micronesia, New Caledonia, Japan, Taiwan, Vietnam Indonesia, East Africa, Sri Lanka |
| | | *S. crispifolium* | Japan, Philippines |

| | | | |
|---|---|---|---|
| Japan (continued) | *Sargassum* | *S. cristaefolium* | Micronesia, Fiji, Indian Ocean, Japan, Malaysia, Indonesia Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Okinawa, Kermadec Islands |
| | | *S. henslowianum* | Japan, China, Vietnam |
| | | *S. ilicifolium*<br>(= *S. sandei*) | Philippines<br>Indonesia, New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka |
| | | *S. oligocystum*<br>(= *S. binderi*) | Japan,<br>Taiwan, Vietnam, Malaysia, Indonesia, Sri Lanka, Indian Ocean, western Pacific, Philippines |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Guam, Thailand |
| | | *S. polyporum* | Japan |
| | | *S. saicifoliodes* | Japan |
| | | *S. ilicifolium*<br>(= *S. sandei)* | Vietnam, Japan<br>Singapore, Malaysia, Philippines |
| | | *S. siliquosum* | Taiwan, Indonesia, Japan, Singapore, Philippines, Vietnam, China, New Guinea |
| | | S. swartzii<br>*(S. acutifolium)* | Western Pacific, Vietnam<br>Indian Ocean, Tahiti*, Indonesia, New Guinea |

Literature: Yendo 1907; Yamada 1942, 1944; Yoshida 1987, 1988; Tseng et al. 1985; Tsuda 1991; Tseng and Lu 1992a, 1992b; Ajisaka et al. 1994; Noro et al. 1994.

| | | | |
|---|---|---|---|
| Korea | *Bactrophycus* | *S. autumnale* | Japan, Korea |
| | | *S. confusum* | Japan, China, Korea |
| | | *S. coreanum* | Japan, Korea |
| | | *S. filicinum* | Japan, Korea, Philippines |
| | | *S. fulvellum* | Japan, Hong Kong, Korea, Philippines, China |
| | | *S. hemiphyllum* | Korea, Japan, China, Taiwan, Hong Kong, Vietnam |
| | | *S. horneri* | Japan, China, Taiwan, Hong Kong, Korea |
| | | *S. macrocarpum* | Japan, Korea |
| | | *S. micracanthum* | Japan, Korea |
| | | *S. microceratium* | Japan, Korea |
| | | *S. miyabei* | Japan, Korea |
| | | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |

| | | | |
|---|---|---|---|
| Korea (continued) | *Bactrophycus* | *S. nipponicum* | Japan, Korea |
| | | *S. pallidum* | Japan, Korea |
| | | *S. sagamianum* | Japan, Korea |
| | | *S. serratifolium* | Japan, Korea, New Zealand, Philippines |
| | | *S. siliquastrum* | Japan, China, Korea, Hong Kong |
| | | *S. thunbergii* | Japan, China, Hong Kong, Korea |
| | | *S. yamadae* | Japan, Korea, Philippines |
| | | *S. yezoense* | Japan, Korea |

Literature: Kang 1966, Kang 1968, Yoo 1976, Lee and Kang 1986, Lee and Yoo 1992.

| | | | |
|---|---|---|---|
| China | *Bactrophycus* | *S. confusum* | China, Japan, Korea |
| | | *S. emarginatum* | China |
| | | *S. fulvellum* | Hong Kong, Japan, China, Korea, Philippines |
| | | *S. hemiphyllum* | Hong Kong, China, Japan, Taiwan, Vietnam, Korea |
| | | *S. herklotsii* | Vietnam, China |
| | | *S. horneri* | Japan, China, Taiwan, Hong Kong, Korea |
| | | *S. mcclurei* | Vietnam, China |
| | | *S. muticum* | Japan, China, north Atlantic, north Pacific (British Columbia to Mexico) |
| | | *S. phyllocystum* | China |
| | | *S. rostratum* | Hong Kong, Taiwan, China |
| | | *S. siloquastrum* | Japan, China, Hong Kong |
| | | *S. thunbergii* | China, Japan |
| | *Sargassum* | *S. aemulum* | Australia*, China, Philippines |
| | | *S. agaviforme* | China |
| | | *S. angustifolium* | India, China, Japan |
| | | *S. assimile* | Indowest Pacific, Japan, China, Vietnam, Ceylon |
| | | *S. baccularia* | Singapore, Indonesia, Vietnam, China, Philippines |
| | | *S. capilliforme* | China |
| | | *S. carpophyllum* | Ceylon, China, Taiwan, India |
| | | *S. cinereum* | Ceylon, Australia*, China, Singapore |
| | | *S. frutescens* | China |
| | | *S. fruticulosum* | China |
| | | *S. glaucescens* | China, Taiwan, Vietnam, Singapore |
| | | *S. graminifolium* | China, Vietnam |
| | | *S. guangdongii* | China |
| | | *S. henslowianum* | China, Vietnam |
| | | *S. incanum* | Japan, China, Vietnam |
| | | *S. kuetzingii* | China, Vietnam |
| | | *S. laxifolium* | China |
| | | *S. leizhouense* | China |

| | | | |
|---|---|---|---|
| China (continued) | *Sargassum* | *S. logicaulis* | China |
| | | *S. longifructum* | China |
| | | *S. nozhouense* | China |
| | | *S. paniculatum* | China, Indian Ocean, Vietnam |
| | | *S. parvivesiculosum* | Japan |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Guam, Japan, China, Sri Lanka, India, Okinawa, Taiwan, Tonga, Fiji, Thailand |
| | | *S. polyporum* | China, Vietnam |
| | | *S. qinzhouense* | China |
| | | *S. shangchuanii* | China |
| | | *S. siliquosum* | Singapore, Indonesia, Philippines, Vietnam, Japan, China |
| | | *S. subtilissimum* | China |
| | | *S. tenerrimum* | India, Ceylon, China, Vietnam, New Guinea |
| | | *S. tenue* | India, China |
| | | *S. vachellianum* | China, Vietnam |

Literature: Tseng et al. 1985; Tseng and Lu 1988, 1992a, 1992b.

| | | | |
|---|---|---|---|
| Vietnam | *Bactrophycus* | *S. mcclurei* | Vietnam, Hong Kong |
| | | *S. hemiphyllum* | Vietnam, China |
| | | *S. herklotsii* | Vietnam, China |
| | *Sargassum* | *S. angustifolium* | Japan, Vietnam |
| | | *S. baccularia* | Vietnam, China, Indonesia |
| | | *S. cinereum* | Ceylong, Australia*, China, Singapore |
| | | *S. crassifolium* | Micronesia, New Caledonia, Japan, Taiwan, Vietnam, Indonesia, East Africa, Sri Lanka, India, Philippines |
| | | *S. cymosum* | Vietnam |
| | | *S. duplicatum* | New Caledonia, Malaysia, Singapore, Philippines |
| | | *S. feldmannii* | Vietnam, Philippines |
| | | *S. glaucescens* | China, Taiwan, Vietnam, Singapore |
| | | *S. gracillimum* | Indonesia, Philippines, Vietnam |
| | | *S. graminifolium* | China, Vietnam |
| | | *S. henslowianum* | Japan, China, Vietnam |
| | | *S. incanum* | Japan, China, Vietnam |
| | | *S. paniculatum* | China, Indian Ocean, Vietnam |
| | | *S. piluliferum* | Vietnam |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |

| | | | |
|---|---|---|---|
| Vietnam (continued) | Sargassum | *S. polyporum* | China, Vietnam |
| | | *S. siliquosum* | Singapore, Indonesia, Philippines, Vietnam, Japan, China |
| | | *S. swartzii* | Western Pacific, Vietnam |
| | | *S. tenerrimum* | India, Ceylon, China, Vietnam |
| | | *S. vachellianum* | Vietnam, China |
| | | *S. vietnamense* | Vietnam |
| | | *S. virgatum* | Vietnam |

Literature: Dawson 1954, Dinh et al. 1993.

| | | | |
|---|---|---|---|
| Thailand | *Sargassum* | *S. grevillei* | Malaysia*, Indonesia |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |

Literature: Velasquez and Lewmanomont 1975.

| | | | |
|---|---|---|---|
| Malaysia | *Sargassum* | *S. asperifolium* | Singapore |
| | | *S. cristaefolium* | Micronesia, Fiji, Indian Ocean, Japan, Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines, Okinawa, Kermadec Islands |
| | | *S. duplicatum* | New Caledonia, Malaysia, Singapore, Philippines |
| | | *S. filipendula* | Malaysia |
| | | *S. granuliferum* | Malaysia |
| | | *S. grevellei* | Malaysia, Indonesia* |
| | | *S. hornschuchii* | Malaysia |
| | | *S. ilicifolium* (= *S. sandei*) | Philippines, Indonesia, New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka |
| | | *S. myriocystum* | Singapore, Malaysia, New Caledonia, Philippines |
| | | *S. oligocystum* (= *S. binderi*) | Japan, Taiwan, Vietnam, Malaysia, Indonesia, Sri Lanka, Indian Ocean, western Pacific, Philippines |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |
| | | *S. spathulaefolium* | New Caledonia, Singapore, Malaysia |
| | | *S. tenerrimum* | Micronesia, China, Malaysia |

| | | | |
|---|---|---|---|
| Malaysia (continued) | *Sargassum* | *S. torvum* | Singapore, Malaysia, New Caledonia, Japan |
| | | *S. virgatum* | Malaysia |
| | | *S. vulgare* | Malaysia |
| | | *S. wightii* | Malaysia |

Literature: Phang 1985, 1986; Ajisaka et al. 1994.

| | | | |
|---|---|---|---|
| Singapore | *Sargassum* | *S. asperifolium* | Malaysia, Singapore |
| | | *S. baccularia* | Singapore, China, Vietnam, Indonesia, Philippines |
| | | *S. cinereum* | Ceylon, Australia, China, Singapore |
| | | *S. duplicatum* | New Caledonia, Malaysia, Singapore, Philippines |
| | | *S. ilicifolium*<br>(*S. sandei*) | Philippines, Indonesia, New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka |
| | | *S. myriocystum* | Singapore, Malaysia, New Caledonia, Philippines |
| | | *S. polycystum* | Micronesia, Fiji, Indonesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |
| | | *S. spathulaefolium* | New Caledonia, Singapore, Malaysia |

Literature: Wei and Chin 1983.

| | | | |
|---|---|---|---|
| Philippines | *Arthrophycus* | *S. biforme* | Philippines |
| | *Bactrophycus* | *S. confusum* | Japan, Korea, China, Philippines |
| | | *S. filicinum* | Japan, Korea, Philippines |
| | | *S. fulvellum* | Japan, Hong Kong, Korea, China, Philippines |
| | | *S. giganteifolium* | Philippines, Japan |
| | | *S. hemiphyllum* | Japan, Hong Kong, Philippines, Korea, China, Taiwan |
| | | *S. miyabei* | Japan, Philippines |
| | | *S. nigrifolium* | Japan, Philippines |
| | | *S. sagamianum* | Japan, Korea |
| | | *S. serratifolium* | New Zealand, Japan, Korea, Philippines |
| | *Phyllotricha* | *S. patens* | Philippines |
| | | *S. abbottiae* | Philippines |
| | *Sargassum* | *S. aemulum* | Australia, China |
| | | *S. agardhianum* | California, Baja California, Mexico |

| | | | |
|---|---|---|---|
| Philippines (continued) | *Sargassum* | *S. baccularia* | Singapore, China, Indonesia, Vietnam, Philippines |
| | | *S. balingasayense* | Philippines |
| | | *S. bataanense* | Philippines |
| | | *S. belangeri* | Indonesia, Java, Sunda Straight, Philippines |
| | | *S. oligocystum* (= *S. binderi*) | Japan, Taiwan, Vietnam, Malaysia, Indonesia, Sri Lanka, Indian Ocean, western Pacific, Philippines |
| | | *S. cinctum* | New Caledonia, Japan, Indonesia, Indian Ocean, Philippines |
| | | *S. crassifolium* | Micronesia, New Caledonia, Japan, Taiwan, Vietnam, Indonesia, East Africa, Sri Lanka, India, Philippines |
| | | *S. crispifolium* | Japan, Philippines |
| | | *S. cristaefolium* | Micronesia |
| | | (*S. berberfolium*) | Fiji, Indian Ocean, Japan, Malaysia, Indonesia, Sri Lanka, India, Taiwan, Guam, Vietnam, Philippines |
| | | *S. currimaoense* | Philippines |
| | | *S. cystocarpum* | Philippines |
| | | *S. cystophyllum* | Philippines |
| | | *S. duplicatum* | Singapore, New Caledonia, Malaysia, Philippines |
| | | *S. dotyi* | Philippines |
| | | *S. droserifolium* | Philippines |
| | | *S. filifolium* | Australia, New Caledonia, Philippines |
| | | *S. filiforme* | Philippines |
| | | *S. feldmannii* | Vietnam, Philippines |
| | | *S. gaudichaudii* | Philippines |
| | | *S. giganteifolium* | Japan, Philippines |
| | | *S. gracile* | Indian Ocean, Indonesia, Java, Philippines |
| | | *S. granuliferum* | India,Indonesia, Malaysia, Philippines, New Guinea |
| | | *S. gracillimum* | Indonesia, Philippines |
| | | *S. hemiphyllum* | Korea, Japan, China, Taiwan, Hong Kong, Vietnam, Philippines |
| | | *S. heterocystum* | Philippines, Indonesia, New Guinea |
| | | *S. ilicifolium* | Philippines, Indonesia, |

| | | | |
|---|---|---|---|
| Philippines (continued) | *Sargassum* | (*S. sandei*) | New Caledonia, Japan, Taiwan, Indian Ocean, Singapore, Vietnam, Malaysia, Australia, Sri Lanka, Philippines |
| | | *S. kushimotense* | Japan, Taiwan, Philippines |
| | | *S. latifolium* | Red Sea, Philippines |
| | | *S. microcystum* | Singapore, Philippines |
| | | *S. myriocystum* | Indonesia, Philippines, New Caledonia |
| | | *S. ohnoi* | Philippines |
| | | *S. oligocystum* | Indonesia, , New Caledonia, Philippines |
| | | *S. oocyste* | Indonesia |
| | | *S. paniculatum* | Indian Ocean, China, Pacific coast, Indonesia |
| | | *S. parvifolium* | Philippines, Indonesia, Singapore*, China*, Australia* |
| | | *S. polyceratum* | Cuba, Philippines |
| | | *S. polycystum* | Indonesia, Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, India, Thailand |
| | | *S. pteropleron* | Bahamas, Philippines |
| | | *S. samarense* | Philippines |
| | | *S. siloquosum* | Japan, Vietnam, Indonesia, Philippines |
| | | *S. spinifex* | China Sea, Philippines |
| | | *S. subspathulatum* | Indonesia, Philippines |
| | | *S. sullivanii* | Philippines |
| | | *S. tenerrimum* | India, China, Ceylon, Vietnam, Philippines |
| | | *S. turbinarioides* | Vietnam, New Caledonia, Philippines |
| | | *S. umezakii* | Philippines |
| | | *S. velasquezii* | Philippines |
| | | *S. vulgare* | Atlantic Ocean, Philippines |
| | | *S. yamadae* | Philippines, Japan, Korea |
| | | *S. yoshidae* | Philippines |
| | Unknown | *S. elongatum* | Philippines |
| | | *S. furcatum* | Philippines |
| | | *S. microphyllum* | Philippines |
| | | *S. natans* | Atlantic Ocean, Caribbean, Sargasso Sea, Philippines |
| | | *S. piluliferum* | Japan, Philippines |
| | | *S. yendoi* | Japan, Philippines |

Literature: Silva et al. 1987, Trono 1992, 1994.

winds. As Munk proposed in 1955, the basic pattern of oceanic currents is generated in an idealized rectangular basin (Fig. 4). This pattern is found in all three ocean basins (Pacific, Atlantic, and Indian) and includes four wind-driven gyres. In the Pacific, these include a well-developed large clockwise subtropical gyre in the Northern Hemisphere, two smaller gyres around the equator, and a well-developed large counterclockwise subtropical gyre in the Southern Hemisphere. The bulk of the water flow for the Pacific basin is westerly via the North and South Equatorial currents, with a relatively minor amount of water flowing back easterly via the Equatorial Countercurrent in normal years (Jokiel and Martinelli 1992). Consequently, the North and South Equatorial currents are the major pathways of transport for the tropical Pacific Ocean basin. Areas where water and drift material accumulate develop as a result of western equatorial boundaries for these currents. In the Pacific region, these collection loci include Indonesia, the Philippines, Papua New Guinea, and eastern Australia (McNally et al. 1983, Koga and Yaki 1989). However, El Niño also has dramatic effects on these long-term average current patterns and diversity loci. With the onset of El Niño, a Kelvin wave is initiated that disrupts westward bulk water flow and results in bulk eastward water flow along the equator (Richmond 1989). Thus, in El Niño years, an alternative collection locus may develop around Baja California. Thus, understanding and acknowledging the potential influence of oceanic currents on diversity patterns are pertinent because the currents can effectively disperse marine organisms (Zinsmeister and Emerson 1979, Scheltema 1986).

The major models of biogeography are vicariance, dispersal and vortex models. In the vicariance model, species develop because of long-term geographical separation, with allopatric speciation as the mechanism for speciation (McCoy and Heck 1976, Nelson and Rosen 1981, Rosen 1988, Cox and Moore 1993). In the dispersal model, new species develop in the center of diversity, with subsequent spread to outlying areas (Ekman 1953, Dana 1975, Briggs 1984). In this model, sympatric speciation is the implied mechanism for speciation. In the vortex model, species are formed outside diversity centers and carried back to these centers via oceanic currents (Jokiel and Martinelli 1992). Intrinsic in this model are both vicariance and dispersal theories and allopatric and sympatric speciation mechanisms. In other words, diversity centers are created by oceanic currents because species accumulate there rather than being formed there. However, this model also allows sympatric speciation, thus not excluding formation of species within diversity centers. For the Pacific basin, areas of accumulation likely include the Philippines, Indonesia, Papua New Guinea, and eastern Australia, and, for the most part, mirror coral diversity centers (Jokiel and Martinelli 1992).These models were largely developed for marine invertebrates, and fundamental differences exist between marine invertebrates and marine algae as to longevity in the water columm and dispersal capabilities.

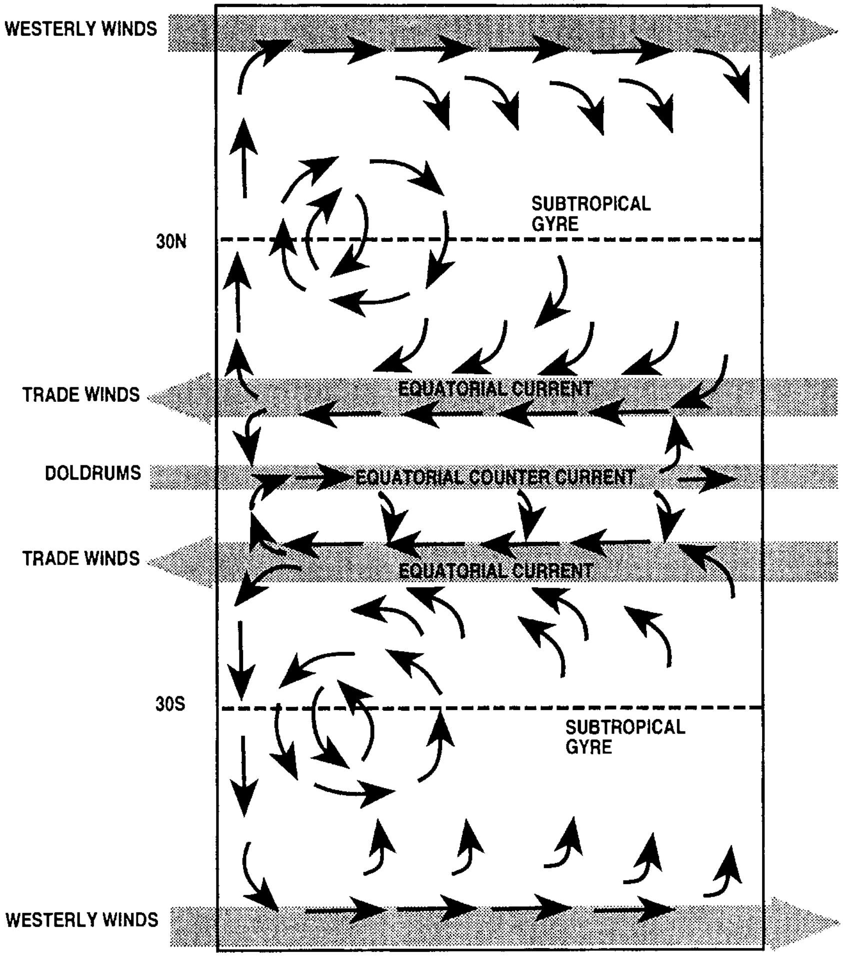

**Fig. 4. Idealized circulation gyres for the world's ocean basins (after Munk 1955).**

## Evolution of *Sargassum* and Its Subgenera and Species

*Phyllotricha* and *Arthrophycus* are interesting Pacific basin subgenera. They have centers of diversity in Australia, few species compared with the other subgenera, and an extremely high degree of endemism (86–100%; Table 4). This diversity center may be both the center of origin for the two subgenera and a species accumulation area (Jokiel and Martinelli 1992). Evidence comes from the views that areas of endemism are generally considered regions of species formation and that few endemic species exist outside those regions (Kay 1984, Jokiel and Martinelli 1992). These species when dispersed may also be caught in feedback loops in oceanic circulation that result in low gene flow outside the

**Table 4. Diversity and Endemism of *Sargassum* Subgenera in the Pacific Basin[1]**

| **Geographical Category** | **Number of Endemic Species Per Total Number of Species** | | | |
|---|---|---|---|---|
| | ***Arthrophycus*** | ***Bactrophycus*** | ***Phyllotricha*** | ***Sargassum*** |
| Continental | | | | |
| California/Baja | 0/0 | 0/1 | 1/1 (100) | 3/4 (75) |
| Columbia | 0/0 | 0/0 | 0/0 | 1/1 (100) |
| Peru | 0/0 | 0/0 | 0/0 | 1/2 (50) |
| Chile | 0/0 | 0/0 | 0/0 | 1/1 (100) |
| Australia | 5/5 (100) | 0/0 | 6/7 (86) | 4/6 (66) |
| Korea | 0/0 | 0/20 | 0/0 | 0/0 |
| China | 0/0 | 2/12 (16) | 0/0 | 16/32 (50) |
| Vietnam | 0/0 | 0/0 | 0/0 | 1/19 (8) |
| Malaysia | 0/0 | 0/0 | 0/0 | 7/17 (41) |
| Singapore | 0/0 | 0/0 | 0/0 | 0/8 |
| **Total** | 5/5 (100) | 2/36 (6) | 7/8 (88) | 34/92 (33) |
| **Total for all subgenera** | | 48/141 (34) | | |
| Continental islands | | | | |
| New Caledonia | 0/0 | 0/0 | 2/2 (100) | 3/18 (17) |
| New Zealand | 1/1 (100) | 0/1 | 2/3 (67) | 2/2 (100) |
| Japan | 0/0 | 10/29 (34) | 0/0 | 3/16 (19) |
| Philippines | 1/1 (100 | 0/9 | 2/2 (100) | 17/53 (33) |
| Indonesia/New Guinea | 0/0 | 0/0 | 0/0 | 4/27 (15) |
| **Total** | 2/2 (100) | 10/39 (25) | 6/7 (86) | 25/90 (28) |
| **Total for all subgenera** | | 46/165 (29) | | |
| Oceanic islands | | | | |
| Easter Island | 0/0 | 0/0 | 0/0 | 1/1 (100) |
| Galapagos | 0/0 | 0/0 | 1/1 (100) | 3/3 (100 |
| Hawaii | 0/0 | 0/0 | 0/0 | 5/5 (100) |
| Micronesia | 0/0 | 0/0 | 0/0 | 0/4 |
| Solomons | 0/0 | 0/0 | 0/0 | 0/1 |
| Fiji | 0/0 | 0/0 | 0/0 | 2/4 |
| Society islands | 0/0 | 0/0 | 0/0 | 4/4 |
| **Total** | **0/0** | 0/0 | 1/1 (100) | 15/22 (68) |
| **Total for all subgenera** | | 16/23 (70) | | |

[1] Percentage of endemism (numbers in parentheses) is the total number of endemic species divided by the total number of species for a given geographical area multiplied by 100. Total diversity and endemism values are included for each geographical category (e.g., oceanic islands or continental areas). These calculations are based on geographic category totals.

region, with more species formation within the diversity center by sympatric speciation.

*Bactrophycus*, also a Pacific basin subgenus, has an apparent center of diversity in eastern Asia. This subgenus has numerous species, with an average endemism rate of 6% (Table 4). However, unlike *Phyllotricha* and *Arthrophycus*, *Bactrophycus* species are widely distributed outside their diversity center, at least in the western Pacific (Philippines or New Zealand), and are not typically endemic outside eastern Asia. This lack of endemism outside eastern Asia may be attributable to circulation patterns that result in high gene flow between eastern Asia and the Philippines or to the taxonomic state of the Philippine flora or to both. Because eastern Asia is not considered a water accumulation area, the high diversity here is difficult to explain but may be the result of recent radiation. On the other hand, the low rates of endemism could be attributable to high gene flow within eastern Asia. If this is an eastern Asian radiation, it may be, in part, attributable to physiological tolerance and dispersal capabilities of *Bactrophycus* species. The distribution of *Bactrophycus* suggests that this subgenus is a temperate subgenus unable to populate subtropical to tropical areas, or possibly, cross these thermal boundaries to temperate areas. Evidence comes from inability of *S. muticum* to have naturally invaded northern Pacific or Atlantic temperate regions. However, once artificially introduced, it easily grows to nuisance-weed proportions (Abbott and Hollenberg 1976, Critchley et al. 1983).

*Sargassum* is the most widespread subgenus, with a reported average endemism of 60% (Table 4). This subgenus is subtropical to tropical in its distribution and is primarily limited to these areas in the Pacific basin. It is difficult to pinpoint a single center of diversity for this subgenus; many continental and oceanic island areas have numerous species, for example, New Caledonia, Japan, China, Malaysia/Singapore, and the Philippines. Given this range of distribution, this subgenus is apparently very adept in dispersal, resulting in the greatest potential for high gene flow despite the greatest distances for dispersal. This pattern of wide distribution may explain why this subgenus has a lower rate of endemism compared with other subgenera. Another interesting note is that this lower endemism occurs mainly in continental areas. Among oceanic islands such as Hawaii, Tahiti, or the Galapagos, where only a handful of species exist, the rate of endemism approaches 100%. This pattern is in accordance with the vortex model, in which diversity develops in the west because of species accumulation and is attenuated to the east with low gene flow (Jokiel and Martinelli 1992). In accordance with this, Baja California becomes a possible point of origin for the *Sargassum* subgenus. This is an interesting hypothesis because during El Niño years, with bulk water flow along the equatorial countercurrents, Baja becomes a potential area of species accumulation. Also, a fair number of species are found in Baja California and a high degree of local endemism exists.

This eastward attenuation is also evident when continental areas are compared with continental islands and oceanic islands with continental islands. In the first comparison, areas with the greatest number of subgenera (three to four) include both continental areas and continental islands: Australia, New Zealand, Philippines, and artificially (because of the introduced *S. muticum*), California (Table 4). With the exception of California, these areas include the main centers of species accumulation for the Pacific basin. Most of continental eastern Asia and the continental islands of Japan and New Caledonia have two subgenera, as do the oceanic islands of the Galapagos. In contrast, many of the oceanic islands of the central Pacific region and continental South America have only a single subgenus (*Sargassum*), which indicates eastward attenuation.

These apparent areas of diversity for subgenera are not always in congruence with the center of diversity for species. Continental islands have the greatest number of total species (165); next, in order, are continental areas (141) and oceanic islands (23). On the other hand, the areas with the highest rates of endemism are relatively isolated oceanic islands (70%); continental areas have lower rates (34%) and continental islands have the lowest (29%; Table 4). It is interesting that the most species-rich areas have the lowest rate of endemism and the least rich areas have the highest rate. This pattern apparently is in accord with the vortex model, indicating westward species accumulation in continental island areas and eastward species attenuation from reduced gene flow and island isolation. These insights may indicate that *Sargassum* species evolved in peripheral areas (for example) and were then carried back into diversity centers via oceanic currents. It does seem that the stepping-stone theory of species dispersal can be invoked here, because a pattern exists of a decreasing number of species with increasing distance as one moves from the west to the east across the Pacific basin (Kay 1984). However, this model must be used cautiously because it was developed for marine mollusks, which are intrinsically different dispersers from *Sargassum*.

So how do Pacific *Sargassum* species disperse? Both Pacific currents and the biogeographical models of dispersal and vortex dictate a westward movement of species across the Pacific basin. This implies that local floras could be made up of several different regional components, resulting in some complex floras. For instance, Japanese flora could be composed of components from California, oceanic islands, or Indonesia-Malayasian regions. This makes sorting out the progenitors difficult. Did these floras evolve from many species or just a handful? It may be useful to examine widespread species as possible dispersal agents for the Pacific region. For example, the central Pacific species of *Sargassum* could have evolved from widespread species such as *S. cristaefolium* or *S. polyphyllum*. However, much of this is speculative. Definitive methods are needed to test hypotheses of this sort.

## Summary

In conclusion, we have a better framework for *Sargassum* taxonomy today than we did at the turn of the century. However, much research in both systematics and nomenclature is needed to give stability to the taxonomy. Much of the

Pacific basin flora is well known; adequate collections and descriptions of species are lacking for only a few areas.

Understanding of oceanic currents and use of biogeographical models provides a framework to begin to understand and unravel the evolution and biogeography of *Sargassum* in the Pacific basin. The vortex model seems the most appropriate and supports the patterns of diversity and endemism found in many areas of the basin. Evidence suggests species and subgenera diversity centers occur in the west and attenuate eastward. Although some hypotheses have been proposed for evolution of the genus as a whole and for evolution of the specific subgenera, definitive centers of origin for the subgenera or species have not been resolved.

As stated, much of this is speculative. With application of current molecular techniques, we should be able to test these hypotheses. Taxonomic affinities, biogeography, and phylogeny of many seemingly intractable terrestrial groups and of marine algae have begun to be resolved with application of these techniques (see Kooistra et al. 1992, DeJoode and Wendel 1992, Doyle 1993, van Oppen et al. 1994). We are at an exciting and challenging turning point in *Sargassum* taxonomy and biogeographical research. The next stage calls for novel and insightful approaches that may open the door to another level of understanding.

## Acknowledgments

The author would like to thank C. M. Smith and I. A. Abbott for critical manuscript reviews, and the Office of Naval Research for financial support through the ASSERT fellowship program.

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# Section II. *Gelidiales*

## INTRODUCTION

### Isabella A. Abbott

The taxonomy of *Gelidium/Pterocladia* is currently in a state of "suspended animation" because of the necessity of finding stable, suitable, repeatably observed features that can be used to distinguish one genus from the other. Earlier it was noted in cross-sections that cystocarps of *Pterocladia* species occasionally had more than one cavity and that cystocarps of *Gelidium* species sometimes had fewer than two cavities, so that the number of locules (cavities) used to define each genus sometimes overlapped and therefore was an unreliable basis for differentiating the two genera. Distinguishing characteristics are still being sought, even though Norris (1992) advocated the abandonment of *Pterocladia,* to be subsumed with *Gelidium.* He did not, however, transfer *Pterocladia* species to *Gelidium.*

When a genus is "too big," with too many species (e.g., *Sargassum* with more than 400, and *Gracilaria* with more than 100), sorting the species is difficult. A simple key for sorting 28 species of *Sargassum*, for example, requires two pages of single-spaced 8-point type. Hence, it is necessary to continue to seek other features that might be used to distinguish genera (and species). In addition, in many genera, most of the specimens found by researchers are sterile, yet most of the features used for differentiation are features of reproductive structures. Vegetative features are sometimes helpful.

At the second workshop, in 1988, Deni Rodríguiz and Bernabé Santelices examined the apices and other vegetative features of 24 species of *Gelidium* and *Pterocladia* and concluded that the position of the apical cell in relation to cortical cells and the initial cells of lateral branches (lateral initials) allowed generic segregation in 23 of the 24 species. At the fifth workshop, in 1993, the same authors closely studied the apical architecture of two Chilean species of *Gelidium* that grow in the same zone. The ontogeny of the apical cells of these two is different from the start. Once established, seasonal changes in the activities of the apical cell are synchronized with activities in lateral initials and cortical cells. Thus, differences in apical cells can be found among species, as well as between the two genera.

New records and a reevaluation of previously described Gelidiales are provided in this volume by Hae Bok Lee in the chapter on Korean species in this order. Six previously reported species are removed from the Korean flora, and three are uncertain.

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# TEMPORAL VARIATIONS IN THE APICAL ARCHITECTURE OF TWO SPECIES OF *GELIDIUM* FROM CENTRAL CHILE

D. Rodríguez and B. Santelices

## Abstract

The apical architecture of two species of *Gelidium* from the coast of central Chile showed ontogenic and seasonal changes. In both species, the first stage of apical development corresponded with the presence of pointed tips, with smooth margins, and a distinctive apical cell. Both species then differentiate by producing the initial cells of lateral branches (lateral initials) on both sides of the axial apical cell. In *G. chilense*, the lateral initials first divided transversely and later obliquely or longitudinally. In *G. rex*, lateral initials divided obliquely as well as longitudinally from the beginning of development. Once the apical architecture typical of the species was established, seasonal changes in apical morphology involved the alternating activities of the axial apical cell, the lateral initials, and the cortical cells. In both species, regenerating branches skipped the first stages of ontogenic differentiation. Branch fragments regenerated to the corresponding morphological stage by starting from some later stage of development.

## Introduction

Earlier, we reported significant interspecies differences in apical architecture among *Gelidium* and *Pterocladia* (Rodríguez and Santelices 1987). These included (1) the position of the initial axial apical cell (apical initial) with respect to the cortical cells and (2) the shape, type of division, and position of the initial cells of lateral branches (lateral initials) with respect to the axial apical cell and the cortical cells. The complexity of the apical morphology of different species of *Pterocladia* and, especially, of *Gelidium* seemed to vary. Whereas the apical growth of some species resulted from the alternating activities of a single apical initial and the cortical cells, growth of other species seemingly included the additional activity of morphologically different lateral initials.

Because the apical architecture of the species of *Gelidium* appeared different from that of species of *Pterocladia*, we (Rodríguez and Santelices 1987) suggested that this feature could be used to distinguish one genus from the other if the apical architecture was little affected by abiotic factors and the results of tests with more species indicated the validity of the differences.

Study of more species of *Gelidium* and *Pterocladia* has revealed limitations in the use of apical architecture as a characteristic for separating the two genera. Although many large-sized species of *Gelidium* and *Pterocladia* conform to the pattern (Rodríguez and Santelices1988, Renfrew et al. 1989), small-sized species of *Pterocladia* (e.g., *P. bulbosa*, *P. caloglossoides*, *P. media*) have *Gelidium*-type apices (Rodríguez and Santelices 1988, Santelices 1990).

Recent morphological studies with species of both genera have revealed clear intrageneric heterogeneity in cystocarpic (Santelices 1991a, 1991b) and medullary structures (unpublished observations). Therefore, determining clear-cut generic differences between *Gelidium* and *Pterocladia* is no longer important, because each taxon will likely be split into several genera. However, the effect of season or other environmental factors on apical architecture remains to be studied. This chapter focuses on the temporal variations in apical morphology in two common species of *Gelidium* from the coast of central Chile. We have followed the ontogenic development of apical architecture from sporeling to adult plants. Through monthly surveys of representative field populations, we measured the seasonal changes in apical structure of both taxa, and through observations on regenerating fronds, we determined how much regeneration recapitulates differentiation.

## Materials and Methods

### Species

Intertidal–shallow subtidal populations of *G. chilense* (Montagne) Santelices et Montalva and *G. rex* Santelices et Abbott were used for this study. The apical structure of adult sterile plants of these two species includes an apical initial present in depressions between cortical lobes or at the same level as other cortical cells (Rodríguez and Santelices 1978, Fig. 5). In addition, the apex has several lateral initials that are morphologically different from the apical initial. Whereas apical initials are globose or dome-shaped, lateral initials are smaller and have the shape of an inverted cone. In addition, in these two species, the lateral initials divide longitudinally, whereas the corresponding apical initials divide transversely only.

### Ontogenetic Studies

In April 1990, tetrasporangial specimens of *G. chilense* and *G. rex* were collected in Pelancura, 5 km north of Puerto San Antonio (lat. 33° 32′S, long. 71° 38′W). They were transported in plastic buckets filled with seawater. At the laboratory, plants were washed with tap water and carefully brushed to reduce contaminants. Tetrasporangial branches were separated, placed in 30 ml of SWM-3 culture medium in small Petri dishes (60 mm in diameter), and left overnight at 15 °C with low irradiance (20 $\mu$E m$^{-2}$ s$^{-1}$) to allow release and settlement of spores. After spore release, fertile branchlets and the culture medium were discarded. The released spores were incubated in fresh SWM-3, at 15 °C, with higher irradiance (50 $\mu$E m$^{-2}$ s$^{-1}$). Ten replicates per species were used. The culture medium was changed every 7 days. Cultures of *G. rex* were maintained for 80 days; those of *G. chilense*, 420 days. After 7 months of growth, the plantlets of *G. chilensis* were transplanted to clam shells inside larger (100 × 80 mm) Petri dishes filled with 150 ml of SWM culture medium. Alternating periods of immersion and emersion were produced by placing the dishes on a rotating platform.

Apical development was determined in both species every 3–5 days during the first 3 weeks of growth and every week thereafter. In the case of *G. chilense*, after 7 months of growth, observations were made every 3 weeks. Apical architecture was also determined in specimens gathered from the same study site in Pelancura in the spring (September 1990) and summer (February 1991). Plants of *G. chilense* 0.03–4.00 cm long and plants of *G. rex* 0.05–15.00 cm long were preserved in a 5% solution of formaldehyde in seawater immediately after collecting.

### Seasonal Changes in Apical Morphology

Representative samples of field populations of both species were collected monthly in Pelancura, from May 1990 to April 1991. All erect axes of *G. chilense* longer than 2 cm and all erect axes of *G. rex* longer than 5 cm found inside 10 randomly settled 100-$cm^2$ quadrats were collected. Quadrats were selected in rocky intertidal areas judged to have high densities of *G. chilense* or *G. rex*. The minimum axial length selected for each species corresponded in each case to the shortest plants exhibiting reproductive branches. Thus, all axes examined for seasonal growth presumably had reached the minimum reproductive size and therefore presumably had completed the apical differentiation associated with ontogeny.

### Apical Differentiation During Branch Regeneration

The samples of field populations were also used to obtain axes that had lost apical tips. These axes, which were excluded from the determination of ontogenic or seasonal changes in apical development, were used to study regeneration patterns.

### Data Collection

In all cases, morphological changes of apical structure were recorded by using a camera lucida. Whenever necessary, photographs were obtained with a Nikon Biophot compound microscope.

## Results

### *Gelidium chilense*

**Ontogenic development**. After embryo formation and differentiation of an apical cell, the erect axes of *G. chilense* remained cylindrical and devoid of lateral branches. The apex was attenuate, with smooth margins and with a distinctive apical cell that at times projected itself over the apex and had evidence of transverse cell divisions (Figs. 1A, 1B, and 2a). No lateral initials were found at this stage. This type of apical architecture was found in all axes 0.1–0.3 cm long (Fig. 3) and in about 17% of axes between 0.3 and 0.6 cm long.

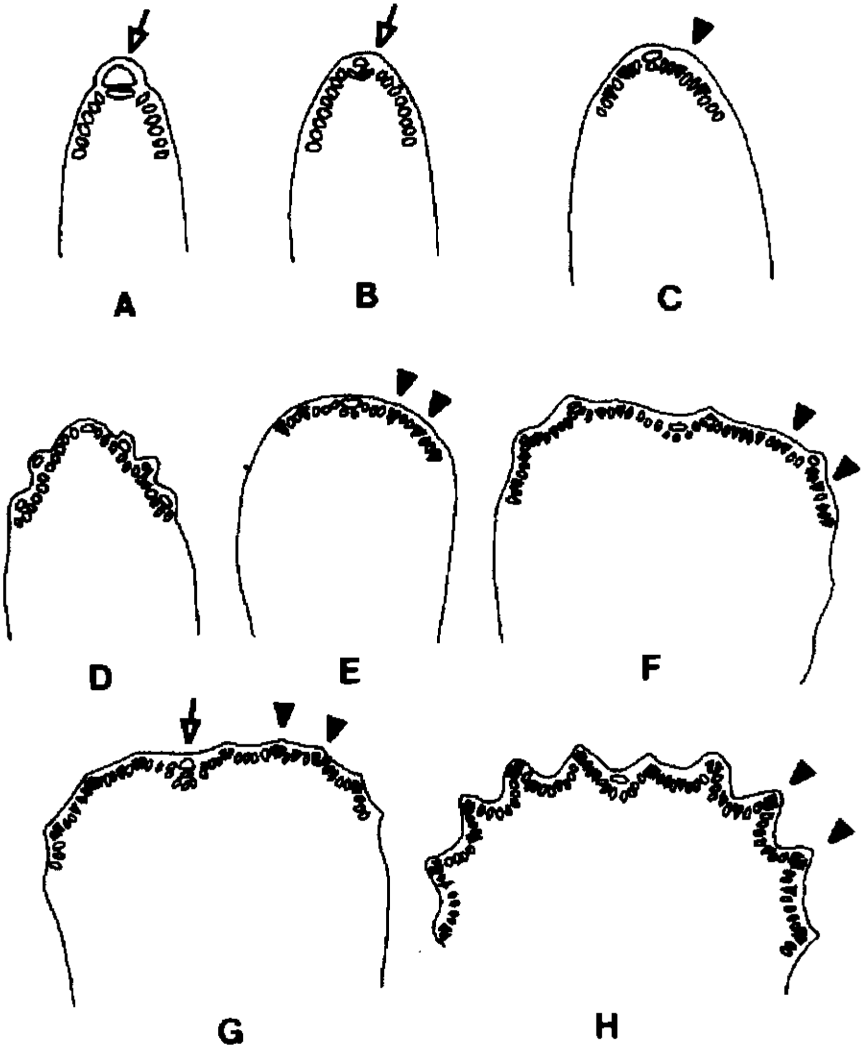

Fig. 1. Pattern of ontogenic development of the apical architecture of *Gelidium chilense*. A and B, Stage 1. A distinctive apical cell (arrows) is present, sometimes projecting over the tip of the apex. C, Stage 2. Lateral initials (arrowhead) appear. D and E, Stages 3 and 4. Lateral initials (arrowheads) divide transversely. F, Stage 5. Lateral initials (arrowheads) divide longitudinally rather than transversely. G and H, Adult plants. Two types of apical architecture found most often.

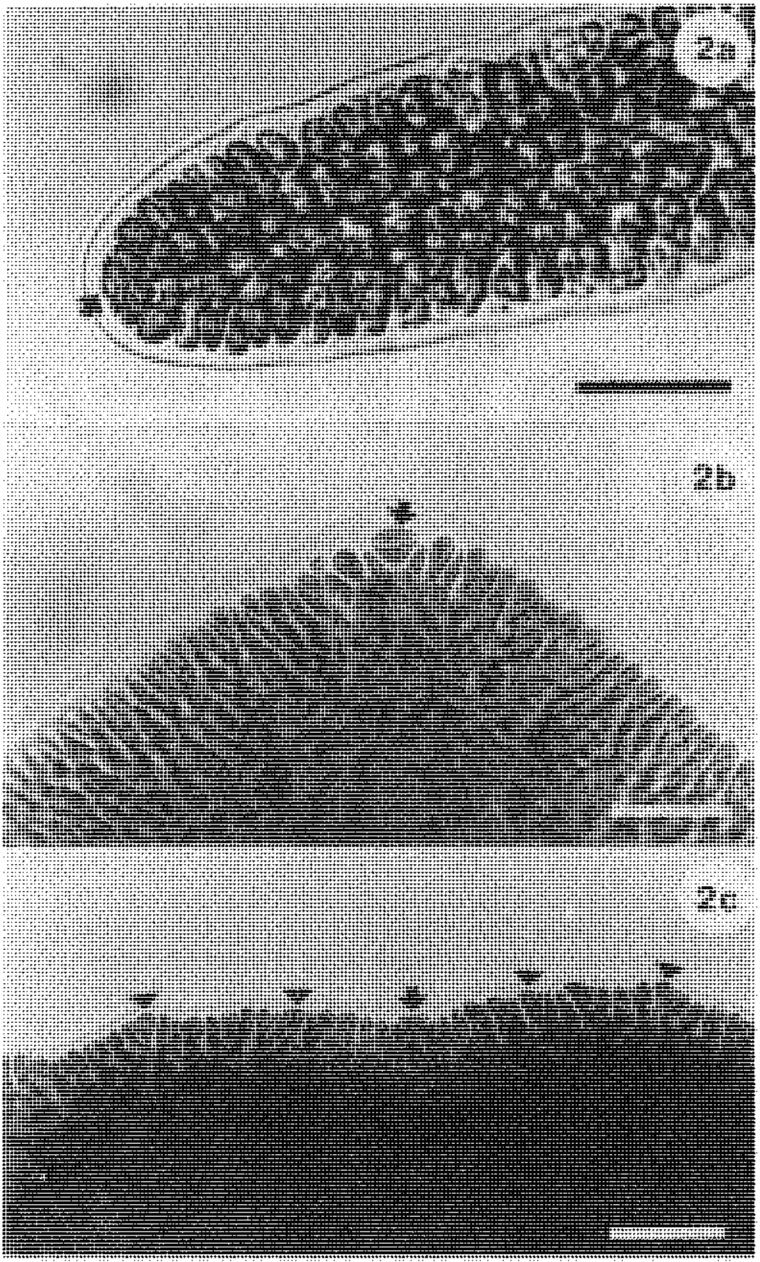

Fig. 2. Stages of apical architecture in the ontogenic development of the apex of *Gelidium chilense*. a, Stage 1. b, Stage 2. c, Stage 7. Scale bars: a, 15 µm; b and c, 25 µm.

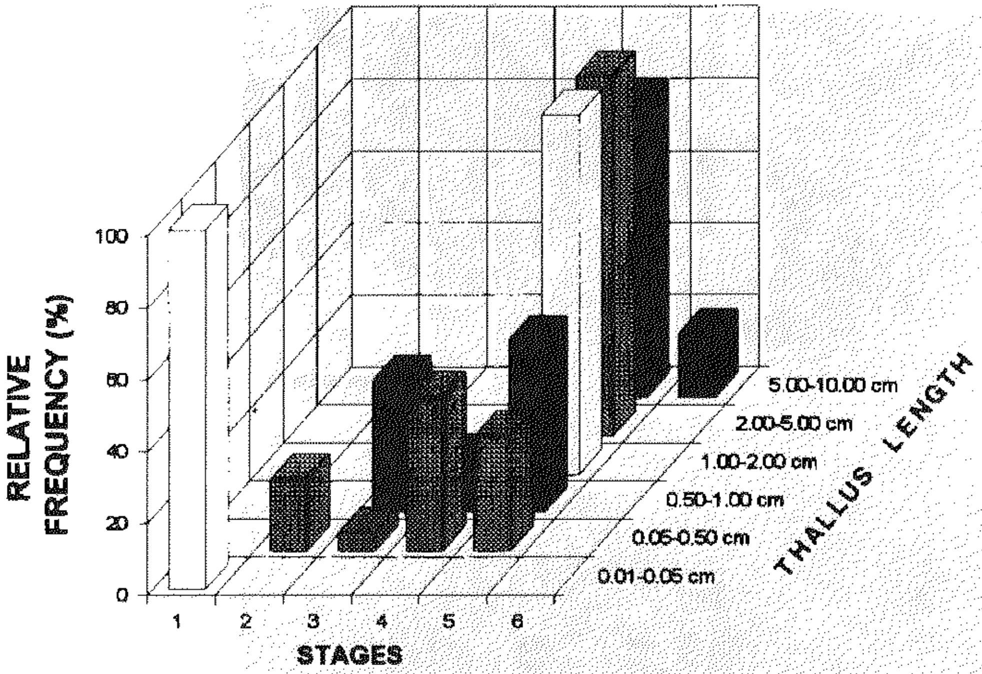

**Fig. 3. Relative frequency of the various stages of ontogenic development in populations of erect axes of *Gelidium chilense* as a function of thallus length.**

The next stage of apical development (stage 2, Figs. 1C and 2b) was characterized by the appearance of lateral initials that had the shape of an inverted cone and were smaller than the dome-shaped apical initial. At this stage, lateral initials showed no evidence of cell division, and the tip margins remained smooth. The axes remained cylindrical, were devoid of branches, and were up to 0.5 cm long.

The next stages in development (stages 3 and 4, Figs. 1D and 1E) were characterized by transverse cell division in the lateral initials. When actively dividing (Fig. 1D), the lateral initials protruded beyond the thallus border, forming small lobes resembling branch primordia. After division (Fig. 1E), the lateral initials recovered their inverted-cone shape, and the smooth margins were restored by divisions of the external cortical cells. On some plants, the dome-shaped apical initials sometimes also showed evidence of transverse cell divisions.

Apical tips in stages 3 and 4 of development were found in plants of up to about 1 cm long (Fig. 3). Through the activity of the lateral initials, the tips gradually became wider and flattened, approaching the typical apical morphology described for the species. Stage 5 (Fig. 1 F) was characterized by the occurrence of longitudinal rather than transverse cell division in the lateral initials. This morphology was first found in axes about 0.5 cm long and sometimes persisted in axes up to 2 cm long. Some tips had lateral initials dividing transversely, close to others dividing longitudinally.

The last two stages of development (stages 6 and 7, Figs. 1 G and 1 H) corresponded to the apex described for adult plants. Depending on divisions from apical initials, alternating with divisions of lateral initials, the tips changed from having finely dentate margins, with a prominent apical initial in the center and longitudinally dividing lateral initials (Fig. 1G), to having multilobed margins, with the apical initial sunk in one of many depressions in the thallus margins and the longitudinally divided lateral initials protruding beyond the margins of the cortical cells (Figs. 1 H and 2c). Stages 6 and 7 were found in plants longer than 1 cm (Fig. 3). Because any given tip had many lateral initials and only one apical initial, the alternating activities of lateral and apical initials resulted in the gradual widening of the tips during development.

### Seasonal Changes

The specimens of entire axes found in field populations of *G. chilense* were all in either stage 6 or stage 7 of development (Fig. 4), indicating that at the level of a population of axes, growth activity of the apical tips occurs at all times of the year. Stage 6, is the most frequently found pattern all year round, was especially frequent during late fall, winter, and early spring (April through October). Stage 7 did not include more than 40% of the population of tips at any one time and was slightly more frequent during summer (December through February).

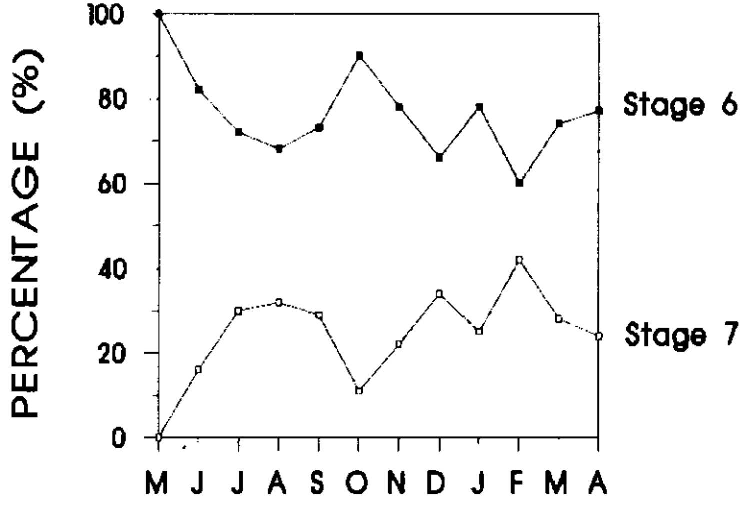

**Fig. 4. Seasonal changes in apical architecture in populations of erect axes of *Gelidium chilense* in central Chile.**

### Branch Regeneration

Regenerating branches found in samples of field populations were in stages 4–7. Without a precise knowledge of the time elapsed since the damage, we could not correlate time with developmental stages of apical architecture. However, it was clear that branch regeneration in this species did not start at stage 1 of apical development. At least three early stages of apical development were never observed in the regenerating branches.

### *Gelidium rex*

**Ontogenic Development**. The first stage of development in *G. rex* (Figs. 5A, 5B, and 6a) was similar to that of other species of *Gelidium*. The axes had attenuated, pointed apices, with smooth cortical margins. The dome-shaped apical initials sometimes projected beyond the apical margins and were prominent because of the absence of lateral initials. The axes were cylindrical, 0.01–0.05 cm long, and devoid of branches (Fig. 7).

The next stage of development (stage 2, Fig. 5C) was characterized by the activity of the cortical cells. These cells appeared elongated in periclinal position, often masking the presence of the dome-shaped apical initials. This type of tip occurred in plants 0.05–0.4 cm long (Fig. 7), which generally were cylindrical and devoid of branches. In slightly larger plants, the axial tips had differentiated lateral initials that showed evidence of transverse cell division followed by longitudinal division (Figs. 5D and 5E). Depending on the alternating activities of the apical initials, the lateral initials, and the cortical cells, the thallus margins were smooth or irregularly undulate, and the apical initials were more or less evident (stages 3 and 4). Axes with this type of organization were up to 1 cm long (Fig. 7). Tips were more flattened, and a few had branch primordia.

Stages 5 and 6 were characterized by the establishment of the apical architecture characteristic of the species. Depending on the alternating activitiees of the apical and lateral initials, two types of morphology could be distinguished (Figs. 5F, 5G, 6b, and 6c). Those axes dominated by the activities of the lateral initials and external cortical cells (Figs. 5F and 6b) had concealed dome-shaped apical initials because of an increase in the outgrowth of the cortical cells. A pair of longitudinally dividing lateral initials was present, one cell on each side of the apical initial. These tips were proportionately flat and had smooth margins. The other type of morphology seen at this stage of development (stage 6; Figs. 5G and 6c) was a rounded apex with smooth cortical margins. The axial apical cells topped the axes. The lateral initials, even though nearby, were located in a low position along the axes. These two types of apical morphology were found in axes longer than 1 cm (Fig. 7).

**Seasonal Variation**. All specimens of entire axes found in field populations were in either stage 5 or 6 of apical development (Fig. 8). As was the case in *G. chilense*, at the level of a population of axes, apical growth occurred at all times of

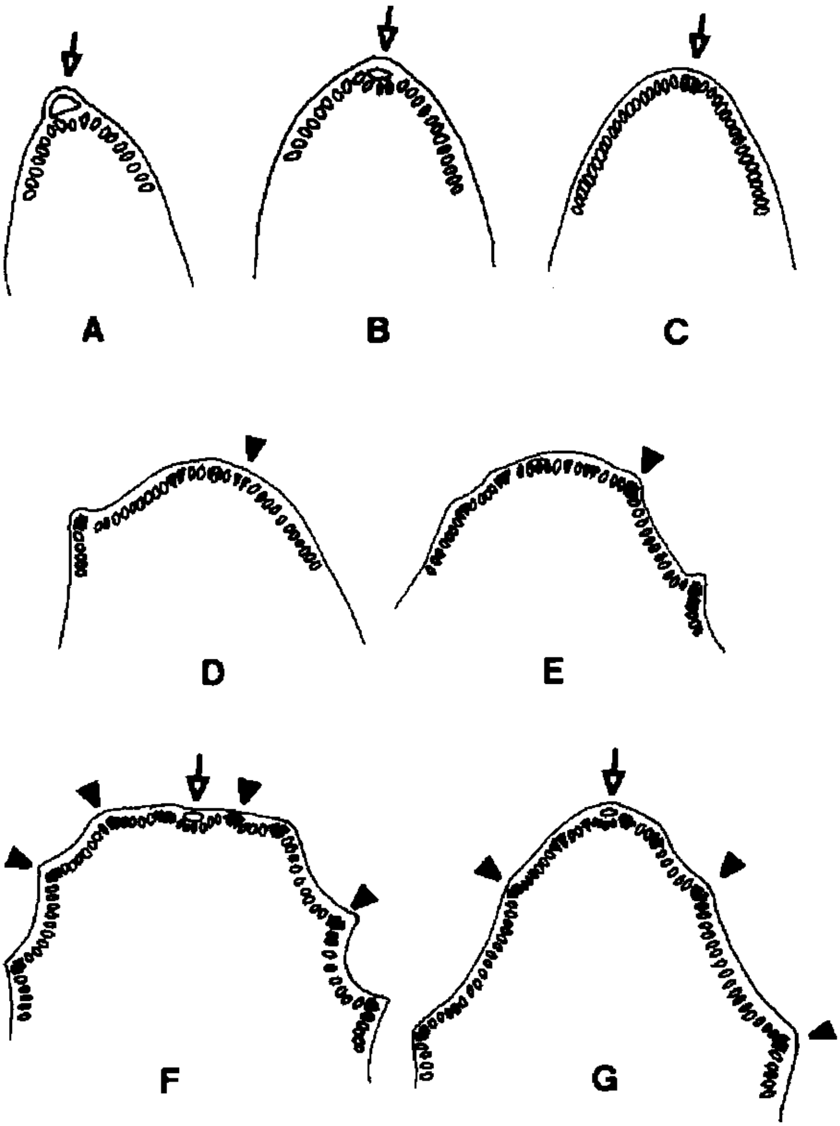

Fig. 5. Pattern of ontogenic development of the apical architecture of *Gelidium rex*. A and B, Stage 1. A dome-shaped apical initial (arrows) is present, sometimes projecting beyond the margin of the apex. C, Stage 2. Activity of cortical cells often masks the presence of the apical initial (arrow). D and E, Stages 3 and 4. Lateral initials (arrowheads) appear and divide. F and G, Stages 5 and 6. Development of the architecture typical of the species. Differences depend on the alternating activities of apical (arrows) and lateral initials (arrowheads).

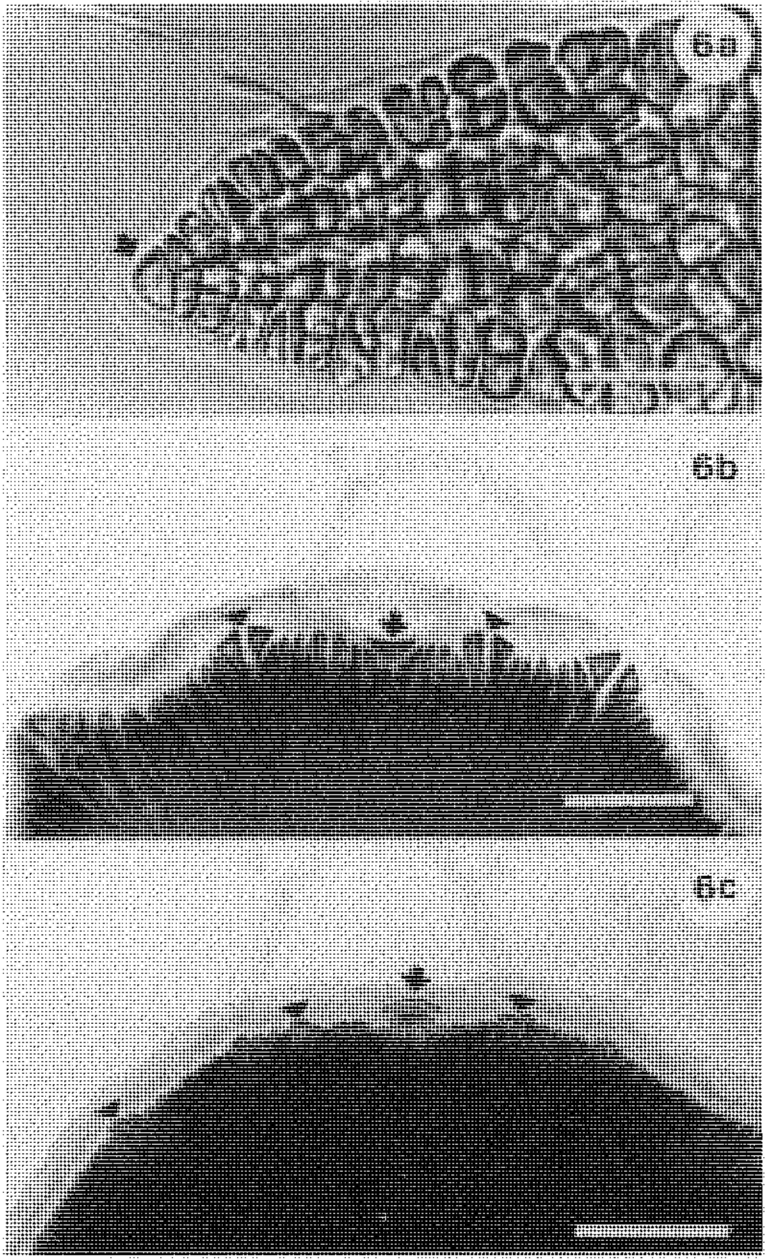

Fig. 6. Stages of apical architecture in the ontogenic development of *Gelidium rex*. a, Stage 1. b, Stage 5. c, Stage 6. Scale bars: a, 15 µm; b 25 µm; c, 50 µm.

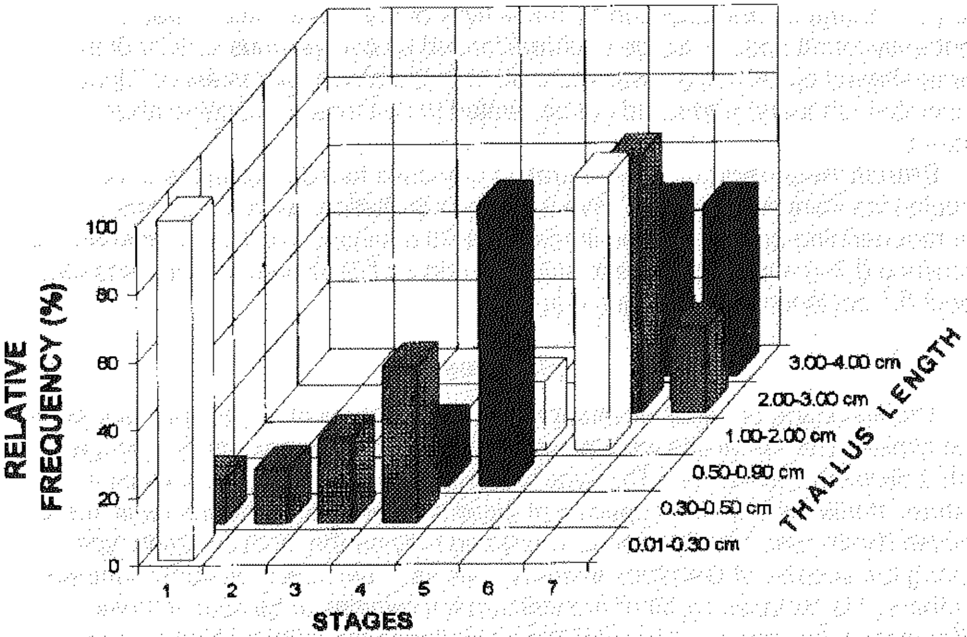

Fig. 7. Relative frequency of the various stages of ontogenic development in populations of erect axes of *Gelidium rex* as a function of thallus length.

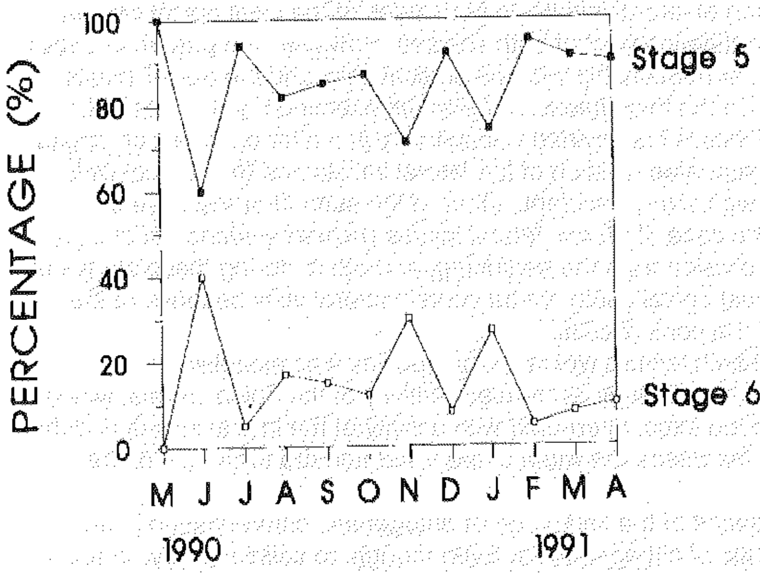

Fig. 8. Seasonal changes in apical architecture in populations of erect axes of *Gelidum rex* in central Chile.

the year. Stage 5, characterized by the activity of the lateral initials, was the most frequently found pattern. Stage 6, characterized by conspicuous activity of the dome-shaped apical initials, was more often found at irregular intervals (June, November, January) and could not be related to seasonally changing abiotic factors.

**Branch Regeneration**. Regenerating branches found in samples of field populations were in stages 1–7. We found no correlation between the length of the regenerating branch and the stage of apical development. Some regenerating branches 0.3–0.4 cm long were in stages 2 and 3 of development, whereas others about 0.1 cm long were in stages 4 and 5.

## Discussion

The first stage of apical development in erect shoots of *G. chilense* and *G. rex* was similar. The apical tips were pointed, attenuated, with smooth margins, and with a distinctive apical cell. This type of apical architecture is also present in mature, sterile axes of other species of *Gelidium*, such as *G. arborescens* and *G. coulteri* (Rodríguez and Santelices 1987) and may be the most common type among the species of *Gelidium*. In some species, it persists to maturity, whereas in others, it is replaced by other architectures. It remains to be seen if these differences have any value in establishing phylogenetic relationships among species within the genus. Up to now, only Norris (1992) has considered the morphology of apical tips as a promising characteristic for establishing phylogenetic relationships.

The differentiation of lateral initials on both sides of the axial apical cell was the next stage in the development of both species. However, the pattern of activity of these cells and their relationship with the cortical cells and the apical initials seem to be different in the two species of *Gelidium* examined. In the case of *G. chilense*, the lateral initials first divided transversely and later obliquely or longitudinally. Despite the repeated division of the lateral initials and the cortical cells, the axial apical cell was always evident, either at the summit or the base of marginal lobes. In the case of *G. rex*, lateral initials showed evidence of oblique as well as longitudinal division from the beginning, and often, during these stages of development, the axial apical could not be seen in lateral view because of the dividing activities of the cortical cells.

Once the apical architecture typical of the species was established, the seasonal changes in morphology decreased. Activity of the apical initials, which allows elongation of the axes, alternated with activity of the lateral initials and the cortical cells, which increases the width of the frond and the thickness of the apical tip.

We saw no evidence of the first stage of ontogenetic differentiation in any regenerating branches of either species. Even though no cellular study on apical regeneration of species of *Gelidium* has been completed to date, there is no reason to expect that differentiation would start with an apical cell in the tip of the regenerating axis. Only a minor proportion (less than 10%) of the regenerating fragments of *G. rex* had tips without lateral initials. All other regenerating branches of this species and all those of *G. chilense* had both apical and lateral initials in all regenerating tips. These results suggest that once the basic architecture of the tip has been established, branch fragments can regenerate the corresponding morphology by starting from some stage along the way; starting from the first stage of ontogenetic differentiation is not necessary. Alternatively, the length of these first stages might be so shortened that we could not detect them with our sampling methods. Both alternatives suggest fine-tuned regulation of the activity and differentiation of the regenerating cortical cells into apical and lateral initials. Overall, the results indicate that differentiation of apical architecture in some species of *Gelidium* is a more complex phenomenon than previously described.

## Acknowledgments

We thank I. A. Abbott for reviewing and commenting on the manuscript. The help of Mrs. Verónica Flores is acknowledged with gratitude. We appreciate the financial support of Red Latinoamericana de Botánica (Grant N-90-7) and SAREC-CONICYT (Grant 90-7) that allowed us to undertake this study. D. Rodríguez thanks Universidad Nacional Autónoma de México for their support while she was on leave of absence and Dr. J. González for much help during her stay abroad. B. Santelices thanks I. A. Abbott, J. Sullivan, and the California Sea Grant College for the invitation to and the support to participate in the fifth workshop on the taxonomy of economic seaweeds, held in Honolulu, Hawaii, in June 1993.

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# NOTES ON GELIDIALES SPECIES FROM KOREA

Hae-Bok Lee and Jong-In Kim

## Abstract

Taxonomic notes and distributions are given for 17 species and five varieties of Korean Gelidiales (Rhodophyta) reported previously by several authors. Included are 1 species and two varieties new to Korea. A key is given for 8 species and four varieties whose distribution in Korea has been confirmed: *Acanthopeltis* sp.; *Gelidium amansii*; *G. crinale*; *G. divaricatum*; *G. japonicum*; *G. pusillum*; *G. pusillum* var. *conchicola*, var. *cylindricum*, var. *pacificum*, and var. *pulvinatum*; *G. vagum*; and *Pterocladia capillacea*. This is the first report of the Korean distribution of *G. japonicum*, *G. pusillum* var. *conchicola*, and *G. pusillum* var. *pulvinatum*. We concluded that 6 species, *G. decumbens*, *G. johnstonii*, *G. latifolium*, *G. microphysa*, *G. pacificum*, and *G. tenue*, are not distributed in Korea as reported previously. Three species and one variety, *G. sesquipedale*, *P. densa*, *P. robusta*, and *G. corneum* var. *pinnatum*, are not identified, because it is uncertain that they occur in Korea.

## Introduction

Korean plants of Gelidiales, including *Gelidium australe* (non J. Agardh, =*G. amansii* f. *teretiusculum*), *G. latifolium*, and *Pterocladia capillacea*, were first reported by Cotton (1906). Later, Okamura (1913, 1915a, 1915b) published reports on *G. australe*, *G. amansii*, *G. divaricatum*, *G. latifolium*, *P. capillacea*, *Acanthopeltis japonica*, and one unknown species of *Gelidium* found in Korea.

In his several studies of algae in Korea, the first Korean phycologist, Kang (1956, 1960, 1962, 1966), described three genera, 8 species and two forms of Gelidiales: *A. japonica* (non Okamura), *G. amansii*, *G. amansii* f. *typica* and f. *elegans*, *G. divaricatum*, *G. pusillum*, *G. pacificum*, *G. vagum*, *P. tenuis*, and *P. densa*. I. K. Lee and Kim (1977) reported distribution of *G. crinale* in Kwangyang Bay on the southern coast. Subsequently, Sohn and Kang (1978) described three genera and 13 species, adding *G. microphysa*, *G. tenue*, *G. johnstonii*, *P. robusta*, and *P. densa*. More recently, I. K. Lee and Kang (1986) added *G. decumbens* in their list of Korean algae, Y. P. Lee (1988) added *G. sesquipedale* and *G. corneum* var. *pinnatum* in his list of gelidioid plants from Chejudo Island, and H.-B. Lee (1994) added *G. pusillum* var. *cylindricum* and var. *pacificum*.

Therefore, the total number of Gelidiales species reported until now was 1 species of *Acanthopeltis*; 13 species, three varieties, and three forms of *Gelidium*; and 3 species of *Pterocladia*: *A. japonica* (non Okamura); *G. amansii*; *G. amansii* f. *amansii*, f. *elegans*, and f. *teretiusculum*; *G. corneum* var. *pinnatum*; *G. crinale*; *G. decumbens*; *G. divaricatum*; *G. johnstonii*; *G. latifolium*; *G. microphysa*; *G. pacificum*; *G. pusillum*; *G. pusillum* var. *cylindricum* and var. *pacificum*; *G. sesquipedale*; *G. tenue*; *G. vagum*; *P. capillacea*; *P. densa*, and *P. robusta* (Lee 1994).

However, the total number of species of Gelidiales occurring in Korea is variable because the circumscriptions of the species are not clear, leaving researchers confused. To clarify Korean species of Gelidiales, we provide short taxonomic notes on them, which we derived by comparing herbarium material with descriptions given in previous reports.

### Key to Korean Species of Gelidales

1. Plants appearing sympodially branched ........ *Acanthopeltis* sp.
1. Plants appearing monopodially branched ........ 2
    2. Cystocarps unilocular, apex of main axis obtuse ........ *Pterocladia* (*P. capillacea*)
    2. Cystocarps bilocular, apex of main axis acute ........ 3 (*Gelidium*)
3. Main branches less than 1 mm wide, cylindrical to slightly compressed ........ 4
3. Main branches more than 1 mm wide, compressed ........ 6
    4. Plants prostrate, never erect ........ *G. divaricatum*
    4. Plants both prostrate and erect ........ 5
5. Upper parts of plants compressed to long-lanceolate ........ 8 (*G. pusillum*)
5. Upper parts of plants linear, cylindrical to slightly compressed ........ *G. crinale*
    6. Plants compressed, with midriblike thickening at lower part ........ *G. japonicum*
    6. Plants compressed, without midriblike thickening at lower part ........ 7
7. Main axis broad and thin, branchlets narrow ........ *G. vagum*
7. Main axis narrow and thick, branchlets thickened ........ *G. amansii*
    8. Plants forming loose mat, erect branches simple ........ *G. pusillum* var. *conchicola*
    8. Plants forming compact mat, branching again pinnately to irregularly ........ 9
9. Erect branches grouped, curved downward, not conspicuous ........ *G. pusillum* var. *pulvinatum*
9. Erect branches conspicuous ........ 10
    10. Plants cylindrical to compressed above, frequently with truncate apices ........ *G. pusillum* var. *cylindricum*
    10. Plants compressed at mid to lower parts of frond, with erect, long-lanceolate branches ........ *G. pusillum* var. *pacificum*

## Taxonomic Notes on the Species

*Acanthopeltis* sp. (Fig. 1)

Distribution in Korea: Hongdo Island (Sohn and Kang 1978), Gomundo Island (Lee and Boo 1984) on the southern coast, Songsanpo of Cheju Island (Kang 1966).

Collection Sites: Haengwon, Saesum of Chejudo Island.

Remarks: In comparison with the described features of *A. japonica* Okamura (1936), our plants were characterized by stalked and ovoid leaves enclosing less than half of the axis, lower axis with scars of early deciduous leaves, dichotomous branches frequent at the upper part of fronds, and a discoidal holdfast with a few fibrous rhizoids on it. Our specimens were monoecious. Although the specimens we examined have been identified as *A. japonica* Okamura by Kang (1966) and Sohn and Kang (1978), we concluded that they are not samples of *A. japonica.*

*Gelidium amansii* (Lamouroux) Lamouroux, Ann. Mus. Hist. Nat. 20:129, 1813.
(Figs. 2–4)

Basionym: *Fucus amansii* Lamouroux, Diss. Fucus, p. 48, pl. 26, figs. 2–5, 1805.

Other Literature: Okamura 1913, p. 22; Sohn and Kang 1978, p.31, pl. III, fig. 6; Y. P. Lee 1988, p. 3, figs 1–12; H.-B. Lee 1994, p. 68. figs. 1–4.

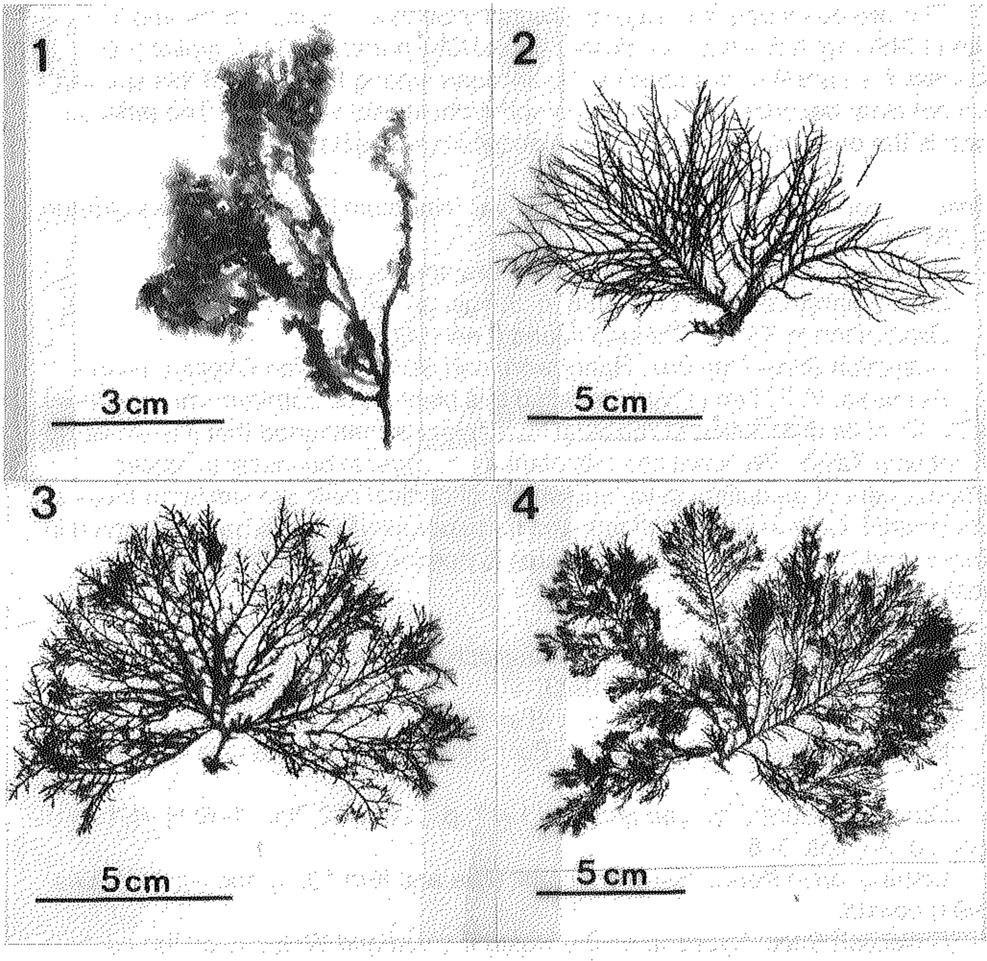

**Fig. 1. Vegetative thallus of *Acanthopeltis* sp. collected from Chejudo Island in May 1989. Figs. 2–4. *Gelidium amansii* (Lamouroux) Lamouroux collected from Namhaedo Island. Fig. 2, Vegetative thallus of plant collected in April 1991. Fig. 3, Female gametophyte of plant collected in November 1990. Fig. 4, Tetrasporophyte of plant collected in September 1991.**

Distribution in Korea: All coasts, including Chejudo Island.

Collection Sites: Padori on the western coast, Gampo on the eastern coast, Namhaedo Island on the southern coast, Sungsanpo on Chejudo Island.

Remarks: The main branches of Korean plants are frequently slightly sympodial, and the terminal branches are cylindrical or compressed. Kang (1956) was the first to collect and to recognize f. *amansii* and f. *elegans* from the southern coast of Korea.

The two descriptions of Korean plants by Sohn and Kang (1978) and Y. P. Lee (1988) are in line with the description of Okamura's (1934) f. *typica* (=*G. amansii f. amansii*) of this species. Distinctions among the forms of this species are not clear because of a continuum of morphological variations. The *amansii* form is the one collected most often along Korean coasts.

*Gelidium corneum**(Hudson) Lamouroux var. *pinnatum* Kützing, Species algarum, p. 764, 1849.

Basionym: *Fucus corneum* Hudson Flora anglica. p. 474, 1762.

Other Literature: Y. P. Lee 1988, p. 8, figs. 30–38.

Distribution in Korea: Chejudo Island (Lee 1988).

Collection Sites: Hamdok, Haengwon, and Songsanpo on Chejudo Island.

Remarks: Y. P. Lee (1988) identified this plant as *G. corneum* var. *pinnatum* because of its distribution of rhizoidal filaments. He mentioned that it is similar to *P. robusta* Taylor. We identified this plant as *P. robusta* because its apices, arrangement of medullary cells, and shape of cortical cells are similar to those of *Pterocladia*. Only vegetative plants and tetrasporophytes have been observed in Korea, and the observation of cystocarps is needed to clarify the taxonomic position of the species.

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

(Fig. 5)

Basionym: *Fucus crinalis* Turner, Fuci...vol. 4, p. 4, pl. 198, figs. a–c, e–g., 1819.

Other Literature: I. K. Lee and Kim 1977, p. 128, pl. 2, figs. 1–6; H.-B. Lee 1994, p. 70, figs. 5–8.

Distribution in Korea: Southern coast (Lee and Kim 1977) and western (Lee 1994) coasts.

Collection Sites: Byonsan on the western coast and Wolsong on the eastern coast.

Remarks: This species is distinguishable from *G. pusillum* on the basis of the

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*This name is the subject of much controversy, and its use has been abandoned in favor of *G. sesquipedale* (Clemente) Thuret, Bornet and Thuret p. 61, 1876 (Dixon and Irvine, *Seaweeds of the British Isles*, pp. 132–133, 1977). [Ed.]

erect thalli more than 3 cm high, the lower fronds without branches, and the mainly cylindrical frond of *G. crinale*. However, differences between the two species in internal structure are not clear. *Gelidium crinale* was reported first by Lee and Kim (1977) from Kwangyang Bay on the southern coast, but Lee and Kang (1986) recorded it in their list as a synonym of *G. pusillum*. *Gelidium crinale* is widely reported in the literature but remains poorly understood.

*Gelidium decumbens* Okamura, J. Imp. Fish. Inst. 29(2):60, 1934.

Distribution in Korea: Not recorded.

Remarks: This species is recorded in the list of Korean algae of I. K. Lee and Kang (1986), but no specimens were reported before or since then. Therefore, the occurrence of this species in Korea is questionable. Also the characteristics used to distinguish this species from other species are disputable. We concluded that this species is not distributed in Korea.

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

(Fig. 6)

Other Literature: Okamura 1913, p. 22; Sohn and Kang 1978, p. 30, pl. 1, figs. 1–3; Y. P. Lee 1988, p. 10, figs. 39–44; and H.-B. Lee 1994, p. 72. figs. 9–12.

Distribution in Korea: All coasts.

Collection Sites: Gampo on the eastern coast, Padori on the western coast, Namhaedo Island on the southern coast, and Wimi on Chejudo Island.

Remarks: Korean plants of this species grow on rocks or oyster shells in the intertidal belt and form mats. The specimens we examined are are not variable in external appearance, and plants with gametophytes are not distinctly different from vegetative ones. Tetrasporangia in transverse section are divided cruciately and elongated anticlinally. Zonate forms (Santelices 1988) were not observed.

*Gelidium japonicum* (Harvey) Okamura, Illust. Mar. Alg. Jpn. 1:57, 1901.

(Fig. 7)

Other Literature: Okamura 1934, p. 52, pl. 18, fig. 2.

Distribution in Korea: Southern coast.

Collection Sites: Gomundo Island on the southern coast.

Remarks: Plants are 3.0–5.5 cm tall, and more than 2 mm wide. The lower part of the main branches is thickened longitudinally in a midriblike manner. The middle parts of the thalli have many short, thin branchlets on the margin and surfaces. The apices are rounded.

*Gelidium johnstonii* Setchell et Gardner, Proc. Calif. Acad. Sci., Series 4, 12:742, 1924.

Other Literature: Sohn and Kang 1978, p. 32, pl. II, figs. 7–9, pl. III, fig. 4.

Distribution in Korea: Namhaedo Island on the southern coast (Sohn and Kang 1978).

Remarks: Sohn and Kang (1978) reported that this species is 5.5–8.0 cm tall, and branches distinctly in a pinnate manner, as described by Segi (1955). However, the typical plant of this species is rare in Korea, and any features distinguishing *G. johnstonii* from *G. amansii* are not clear. We concluded that *G. johnstonii*, as identified in Korea, is a morphological variant of *G. amansii*.

*Gelidium latifolium* (Greville) Bornet et Thuret, Notes algologiques, Fasc. 1, p. 58, 1876.

Basionym: *Gelidium corneum* var. *latifolium* Greville, *Algae brittanicae*. p. 143, 1830.

Other Literature: Cotton 1906, p. 366; Okamura 1913, p. 22.

Distribution in Korea: Coast between Pusan and Kunsan (Okamura 1913).

Remarks: This species was reported by Cotton (1906) without any record of distribution. Okamura (1913) estimated that the distribution was Fusan (=Pusan) and the coast between Pusan and Kunsan. The occurrence of this species in Korea is questionable, because no record or description has been reported since that of Okamura (1913).

*Gelidium microphysa* Setchell et Gardner, Proc. Calif. Acad. Sci., Series 4, 19:154, 1930.

Other Literature: Sohn and Kang 1978, p. 31, pl. I, figs. 10–12.

Distribution in Korea: Pusan on the southern coast (Sohn and Kang 1978).

Remarks: Sohn and Kang (1978) reported that this species grows up to 0.6–1.5 cm high on rocks and has a pinnate or flabellate form, with round apices and rhizoids developing in various directions, as described by Dawson (1952). The typical form of this species is rare in Korea, and any features distinguishing it from *G. amansii* are not clear. We concluded that this species, as previously identified in Korea, is a morphological variant of *G. amansii*.

*Gelidium pacificum* Okamura, Icon. Jpn. Alg., vol. III, p. 99, 1914.

Other Literature: Kang 1966, p. 64; Sohn and Kang 1978, p. 31, pl. II, figs. 1–3, pl. III, fig. 7.

Distribution in Korea: Pusan, Bangojin (Kang 1966), and Yosu (Sohn and Kang 1978) on the southern coast.

Remarks: *Gelidium pacificum* is described as large, robust, 30 cm tall, with ramuli branching closely and pinnately on the distal parts of branches, and similar to *G. amansii* (Okamura 1934) in internal structure. Sohn and Kang (1978) recorded specimens with regenerating whorl branchlets on the branch tips as *G. pacificum* Okamura. After reading the three papers (Okamura 1934, Sohn and Kang 1978, Santelices and Miyata 1994), we concluded that the plants of *G. pacificum* reported from Korea are a variation of *G. amansii*.

*Gelidium pusillum* (Stackhouse) Le Jolis, Mem. Soc. Imp. Sci. Nat. Cherbourg 10, p. 139, 1863. (Fig. 8)

Basionym: *Fucus pusillus* Stackhouse, *Nereis brittanica*. p. 16, pl. vi, 1795.

Other Literature: Kang 1966, p. 63; Sohn and Kang 1978, p. 31, pl. 1, figs. 8–9; Y. P. Lee 1988, p. 12, figs. 45–52; H.-B. Lee 1994, p. 72.

Distribution in Korea: Sockcho on the eastern coast, Yosu on the southern coast (Kang 1966, Sohn and Kang 1978), and Chejudo Island (Lee 1988).

Collection Sites: Wolsong on the eastern coast, Namhaedo Island on the southern coast, Padori on the western coast, and Chejudo Island.

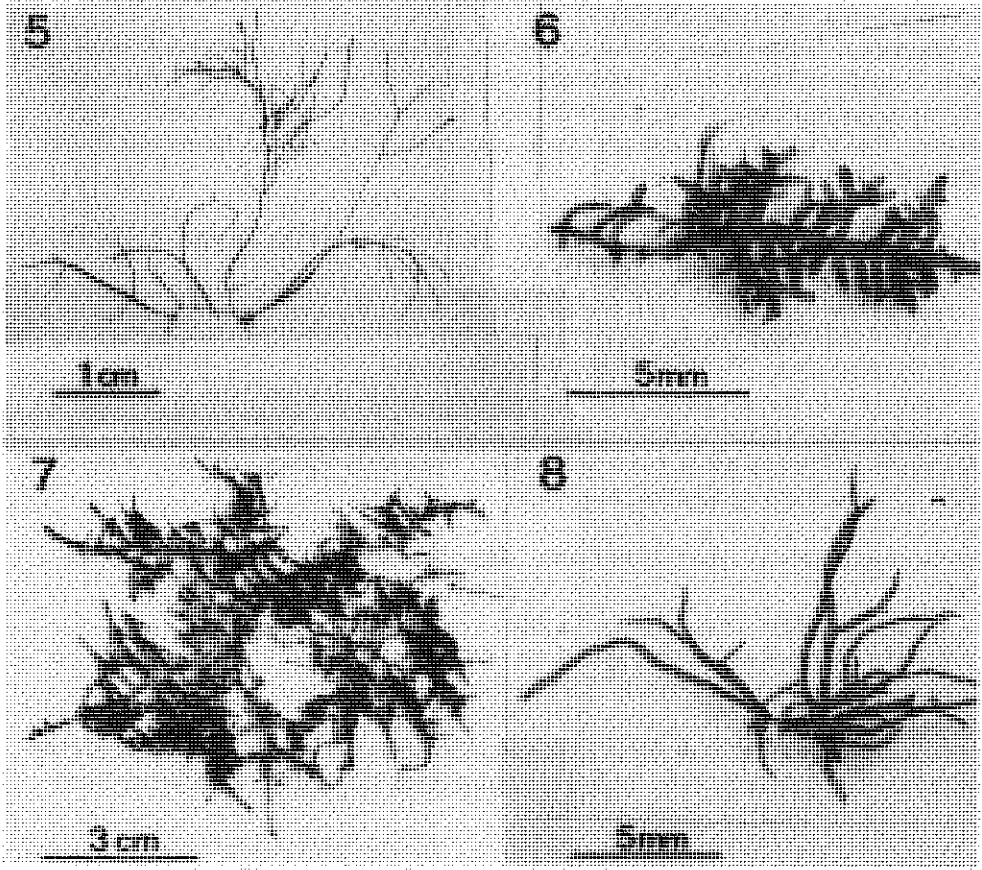

**Fig. 5.** **Vegetative thallus of *Gelidium crinale* (Turner) Gaillon collected from Byonsan in July 1993. Fig. 6. Vegetative thallus of *Gelidium divaricatum* Martens collected from Chejudo Island in July 1993. Fig. 7. Tetrasporophyte of *Gelidium japonicum* (Harvey) Okamura collected from Gomundo Island in July 1990. Fig. 8. Vegetative thallus of *Gelidium pusillum* (Stackhouse) Le Jolis collected from Namhaedo Island in May 1991.**

Remarks: Korean plants of this species grow in fissures of rock, and occasionally mixed with *G. divaricatum*. Plants grow on the substratum; they have short holdfasts that develop from creeping axes at irregular intervals and short cylindrical to compressed erect branches. We identified four varieties of this species: *conchicola, cylindricum, pacificum*, and *pulvinatum*. However, structural characteristics that distinguish this species from *G. crinale* are not clear.

*Gelidium pusillum* var. *conchicola* Piccone et Grunow, in Piccone, Nouovo Giorn. Bot. Ital. 16, p. 316, 1884. (Fig. 9)

Other Literature: Okamura 1934, p. 51, pl. 17, figs. 5–6.

Collection Sites: Euihang on the western coast, Gomundo Island on the southern coast, and Chejudo Island.

Remarks: These plants lie flat (prostrate) and spread out on rocks in tidal pools; they do not form mats. Holdfasts and erect branches develop at the same point on creeping axes at irregular intervals. Erect branches form broadly ovate foliages. The spread-out prostrate mode of growth distinguishes these plants from other varieties of *G. pusillum*.

*Gelidium pusillum* var. *cylindricum* Taylor, Allan Hancock Pac. Exped. 12, p. 154, 1945. (Fig. 11)

Other Literature: Lee 1994, p. 72, figs. 13–16.

Distribution in Korea: All coasts (Lee 1994).

Collection Sites: Euihang on the western coast.

Remarks: In these plants, erect branches develop in a tuft from cylindrical axes. The branches are cylindrical and branch pinnately or dichotomously. The distal parts of the branches are compressed, frequently truncate or branching again, as described by Santelices (1988).

*Gelidium pusillum* var. *pacificum* Taylor, Allan Hancock Pac. Exped. 12, p. 153, 1945. (Fig. 10)

Other Literature: Lee 1994, p. 75, figs. 17–20.

Distribution in Korea: All coasts (Lee, 1994).

Collection Sites: Hamdok on Cheju Island.

Remarks: The creeping axes are cylindrical and erect axes lanceolate. The branches are broad in the middle to lower parts, are narrow and elongated above, and branch pinnately distally. These characteristics distinguish this variety from other varieties within *G. pusillum*.

*Gelidium pusillum* var. *pulvinatum* (C. Agardh) J. Feldmann in Feldmann and Hamel, Rev. Alg. 9, 113–114, fig. 19a–19c, 1936. (Fig. 12)

Collection Sites: Gojedo Island on the southern coast and Osan on the eastern coast.

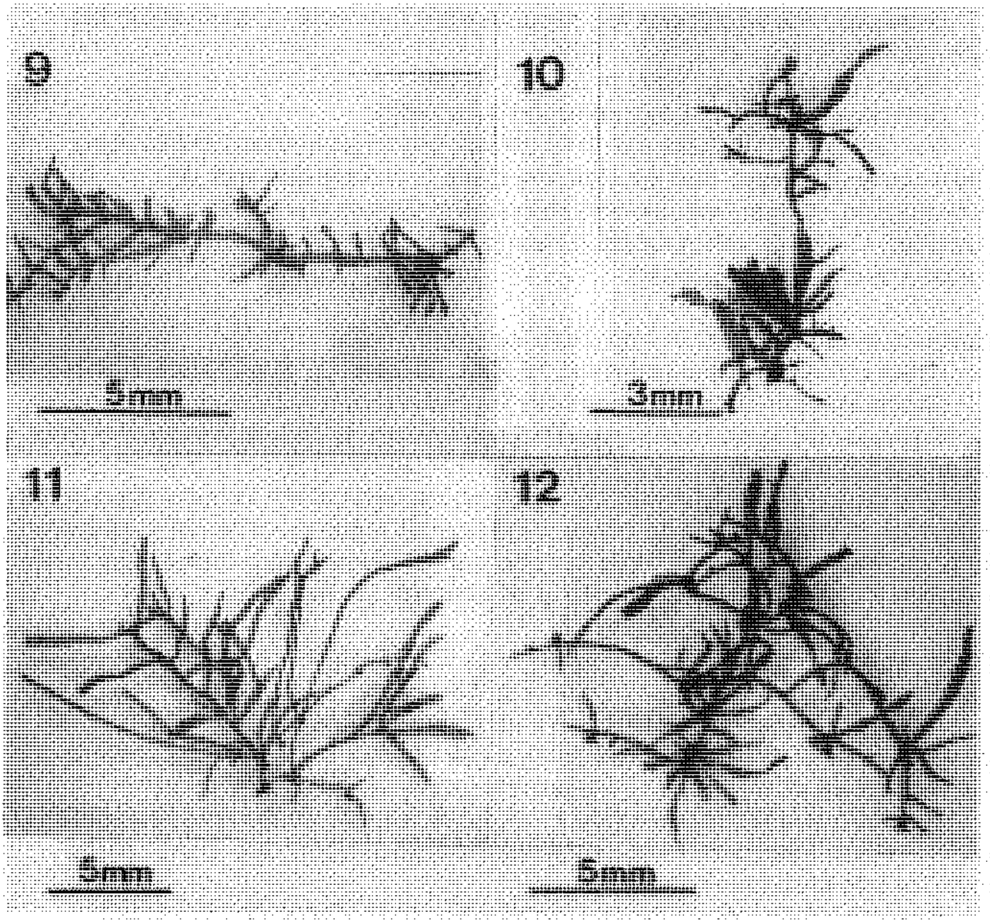

**Fig. 9.** Tetrasporophyte of *Gelidium pusillum* var. *conchicola* Piccone et Grunow collected from Gomundo Island in September 1989. **Fig. 10.** Vegetative thallus of *Gelidium pusillum* var. *pacificum* Taylor collected from Chejudo Island in July 1993. **Fig. 11.** Vegetative thallus of *Gelidium pusillum* var. *cylindricum* Taylor collected from Euihang in December 1993. **Fig. 12.** Vegetative thallus of *Gelidium pusillum* var. *pulvinatum* (C. Agardh) J. Feldmann collected from Gojedo Island in May 1990.

Remarks: The cylindrical and compressed erect branches of this variety develop in tufts. The branches arising from erect branches curve downwards and are mixed with long slender cylindrical proliferations. This variety has also been treated as an independent species (Kützing 1849, Grunow 1867, Desikachary et al. 1990).

*Gelidium sesquipedale* (Clemente) Thuret, in Bornet et Thuret, Notes algologiques, Fasc. 1, p. 61, 1876. (See footnote for *Gelidium corneum* var. *pinnatum*.)

Basionym: *Fucus corneus* var. *sesquipedalis* Clemente, Ensayo sobre las variedades...Andalucia. p. 317, 1807.

Other Literature: Lee 1988, p. 5, figs. 13–29.

Distribution in Korea: Chejudo Island (Lee 1988).

Remarks: Korean plants are 7–10 cm tall, and cross-sections of the stipe show two acute ridges, one opposite the other. In comparison with *G. subcostatum*, *G. sesquipedale* also branches at various intervals and has short branches. Unlike *G. subcostatum*, it has no parenchymatous tissue between the cortex and medulla (Lee 1988).

*Gelidium tenue* Okamura, J. Imp. Fish. Inst. 29:56, 1934.

Other Literature: Sohn and Kang 1978, p. 32, pl. II, fig. 6, pl. IV, fig. 1.

Distribution in Korea: Kuryongpo on the eastern coast (Sohn and Kang 1978).

Remarks: Song and Kang described this species as having pinnate branches developed at right angles from the main branch. *Gelidium tenue* is distinguished from the morphologically similar *G. vagum* on the basis of the former's short acute branches. It is not clear which characteristics of *G. tenue* are different from those of *G. amansii*. We concluded that this species, as recognized in Korea, should be included within the limits of variation of *G. amansii*.

*Gelidium vagum* Okamura, J. Imp. Fish. Inst. 29: 58, 1934.
(Fig. 13)

Other Literature: Kang 1966, p. 64, pl. IV, fig. 2; Sohn and Kang 1978, p. 32, pl. II, fig. 5, pl. IV, fig. 2; Y. P. Lee 1988, p. 14, figs. 53–63; H.-B. Lee 1994, p. 76, figs. 21–24.

Distribution in Korea: Odongdo, Heuksando Islands, on the southern coast (Kang 1966), Ochongdo Island on the western coast (Sohn and Kang 1978), and Chejudo Island (Lee 1988).

Collection Sites: Yongil bay on the eastern coast; Padori on the western coast; and Sorock, Jindo, and Namhaedo Islands on the southern coast.

Remarks: Korean specimens of this species are thin and mostly bright red. The lateral branches and branchlets issue from main branches, and the distal parts of main branches are all elongated narrowly. The thinness of its thallus, elongation of branches, and proliferations on the surfaces of fronds distinguish this species from *G. amansii*.

*Pterocladia capillacea* (Gmelin) Bornet et Thuret, Notes algologiques. Fasc. 1, p. 57, 1876.
(Fig. 14)

Other Literature: Cotton 1906, p. 371; Sohn and Kang 1978, p. 32, pl. II, fig. 10, pl. IV, fig. 6.

Distribution in Korea: Pusan, Jindo, and Heuksando Islands on the southern coast (Kang 1966); Ullungdo Island on the eastern coast (Sohn and Kang 1978); and Chejudo Island (Kang 1966).

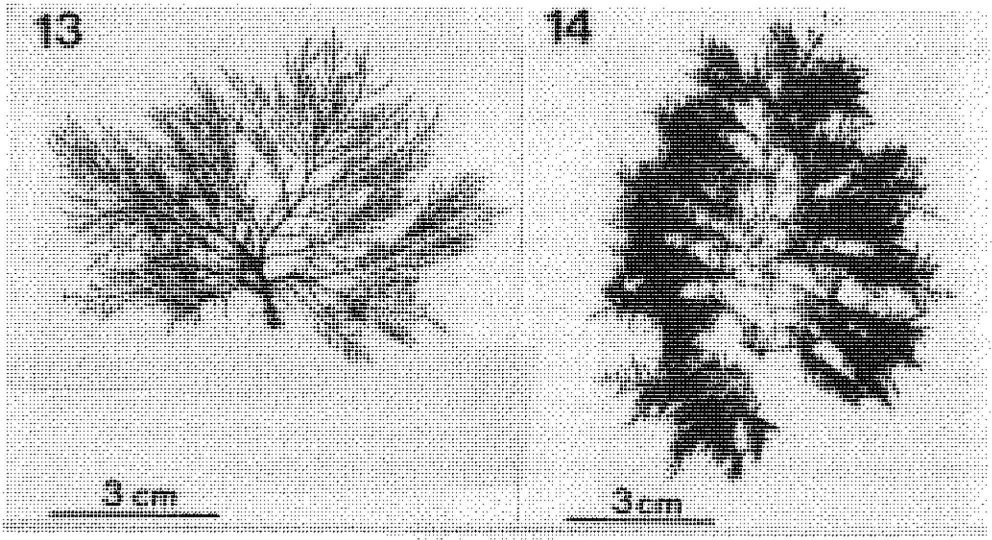

**Fig. 13. Tetrasporophyte of *Gelidium vagum* Okamura collected from Namhaedo Island in May 1991. Fig. 14. Tetrasporophyte of *Pterocladia capillacea* (Gmelin) Bornet et Thuret collected from Chejudo Island in August 1993.**

Collection Sites: Gampo on the eastern coast; Euihang on the western coast; Namhaedo on the southern coast; and Sinchang and Haengwon on Chejudo Island.

Remarks: Korean plants of this species vary in branching density according to the depth of habitat and the branching position of the frond (Sohn and Kang 1978). Many terminal branches of specimens with broad branches, narrow branches, or both broad and narrow branches, had slender extensions.

*Pterocladia densa* Okamura, J. Imp. Fish. Inst. 29(2):63, 1934.

Other Literature: Kang 1956, p. 7; Sohn and Kang 1978, p. 33, pl. II, fig. 11, pl. IV, fig. 4.

Distribution in Korea: Sockcho on the eastern coast and Gomundo Island on the southern coast (Sohn and Kang 1978).

Collection Sites: Gampo on the eastern coast, Padori on the western coast, Impo on the southern coast, and Sungsanpo of Chejudo Island.

Remarks: Korean plants of this species are characterized by aggregated branches; compressed main branches; cylindrical branchlets; small plants less than 10 cm high; and slender, prolonged, and irregularly branching apices (Sohn and Kang 1978), as Okamura (1934) described. However, plants with these characteristics are rare. *Pterocladia densa* cannot be distinguished from *P. capillacea* on the basis of these features alone, because many of these features are seen in both species.

*Pterocladia robusta* Taylor, Allan Hancock Pac. Exped. 12:160, 1945.

Other Literature: Sohn and Kang 1978, p. 33, pl. II, figs. 12–14, pl. IV, fig.5.

Distribution in Korea: Hongdo, Kukdo, and Galdo Islands on the southern coast (Sohn and Kang 1978).

Collection Sites: Chejudo Island.

Remarks: The broad main branches of this species do not have lateral branches below; instead they bear pinnate branches above and have acute ends distally. The cortical cells are irregularly shaped (Sohn and Kang 1978). We concluded tentatively that this plant belongs to the genus *Pterocladia*, because it has a round apex with a central depression; cells in the medulla are compactly aggregated; and in longitudinal section, outermost cortical cells have the shape of elongated cubes. Without observation of cystocarps, discrimination between this species and *G. corneum* var. *pinnatum* (=*G. sesquipedale*) is difficult. So far, female reproductive organs have not been observed on *P. robusta*.

## Discussion

Kang (1960) identified a species of Korean *Acanthopeltis* as *A. japonica* Okamura, and Sohn and Kang (1978) described it in more detail. However, the plant they examined is now recognized as a different species. We recorded the differences in external appearance only for the specimen of *Acanthopeltis* examined in this study and the specimen described by Okamura (1936). A comparison is needed of the internal structures of both the species we examined and specimens of *A. japonica*.

The descriptions of Korean species of *G. amansii* by Sohn and Kang (1978), Y. P. Lee (1988), and H.-B. Lee (1994) all fit the description of the *amansii* form of the species. Establishing a clear limitation of the forms belonging to *G. amansii* is difficult, because variations among the forms overlap and are continuous. An analysis of the limits in variation among the Korean plants of *G. amansii* is needed.

In external appearances, *G. corneum* var. *pinnatum* as reported by Y. P. Lee (1988) is similar to *P. robusta* reported by Sohn and Kang (1978). We concluded that these are the names for the same plants of a species identified without observaton of cystocarps. The taxonomic positions of these two cannot be fixed until plants with female reproductive organs have been examined.

*Gelidium pusillum* var. *pulvinatum* (C. Agardh) J. Feldmann is treated as an independent species: *G. pulvinatum* (C. Agardh) Grunow (1867) or *G. pulvinatum* (Kützing) Thuret ex Bornet (Desikachary et al. 1990). We recorded this taxon as a variety, because the reproductive isolation of this plant from *G. pusillum* has not been confirmed.

Okamura (1934) described a new species, *P. densa*, as a linear, filiform plant with compressed main branches and cylindrical branchlets. The thalli in this species are slenderer, branch more densely, and have denser rhizoidal filaments in the medulla than *P. tenuis* (=*P. capillacea*), and the broader branches taper toward the base. The characteristics of this species described by Okamura (1934) are variable and are often observed among *P. capillacea* specimens, so the circumscription of this species is not clear. In clarifying the limits of variation of *P. capillacea*, Stewart (1968) and Santelices (1988) pointed out that the distinguishing characteristics of *P. densa* are not clear.

## Acknowledgments

We thank Professor I. A. Abbott and the California Sea Grant College for inviting and helping us to do this work. We also thank Professor I. K. Lee for his encouragement to study Korean Gelidiales.

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# Section III. *Gracilaria*

## INTRODUCTION

Isabella A. Abbott

When I think about my flowering-plant colleagues who look down their individual and collective noses at phycologists who are still describing new species ("You must be a splitter. There can't be that many new species of algae to be described. When someone discovers a new area where botanists have never been—that's when 'we' find new species. Yet you are discovering them where people swim or surf every day. You must be kidding!"), I think about *Gracilaria* and realize that there are many species to be described, but many more to be resurrected and recovered. In addition, most of them should be grown in culture and hybridized as Dr. Yamamoto is doing—and even after growing them in culture, he is not always sure what species he has. So some species need not be *new* species, but they do need to be described well so that the names do not multiply needlessly. Many students of *Gracilaria*, however, have been restudying "old" species. For example, *G. verrucosa* (probably the most widely used name for a species in the genus) currently has a narrow geographical range, and "look-alikes" could even be placed in *Gracilariopsis*, if you recognize that genus.

Actually, discrimination of *Gracilaria* species is kind of a nightmare, because when researchers find features that might be used for systematics, they must then assess the stability of those features. The configuration of spermatangia, which seemed such a useful and easily observable way of dividing species groups within the genus, has become a sticky trap, with different kinds of configuration grading into one another (but not necessarily consistently). I think that Dr. Yamamoto with his culture system and Dr. Goff with her molecular toolbox may have the clues to help us to avoid such traps.

The description of two new Chinese species in this section includes the contributions of colleagues from the Shantou (Guangdong province) Laboratory and represents an increase in the number of Chinese investigators working in systematics. The description of a new species and a new variety from Japan by Dr. Yamamoto and the description of a Korean "verrucosa" (it is *not* like the British species, because it has almost no traversing or nutritive filaments and shows intergrading textorii-verrucosa types of spermatangia) by Dr. Lee and his students are interesting contributions from Asia.

It may be time to establish connections with other researchers on gracilarioid algae who have species that we do not know. Investigation of those species might provide light on how to restructure the systematics of the genus. Just as the attention of our *Sargassum* colleagues has moved from subgenus to lower categories, *Gracilaria* systematists might focus on higher categories than species. More than 100 species of *Gracilaria* have been examined in the past 10 years, mostly with support from the Sea Grant Program. This section contains a list of these species and their major bibliographic citations, for easy reference.

# *GRACILARIA MARAMAE* SP. NOV. (GRACILARIACEAE, GRACILARIALES, RHODOPHYTA), AN ECONOMICALLY IMPORTANT SPECIES FROM THE FIJI ISLANDS, SOUTH PACIFIC

G. Robin South

## Abstract

*Gracilaria maramae* sp. nov. is a new terete species of *Gracilaria sensu stricto* from the Fiji Islands. An important food species for ethnic Fijians, *G. maramae* is distinguished by branches that are constricted at the base; nonconcurrent verrucosa-type male conceptacles; and nonrostrate cystocarps with numerous tubular nutritive filaments, a large-celled gonimoblast lacking a fusion cell, and a thin-walled pericarp lined with cells containing stellate chloroplasts.

## INTRODUCTION

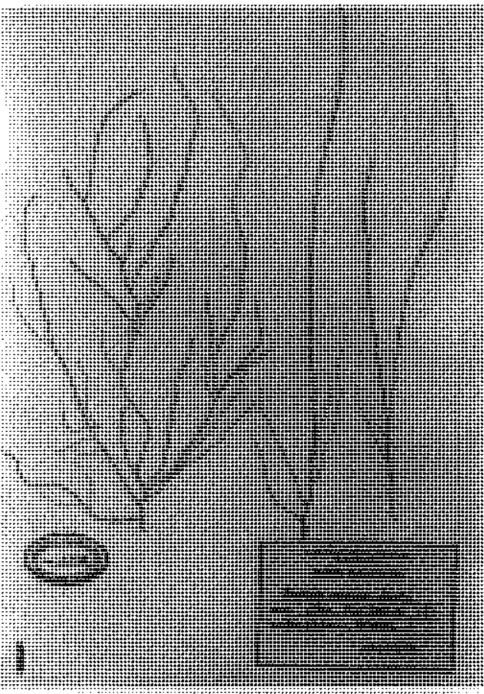
*Gracilaria* is an important food species in the Fiji Islands, where it is gathered and marketed by Fijian women (South 1993). The species does not fit any of the descriptions of eight reported species from Fiji (South and Kasahara, 1992), and until recently it could not be identified because no male specimens were available for examination. All stages are now available, and a comparison with related species has indicated that the Fijian plants belong to an undescribed taxon. They have been assigned to *G. maramae* sp. nov.

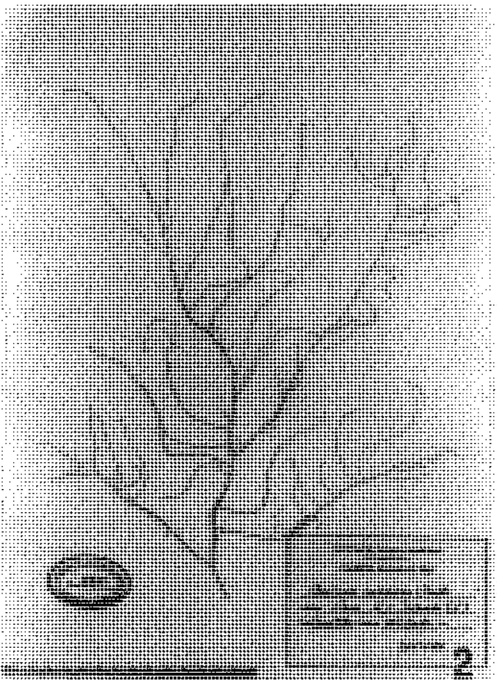
### Description of the Species

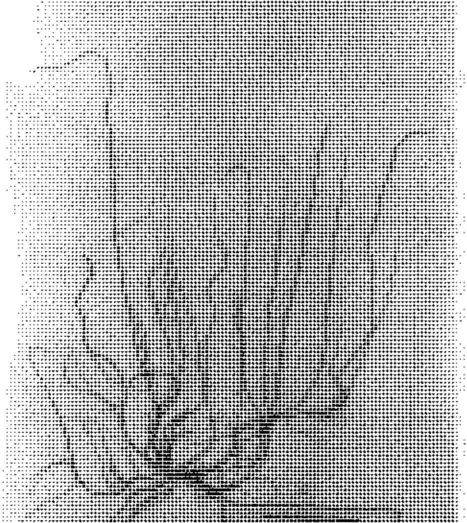
*Gracilaria maramae* sp. nov. (Figs. 1–14)

Planta erecta, usque 25 (40) 60 cm longa; solitaria vel caespitosa; axes et rami teretes, 1.0 (1.5) 2.5 mm diametro; ramificatio flagelliformis, 1–4 ordinum, secunda, constricti abrupte basibus suis. Collaocatio spermatangiorum "verrucosa" typus in conceptaculis corticalibus elongato-ovalibus, 27.5–38.0 × 50 µm. Cystocarpia protrudentia manifeste, hemisphaerica, nonrostrata, non constricta basi, 800 µm diametro; gonimoblastus ramosus, pseudoparenchymatus; superna fila absorbentia mul ta, basali fila absorbentia pauca. Pericarpium ex 6–7 stratis constante, 130 (170) 200 µm crassum; cellulae pericarpii contentis stellatis. Tetrasporangia in strato externo dispersa, cruciatum divisor, 30.0–37.5 × 25–30 µm, cellulis corticalibus normalibus circumfusa.

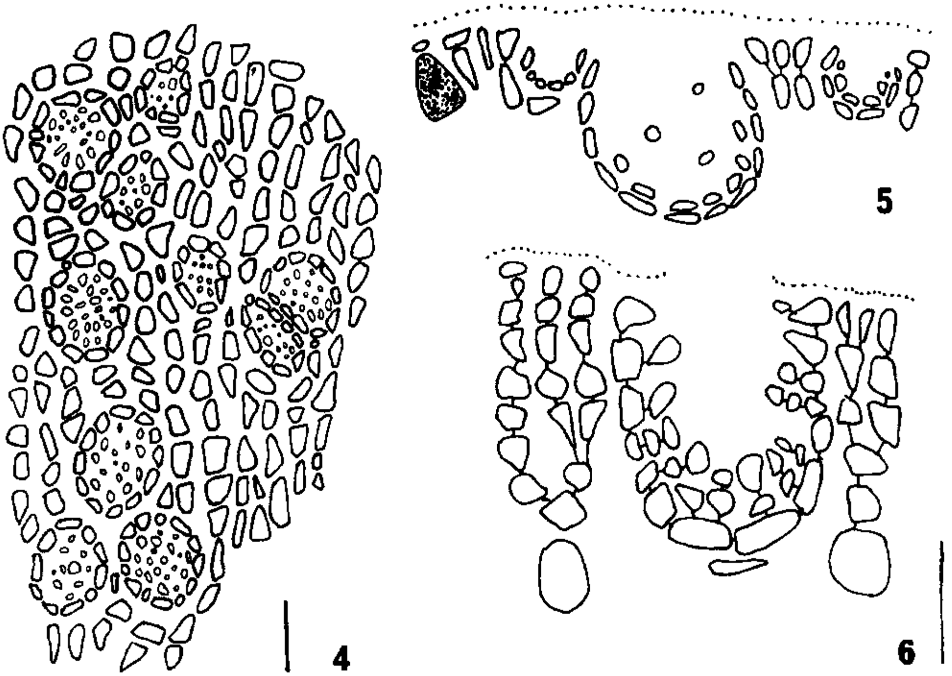
Thallus succulent, erect, solitary or caespitose, arising from a small disc 1.5–2.0 mm in diameter. Plant terete throughout, 25–60 cm tall (average, 40 cm), axes 1.0–2.5 mm in diameter (average, 1.5 mm), with two to four orders of branching, the branches flagelliform. Main axis persistent, or limited to the lowermost part; in very sheltered locations, lower laterals showing a tendency to become decumbent, or becoming the lead branches. First-order branches alternate, second-order branches predominantly secund, unilateral branches arranged







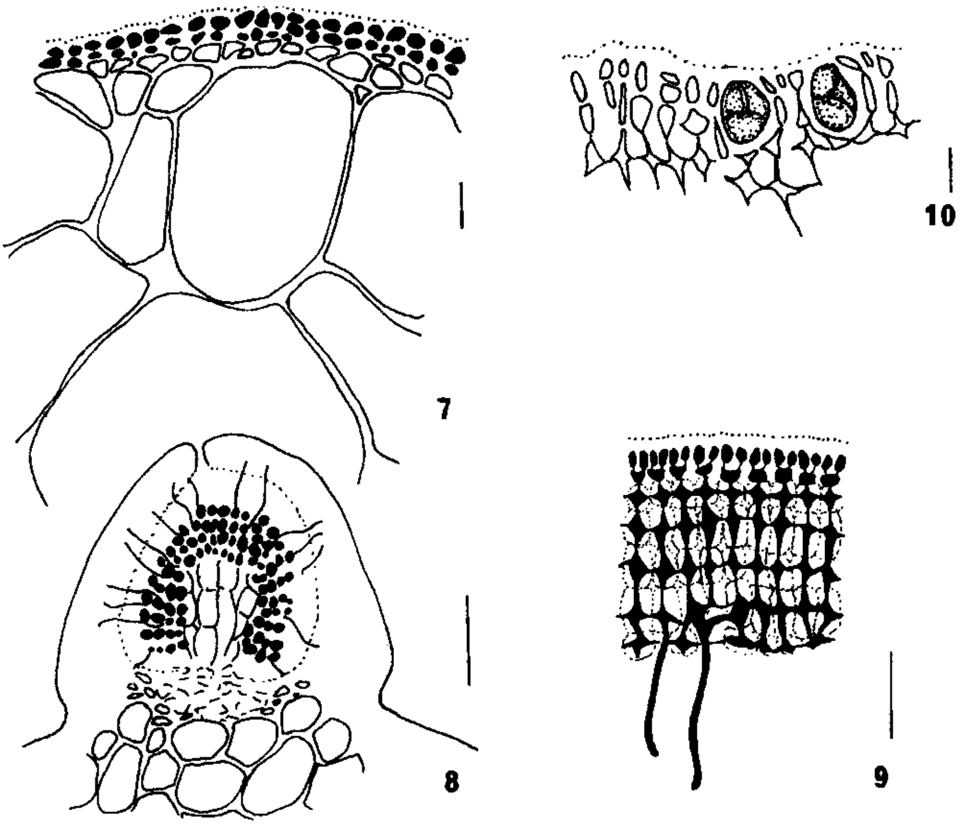
Figs. 1–3. *Gracilaria maraenae* sp. nov. collected by G. R. South at Suva, Fiji Islands, June 19, 1993. Fig. 1, cystocarpic holotype specimen (USP 0505). Fig. 2, Spermatangial isotype specimen (USP 0506). Fig. 3, Tetrasporic isotype specimen (USP 0507). Scale bars = 15 cm.



**Figs. 4–6. Spermatangial conceptacles of *Gracilaria maramae* sp. nov. collected by G. R. South at Suva, Fiji Islands, June 19, 1993. Fig. 4, Surface view (from the isotype material). Fig. 5, Transverse section of immature and mature conceptacles and a hair base cell (shaded) (from the type material). Fig. 6, Enlarged view (from the type material). Scale bars = 50 μm.**

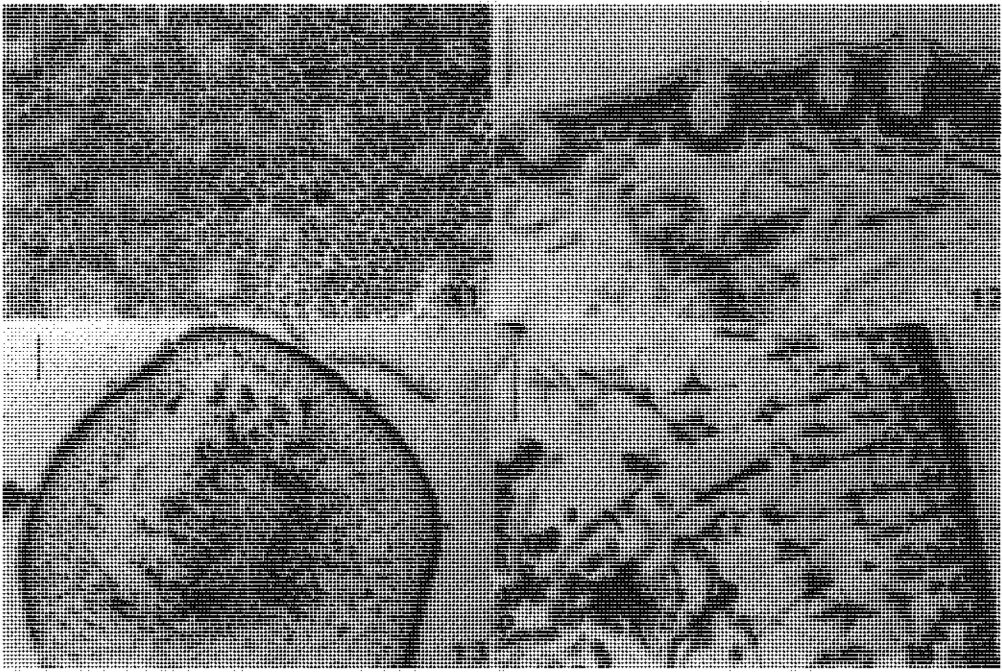
predominantly abaxially. Branches markedly fine tip at the base, tapering terminally to a fine tip. In transverse section, inner medulla consisting of large, pseudoparenchymatous cells, 250–480 μm in diameter, with thin walls 2.0–5.0 μm thick; transition from inner to outer medulla and from medulla to cortex abrupt. Cortex consisting of two to four cell layers, with outermost cells rounded, 10.0–12.5 μm tall and 7.5 μm wide.

Tetrasporangia scattered over most of thallus, among cortical cells; ovoid or subspherical, regularly cruciate, 30.0–37.5 μm tall, 25–30 μm wide, surrounded by elongated cortical cells. Hair basal cells numerous in cortex of tetrasporangial plants. Spermatangial conceptacles of verrucosa type, scattered over surface of thallus, round to oval in cross section, 27.5–38.0 μm diameter, up to 50 μm deep; conceptacles usually separated by several cortical cells, not merged, and when adjacent, separated by the walls of the two conceptacles. Cystocarps prominent, conical, or hemispherical, to 800 μm wide and 600 μm tall, not or scarcely constricted at the base, and not beaked when mature. Gonimoblast consisting of



**Figs. 7–10. *Gracilaria maramae* sp. nov. collected by G. R. South at Suva, Fiji Islands. Fig. 7, Transverse section of sterile axis (from the type material). Collected June 19, 1993. Scale bar = 20 μm. Fig. 8, Vertical section of cystocarp showing gonimoblast of large, pseudoparenchymatous cells and numerous tubular nutritive filaments (from the type material). Collected June 19, 1993. Scale bar = 200 μm. Fig. 9, Detail of the pericarp (stylized) showing tubular nutritive filaments with transverse connections and stellate cells. Collected September 26, 1992. Scale bar = 50 μm. Fig. 10, Transverse section showing tetrasporangia and tetraspores (from the type material). Collected June 19, 1993. Scale bar = 20 μm.**

large, pseudoparenchymatous cells, lacking a conspicuous or persistent fusion cell; numerous upper, and rather fewer, basal tubular nutritive filaments present, with upper filaments connecting and anastomosing with innermost two layers of pericarp; carpospores terminal, rounded or ovoid, 25–30 μm × 10–15 μm. Walls of pericarp thin, 130–200 μm thick, composed of six to seven layers, outermost layer pigmented, cells rounded to ovoid, remaining five to six layers consisting inwardly of progressively larger cells in conspicuous vertical rows, containing stellate chloroplasts and many pit connections.



Figs. 11–14. Fig. 11, *Gracilaria maramae* sp. nov. collected by G.R. South at Suva, Fiji Islands, June 19, 1993. Surface view of spermatangial conceptacles (from the type material). Fig. 12, Transverse section of male plant showing mature spermatangial conceptacles (from the type material). Fig. 13, Vertical section of cystocarp showing tubular nutritive cells (arrowheads) (from the holotype material). Fig. 14, Section of pericarp showing stellate cells and tubular nutritive filaments (from the type material). Scale bars: Figs. 11–13, 50 µm; Fig. 14, 100 µm.

Etymology: The specific epithet is derived from the Fijian word *marama* (lady), in recognition of the important role played by ethnic Fijian women in the harvesting and marketing of *G. maramae*.

Holotype Specimen: USP 0606, cystocarpic, collected at Suva, Fiji Islands, June 19, 1993, by G. R. South.

Isotypes: USP 0607, tetrasporic, collected at Suva, Fiji Islands, June 19, 1993, by G. R. South; USP 0608, spermatangial, collected at Suva, Fiji Islands, June 19, 1993, by G. R. South.

Representative Material: Suva Lagoon, Nukubuco Passage, Laucala Bay (*Carlson*; January 14, 1972, USP 0141 and 0142); Beqa (ex Suva Market) (*South*, October 26, 1991, USP 0143 and 0144); Suva Lagoon (*South*, September 26, 1992, cystocarpic, USP 0424 and 0575); Suva Lagoon (*South*, November 14, 1992, tetrasporic and cystocarpic, USP 0574); Beqa (ex Suva Market) (*South*, September 28, 1992, USP 0423); Suva (*South*, March 6, 1993, USP 0610 [cystocarpic], USP 0611 [male]); Suva Market (probably from Suva Lagoon)

(*South*, March 10, 1993, cystocarpic, USP 0590); Suva Lagoon (*South*, March 13, 1993, cystocarpic, USP 0576).

Distribution: *Gracilaria maramae* sp. nov. is common throughout Viti Levu and probably the remainder of the larger islands of the Fiji group. It grows in the upper subtidal to lower intertidal areas on the backreefs, favoring sites with good currents and water exchange. The species is regularly harvested and marketed for human consumption (South 1993) and may have considerable potential for development as an aquaculture species.

Remarks: *Gracilaria maramae* sp. nov. fits in the genus *Gracilaria sensu stricto* according to Fredericq and Hommersand (1990), because tubular nutritive filaments are present in both the pericarp and the floor of the cystocarp, and spermatangial conceptacles are generally not confluent (i.e., are not the polycavernosa type, or the *Hydropuntia* type *sensu* Fredericq and Hommersand 1990).

*Gracilaria maramae* sp. nov. shares a number of characteristics (Table 1) with other terete *Gracilaria* species from China that have verrucosa-type male conceptacles and stellate cells in the pericarp, such as *G. asiatica* Chang et Xia, *G. rubra* Chang et Xia, and *G. hainanensis* Chang et Xia, (Zhang and Xia 1992). *Gracilaria asiatica* has a more gradual reduction in cell size from the inner to outer medulla than *G. maramae* does, and it lacks constrictions of the branch bases; it also has only a few tubular filaments in the cystocarp, as does *G. hainanensis* (Zhang and Xia 1992). The wall of the pericarp is much thinner in *G. maramae* than in *G. rubra*, the most similar species of this group. Xia Bangmei and Zhang Junfu kindly examined the type material of the new species and remarked that the wall of the pericarp is the most distinctive feature of *G. maramae* and can be used to separate it from Chinese species.

**Table 1. Comparison of Selected Characteristics of *Gracilaria maramae* sp. nov. and Similar Terete Species from Asia and the Western Pacific**

| | **Characteristics** | | | | | |
|---|---|---|---|---|---|---|
| **Species** | **1** | **2** | **3** | **4** | **5** | **6** |
| *Gracilaria maramae* sp. nov. | + | | | + | + | + |
| *Gracilaria asiatica* Chang et Xia | + | | | ± | | + |
| *Gracilaria hanainensis* Chang et Xia | + | | | ± | + | + |
| *Gracilaria rubra* Chang et Xia | + | | | + | + | + |
| *Gracilaria stellata* Abbott, Zhang et Xia | | + | | | | + |
| *Gracilaria mixta* Abbott, Zhang et Xia | + | + | | | | |
| *Gracilaria fisheri* (Xia et Abbott) Abbott, Zhang et Xia | | + | | + | ± | |
| *Gracilaria edulis* (Gmelin) Silva | | + | | | | |
| *Gracilaria subtilis* (Xia et Abbott) Xia et Abbott | | + | | + | ± | |

Note. 1 = verrucosa-type male conceptacles, 2 = polycavernosa-type male conceptacles, 3 = textorii-type male conceptacles, 4 = presence of tubular nutritive filaments in the cystocarp, 5 = branches of first and subsequent orders markedly constricted at the base, 6 = cells of the pericarp with stellate chloroplasts.

The discrete verrucosa-type conceptacles of *G. maramae* sp. nov. distinguish it from the polycavernosa-type species of *Gracilaria* from the western Pacific: *G. changii* (Xia et Abbott) Abbott, Zhang et Xia; *G. fisheri* (Xia et Abbott) Abbott, Zhang et Xia; *G. edulis* (Gmelin) Silva (=*Polycavernosa fastigiata* Chang et Xia); *G. subtilis* (Xia et Abbott) Xia et Abbott; and *G. stellata* Abbott, Zhang et Xia (=*P. divergens* Xia et Abbott) (Abbott et al. 1991). Various features of the cystocarp of *G. maramae* sp. nov. also distinguish it from these other species.

Specifically, in comparison with *G. changii*, *G. maramae* sp. nov. has a much thinner pericarp, stellate chloroplasts in the pericarp cells, and no compressed cells in the inner pericarp. It also has large pseudoparenchymatous gonimoblast cells and numerous tubular absorbing filaments, features not found in *G. changii*.

Although it superficially resembles *G. mixta* Abbott, Zhang et Xia from South China (Abbott et al. 1991), *G. maramae* has several features not found in *G. mixta*, including the following:

- Lack of polycavernosa-type male conceptacles.
- Much thinner medullary cell walls.
- Spermatangial conceptables not arranged in elongate groups with lobed margins.
- Smaller cystocarps.
- Thinner pericarp, with fewer cell layers.
- Stellate chloroplasts in the wall of pericarp.

In some respects, *G. maramae* sp. nov. superficially resembles *G. stellata* from the Philippines. Xia and Abbott (1987) noted that *G. stellata* (as *P. divergens*) might also occur in the Solomon Islands, because a specimen in the British Museum from the Royal Society of London Expedition to the Solomon Islands (252a) has characteristics close to if not the same as those of *G. stellata*. The Solomon Island plants were identified as *G. edulis* (Gmelin) Silva (Womersley and Bailey 1970). Both *G. stellata* and *G. maramae* sp. nov. have stellate chloroplasts in the cells of the pericarp, but *G. stellata* has more cell layers (9–12 compared with 6–7), and the innermost layer of *G. stellata* consists of smaller, nonstellate cells, whereas those of *G. maramae* sp. nov. are stellate (Xia and Abbott 1987). In addition, *G. stellata* has fewer tubular nutritive filaments in the cystocarp than *G. maramae* sp. nov. does, and the mature cystocarps of *G. stellata*, unlike those of *G. maramae* sp. nov., are beaked. *Gracilaria stellata* also has a subcortex in the tetrasporangial plants, a feature lacking in *G. maramae*. Other differences in the overall morphology of the plants includes the divergent branching pattern characteristic of *G. stellata* but not *G. maramae* (Xia and Abbott 1987).

Previous records of *G. maramae* sp. nov. from Fiji may have been confused under the names *G. edulis*, *G. verrucosa* (Hudson) Papenfuss, and *G. confervoides* (Linnaeus) Greville (Chapman 1971, South and Kasahara 1992). In surveys conducted by the Fiji Fisheries Division, the plants are referred to as *G. verrucosa* (Fiji Fisheries Division 1981–1991). The record of *G.* sp. aff. *G. parvispora* Abbott in South and Kasahara (1992, p. 61) is certainly referable to *G.*

*maramae* sp. nov., because the plants (17971 in the herbarium of I. A. Abbott) are identical with the type specimen. The occurrence of *G. verrucosa* in Fiji must be ruled out, because of the current understanding of the features and distribution of this British species (Bird et al. 1982, Fredericq and Hommersand 1989).

## Acknowledgments

I thank Isabella A. Abbott for the invitation to participate in the fifth workshop, and the California Sea Grant Program and James Sullivan for assistance. Financial support was largely provided by the Canadian International Development Agency (Project C-046) and is warmly acknowledged. Collections and study of *G. maramae* in Fiji were made possible through a research grant from the University of the South Pacific. I also extend my appreciation to Xia Bangmei, Zhang Junfu, and Khanjanapaj Lewmanomont for kindly sharing their extensive *Gracilaria* experience with me and to Isabella A. Abbott for reviewing the manuscript and offering helpful advice.

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Xia Bangmei, and Abbott, I .A. 1987. New species of *Polycavernosa* Chang et Xia (Gracilariaceae, Rhodophyta) from the western Pacific. Phycologia 26:405–418.

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, pp. 195–206.

# A DECADE OF SPECIES OF *GRACILARIA* (*SENSU LATU*)

Isabella A. Abbott

## Abstract

A listing of 97 species of *Gracilaria* in the broad sense is provided along with the major bibliographic references to these species published in the past decade, a period of Sea Grant support for taxonomy workshops. Because numerous papers on *Gracilaria* and its relatives have been included in the Sea Grant series of workshop publications, and in other publications, the status of species of this genus that occur in the tropics and subtropics, especially in the warm Pacific areas, may have changed. This summary provides the most recent name changes and indicates the previous status.

## Introduction

A decade of studies of the genus *Gracilaria* and its close relatives has yielded a wider recognition of some of the species, as well as many new species. If the years have not resolved the limits of *Gracilaria verrucosa* (Hudson) Papenfuss (the type species of the genus), they also have not clearly demarcated the generic limits between *Gracilaria* and *Gracilariopsis*, which seemed straightforward in earlier times. At this writing, according to some students of the genera, of which I am one, the genus *Gracilaria* contains species that formerly were placed in *Gracilaria, Gracilariopsis*, and *Polycavernosa* (=*Hydropuntia*).

Although the careful studies of Fredericq and Hommersand (1989a, 1989b) have shown embryological and ontogenic differences between *Gracilaria* and *Gracilariopsis*, these distinctions are too technical for easy acceptance, even by other phycologists. To expect those who are not technically trained to accept these differences and to apply names to species that they cannot distinguish easily is impractical. Until further studies show other differences, it is useful to retain all species in *Gracilaria*. At such a time, a further sorting of categories may be possible. Additional grounds may justify retaining distinctions based on classification of spermatangial types (Yamamoto 1975), which have been in use for more than 15 years, but which studies in recent years show grade into each other.

Many will not accept the present circumscription of the numerous taxa that the genus comprises in the narrow or large sense. Perhaps, students of this group should aim for a compromise that will satisfy colleagues who have not become specialists in this group of algae, but who might be willing to learn the distinctions if the distinguishing features are easily recognized. The persons who grow, harvest, and sell gracilarioid material are interested in getting the algae to market, and only superficially interested in the fact that certain species yield a better grade of agar, or have a higher fraction of agarose that brings top dollar. For them, the biomass is simply not enough to warrant worrying about species names.

In the following alphabetical list, each entry contains the most meaningful references published in the past decade under each species name; the starred references which are from a list of many, are the most important ones. Each of these references may, in turn, have other references but, for the most part, these internal references serve only as supporting material for the use of the name, on the basis of one or more earlier reports. Identification or misidentification in a checklist may not constitute anything more than casual listing of a species name; such references are omitted. The emphasis is on references published in the past decade, but some earlier accounts give greater detail than the recent ones, and for that reason the earlier ones are included. No bibliography is included for the list, because the citations with the species names are sufficient to aid in locating the literature cited.

Clearly, a large amount of work has been going on in *Gracilaria*, yet we know that a great deal remains to be done. More important than describing new species will be redescribing old species whose names have been published for more than 100 years but are as poorly known now as when their names were first published.

### Species of *Gracilaria*

1. *Gracilaria abbottiana* Hoyle
   Abbott, I. A. Tax. Econ. Seaweeds 1, p. 85, fig. 49, 1985.
   Hoyle, M. D. Phycologia 17:299–303, 1978.
2. *Gracilaria aculeata* (Hering) Papenfuss
   Doty, M. S. Tax. Econ. Seaweeds 2, p. 203, 1988.
3. *Gracilaria albornozii* (Rodriguez) Abbott
   =*Polycavernosa albornozii* Rodriguez
   Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:12–27, 1991.
   * Rodriguez de Rios, N. Ernstia 15:12–31, 1986.
4. *Gracilaria arcuata* Zanardini
   * Abbott, I. A. Tax. Econ. Seaweeds 1, p. 89; 2, pp. 151, 153–154, 1985.
   Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, p. 69, 1985.
5. *Gracilaria arcuata* var. *arcuata*
   * Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 153–155, fig. 3, 1988.
6. *Gracilaria arcuata* var. *snackeyi* Weber-van-Bosse
   Trono, G. T., Jr., Azanza-Corrales, R., and Manuel, D. Philip. J. Biol. 12:32, 1983.
   * Abbott, I. A. Tax. Econ. Seaweeds 2, p. 155, fig. 4, 1988.
7. *Gracilaria articulata* Chang et Xia
   * Chang, C. F., and Xia Bangmei. Stud. Mar. Sin. 11:91–163, 1976.
   Xia Bangmei. Tax. Econ. Seaweeds 1, pp. 72–75, 1985.
8. *Gracilaria asiatica* Zhang et Xia
   Formerly *Gracilaria verrucosa* of Chinese authors.
   * Chang, C. F., and Xia Bangmei. Oceanol. Limnol. Sin. 16:175–180, 1985.
   Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–197, 1992.

9. *Gracilaria asiatica* var. *asiatica*
   Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–196, 1992.
10. *Gracilaria asiatica* var. *zhengii* Zhang et Xia
   * Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–197, 203, 1992.
11. *Gracilaria bangmeiana* Zhang et Abbott
   Formerly *Polycavernosa ramulosa* Chang & Xia.
   * Abbott, I. A, Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:23, 27, 1991.
   Dinh Nguyen H. Tax. Econ. Seaweeds 3, p. 208, 1992.
12. *Gracilaria blodgettii* Harvey
   Synonym: *Gracilaria cylindrica* Børgesen
   Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 69, 75, 1985.
   * Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 3, pp. 211–216, 218-221, 224-230, 1992.
   Reading, R. P., and Schneider, C. W. Phycologia 22:395–398, 1986.
13. *Gracilaria bursa-pastoris* (Gmelin) Silva.
   Hawaiian specimens previously published under this name have been transferred to *Gracilaria parvispora* Abbott; Chinese specimens under this name have been transferred to *Gracilaria chouae* Zhang et Xia.
   Yamamoto, H. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, pls. 1–49, 1978.
   * Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–206, 1992.
   Abbott, I. A. Tax. Econ. Seaweeds 1, pp. 118–121, 1985.
14. *Gracilaria cacalia* (J. Agardh) Dawson
   Synonym of *Gracilaria salicornia* (C. Agardh) Dawson
   * Xia Bangmei. Chin. J. Oceanol. Limnol. 4:100–106, pl. 1, 1986.
   Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 127–128, 136, 142, 1988.
15. *Gracilaria canaliculata* (Kützing) Sonder
   Synonym of *Gracilaria salicornia* (C. Agardh) Dawson
   * Xia Bangmei Chin. J. Oceanol. Limnol. 4:100–206, pl. 1, 1986.
16. *Gracilaria cervicornis* Turner
   Norris, J. N. Tax. Econ. Seaweeds 1, p. 101, fig. 69, 1985.
   * de Oliveira, E. C., Bird, C. J., and McLachlan, J. Can. J. Bot. 61:2999–3008, 1983.
   Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, pp. 137–155, figs. 2, 12–13, 22, 24, 1985.
17. *Gracilaria changii* (Xia and Abbott) Abbott, Zhang et Xia
   (=*Polycavernosa changii* Xia and Abbott)
   * Xia Bangmei and Abbott, I. A. Phycologia 26:406–409, figs. 3, 11, 1987.
   Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:23, 1991.
18. *Gracilaria chorda* Holmes
   Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, p. 69, 1985.
   * Yamamoto, H. Mem. Fac. Fish. Hokkaido Univ. 25:119–121, 1978.
19. *Gracilaria chouae* Zhang et Xia
   Formerly known in China as *Gracilaria bursa-pastoris*.

Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–196, 199–204, 1992.

20. *Gracilaria compressa* (C. Agardh) Greville
    Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, p. 69, 1985.
    * Howe, M. A. J. Wash. Acad. 22:167–170, 1932.
    Norris, J. N. Tax. Econ. Seaweeds 1, p. 131, 1985.
21. *Gracilaria confervoides* (Linnaeus) Greville
    =*Gracilaria verrucosa* (Hudson) Papenfuss
    Western Pacific specimens identified as *G. verrucosa* do not match specimens from various areas on the British and Welsh coasts (which themselves may be mismatched). The Asian specimens are now being studied in culture, with hybridization, and critical morphological examination. Previous Chinese specimens under this name have been relegated to *G. asiatica* Zhang et Xia or *G. tenuistipitata* var. *liui* Zhang et Xia, the latter from Taiwan as well. Some of the Japanese specimens previously identified as *G. verrucosa* have been placed in *G. vermiculophylla* Ohmi; others have not been segregated. Plants from the American Pacific coast that previously were identified as *G. verrucosa* are now named *G. pacifica* Abbott.
    Abbott, I. A. Tax. Econ. Seaweeds 2, p. 127, 1988.
    * Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, pp. 138–139, 148, 1985.
    Dinh Nguyen H. Tax. Econ. Seaweeds 3, p. 208, 1992.
    Papenfuss, G. F. Phykos 5:95–105, 1967.
22. *Gracilaria confervoides* forma *ecorticata* Pham
    Dinh Nguyen H. Tax. Econ. Seaweeds 3, p. 208, 1992.
    Pham, H. H. Marine algae of South Vietnam. Ministry of Education, Saigon, 1969 (the Vietnamese material on which this identification was based should be reexamined).
23. *Gracilaria cornea* J. Agardh
    Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45(1):1–27, 1991.
24. *Gracilaria coronopifolia* J. Agardh
    Abbott, I. A. Tax. Econ. Seaweeds 1, p. 85–86, 1985.
    Dawson, E. Y. Allan Hancock Found. Occ. Pap. 7:22, 1949.
    Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 77–78, 80, 1985.
25. *Gracilaria corticata* J. Agardh
    Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, p. 138, 1985.
26. *Gracilaria corymbiata* (Rodríguez) Abbott
    =*Polycavernosa corymbiata* Rodríguez
    * Rodríguez de Rios, N. Ernstia 15(38):12–31, 1986.
    Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:24–25, 1991.
27. *Gracilaria crassa* Harvey ex. J. Agardh.
    Synonym of *Gracilaria salicornia*
    * Xia Bangmei. Chin. J. Oceanol. Limnol. 4:100–106, pl. 1, 1986.
    Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 127–128, 1988.

28. *Gracilaria crassissima* (Crouan et Crouan) Crouan et Crouan
=*Polycavernosa crassissima* (Crouan et Crouan) Fredericq and Norris
* Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, pp. 137–152, 1985.
Rodríguez de Rios, N. Ernstia 15(38):13–17, figs. 5–7, 9, 1986.

29. *Gracilaria crispata* Setchell et Gardner
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 93, 95–96, 123–125, 1985.

30. *Gracilaria cylindrica* Børgesen
Synonym: *Gracilaria blodgettii* Harvey
Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 3, pp. 211–215, 217–219, 224–225, 229–230, 1992.
Note: Western Pacific material under the name *G. cylindrica* or *G. blodgettii* is doubtfully this species.

31. *Gracilaria dactyloides* Sonder
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 89, 1985.

32. *Gracilaria debilis* (Forsskål) Børgesen
=*Polycavernosa debilis* (Forsskål) Fredericq and Norris
* Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, pp. 137–152, 1985.
Rodríguez de Rios, N. Ernstia 15(38):17–23, figs. 8–11, 1986.

33. *Gracilaria dentata* J. Agardh
Synonym of *Gracilaria rangiferina* (Kützing) Piccone
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:24, 1991.

34. *Gracilaria denticulata* (Kützing) Weber van Bosse
Substitute name: *Gracilaria vieillardii* Silva, Smithsonian Contrib. Mar. Sci. 27:44, 1987.
Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 78–80, 1985.
Chiang, Y. M. Tax. Econ. Seaweeds 1, pp. 81–83, 1985.

35. *Gracilaria disticha* J. Agardh
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 89, fig. 56, 1985.

36. *Gracilaria domingensis* Sonder ex Kützing
Norris, J. N. Tax. Econ. Seaweeds 1, p. 101, 1985.
Oliveira, E. de, Bird, C. J., and McLachlan, J. Can. J. Bot. 61:3000, 1983.

37. *Gracilaria dotyi* Hoyle
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 85, 1985.

38. *Gracilaria dura* (C. Agardh) J. Agardh
Abbott, I. A. Tax. Econ. Seaweeds 2, p. 137, 1988.

39. *Gracilaria dura* forma *prolificans* Reinbold
Abbott, I. A. Tax. Econ. Seaweeds 2, p. 137, 1988.

40. *Gracilaria edulis* (Gmelin) Silva
Synonyms: *Gracilaria lichenoides* (Lamouroux) Greville
*Polycavernosa fastigiata* Chang et Xia
Abbott, I. A. Tax. Econ. Seaweeds 2, p. 151, 1988.
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45(1):12–27, 1991.
Abbott, I. A. Tax. Econ. Seaweeds 4, pp. 113–114, 1994.

41. *Gracilaria epihippisora* Hoyle
 Abbott, I. A. Tax. Econ. Seaweeds 1, p. 85, 1985.
42. *Gracilaria eucheumoides* Harvey
 Trono, G. C., Jr., and Ganzon-Fortes, E. T. An illustrated seaweed flora, p. 91, 1980, Filipinas Foundation, Manila.
 Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 77–80, 1985.
 Chiang, Y. M. Tax. Econ. Seaweeds 1, pp. 81, 83, 1985.
 Meneses I. and Abbott, I. A. Micronesica 20:192, 1987.
43. *Gracilaria firma* Chang and Xia
 * Chang, C. F., and Xia Bangmei. Stud. Mar. Sin. 11:91–163, 1976.
 Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 137–138, 1988.
44. *Gracilaria fisheri* (Xia et Abbott) Abbott, Zhang et Xia
 =*Polycavernosa fisheri* Xia and Abbott
 Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:23, 1991.
 * Xia Bangmei and Abbott, I. A. Phycologia 26:411–413, 1987.
45. *Gracilaria foliifera* (Forsskål) Børgesen
 * Norris, J. N. Tax. Econ. Seaweeds 1, p. 101, fig. 70, 1985.
 Dinh Nguyen H. Tax. Econ. Seaweeds 3, p. 208, 1992.
46. *Gracilaria gigas* Harvey
 Xia Bangmei. Tax. Econ. Seaweeds 1, pp. 71, 75, 1985.
 Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 77–80, 1984.
 Yamamoto, H. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, pls. 1–49, 1978.
47. *Gracilaria hainanensis* Chang et Xia
 * Chang, C. F., and Xia Bangmei. Stud. Mar. Sin. 11:91–163, 1976.
 Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, p. 69, 1985.
 Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 208–209, 1992.
48. *Gracilaria henriquesiana* Hariot
 Synonym of *Gracilaria rangiferina* (Kützing) Piccone
 =*Polycavernosa henriquesiana* (Hariot) Chang and Xia
 =*Hydropuntia henriquesiana* (Hariot) Wynne
 Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:24, 1991.
49. *Gracilaria heteroclada* Zhang and Xia
 Now *Gracilariopsis heteroclada* (Zhang and Xia) Zhang and Xia.
 Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 2, pp. 132–136, figs. 2, 10–17, 1988.
 Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:22, 1991.
50. *Gracilaria incurvata* Okamura
 Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 78-80, 1985.
51. *Gracilaria irregularis* Abbott
 Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 141–142, figs. 2, 5–6, 1988.
52. *Gracilaria lacinulata* (Vahl) Børgesen
 Abbott, I. A. Tax. Econ. Seaweeds 1, p. 89, 1985.
53. *Gracilaria lemaneiformis* (Bory) Weber-van Bosse
 Synonym: *Gracilaria sjoestedtii* Kylin

*Gracilariopsis sjoestedtii* (Kylin) Dawson
*Gracilariopsis lemaneiformis* (Bory) Dawson, Acleto, and Foldvik
* Abbott, I. A. Taxon 32:561, 1983.
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 85, 1985.
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 95–99, 1985.

54. *Gracilaria lichenoides* (Linne) Harvey
Synonym: *Gracilaria edulis* (Gmelin) Silva
Abbott, I. A. Tax. Econ. Seaweeds 2, p. 151, 1988.
* Abbott, I. A. Tax. Econ. Seaweeds 4, p. 113, 1994.

55. *Gracilaria mammillaris* (Montagne) Howe
Norris, J. N. Tax. Econ. Seaweeds 1, p. 133, 1985.

56. *Gracilaria megaspora* (Dawson) Papenfuss
=*Gracilariopsis megaspora* Dawson
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 123, 127, 1985.
Chang, C. F., and Xia Bangmei. Stud. Mar. Sin. 11:145–147, figs. 40–41, 1976.

57. *Gracilaria millardetii* (Montagne) J. Agardh
Fredericq, S., and Norris, J. N. Tax. Econ. Seaweed. 1, p. 139, 1985.

58. *Gracilaria minor* (Sonder) Durairatnam
Synonym of *Gracilaria salicornia* (C. Agardh) Dawson
Abbott, I. A. Tax. Econ. Seaweeds 2, p. 127, 1988.
Xia Bangmei. Chin. J. Oceanol. Limnol. 4:100–106, 1986.

59. *Gracilaria mixta* Abbott, Zhang and Xia
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:12–27, 1991.
Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, p. 203, 1992.

60. *Gracilaria multifurcata* Børgesen.
Synonyms: *Polycavernosa multifurcata* (Børgesen) Chang and Xia
*Hydropuntia multifurcata* (Børgesen) Wynne
Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, p. 150, 1985.
Xia Bangmei and Abbott, I. A. Tax. Econ. Seaweeds 1, p. 161, 1985.
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45(1):12–27, 1991.

61. *Gracilaria multipartita* J. Agardh
Fredericq, S., and Norris, J. N. Tax. Econ. Seaweeds 1, p. 138, 1985.

62. *Gracilaria pachydermatica* Setchell et Gardner
Synonyms: *Gracilaria guaymasensis* Dawson
*Gracilaria sinicola* Dawson
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 93, 123–124, 127–128; 1985.

63. *Gracilaria pacifica* Abbott
Previously known as *Gracilaria verrucosa* on Pacific west coast of North America.
Abbott, I. A. Tax. Econ. Seaweeds 1, pp. 97–99, 116–118, 1985.

64. *Gracilaria papenfussii* Abbott
Synonym: *Gracilaria andersonii* Kylin
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 97, 1985.

* Abbott, I. A. Taxon 32:561–564, 1983.

65. *Gracilaria parvispora* Abbott
Hawaiian material previously known as *Gracilaria bursa-pastoris.*
* Abbott, I. A. Tax. Econ. Seaweeds 1, pp. 119–120, 1985.
Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, pp. 195–196, 199–204, 1992.
66. *Gracilaria percurrens* (Abbott) Abbott
=*Polycavernosa percurrens* Abbott
* Abbott, I. A. Tax. Econ. Seaweeds 2, pp. 146–148, fig. 13, 1988.
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:23, 1991.
67. *Gracilaria pinnata* Setchell et Gardner
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 123, 128, 131, 1985.
68. *Gracilaria punctata* (Okamura) Yamada
Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 78–80, 1985.
Dinh Nguyen H. Tax. Econ. Seaweeds 3, pp. 208–209, 1992.
69. *Gracilaria purpurascens* (Harvey) J. Agardh
Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 78–80, 1985.
Yamamoto, H. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, 1978.
70. *Gracilaria radicans* Hauck
Tsuda, R. Tax. Econ. Seaweeds 1, p. 92, 1985.
71. *Gracilaria rangiferina* (Kützing) Piccone
Synonyms: *Gracilaria dentata* J. Agardh
*Polycavernosa dentata* (J. Agardh) Lawson and John
*Hydropuntia dentata* (J. Agardh) Wynne
*Gracilaria henriquesiana* Hariot
*Polycavernosa henriquesiana* (Hariot) Chang and Xia
*Hydropuntia henriquesiana* (Hariot) Wynne
* Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45(1):12–27, 1991.
72. *Gracilaria robusta* Setchell
Abbott, I. A. Tax. Econ. Seaweeds 1, p. 97, 1985.
73. *Gracilaria rubra* Chang et Xia
Xia Bangmei. Tax. Econ. Seaweeds 1, pp. 71–75, 1985.
Zhang Junfu and Xia Bangmei. Tax. Econ. Seaweeds 3, p. 196, 1992.
74. *Gracilaria rubrimembra* Dawson
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 93–96, 1985.
75. *Gracilaria salicornia* (C. Agardh) Dawson
Synonyms: *Corallopsis salicornia* (C. Agardh) Greville
*Corallopsis dichotoma* Ruprecht
*Corallopsis cacalia* J. Agardh
*Gracilaria cacalia* (J. Agardh) Dawson
*Corallopsis opuntia* J. Agardh
*Corallopsis salicornia* var. *minor* Sonder
*Corallopsis minor* (Sonder) J. Agardh
*Gracilaria minor* (Sonder) Chang and Xia

*Gracilaria canaliculata* (Kützing) Sonder
* Xia Bangmei. Chin. J. Oceanol. Limnol. 4:100–106, pl. 1, 1986.
Trono, G. C., Jr., and Ganzon-Fortes, E. An illustrated seaweed flora. Filipinas Foundation, Manila, p. 93, 1980.

76. *Gracilaria sjoestedtii* Kylin
Synonym of *Gracilaria lemaneiformis* (Bory) Weber-van Bosse; the type species of Gracilariopsis if that genus is recognized.
Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, p. 70, 1985.
* Abbott, I. A. Taxon 32:561–565, 1983.

77. *Gracilaria spinulosa* (Okamura) Chang et Xia
Xia Bangmei. Tax. Econ. Seaweeds 1, p. 75, 1985.
* Chang, C. F., and Xia Bangmei. Stud. Mar. Sin. 11:148–150, fig. 42, 1976.
Dinh Nguyen H. Tax. Econ. Seaweeds 3, p. 208, 1992.

78. *Gracilaria stellata* Xia et Abbott
New name for *Polycavernosa divergens* Xia and Abbott when it was transferred to *Gracilaria*, because the species name was already used in that genus.
Xia Bangmei and Abbott, I. A. Phycologia 26:409, 1987.
Abbott, I. A., Zhang Junfu, and Xia Bangmei. Pac. Sci. 45:22, 1991.

79. *Gracilaria sublittoralis* Yamada et Segawa
Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 78–80, 1985.
* Yamamoto, H. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, 1978.

80. *Gracilaria subsecundata* Setchell et Gardner
Norris, J. N. Tax. Econ. Seaweeds 1, pp. 93, 95–96, 123, 128, 131, 1985.

81. *Gracilaria subtilis* (Xia and Abbott) Xia and Abbott
* =*Polycavernosa subtilis* Xia and Abbott, Phycologia 26: 413–414, 1987.
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Xia Bangmei and Yamamoto, H. Tax. Econ. Seaweeds 1, pp. 69–70, 1985.
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    Doty, M. S. Tax. Econ. Seaweeds 2, p. 172, 1988.
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## Miscellaneous Notes

At this time (November 1993), the genus *Gracilariopsis* is separated from *Gracilaria* on the basis of highly technical grounds: female gametophytes must be in just the right stage after fertilization for interpretations. As fewer persons are being trained to recognize these events, I think it is impractical to impose this kind of high specificity on the systematics of algae used commercially by persons who lack the technical training required to recognize the taxa. For that reason, and until a more usable system is forthcoming, I urge the continued use of *Gracilaria* for species that are now in *Gracilaria* and *Gracilariopsis*. However, many species that have been placed in *Gracilariopsis* have not been moved from that genus, and at this time, their anatomy has not been elucidated by modern-day workers. These species should remain in *Gracilariopsis* until it can be determined by reexamination of type specimens and study of new material where they belong.

The following species of *Gracilariopsis* were found in Vietnam but have not been examined by a specialist in gracilarioids.

95. *Gracilariopsis nganii* Pham
    Dinh Nguyen H. Tax. Econ. Seaweeds 3, pp. 207–208, 1992.
    Pham, H. H. Marine algae of South Vietnam. Ministry Education and Youth, Saigon. pp. 179–180, 1969.
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    Pham, H.H. Marine algae of South Vietnam. Ministry Education and Youth, Saigon. pp. 180–181, 1969.
97. *Gracilariopsis rhodotricha* Dawson
    Dinh Nguyen H. Tax. Econ. Seaweeds 3, pp. 207–208, 1992.
    Dawson, E. Y. Pac. Sci. 8:373–481, 1954.
    Pham, H. H. Marine algae of South Vietnam. Ministry Education and Youth, Saigon. p. 179, 1969.

All *Hydropuntia* species have been placed in *Gracilaria* by Abbott, Zhang, and Xia (1991). As a synonym (later homonym) of *Hydropuntia*, all species of *Polycavernosa* have been transferred to *Gracilaria* by Abbott, Zhang, and Xia (1991).

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# ADDITIONS TO THE SPECIES OF *GRACILARIA* OF CHINA

†Zhang Junfu, Xia Bangmei, Wang Yongchuan, and Pan Guoying

## Abstract

On the basis of new materials of *Gracilaria* received from the South China Sea Institute of Oceanology, two new species, *G. longirostris* Zhang et Wang and *G. fanii* Xia et Pan from the eastern coast of Guangdong Province, South China, are described. The former is distinctive and can be easily recognized on the basis of an exceptionally long projection representing the ostiole of cystocarps. This feature is unique, not appearing in any other members of the genus. The second species closely resembles *G. megaspora* (Dawson) Papenfuss. However, unlike *G. megaspora* , it has traversing filaments, is a larger plant, branches more frequently, has no hairs, and has larger cystocarps and a different structure in the pericarp.

## Description of the Species

Additions to the already numerous species of *Gracilaria* in China are due to the exploration of new areas. A description of two new species is given here. The type specimens of the new species are deposited in the Herbarium of the Institute of Oceanology, Chinese Academy of Sciences, Qingdao (AST).

*Gracilaria longirostris* Zhang et Wang sp. nov.

Figs. 1–19

Thallis and 30 cm longis, cylindricis 830–960 µm diametro, 2–4 ordinatos edentibus; tetrasporangiis ovatis, 20–50 µm × 10-36 µm; cystocarpiis proeminentibus, 1992 µm × 1138 µm, longirostris ad 2–3 mm longis, uno vel ramificato subdichomas, cellulae pericarpii 4–7 seriales, 106–145 µm crassa.

Plants (Figs. 1–3) dark brown, subcartilaginous, erect, solitary or caespitose, arising from a small disc, cylindrical throughout, about 30 cm long. Main axis percurrent or not, 830–960 µm in diameter, with two to three or four orders of branching. Specimens, adhering imperfectly to paper on drying. In transverse section (Fig. 19), thallus consisting of a medulla of large parenchymatous cells, 100–165 µm × 66–80 µm, with walls 10.0–16.5 µm thick, surrounded by three to four layers of small, oblong to ovoid cortical cells 6.6–13.0 µm × 3.0–6.6 µm, outermost layer of cell pigmented and with surface jelly 6.6 µm thick; transition from medulla to cortex abrupt.

Tetrasporangia scattered among surface layers of frond, ovoid to oblong in transverse section, 20–50 µm × 10–36 µm, surrounded by slightly modified cortical cells. Cystocarps prominently protruding, 1992 µm × 1138 µm, globose (Fig. 4) to pomegranatelike (Fig. 6) or terminating in an elongated, simple (Fig. 7)

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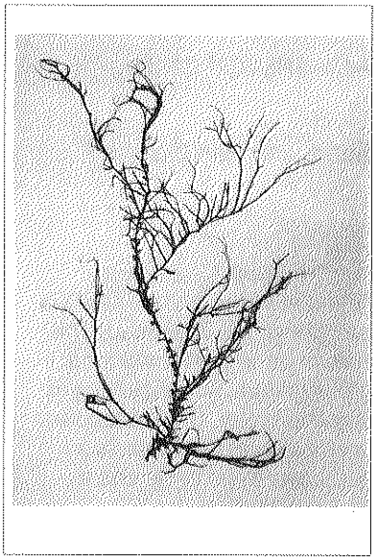
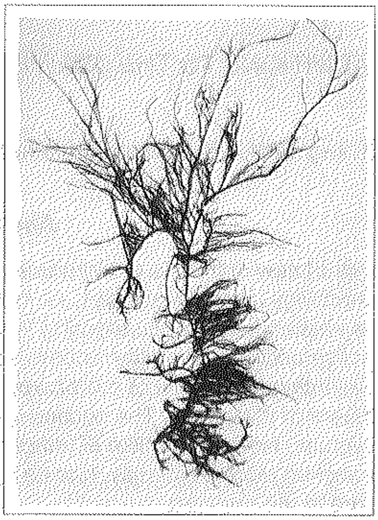
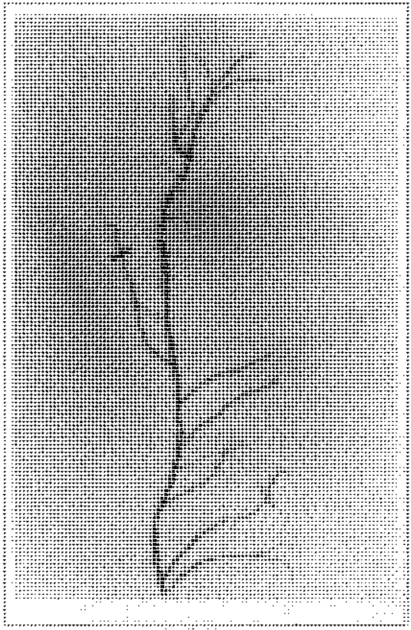
†This publication is dedicated to Zhang Junfu.







Figs. 1–3. *Gracilaria longirostris* Zhang et Wang sp. nov. Fig. 1, Holotype (AST 821022), a cystocarpic plant. Fig. 2, Isotype (AST 821021), a tetrasporangial plant. Fig. 3, A cystocarpic plant (AST 840100).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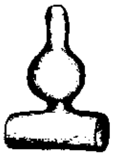
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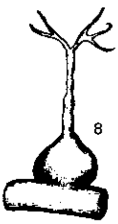
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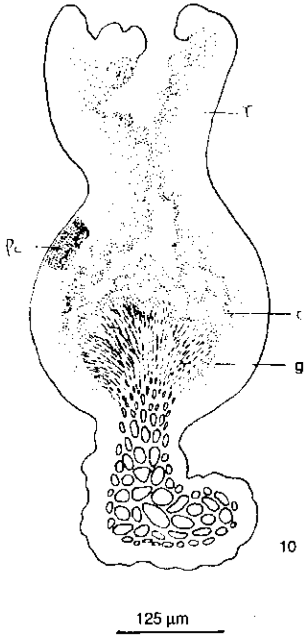

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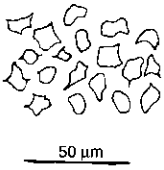

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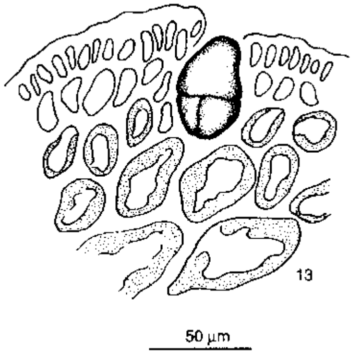

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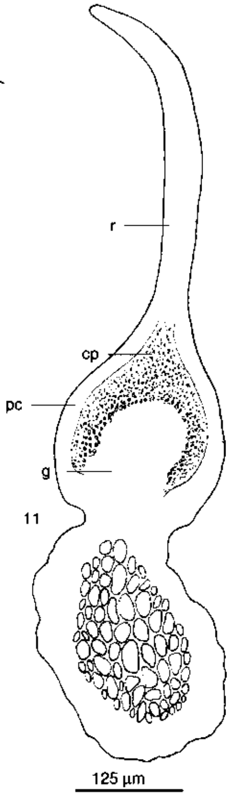

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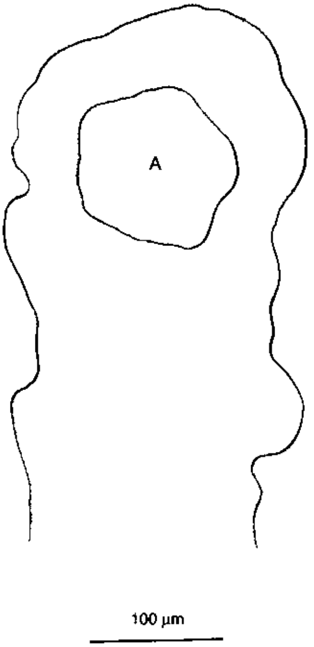
**Figs. 4–13.** ***Gracilaria longirostris*** **Zhang et Wang sp. nov. Figs. 4–9, Variation of the cystocarpic rostrates (4–6, AST 821022; 7–9, AST 840100.) Figs. 10–11, Longitudinal sections through the cystocarp showing rostrate (r), gonimoblast (g), carposporangia (cp), and pericarp (pc). (10, AST 821022; 11, AST 840100.) Fig. 12, Enlargement of part of the gonimoblast of Fig. 11 (AST 840100). Fig. 13, Transverse section of tetrasporangium (AST 821021).**



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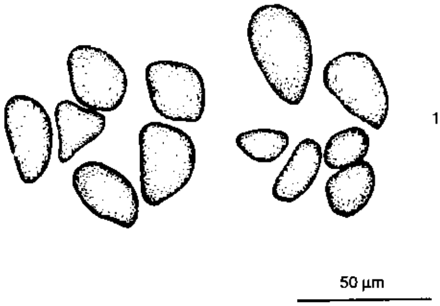

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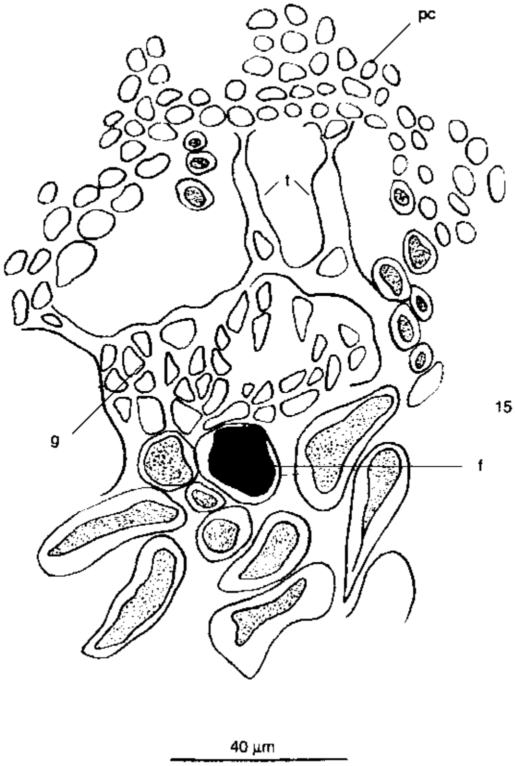

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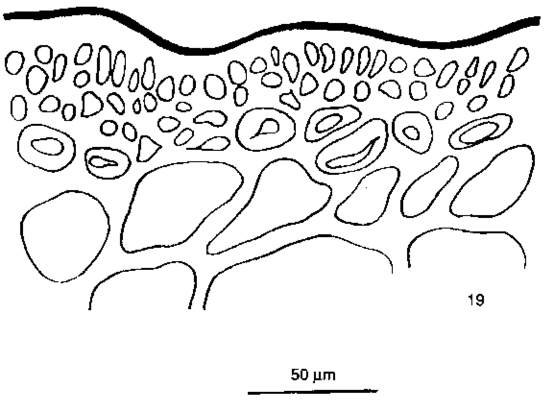
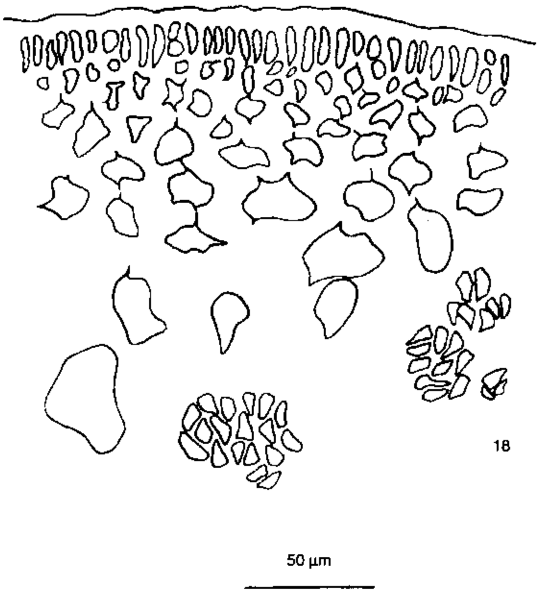
Figs. 14–19. *Gracilaria longirostris* Zhang et Wang sp. nov. Fig. 14, Longitudinal section through young cystocarp (AST 821022). Fig. 15, Enlargement of part of the pericarp of Fig. 14 showing gonimoblast (g), fusion cell (f), traversing filaments (t), and pericarp (pc). Fig. 16, Carposporangia.





**Figs. 17 and 18, Enlargement of part of the pericarp of Fig. 10 (821022). Fig. 19, Transverse section of part of main axis (AST 821022).**

to branched (Fig. 8) beak of up to 2–3 mm (Fig. 9), which may be constricted at the base. Gonimoblast consisting of small cells with obscure cell walls and cell contents irregularly connected to each other. Traversing filaments found only in young cystocarp (Fig. 15). Pericarp (Figs. 17 and 18) thin, 106–145 µm, consisting of four to seven layers of cells, outermost layer pigmented with cells cylindrical or oblong, inner layers with small oval-elliptical to roundish cells with irregular corners and obscure cell walls; in young cystocarp, gonimoblast developing from a large fusion cell (Fig. 15). Carposporangia ovoid or round, 30–33 µm × 13–20 µm. Spermatangia unknown.

Holotype Specimen: AST 821022, cystocarpic, collected from shells or gravel in small canal on shallow intertidal areas, with some fresh water flowing into it, in Sankongqiao, Shenao, Nanao County, Guangdong Province, China, by Pan Guoying and Liao Xiaoshan, June 5, 1982.

Isotypes: AST 821021, tetrasporangial, and AST 830173 and AST 820237, cystocarpic, collected at same place and on same date as holotype specimen.

Other Material: AST 840100, cystocarpic, collected from Jiezigang, Lufeng County, Guangdong Province, China.

Etymology: This species is named for the characteristic long beak of the cystocarp.

Remarks: The large, prominently protruding cystocarps with long, elaborate or simple beaks are distinctive; they have not been found in any other species of the genus. In external appearance, only *G. tenuistipitata* Chang et Xia var. *tenuistipitata* (Chang and Xia, 1976) and *G. bailinae* (Zhang et Xia) Zhang et Xia comb. nov. are similar.

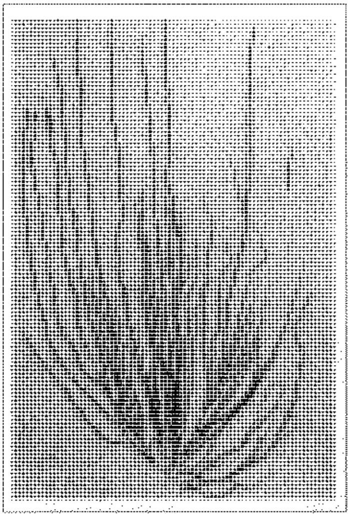
The regular production of vegetative branches from the pericarp can be used as a distinguishing feature. The cystocarps of this species show more variation in ornamentation than any other known species, from the shorter and simple form (less than I mm) to the longer (up to 2–3 mm) and simple to branching form. Among the materials we examined, the cystocarps of a few specimens (AST 821022) had a shorter and swollen beak, resembling pomegranate. Longitudinal sections showed that the beak is an extension of the cystocarp (Figs. 10 and 11), because some carposporangia are found in them.

*Gracilaria fanii* Xia et Pan sp. nov. Figs. 20–29

Thallis ad 33 cm longis, gracilibus, cylindricis, totis minus quam 664 μm diametro, fragilis, fractis, majoribus ramis in seriebus 3–5 irregularibus, longius attenuatis; tetrasporangiis haud in soris congregatis per corticem fabrica fere normali dispersis; spermatangiorum typi "verrucosa"; cystocarpiis 580–996 μm × 1145–1495 μm, subconicsis, basi paullo constrictis; cellulae pericarpii 6–10 seriale, 60–100 μm crass; carposporis ovoideis, 26–36 (-42) μm × 17–26 μm.

Plants (Figs. 20 and 21) light purplish or olive green, membranous-cartilaginous, erect, solitary or caespitose, arising from a small disc, cylindrical throughout, relatively slender, 30–33 cm long. Main axis not percurrent, 531–664 μm in diameter with three to five orders of branches, second and third orders divided near the bases, forming leading branches; branches elongated, flagelliform, brittle and easily broken. Specimens adhering imperfectly to paper on drying. In transverse section, thallus consisting of a medulla of large parenchymatous cells, 46–200 μm × 33-116 μm, with walls 8–17 μm thick, surrounded by two to three layers of small oblong or ovoid cells 17–20 μm × 5–7 μm thick, outermost layer 13.0 μm × 3.0 μm, pigmented and with surface jelly 3.0–6.6 μm thick; transition from medulla to cortex abrupt (Fig. 22).

Tetrasporangia scattered among surface layers of frond, ovoid or oblong (Fig. 24) in surface view, 17–40 μm × 13–36 μm, ovoid or oblong in transverse section,



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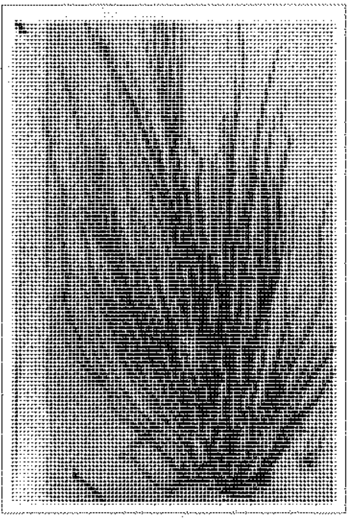

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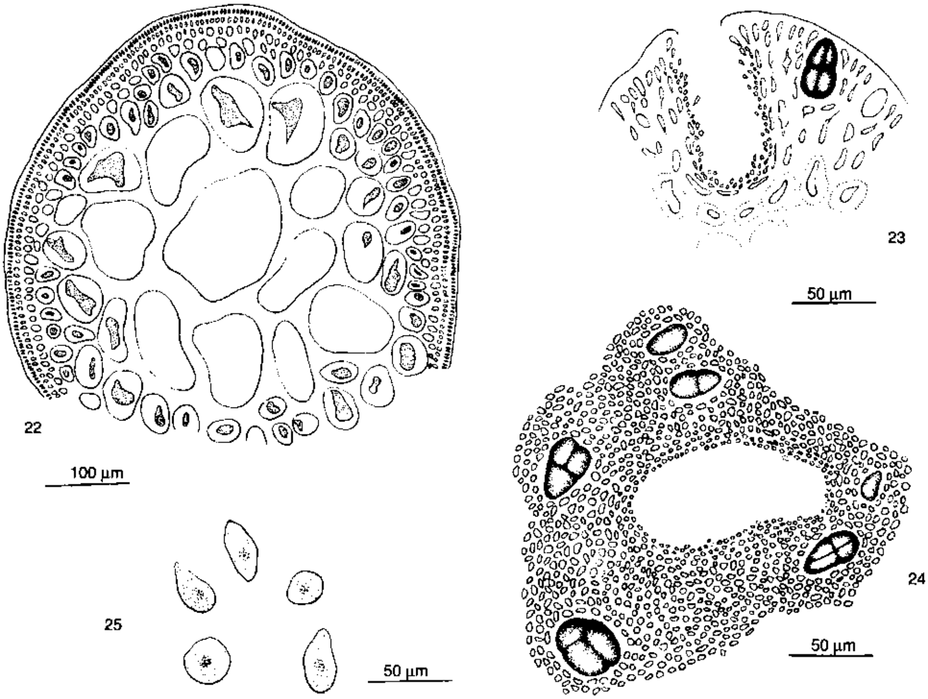
**Figs. 20 and 21. *Gracilaria fanii* Xia et Pan sp. nov. Fig. 20, Holotype (AST 821313) a cystocarpic plant. Fig. 21, Isotype (AST 821312) a tetrasporangial plant mixed with spermatangia.**

40–46 μm × 23–30 μm, surrounded by slightly modified cortical cells, cruciately or occasionally irregularly tetrahedrally divided. Spermatangial conceptacles (Fig. 24) scattered over surface of frond, mixed with tetrasporangia, conceptacle ovoid to elongate-elliptical in sectional view, 112–122 μm × 66 μm, well separated by modified cortical cells (Fig. 23). Cystocarps (Fig. 26) prominently protruding, 580–996 μm × 1145–1494 μm, subconical, slightly constricted at base. Gonimoblast consisting of many small parenchymatous cells (Fig. 26). Pericarp (Figs. 27–29) thin, 60–100 μm thick, consisting of 6–10 layers of cells; outermost layer pigmented, with elliptical cells, cells in inner layers round to ovoid, horizontally elliptical with obscure cell walls; traversing filaments. Carposporangia round or ovoid, 26–36 (-42) μm × 17–26 μm (Fig. 25).

Holotype Specimen: AST 821313 cystocarpic. Isotype: AST 821312, tetrasporangia; mixed with spermatangia, collected from Beilin, Jiaoping County (near Shantou City), Guangdong Province, China, by Chen Haoru, April 12, 1982.

Etymology: The species was named in appreciation of the contributions to phycology of the late Dr. Kung-Chu Fan, who was an inspirational teacher of Pan and Wang.

Remarks: This fine, slender plant seems to be related most closely to *G. megaspora* Dawson. However, unlike *G. megaspora* it has traversing filaments in its cystocarps, larger cystocarps, smaller carpospores, no hairs, cystocarps constricted at the base, and longer and narrower gonimoblast cells. The basal constriction of the cystocarps and the spermatangial configuration are similar to

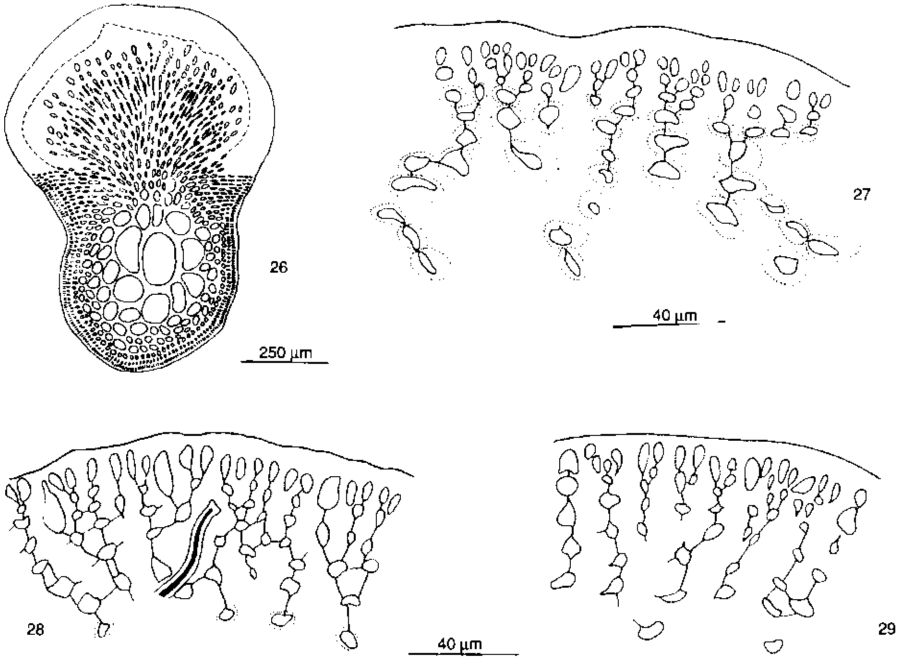


**Figs. 22–25.** ***Gracilaria fanii*** **Xia et Pan sp. nov. Fig. 22, Transverse section of part of main axis (AST 821313). Fig. 23, Part of cortex with tetrasporangia and verrucosa-type spermatangia in surface view (AST 821312). Fig. 24, Part of cortex with tetrasporangia and verrucosa-type spermatangia in surface view (AST 821312). Fig. 25, Carposporangia.**

features found in *G. tenuistipitata* var. *liui* Zhang et Xia. However, the elongate and flagellate branches and verrucosa type of spermatangia of *G. fanii* Xia et Pan distinguish it from *G. tenuistipitata* var. *liui* Zhang et Xia (1988).

## Acknowledgments

This is contribution No. 2281 from the Institute of Oceanology, Chinese Academy of Sciences, Qingdao. We are especially grateful to Dr. I. A. Abbott for reviewing, commenting on, and editing the manuscript. We thank her also for her hospitality when we stayed in Hawaii. Thanks also to Leng Zengfu, Kuang Mei, and Yang Zhaohui for their help in preparing the manuscript. Financial support for participation in the fifth workshop was provided by the California Sea Grant program and Dr. J. Sullivan.



**Figs. 26–29.** ***Gracilaria fanii*** **Xia et Pan sp. nov. Fig. 26, Longitudinal section of cystocarp (AST 821313). Figs. 27–29, Part of longitudinal section of the pericarp (AST 821313).**

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Zhang Junfu and Xia Bangmei. 1988. On two new *Gracilaria* (Gigartinales, Rhodophyta) from south China. In Tax. Econ. Seaweeds 2, pp. 131–136.

# NEW SPECIES AND VARIETY OF *GRACILARIA* FROM JAPAN: *G. RHODOCAUDATA* SP. NOV. AND *G. CHORDA* VAR. *EXILIS* VAR. NOV.

Hirotoshi Yamamoto

## Abstract

A new species and a new variety of *Gracilaria*, *G. rhodocaudata* and *G. chorda* var. *exilis*, from Japan are described. *Gracilaria rhodocaudata* is characterized by lengthy fronds, its red color, and elongated spermatangial conceptacles. It is similar to *G. chorda* var. *exilis*, *G. lemaneiformis*, and *G. vermiculophylla* in general appearance but differs from the first two in spermatangial type and from the last in frond length, color, and shape of spermatangial conceptacle. *Gracilaria chorda* var. *exilis* can be distinguished from var. *chorda* on the basis of the former's thin axes (up to 2 mm wide) and abundant branches. These two varieties are distributed in different regions: the former grows in colder region of Japan and the latter in warmer regions.

## Introduction

Taxonomic studies of *Gracilaria* in Japan have been done by several researchers (Okamura 1936, Ohmi 1958, Yamamoto 1978), and about 16 species are currently recognized. However, some taxa are still indefinite because of the wide range of morphological variations and the lack of information on reproductive organs, especially male organs.

We have removed certain plants previously tentatively identified as *G. chorda* on the basis of the external appearance, because cystocarps and male organs were not found, to a new species on the basis of reproductive structures. We have also divided *G. chorda* into two varieties.

*Gracilaria chorda* was established by Holmes (1895) on the basis of materials from Izu Peninsula, middle Honshu (Japan). Since then this alga has been recorded mainly from the southwestern region of Japan (Yendo 1911, Okamura 1918, Ohmi 1958, Yamamoto 1978). This species characteristically has thick axes (up to 4 mm in diameter) and is sparsely branched or sometimes has a ropelike appearance.

Yamamoto (1973, 1974) identified a group of specimens of *Gracilaria* from Hokkaido (northernmost Japan) that had been identified as *G. verrucosa* by Ohmi (1958) as *G. chorda*, because the specimens had the male structure of the chorda type. However, unlike the typical *G. chorda*, this taxon has thin axes (up to 2 mm in diameter) and abundant branches. No critical differences between the two morphological types are seen in vegetative and reproductive structures. However, we know now that the thick morphological types grow in southwestern Japan (a region with high-temperature seawater), whereas the thin type grows in northern Japan (a region with low-temperature seawater). Accordingly, we have used this phytogeographical difference as the basis for separating *G. chorda* into two varieties.

## Materials and Methods

*Gracilaria rhodocaudata* was collected at Kisarazu, Chiba Prefecture in May and June 1992. *Gracilaria chorda* var. *exilis* was collected mainly at Akkeshi and Hakodate bays in Hokkaido in July to September 1992. The materials were preserved in a solution of approximately 5% formalin in seawater for anatomical studies. Preparations for microscopic observations were made by using the squash method and a freezing microtome. Aniline blue was used when needed.

## Descriptions of the Species and Variety

*Gracilaria rhodocaudata* Yamamoto et Kudo sp. nov.

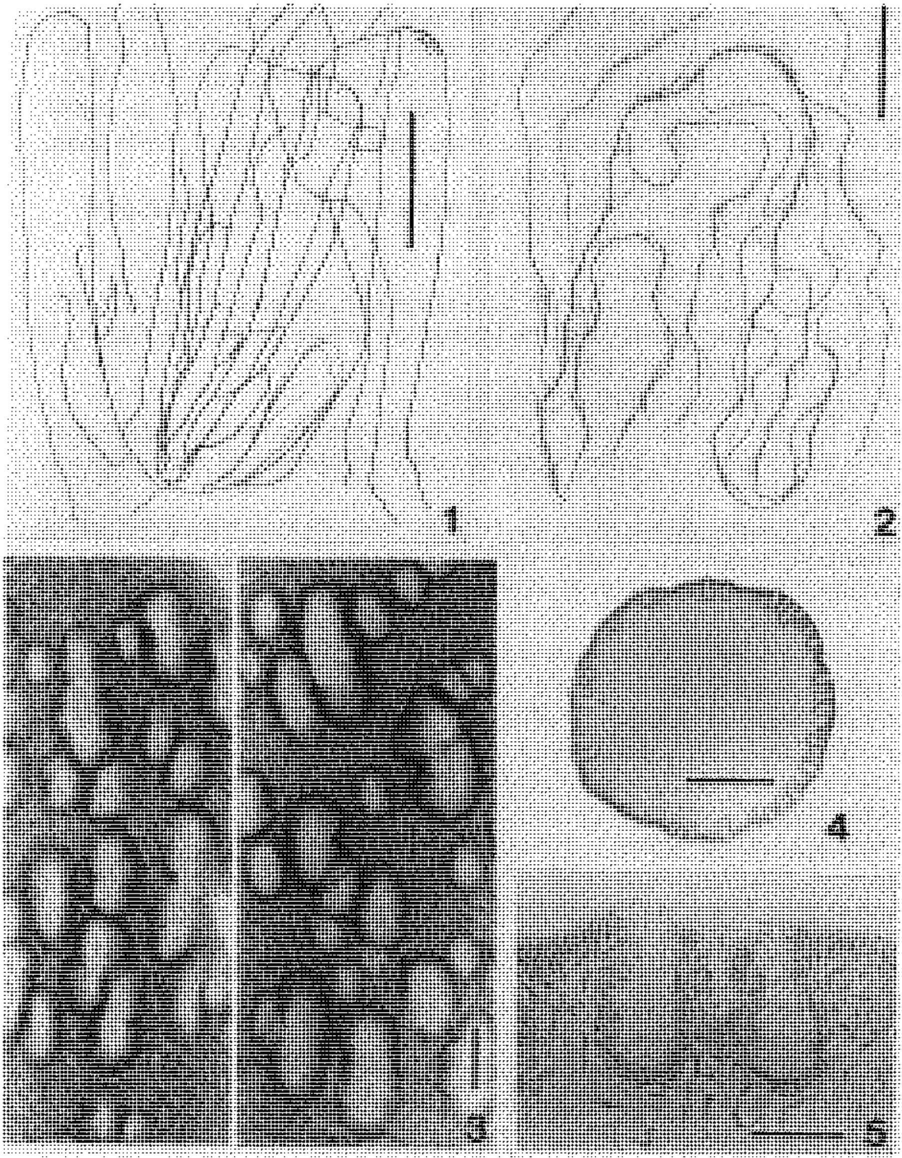
(Figs. 1–5)

Frondes solitariae exorientes disco parvo, omnino cylindratae usque ad 150 (~200) cm longae, usque ad 2.0 mm diametro; axes principales plus minusve percurrentes, ornati ramis sparsis usque ad abundos ramos qui sunt similes axibus principalibus; rami irregulariter alterni vel omnilateraliter in intervallis irregularibus, generaliter ornati ramulis filiformibus longis brevibusve orientibus omnilateraliter alternatim vel irregulatim, leviter vel vix constricti basibus; cartilagineae, brunneolae rubrae. Cellulae extimae corticis 6–12 µm altae, 4–8 µm latae; medulla constans ex magnis cellulis polygoniis, 250–320 (~400) µm diametro; transitio in amplitudine cellulae a cortice ad medullam abrupta.

Tetrasporangia regulatim cruciata, usque ad 60 µm alta, usque ad 40 µm lata; spermatangia formata in conceptaculis ("verrucosa" typus); conceptacula elongata usque ad 240 µm longa parallela axibus frondisin facie aspectu, usque ad 80 µm lata, usque ad 160 (~200) µm alta in sectione transversali aspectu, aggregata sed separata utroque cellulis vegetativis; cystocarpia usque ad 1 mm alta, 1.2 mm lata, cum filis absorbentibus penetrantibus in pericarpio.

Fronds brownish red, cartilaginous, solitary, arising from a small disc, cylindrical throughout, up to 150 cm long (~200) cm, axes 1.4–2.0 mm in diameter (average, 1.6 mm); main axes more or less percurrent, tapering into filiform apical portions, provided with sparse (spermatangial) to abundant (tetrasporangial) branches similar to main axes; branches irregularly alternate or on all sides at irregular intervals, generally provided with long or short filiform branchlets arising alternately or irregularly on all sides, slightly or hardly constricted at bases. Outermost cells of cortex 6–12 µm high, 4–8 µm wide; medulla consisting of large polygonal cells 250–320 µm in diameter, up to 400 µm; transition in cell size from cortex to medulla abrupt; hair basal cells present.

Tetrasporangia regularly cruciate, borne among cortical cells, scattered over entire surface of frond except basal and apical portions, up to 60 µm high, up to 40 µm wide. Spermatangia formed in conceptacles (verrucosa type), on entire



Figs. 1–5. *Gracilaria rhodocaudata* collected from Kisarazu, Chiba Prefecture, in May 1922. Fig. 1, Type specimen (spermatangial) with sparse branching. Fig. 2, Tetrasporophyte with third- and fourth-order abundant branchlets. Fig. 3, Surface view of mature male frond with spermatangial conceptacles elongated parallel to frond axes. Fig. 4, Cross-sectional view of male frond showing arrangement of deep spermatangial conceptacles. Fig. 5, Magnified cross-sectional view of male frond with deep verrucosa-type spermatangial conceptacles. Scale bars: Figs. 1 and 2, 10 cm; Figs. 3 and 5, 100 μm; Fig. 4, 0.5 mm.

surface of frond except basal and apical portions; conceptacles elongated, up to 240 µm long, parallel to frond axes in surface view, up to 80 µm wide, up to 160 (~200) µm deep in cross-sectional view, crowded but separated from each other by vegetative cells. Carpogonial branches two cells; cystocarps formed on entire surface of frond except basal and apical portions, up to 1 mm high, 1.2 mm wide; traversing filaments present in cystocarps.

Etymology: This species is named for its reddish and horsetail-like appearance on the sea bottom at ebb tide.

Japanese Name: Beni-ogonori.

Type Specimen: Holotype specimen (spermatangial, collected May 28, 1992) and other specimens are deposited at the Herbarium of Marine Botany, Faculty of Fisheries, Hokkaido University (HAK).

Type Locality: Kisarazu in Chiba Prefecture.

Materials Examined: Cystocarpic, spermatangial, tetrasporangial collected in Kisarazu May 28, 1992, by H. Kudo; tetrasporangial collected in Kisarazu June 3, 1992, by A. Miyata.

Habitat: This species grows on rocks, pebbles, and shells covered with sandy mud from low tide mark down to upper sublittoral zone in comparatively calm waters and frequently is found with *G. vermiculophylla* (Yamamoto and Sasaki 1988).

Remarks: *Gracilaria rhodocaudata* is similar to *G. chorda* var. *exilis* (see following) which grows in Hokkaido and northern Honshu, and to *G. lemaneiformis* in color and appearance. However, it differs from these taxa in spermatangial type: *G. rhodocaudata* has the verrucosa type,whereas the other two have the chorda type. *Gracilaria rhodocaudata* may also resemble *G. vermiculophylla* externally, but can be easily distinguished from it. The former has much longer fronds, is red, and has elongated spermatangial conceptacles.

*Gracilaria rhodocaudata* has wide morphological variations: from sparse to abundant branches. These variations could cause a confusion in specific identification. Plants with tetrasporic or cystocarpic fronds with abundant branches could be mistaken for *G. chorda* or some other taxa. However, I confirmed that traversing filaments are present in the cystocarps of *G. rhodocaudata* and that both morphological variations coexist in the same habitat.

A population similar to that found in the type locality grows near Miura Peninsula, Kanagawa Prefecture, on the opposite side and across Tokyo Bay from Kisarazu, but the final taxonomic identification is left for future study because so far no gametophytes have been found. It is difficult to distinguish this species from *G. chorda* on the basis of vegetative features only.

### *Gracilaria chorda* var. *exilis* var. nov. Yamamoto

(Figs. 6–7)

Yamamoto 1973, as *Gracilariopsis chorda*.

Yamamoto 1974, as *Gracilariopsis chorda*.

Yamamoto 1978, in part, as *Gracilaria chorda* (pl. 38, figs. 1–4; pl. 39, fig. 1).

Frondes solitariae, omnino cylindratae, usque ad 150 cm longae, usque ad 2 mm diametro; axes principales plus minusve percurrentes, ornati ramis longis similibus axibus; rami orientes alternatim vel irregulatim omnilateraliter in intervallis irregularibus, ornati ramulis longis brevibusve; bases rami leviter constrictae; cartilagineae, brunneolae rubrae.

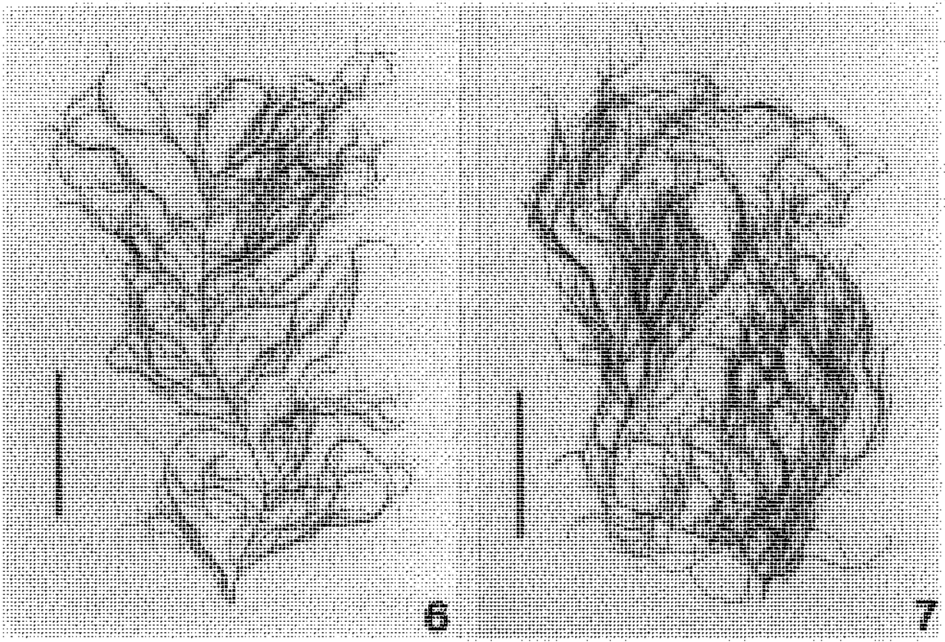
Fronds reddish brown, cartilaginous, solitary, cylindrical throughout, up to 150 cm long, 1.6–2.0 mm in diameter (average, 1.8 mm); main axis more or less percurrent, provided with long branches similar to axes; branches arising alternately or irregularly on all sides at irregular intervals and sometimes in fascicles provided with long or short branchlets; branchbases slightly constricted.

Life history is confirmed to be polysiphonia type by *in vitro* culture (Yamamoto, unpublished). Chromosome number is 24 (Yabu and Yamamoto 1989).

Etymology: This variety is named for its axes which are thinner than those of var. *chorda*.

Type Specimen: Holotype (spermatangial, collected September 14, 1972) and other specimens are deposited at the herbarium of Marine Botany, Faculty of Fisheries, Hokkaido University (HAK).

Type Locality: Hakodate Bay in Hokkaido.



**Figs. 6 and 7. *Gracilaria chorda* var. *exilis* collected from Hakodate Bay (September 1972). Fig. 6, Type specimen (spermatangial). Fig. 7, Tetrasporophyte. Scale bars = 10 cm.**

Remarks: Unlike the *chorda* variety, this variety has thin axes and abundant branches. The fronds grow on shells and pebbles covered with sand in the sublittoral zone (1–3 m) in Hakodate Bay. A large population of this variety drifting on the muddy bottom in Akkeshi Bay was once harvested for agar materials, but the population has almost disappeared now because of water pollution.

In the populations of Hokkaido, almost all the fronds are tetrasporophytes; gametophytes have never been found in Akkeshi Bay, the most northern range, in which the seawater is cold (0.5–18.5°C, average in February and August). A few gametophytes have been seen in Hakodate Bay, a warmer region (5.0–22.0°C, average in March and August; Yamamoto 1978). However, in northern Honshu, its warmest habitat (6–25°C , average in February and August), three reproductive phases appear to be common in summer. In contrast, the var. *chorda* grows in areas in which the temperature of seawater is 11–28°C (average in February and August) and commonly has three reproductive phases from spring to early summer.

The taxonomic relationships between *G. chorda* and *G. lemaneiformis* should be reviewed at some time. These two taxa are similar in general morphology, and they also show similar variations in size, number of branches and patterns of branching, internal anatomy, and so forth. (I. A. Abbott, personal communication). This study, records only the ecotypic morphologies of *G. chorda*.

## Acknowledgments

I thank Dr. I. A. Abbott, University of Hawaii, for her critical reading of the manuscript; Dr. A. Miyata, Natural History Museum and Institute, Chiba, for his cooperation during collection of the materials; and Mrs. Meng S. Doty for preparing the Latin descriptions.

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# A TAXONOMIC APPRAISAL OF KOREAN *GRACILARIA VERRUCOSA* (RHODOPHYTA, GRACILARIALES)

In Kyu Lee, Myung-Sook Kim, and Sung Min Boo

## Abstract

The vegetative and reproductive features of *Gracilaria verrucosa* (Hudson) Papenfuss collected from the coast of Korea were investigated. The plants were characterized by a cylindrical thallus, nondistinct main axis, irregularly alternate to secund or subdichotomous branches, gradually tapering apex, slightly or occasionally abruptly constricted branch base, and gradual increase from cortical to medullary cells. Gonimoblasts were connected to the pericarp by rare tubular nutritive cells or lacked the cells completely, and a morphological continuum from the textorii type of spermatangial conceptacles to the verrucosa type was apparent. Korean plants differed from British specimens of *G. verrucosa*. They also differed from Chinese and Japanese plants in the constriction at the base of branches, the size of carpospores, the abundance of tubular nutritive cells, and the structure of the pericarp.

## Introduction

Specimens from various parts of the world of the alga known as *Gracilaria verrucosa* (Hudson) Papenfuss have produced a lot of taxonomic problems (Fredericq and Hommersand 1989). Plants collected from the northwestern Pacific and previously classified as *G. verrucosa* are now split into *G. vermiculophylla*, *G. verrucosa,* and *G. asiatica* Zhang et Xia.

Chang and Xia (1985) mentioned that specimens of *G. verrucosa* from China could be distinguished from specimens from the United Kingdom on the basis of the deeper spermatangial conceptacles, larger tetraspores, smaller carpospores, and structure of the pericarp of the Chinese plants. They proposed a new name, *G. asiatica,* for the Chinese plants and included Japanese specimens identified as *G. verrucosa*. with the Chinese specimens. Yamamoto and Sasaki (1987, 1988) found a sexual compatibility between *G. vermiculophylla* and specimens of *G. verrucosa* from Japan, and they suggested that a comparative reexamination of *G. asiatica* and *G. verrucosa* was needed. Yabu and Yamamoto (1988, 1989) found that the chromosome number in specimens of *G. vermiculophylla* and *G. verrucosa* from Japan was 24.

In this study we compared the vegetative and reproductive features of so-called Korean *G. verrucosa* and *G. asiatica.*

## Materials and Methods

Materials were collected from several locations on the coasts of Korea and preserved in a solution of 5–10% formalin in seawater. Vegetative and reproductive features were examined in transverse sections and stained with 0.5–1.0 % aniline blue. Illustrations were prepared with the aid of a camera lucida. A micrometer was used to quantitatively measure lengths, widths, and diameters.

## Results

### Vegetative Thallus

Plants are erect, solitary or caespitose, arising from a small disc. They are cylindrical throughout, usually 7–30 cm long, but up to 60 cm long, and 1–2 mm in diameter, with two to four orders of branches. Branches are irregularly alternate or secund, gradually taper toward apices, and are slightly or abruptly constricted at the base (Fig. 1A). In transverse section, the medulla consists of pseudoparenchymatous cells 200–250 µm in diameter with walls and is surrounded by one to two layers of cortical cells. The outermost cortical layer is pigmented, consists of small roundish cells 5 µm × 15 µm, and gradually decreases in cell size from medulla to cortex (Fig. 1B).

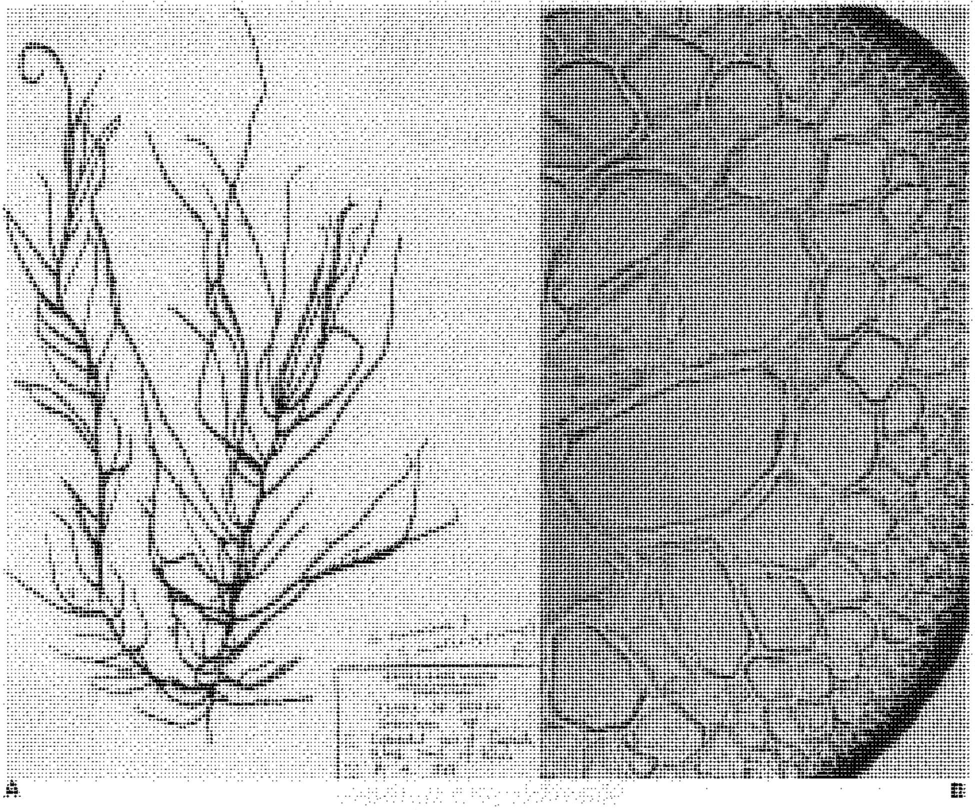

**Fig. 1.** ***Gracilaria verrucosa*** **(Hudson) Papenfuss from Korea. A, Mature plant B, Transverse section of main axis.**

### Cystocarp Development

In the female reproductive organ, a supporting cell bears a two-celled carpogonial branch flanked by a pair of sterile cell groups. This supporting cell cuts off a conical carpogonial branch initial toward the surface of the thallus (Fig. 2A). The initial cell divides transversely to produce a roundish carpogonium and a rectilinear hypogynous cell (Fig. 2B). The carpogonium forms a straight trichogyne extending toward the surface of the thallus (Figs. 2C–E).

Soon after fertilization, the sterile cell groups flanking the carpogonial branch fuse directly into the expanding carpogonium, excluding the hypogynous cell and forming a carpogonial fusion cell (Fig. 2F). Each of the primary gonimoblast cells cuts off derivatives from its upper side and then expands rapidly (Fig. 2G). Carposporangia form irregular clusters or chains (Fig. 2H). Mature cystocarp typically consists of a persistent fusion cell, even after the formation of gonimoblast and carposporangia, and a pericarp with a central ostiole (Fig. 2I).

Although tubular nutritive cells are rarely present, the gonimoblast cells in the floor of the cystocarp typically elongate and connect with the pericarp (Fig. 3A). The pericarp consists of 7–10 layers 95–200 μm thick. Inner cells of the pericarp are connected anticlinally and periclinally with distinct star-shaped cell contents. However, in mature thalli they differ according to the condition of the samples: fresh are roundish rather than star-shaped (Figs. 3B–3D). Hemispherical and globose cystocarps project considerably from the thallus, up to 0.8–1.1 mm in diameter and 0.6–0.8 mm in height, and are not constricted at the base.

### Male Reproductive Organs

The spermatangial parent cell is an intercalary cell that is pit-connected to one or two outer cortical cells. It is formed from an outer cortical cell that divides obliquely and longitudinally by means of a concavo-convex septum. After this division, the subapical cell divides obliquely roughly perpendicular to a plane of the first cell division (Figs. 4A–4E). Successive spermatangial parent cells are formed peripherally by oblique longitudinal divisions, resulting in a branched filament that fills the intercellular space among distal cortical cells. Spermatangial conceptacles are 50–160 μm deep and 40–110 μm wide (Fig. 4F). A morphological continuum is also shown in spermatangial conceptacles, from the textorii type to the verrucosa type (Fig. 5).

### Tetrasporangia

Tetrasporangial initial cells are produced from the cortical cells (Figs. 6A and 6B). A tetrasporangial initial cell expands in length and width and undergoes two successive divisions to produce four cruciately divided tetrasporangia (Figs. 6C and 6D), each 32 μm × 40 μm.

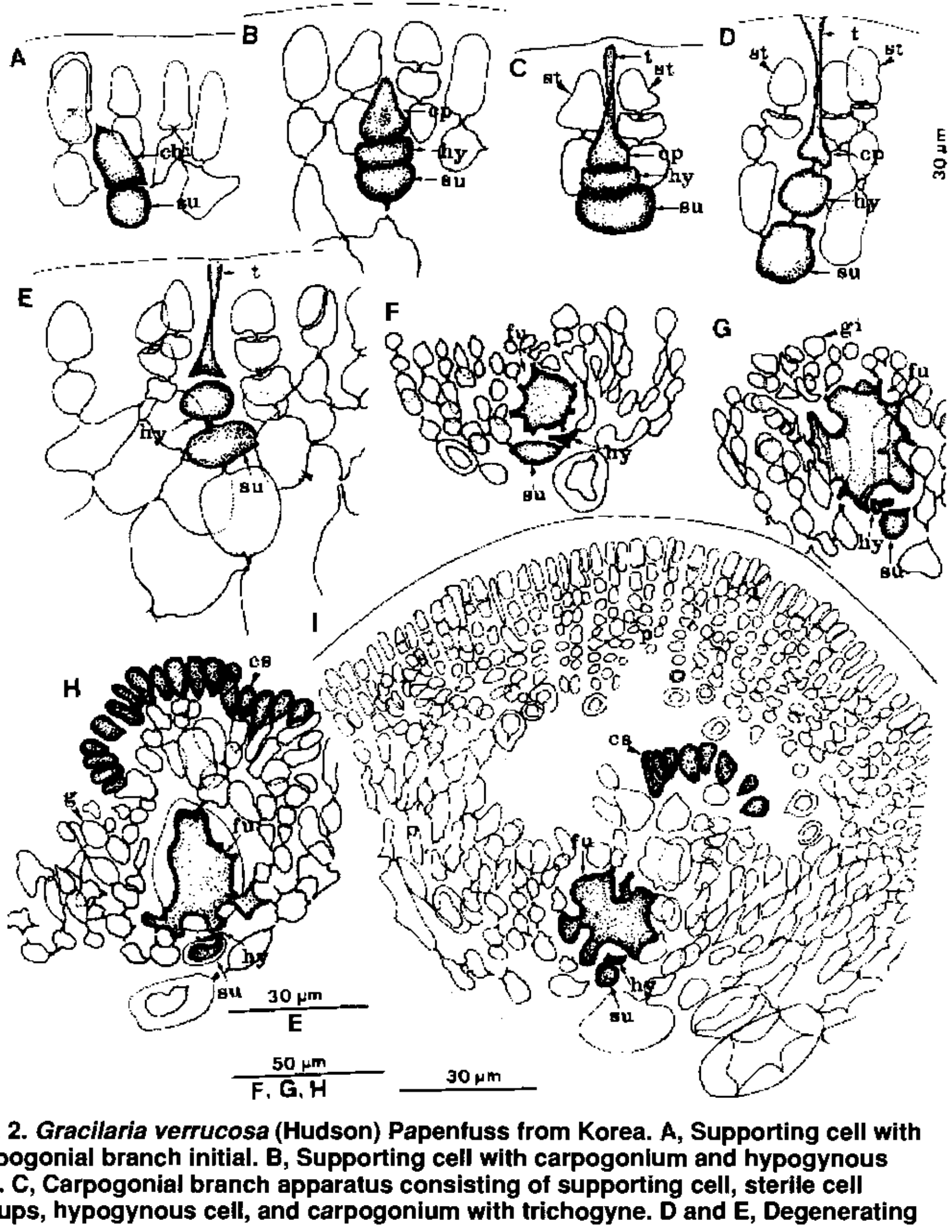

Fig. 2. *Gracilaria verrucosa* (Hudson) Papenfuss from Korea. A, Supporting cell with carpogonial branch initial. B, Supporting cell with carpogonium and hypogynous cell. C, Carpogonial branch apparatus consisting of supporting cell, sterile cell groups, hypogynous cell, and carpogonium with trichogyne. D and E, Degenerating carpogonium with trichogyne. F, Fusion cell after fertilization. G, Gonimoblast initial cut off from lobe of fusion cell. H, Carposporangial initials dividing from gonimoblast clusters. I, Cystocarp showing remnants of fusion cell, hypogynous cell, and pericarp. cbi = carpogonial branch initial, cp = carpogonium, cs = carposporangia, fu = fusion cell, gi = gonimoblast initial, hy = hypogynous cell, st = sterile branches, su = supporting cell, t = trichogyne.

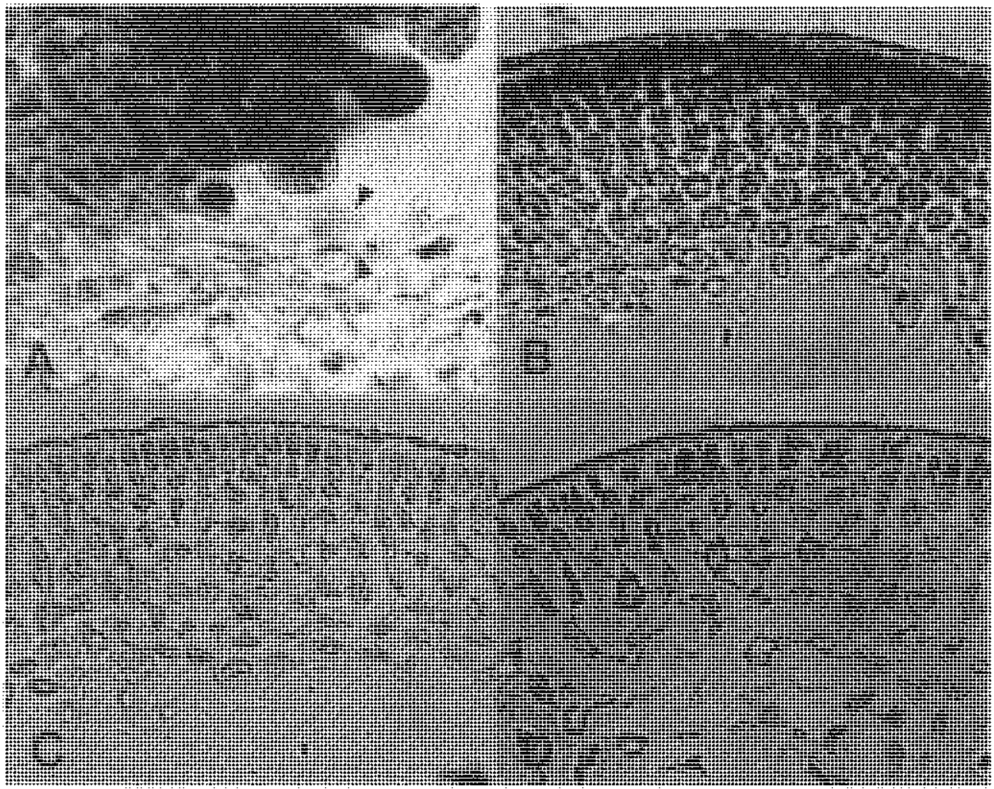

Fig. 3. *Gracilaria verrucosa* (Hudson) Papenfuss from Korea. A, Transverse section through mature cystocarp showing elongated cells in the floor of the cystocarp (arrowheads). B–D, Longitudinal sections through pericarps of fresh (B), dry (C), and liquid-preserved (D), materials.

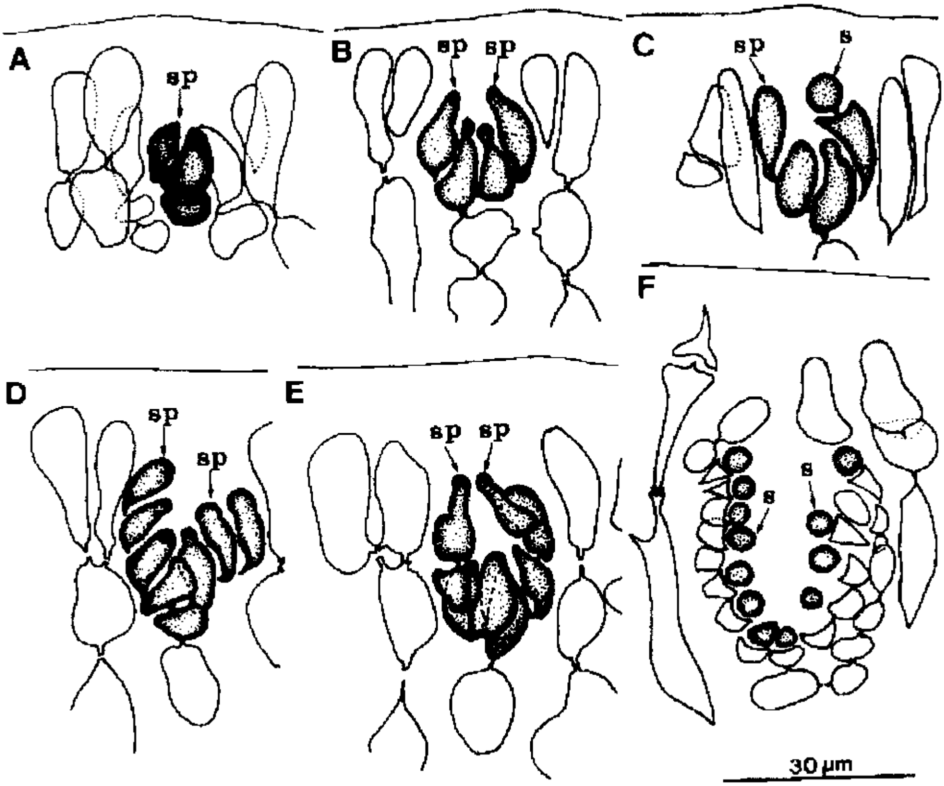

Fig. 4. *Gracilaria verrucosa* (Hudson) Papenfuss from Korea. A, Intercalary initials of spermatangial parent cell. B, Four spermatangial parent cells. C, Spermatangium cut off from spermatangial parent cell. D and E, Short branched filament of spermatangial parent cells with spermatangia. F, Spermatangia cut off from terminal spermatangial parent cell. sp = spermatangial parent cell, s = spermatangium.

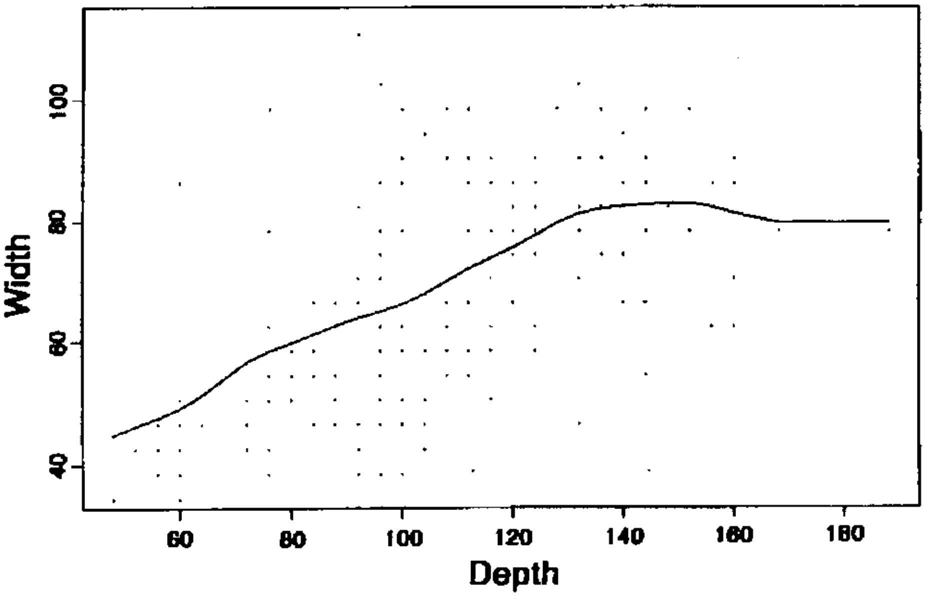

Fig. 5. Scatter diagram of depth and width of spermatangial conceptacles of *Gracilaria verrucosa* from Korea.

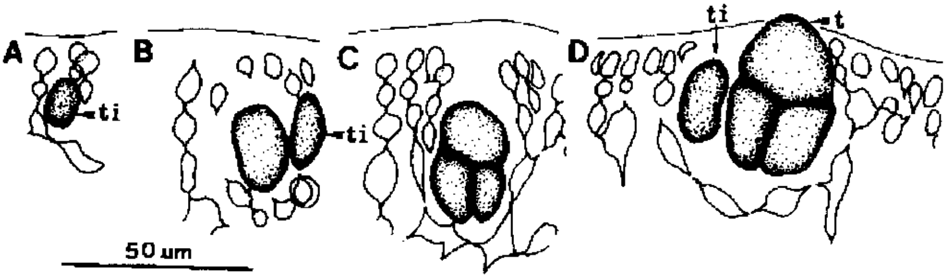

Fig. 6. *Gracilaria verrucosa* (Hudson) Papenfuss from Korea. A and B, Tetrasporangial initial cells. C and D, Cruciately divided tetrasporangium. t = tetrasporangium, ti = tetrasporangial initial cell.

## Discussion

Asian plants of *G. verrucosa* are characterized by cylindrical and erect fronds and slightly constricted branches at the bases. The branches are alternate or secund with many orders. Cystocarps are semiglobose, with no or slight constrictions at the bases with the pericarp of tubular nutritive cells. Spermatangia are in deep oval conceptacles (Xia and Yamamoto 1985). In Korean plants, however, the gonimoblast is rarely connected to the pericarp by tubular nutritive cells, and the spermatangial conceptacles show a morphological continuum from the textorii type to the verrucosa type, which agrees with observations of Bird and Rice (1990). The diameter of carpospore is 30–50 µm in plants from Korea and Japan (Ohmi 1956), 30–40 µm in plants from England, and 15-20 µm in plants from China (Fig. 7A).

Chang and Xia (1984) considered the structure of the pericarp a primary characteristic for distinguishing species. They pointed out the difference between Chinese and British plants in this feature. In Korean and Chinese plants, it is 95–170 µm thick and has distinct star-shaped cell contents. In British plants, the pericarp is 280–430 µm thick. In fresh materials, however, star-shaped cell contents are indistinct in Korean plants. Accordingly, the difference between Chinese plants and Korean plants is the more roundish shape of the cells of the pericarp in fresh samples (Fig. 3B).

The size of mature conceptacles in male plants is an important characteristic for distinguishing species (Yamamoto 1978). Various studies reported that the male conceptacles were 60 µm deep in *G. verrucosa* from England (Chang and Xia 1985) 80–180 µm × 30–100 µm, *G. asiatica* from China (Chang and Xia 1985), and 100–120 µm × 55–80 µm in *G. verrucosa* and 70–150 µm × 45–120 µm in *G. vermiculophylla* from Japan (Ohmi 1956, Yamamoto 1978). In Korean plants, the male conceptacles are 45–160 µm × 35–110 µm. This size includes dimensions reported for British and Japanese plants and some Chinese plants (Fig. 7B). Male conceptacles of Korean plants make up a continuum between the textorii type and the verrucosa type, as is the case in plants from North Carolina (Reading and Schneider 1986). The size of tetraspores, however, differs markedly between Asian and British plants (Fig. 7C).

Thus, Korean plants are recognized as a distinct taxon from English *G. verrucosa*. They also differ from Chinese and Japanese plants in constriction at the base of branches, size of carpospores, existence of tubular nutritive cells, and the structure of the pericarp (Kim et al. 1993). Rice and Bird (1990) mentioned that the reservations of Yamamoto and Sasaki (1988) about referring Japanese plants to *G. asiatica* were justified because of the restriction profiles of the DNA and the chromosome number. Until the crossing experiments among the three taxa, *G. asiatica* from China, *G. vermiculophylla* from Japan, and *G. verrucosa* from Korea, are carried out, adoption of a species epithet between *G. asiatica* and *G. vermiculophylla* should be postponed.

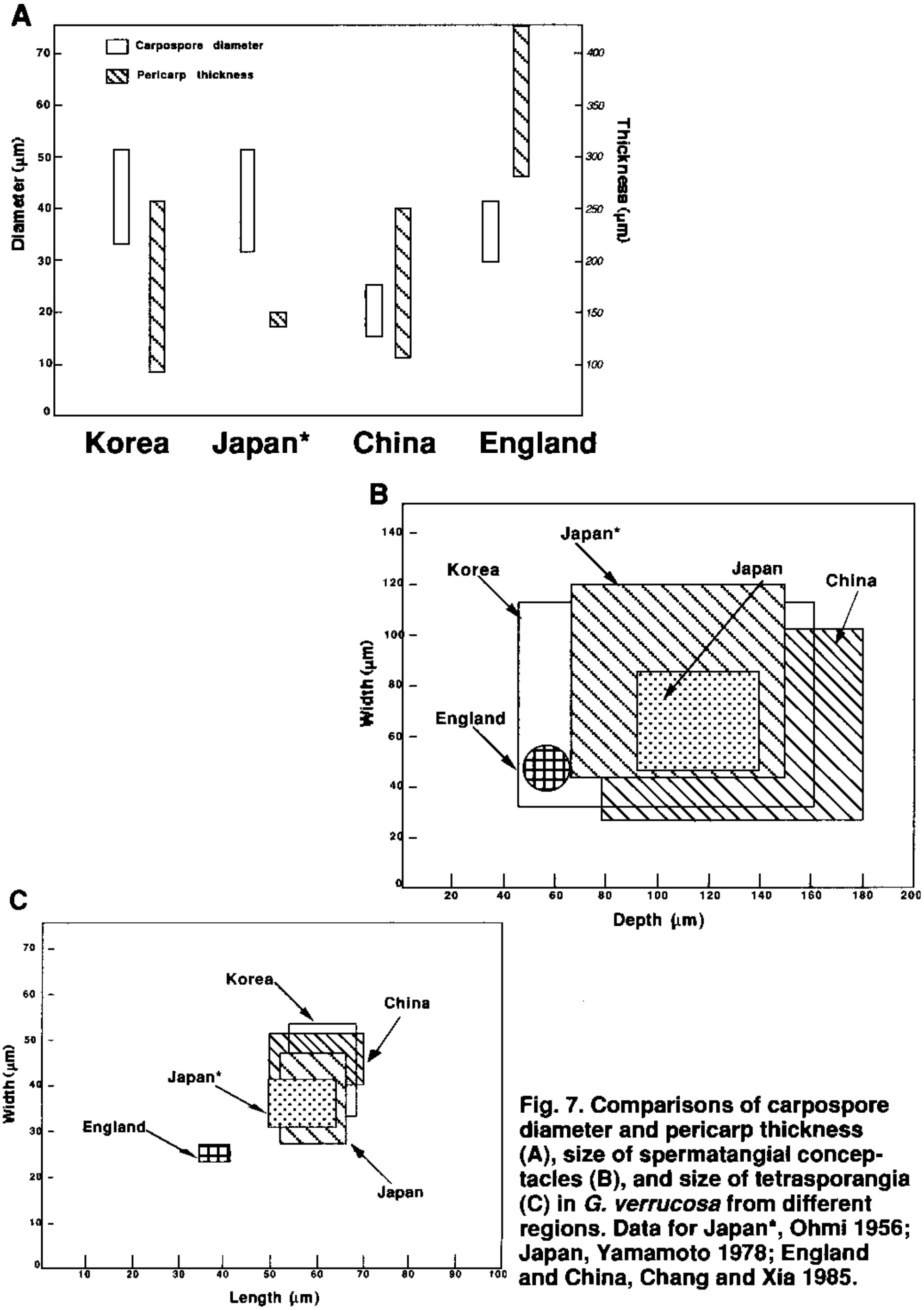

Fig. 7. Comparisons of carpospore diameter and pericarp thickness (A), size of spermatangial conceptacles (B), and size of tetrasporangia (C) in *G. verrucosa* from different regions. Data for Japan*, Ohmi 1956; Japan, Yamamoto 1978; England and China, Chang and Xia 1985.

## Acknowledgments

We thank Isabella A. Abbott for the invitation to participate in the fifth workshop and for a critical reading of the manuscript, Dr. K. Y. Kim for preparing the diagrams, and Dr. J. H. Lee for material used in this study. We acknowledge the financial support of the California Sea Grant College and Dr. J. Sullivan for participation in the workshop.

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# *GRACILARIA URVILLEI* (MONTAGNE) ABBOTT: A NEW RECORD FOR THAILAND

Khanjanapaj Lewmanomont

## Abstract

Preserved specimens of *Gracilaria* collected from Satun Province in southern Thailand along the Andaman Sea and stored in the Kasetsart University Museum of Fisheries, Bangkok, were examined. The specimens were identified as *G. urvillei* (Montagne) Abbott and are reported here as a new record for Thailand.

## Introduction

Studies on the marine red algal genus *Gracilaria* from Thailand have received more careful attention recently, and species have been described in detail. Abbott (1988) reported 4 species of *Gracilaria* and 4 species of *Polycavernosa* from Thailand, 2 of which were new species. Lewmanomont (1994) described 13 species of *Gracilaria* from Thailand, with 1 new species. This paper reports *G. urvillei* as a new record for Thailand.

## Materials and Methods

Specimens preserved in 5% formalin and stored in the Kasetsart University Museum of Fisheries (KUMF), Bangkok, were examined. These specimens were collected from Satun Province in southern Thailand along the Andaman Sea in August 1972. A small piece of preserved material was cut into thin sections by hand and stained with 1% aqueous aniline blue, fixed with 1% HCl, washed with distilled water, and mounted with corn syrup (Karo syrup) (Tsuda and Abbott, 1985). Stained sections were examined with a light microscope.

## Description of the Species

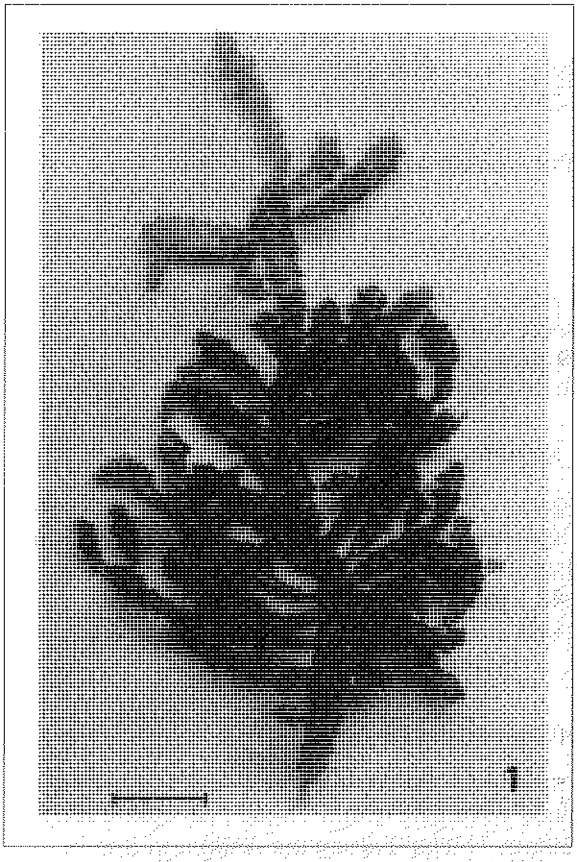
*Gracilaria urvillei* (Montagne) Abbott Pac. Sci. 45:23, 1991.

(Figs. 1–3)

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

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

Thallus succulent, cartilaginous, 11–14 cm high. Percurrent axis terete, 0.6–1.0 cm in diameter, with constrictions differentiating it into segments 4–6 cm long. Branching irregular, of one to three orders, with branches growing from tips of



**Figs. 1–3** ***Gracilaria urvillei*****. Fig. 1, Appearance of plant.**

surface projections; branches with conspicuous articulation at the base, ultimate branchlets short and stipitate, 0.6–20.0 cm long, teardrop in shape; axes and branches covered with short projections from the surface throughout (Fig. 1).

Transverse section of frond consisting of a cortex of three to four layers of small pigmented cells and a medulla of many layers of rounded cells 60–100 μm in diameter near the cortex with a gradual transition to 300–400 μm diameter in the center. All specimens tetrasporangial plants. Tetrasporangia scattered over surface of frond, oval in transverse section, 30 × 50 μm. Tetraspores 25–30 μm in diameter with distinct stellate plastid (Figs. 2 and 3).

Type Locality: Torres Strait, northeastern Australia.

Distribution: Indonesia, Malaysia, Singapore, and northern Australia.

Habitat: Growing on rock in coral reef area of clear water about 8 m deep.

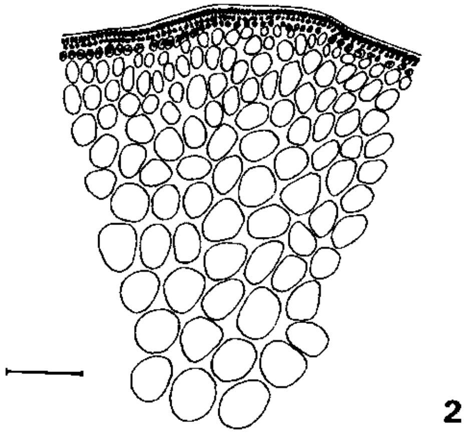


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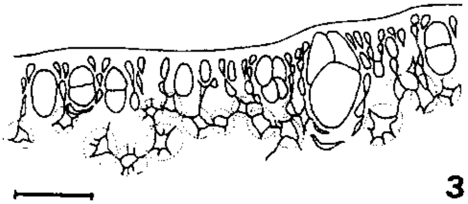
**Fig. 2, Transverse section of thallus showing a gradual transition of medullary cells. Fig. 3, Transverse section of cortex with tetrasporangia. Scale bars: Fig. 1, 2 cm; Fig. 2, 500 μm; Fig. 3, 50 μm.**



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## Discussion

The first descriptions of *G. urvillei* were of specimens from Torres Strait, northeastern Australia; Montagne (1842) identified them as *H. urvillei*. In 1876, the species was transferred by J. Agardh (1876) to *C. urvillei* (Montagne) J. Agardh. Xia and Abbott (1987) examined *H. urvillei* Montagne, decided it was a species of *Polycavernosa*, and named it *P. urvillei* (Montagne) Xia et Abbott. Wynne (1989) pointed out that *Hydropuntia* Montagne (Montagne 1842) had priority over *Polycavernosa* Chang et Xia (Chang and Xia 1976), and restored *Hydropuntia,* making 14 transfers. In 1991, Abbott et al. examined male plants of several species of *Polycavernosa (= Hydropuntia)* and transferred the species to *Gracilaria*. In this description, *H. urvillei* Montagne became *G. urvillei* (Montagne) Abbott. Seventeen species, including 1 new, were recognized in these changes.

When Xia and Abbott (1987) examined the holotype specimens, they described the prostrate axes as cylindrical to slightly to strongly compressed. However, the specimens I examined are cylindrical throughout. *Gracilaria urvillei* has typical characteristics of succulent multisegments with stipitate branches and surface projections that can be used to distinguish it from other species even though gametophytic plants were not examined.

## Acknowledgments

I thank Drs. I. A. Abbott and Virginia Harden for reading and correcting the manuscript and Miss Chatcharee Supanwanid for photographic preparation.

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# Section IV. *Eucheuma*

## INTRODUCTION

Isabella A. Abbott

The genus *Eucheuma* is included in volumes 1 and 2 of the workshop publications, with contributions by M. S. Doty, J. N. Norris, and D. P. Cheney. The segregation of one of the important commercial species as *E. alvarezii* by Doty (1985) led to this species being used as the type species for *Kappaphycus* Doty (1988). In circumscribing the species to be included in *Kappaphycus*, a number of vegetative and reproductive features were named, but mainly the species to be included must have a preponderance of kappa-carrageenan in their cell walls. They are thus different from the species of *Eucheuma* in the Doty classification, because *Eucheuma* species have iota-carrageenan. The new genus described in this volume, *Betaphycus*, contains beta-carrageenan. Although these are large-molecule colloids and structurally different (recognized by a number of microorganisms that have specifically different enzymes for degrading the colloids), generally speaking, when extracted, they can be recognized by nonchemists.

Kappa-carrageenan is relatively firm, beta-carrageenan is "stiff" (extremely firm), and iota-carrageenan is "soft." With this explanation, it can be realized that these colloids have different commercial uses, and providing a scientific "handle" or name for the different species helps growers and academics know that they are talking about the same (or different) species.

Many other carrageenans are present in other genera—are we to expect that other generic names will change because of the chemicals the plants contain? Probably not. Other carrageenans are present in small quantities (of interest to academics, not to commercial growers). Moreover, in some species of red algae (*Mazzaella* and *Chondracanthus*, formerly containing many commercial species of *Iridaea* and *Gigartina*, respectively), the gametophyte may have cell walls with kappa-carrageenan, and the sporophyte may have cell walls with lambda-carrageenan. Because of the cost of separating these life phases for extracting purposes, these two genera are probably not candidates for similar taxonomic treatment, and they are not of great interest to growers at this time. (The market price for these colloids depends on the new uses and new products developed for them.) Beside the commercial aspects, the systematics of the Gigartinaceae is at least 90% easier (in my opinion) than that of the Solieriaceae (or Gracilariaceae), and any method for separating these two families that can be taught to others should be greeted with joy!

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# SPECIES OF *EUCHEUMA* AND *KAPPAPHYCUS* IN VIETNAM

Nguyen Huu Dinh and Huynh Quang Nang

## Abstract

*Eucheuma gelatinum* (Esper) J. Agardh, *E. arnoldii* Weber van Bosse, *Kappaphycus inerme* (Schmitz) Doty, and *K. cottonii* (Weber van Bosse) Doty from Vietnam are reported for the first time.

## Introduction

A survey of the species of marine algae that might provide a sustainable source of raw material or have marine farming potential has been under way in Vietnam for some years. Dinh (1992) studied the species of *Gracilaria* and related taxa and found 15 species for which there are voucher specimens for documentation, including three previously reported ones of uncertain status. None of these 15 species is being used in adjacent countries as a source of agar, but species that are used in Thailand, China, and Taiwan might be investigated and perhaps transferred to Vietnam for experimental purposes. Vietnam has suitable habitats, similar to those in Thailand and southern China, that could support *G. changii*, *G. fisheri* (both from Thailand), and *G. tenuistipitata* var. *liui* (holotype from Hainan Island, but widely distributed in Guangdong and Guangxi provinces of China and in Thailand and Taiwan).

Although the two major articles on marine algae of Vietnam belong to a previous generation (Dawson 1954, Pham 1969), both were comprehensive reports of the seaweeds of Vietnam. Although many more species likely will be found (especially from deep water), the first-time discovery of relatively common algae of large size such as *Eucheuma* species in Vietnam is surprising. The previous collections were made in the southern part of the country; exploration of the northeastern shores of Vietnam should yield many interesting species.

This chapter reports four species of *Eucheuma* and *Kappaphycus* found in Vietnam. One of the species of *Eucheuma*, *E. gelatinum*, has been placed in a new genus, *Betaphycus*, by Doty (this volume). The locations where the reported species were collected are shown on the map (Fig. 1). More locations where these species may occur should be sought, and estimates of standing stock made. Possibilities for farming these species will be investigated in the future.

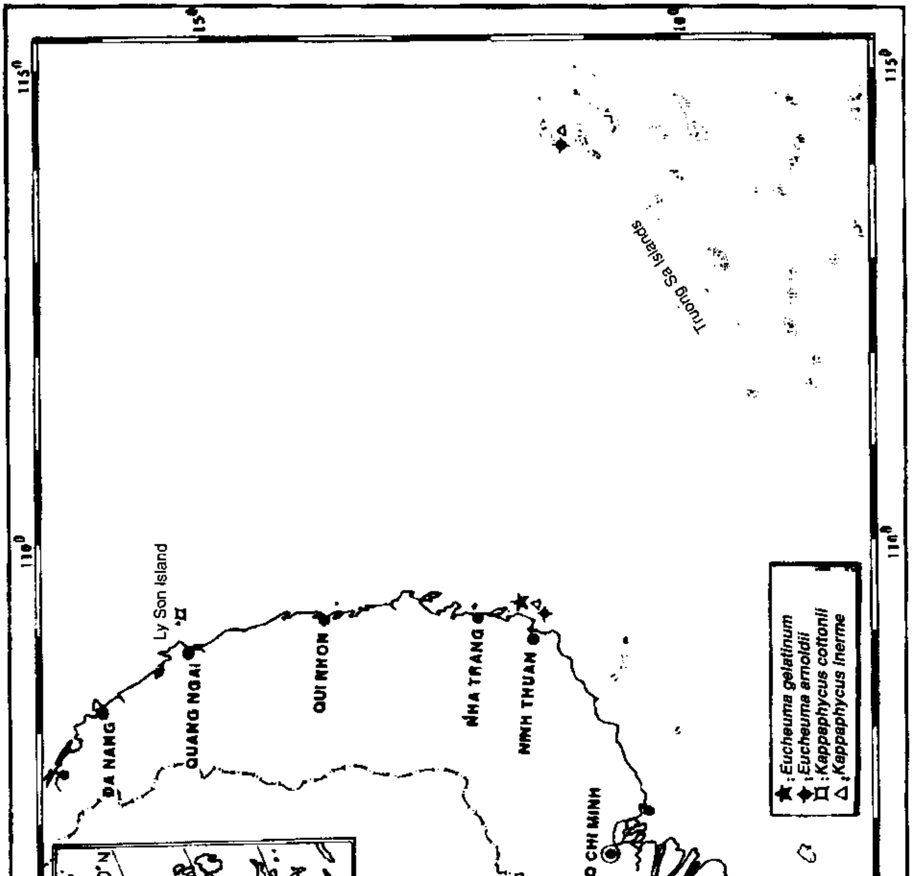


Fig. 1. Distribution of *Eucheuma* and *Kappaphycus* in Korea.

## Description of the Species

*Eucheuma gelatinum* (Esper) J. Agardh, Kongl. Vet.-Akad. Förhandl. 4:5–17, 1847 (=*gelatinae*).

(Fig. 2)

Basionym: *Fucus gelatinus* Esper, Icones fucorum, Fasc. 4, p. 188, pl. 101, 1800 (See *Betaphycus gelatinum* (J. Agardh) Doty, this volume).

Fronds compressed, 3–5 mm wide, 5–7 cm long, (up to 15 cm), prostrate, decumbent, entangled, forming plants up to 20 cm in diameter; branches numerous, arising from blade margins. Tubercles arising from lateral, ventral, and dorsal surfaces, swollen; haptera swollen, attached on rocky coralline substrate. Dorsal surface densely covered with simple or compound spinose processes. Frond coarse, surfaces rough and firm, purple when fresh, becoming cartilaginous and black on drying.

In cross section, medulla consisting of many rhizoidal cells, arranged closely; inner cortex of many rows of large with round, ovoid or polygonal cells; the outer cortex consisting of two to three rows of pigmented small cells. Sexual reproduction not seen.

Habitat: Found growing at a depth of 1.0–2.5 m, exposed to strong wave action and turbulence. Salinity 29–34‰, temperature 20–33°C.

Distribution: Along the coast of Ninh Thuan Province. According to Doty (1988), the species can be found in the Philippines and southern China.

Economic Potential: As human food and as a source of beta-carrageenan, a colloid of high demand in the marketplace.

Remarks: The separation of *E. gelatinum* from *Eucheuma* to *Betaphycus* by Doty (this volume) is based primarily on the high preponderance of beta-carrageenan over kappa-carrageenan in the cell walls of this species. Because of the high quality of agarose that can be obtained from it, the species should be seriously considered for maricultural operations.

*Eucheuma arnoldii* Weber van Bosse, Siboga Exped. 59d, p. 421, pl. 13, 1928; Doty, Tax. Econ. Seaweeds 3, p. 185, figs. 19a, 21, 1988.

(Fig. 3)

Fronds cylindrical, 3–17 cm high, entangled, forming a cushionlike plant, 10–20 cm in diameter, with dense upright branching. Erect axes with numerous short branchlets, arranged irregularly or in whorls, covered by simple or compound tubercles or spines, with obtuse or acute apices. In cross section, medulla consisting of small rhizoidal cells, interspersed with large cells; inner cortex consisting of many rows of large oval or polygonal cells; outer cortex consisting of one to two rows of cortical cells. Sexual reproduction not seen.

Habitat: Found growing on living or eroded corals where exposed to strong wave action. Living specimens strongly resemble the coral *Acropora* in appearance and color.

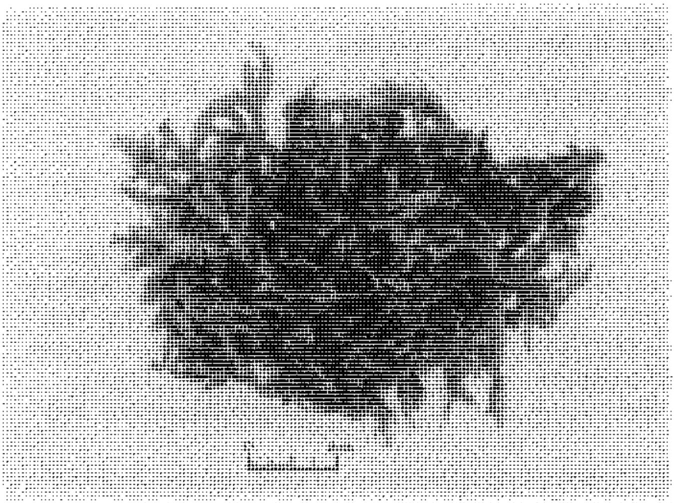
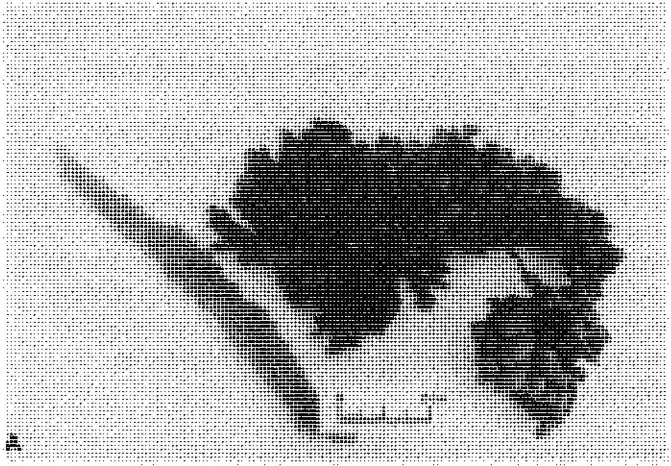


Fig. 2. Thallus of *Eucheuma gelatinum.*



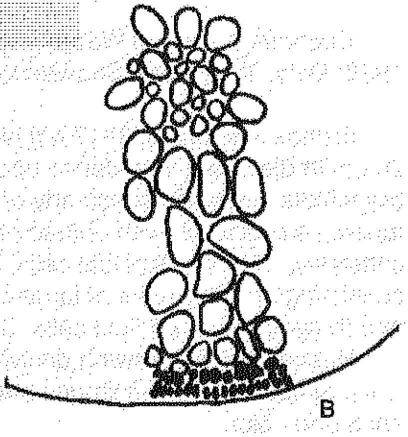


Fig. 3. *Eucheuma arnoldii.* A, Whole thallus. B, Diagram of cross-section of thallus.

Distribution: Ninh Hai-Ninh Thuan Province, Truong Sa Islands, and Khanh Hoa Province. Specimens: TS 901, NTL 931. According to Doty (1988), the species is known from northern Queensland, Australia, to Taiwan and the Ryukyu Islands.

Economic Potential: As a source of iota-carrageenan, with probably small economic potential, unless large numbers of plants are available.

*Kappaphycus inerme* (Schmitz) Doty, Tax. Econ. Seaweeds 3, p. 173, 1988.
(Fig. 4)

Basionym: *Eucheuma inerme* Schmitz, Bot. Jahrb. Syst. 21:150, 1895.

Plants partly decumbent, axes cylindrical-compressed, apices blunt, 3–5 cm in diameter, 5–7 cm tall, branching irregular. Apically inflated apices of branches (Doty 1988, fig. 13) not seen. In cross section, medulla consisting of elongated cells, inner cortex of polygonal-ovoid cells irregularly arranged, outer cortex of two cell rows. Sexual reproduction not seen. Plants slippery when living, attached to rocky or coral substrate, often forming haptera from apices of branches.

Habitat: Found growing at a depth of 1.0–1.5 m.

Distribution: Truong Sa Islands, and Khanh Hoa Province. Specimen: TS 902. Distributed from eastern Africa (Tanzania, type locality) to southwestern Indian Ocean.

Remarks: The massive haptera with ascending axes from various levels found by Doty (1988, fig. 12) in the isotype and other material of this species were not observed and should be looked for if this is characteristic of this species.

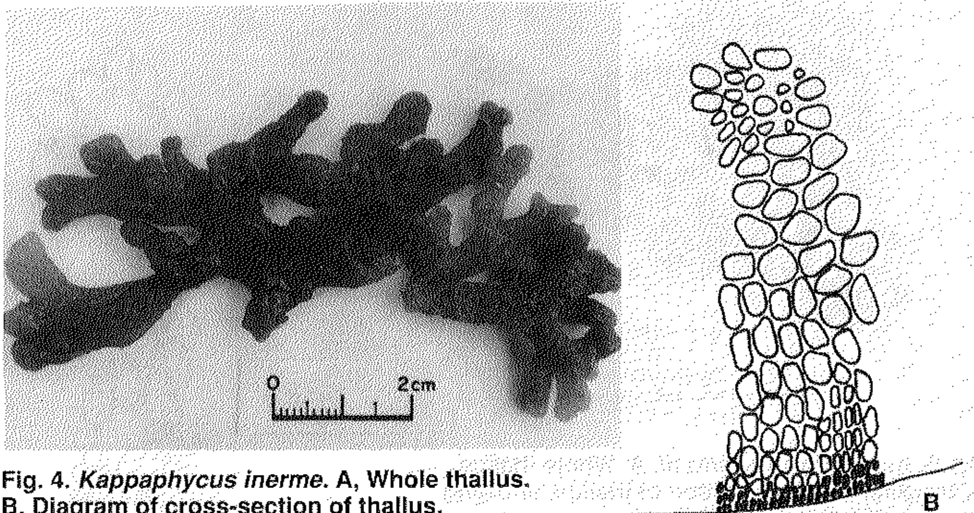


**Fig. 4.** ***Kappaphycus inerme*****. A, Whole thallus. B, Diagram of cross-section of thallus.**

*Kappaphycus cottonii* (Weber van Bosse) Doty, Tax. Econ. Seaweeds 2, p. 177, fig. 16, 1988. (Fig. 5)

Basionym: *Eucheuma cottonii* Weber van Bosse, Trans. Linn. Soc., Ser. 2, Bot. 8, p. 115, pl. 12, fig. 2, 1913.

Plants growing in clumps, congested or simple; axes cylindrical, compressed to flattened, 9–10 mm wide, with branches of irregular lengths, and irregular patterns. Tubercles spiny on dorsal surface, some elongated and swollen, forming haptera; others on ventral surfaces crowded, with obtuse apices 1–2 mm tall; those from margin elongating to form new branches, which often zig-zag and attach here and there. Fronds firm to cartilaginous. In cross section, medulla consisting of elongated cells, surrounded by large cells; inner cortex consisting of rows of round, ovoid cells, becoming smaller toward the margin; outer cortex consisting of one to two rows of small ovoid cells. Tetrasporangia zonately divided, immersed in outer cortex; sexual organs not seen.

Habitat: Found growing at a depth of 0.7–2.0 m; often in sandy mud, although when exposed to strong wave action and turbulence, the salinity can be 30–34‰ and temperature 20–27°C.

Distribution: Ly Son Island, Quang Ngai Province, Ninh Hai-Ninh, and Thuan Province. Also found in eastern Africa (Tanzania) to southern China, Philippines, and Guam (Doty 1988).

Economic potential: As human food and as a source of kappa-carrageenan.

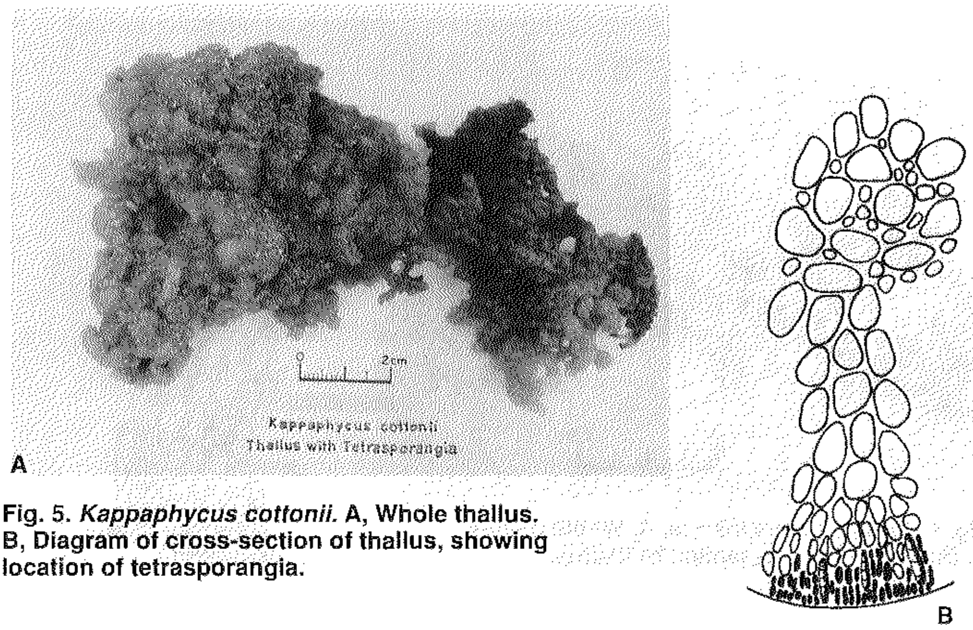


**Fig. 5.** ***Kappaphycus cottonii.*** **A, Whole thallus. B, Diagram of cross-section of thallus, showing location of tetrasporangia.**

## Acknowledgments

We thank Professor M. S. Doty, University of Hawaii, for his help in identifying our specimens and Dr. I. A. Abbott for substantial help in reviewing and rewriting this chapter. We acknowledge the financial support of the California Sea Grant College and the University of Hawaii Sea Grant College Program for our participation in this workshop and for making it possible for us to join others in learning how to distinguish different species of marine algae.

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# *BETAPHYCUS PHILIPPINENSIS* GEN. ET SP. NOV. AND RELATED SPECIES (SOLIERIACEAE, GIGARTINALES)

Maxwell S. Doty

## Abstract

*Betaphycus*, with *B. philippinensis* as its type species, is described to receive species formerly assigned to *Eucheuma* that differ from *Eucheuma* in the main type of gel found in their cell walls and that, with the earlier segregated genus *Kappaphycus* Doty, form a tribe (Eucheumateae) containing commercially important species. *Betaphycus gelatinum* (formerly *E. gelatinum*); *B. speciosum* (previously *Gigartina speciosa*, the name-bringer for *E. speciosum* (Sonder) J. Agardh); and *B. philippinensis* have predominantly beta-carrageenan in their cell walls. Species in *Kappaphycus* have mostly kappa-carrageenan, and species in *Eucheuma* (*sensu stricto*) have mostly iota-carrageenan.

## Introduction

In studies of the Solieriaceous generic tribe *Eucheumateae* over the years, a few species placed in the genus *Eucheuma* have stood out as different in many ways. Among them are some with unique ecological, morphological, and phycocolloid features that distinguish a genus neither previously named nor described. This genus is typified by a new species as follows.

## Description of the Type Species

*Betaphycus philippinensis* gen. et sp. nov.

(Figs. 1–5)

Thalli horizontales vel erectes. Frondes generaliter complanatae et dorsiventraliter asymmetricae e basi crustacea exorientes. Pinnae saepe oppositae et compressae, non in verticillis, elementa texturae cortice exteriore plerumque filamentoso, cortice interiore non filamentoso et pseudoparenchymatico. Medulla centrali axe complanato rhizoideorum tortuosorum. Cystocarpia portata lateraliter determinatis ramulis ventralibus. Tetrasporangia in cortice exteriore inclusa. Tetrasporae seriatim dispositae. Capientes beta et kappa carrageenan in complexione pro maioribus partibus parietum cellulosorum.

Typus Generi: *Betaphycus philippinensis*. Holotypus speciei *Betaphycus philippinensis* numero auctoritatis 33052 depositus in Herbario Pacifico B. P. Bishop Musei, Honolulu, Hawaii pro No. 636-903. Illa species typica pro hoc genere differt ab aliis speciebus generis structuris reproductivis in paginis inferioribus vel ventralibus. Thalli usque 15 cm alti.

Thalli with fronds generally flattened and dorsiventrally asymmetrical, horizontal or erect from crustose bases by means of short cylindrical erect basal segments. Frond branches often opposite and compressed, not in whorls. Tissues

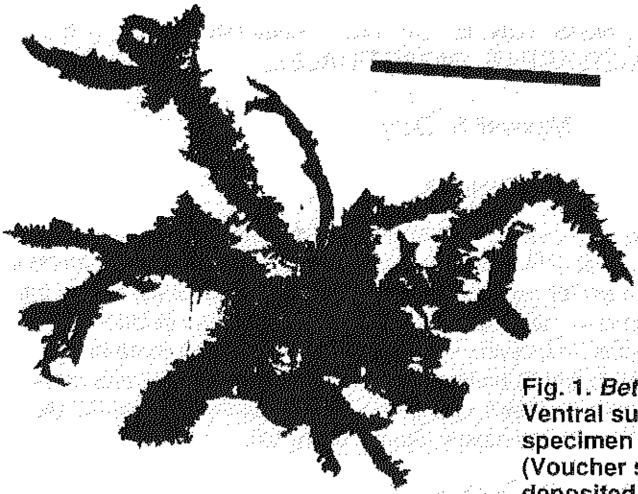


Fig. 1. *Betaphycus philippinensis.* Ventral surface of cystocarpic specimen from holotype preparation (Voucher specimen Doty No. 33052 deposited in the B. P. Bishop Museum herbarium as BISH 636-903). Scale bar = 3 cm.

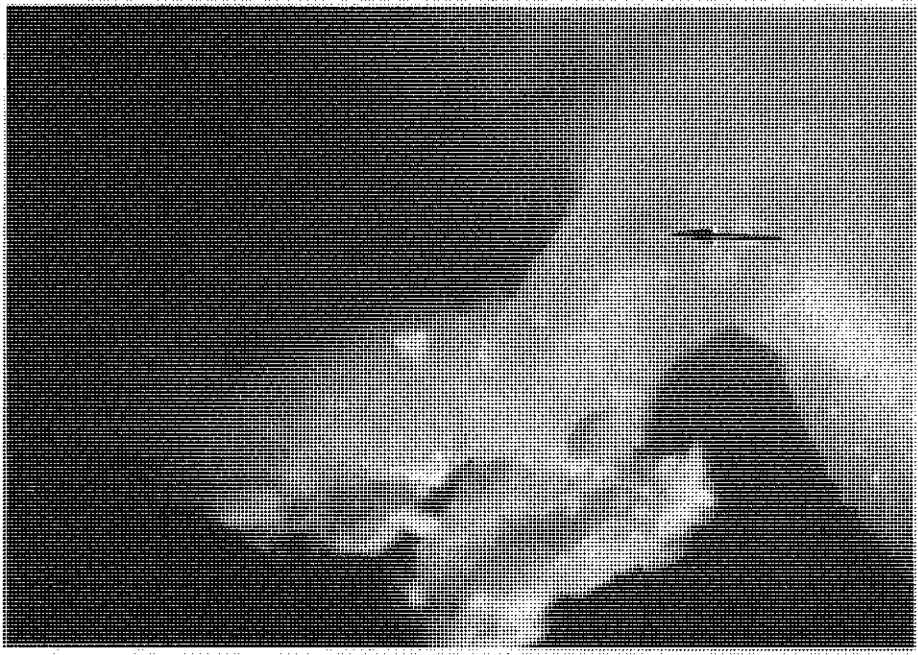


Fig. 2. *Betaphycus philippinensis.* Holdfast spreading to left from possible initial cushionlike central disk below. Frond blade extends to upper right corner. Arrow = young lateral conical proliferation. A horizontal terete branch extends downward at right. Arrow shaft = scale bar = 0.5 mm. (Photo MSD 33570.20).

with outer cortex for the most part filamentous, with inner cortex pseudoparenchymatous and not filamentous. Medulla with central axis flattened and with contorted rhizoids. Cystocarps borne subterminally or laterally on short ventral cylindrical to compressed branchlets. Tetrasporangia ventral, enclosed in outer cortex, and arranged in a row. Greater part of vegetative cell walls consisting of beta- and kappa-carrageenans in combination.

Holotype: BISH 636-903, a preparation (Doty voucher No. 33052) deposited in the Herbarium Pacificum of the B. P. Bishop Museum, Honolulu, Hawaii.

The type material is a preparation consisting of four herbarium sheets, each bearing fronds selected from about 5 kg of dried thalli obtained from eastern Sorsogon Province, Philippines, in October and November 1987. One cystocarpic thallus (Fig. 1) provided fronds for each of the four exsiccati preparations. Tetrasporic specimens are also present on each sheet. One sheet is marked "holotype." The others are marked "isotype 2," "isotype 3," and "isotype 4." The holotype and one isotype are deposited in the Herbarium Pacificum of the B. P. Bishop Museum, Honolulu, Hawaii. Isotype materials have been provided to the Botany Department Herbarium of Melbourne University, Parkville, Victoria, Australia.

Remarks: In having the reproductory structures on the lower or ventral surfaces, this species differs from other species in the genus. The type species for the genus is *B. philippinensis* as described here.

The generic name is neuter, combining "beta" from the name of its principal carrageenan with "phycus" as an alga. The type species for the genus, *B. philippinensis*, is named for the place of collection of the voucher materials for this species, which is reef crests along the east-facing Pacific Philippine shores. Although it grows on limestone, *B. philippinensis* is usually near volcanic rock of recent but prehistoric age.

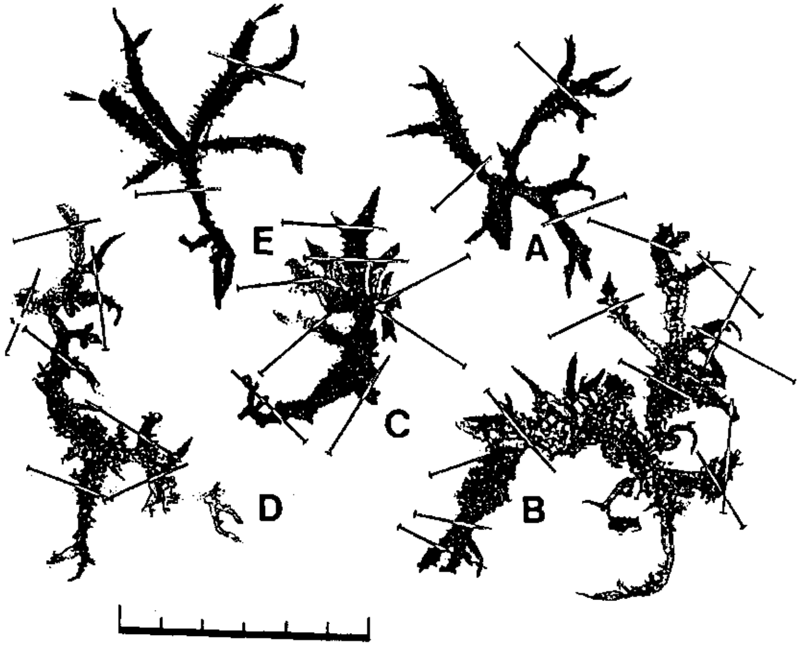
The type species as understood thus far tends to arise from cylindrical primary shoots, with the most basal portion pulvinate or cylindrical, and may be obscured in a hole or depression in the substratum. Basal segments (Fig. 2) give rise to lateral branch initials that when first appearing are conical, and some basal lateral branches grow horizontally and attach apically somewhat, as is the case in most juvenile plants of *Gelidium* species and their relatives. A few juvenile fronds less than 3 mm tall arise as thin blades from a thin crustose superficial base growing on a crustose corralline alga.

Tetrasporangia divide seriately and are borne in the outer cortices of cylindrical proliferations on the ventral surfaces of fronds. Tetrasporangial plants are common and dominate the communities of this species almost to the exclusion of all other life-history stages. Male structures are unknown. Cystocarps first appear subapically on ventral initially terete proliferations and so tend to bear an asymmetric spine as they enlarge. Older cystocarps may become marginal (as shown in Doty 1988, fig. 24A of a different species), if their supporting proliferations lengthen and flatten.

Along approximately the 60-km stretch of coast where it has been collected, this species has a number of variations in distinct form that appear to be responses to different environments. Only four are mentioned informally here.

Most common is the type variety, *B. philippinensis* var. *philippinensis* (Figs. 1 and 3), which may be nearly rigid and is often found bent immediately above its primary segments so that its fronds become horizontal. Primary branches are predominant in this variety (i.e., they originate near the apex), but in this case, they lead to pinnate fronds. The gels in the cell walls appear to be stronger in the smooth nonproliferous top (dorsal) surfaces of flattened fronds and lateral primary and indeterminate and determinate secondary branches. This dorsiventral difference in gel material results in strong longitudinal and some lateral incurving of fronds as they dry.

The illustrations of *B. philippinensis* var. *philippinensis* (Figs. 3A–E), are of normal-sized fronds, several of which are commonly found on a given specimen in nature. When soaked, dried fronds seem to swell to about the weight and size they were when fresh and alive. Drying and soaking are necessary to get specimens to spread flat on herbarium sheets so they will show branching patterns and the differences between and locations of secondary branching and proliferation. Measurements of wet fronds and the same fronds when dry showed average shrinkage of 9% in length and 28% transversely for the broadest portions.



**Figs. 3. *Betaphycus philippinensis* var. *philippinensis*. A–E, Dry fronds soaked in fresh water to simulate natural size of live specimens. Dorsal side is up in all cases. B–E, Nearly whole thalli. Note spatulate blade (arrows in E). Scale bar = 6 cm. (Retouched xerograph from MSD 33677).**

A second form is found in the calm deeper water just offshore of the reef-top seaward-edge position of the type variety. Its ultimate blades are erect, thin, and spatulate, similar to some ultimate blades of fronds of the first form (arrows in Fig. 3E). Although specimens of this variety are included in the collections of Dr. G. T. Kraft, from Bulusan, Sorsogon Province, Philippines, it is not illustrated here. No fertile plants have been found.

A third form (Fig. 4) also tends to have slender but not rigorously erect spatulate blades. Marginal denticulations are common on broader frond segments. It is considered a shallow high-elevation form possibly found in tide pools in which the water is exchanged gently with almost each wave. Its pseudodichotomies are more conspicuous than those of other forms.

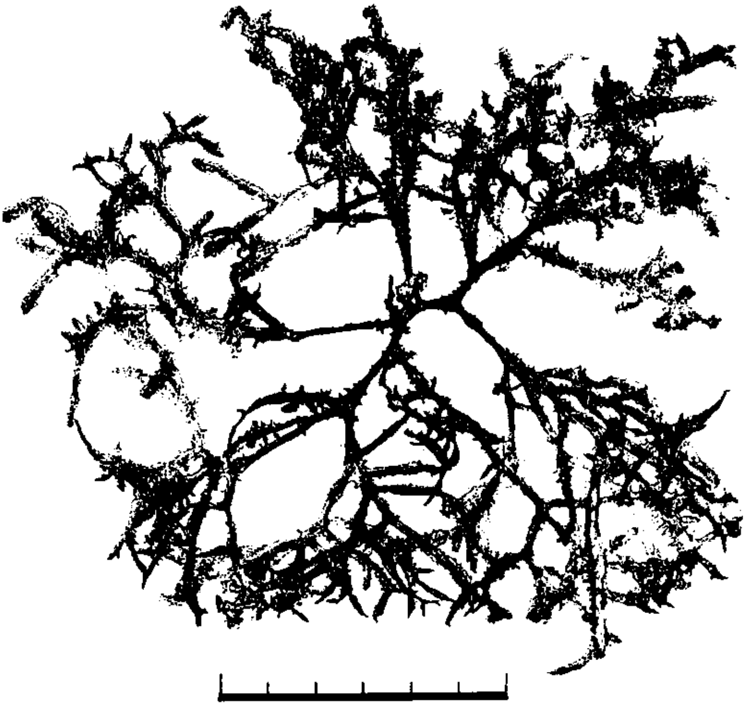


**Fig. 4.** ***Betaphycus philippinensis.*** **Whole thallus with limestone substratum and holdfast of specimen with primary pseudodichotomous branching. Scale bar = 6 cm. (Retouched xerograph of a specimen selected from an eastern Sorosogon, collection, MSD Voucher No. 33675).**

The fourth form (Fig. 5) is slender and often unilaterally branched and somewhat fastigiate. Its main frond segments are less compressed than are segments of the other forms. Major frond axes may be twisted as though they grew under the influence of gentle but occasionally reversing currents.

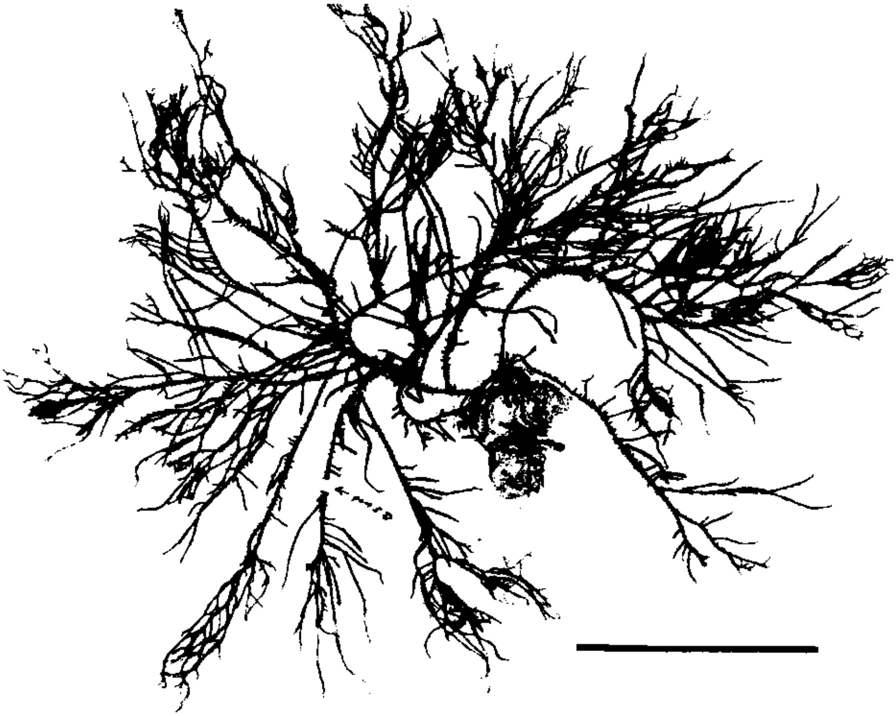


**Fig. 5.** ***Betaphycus philippinensis.*** **Whole thallus with limestone substratum of slender specimen with fastigiate, sometimes unilateral branching. Scale bar = 6 cm. (Retouched xerograph from an eastern Sorsogon, Philippines, collection, MSD Voucher No. 33674).**

Unfortunately, these associations of form and their biospaces must remain hypothetical for the present, because of a lack of reliable information. In the intense mixing of the seawater coming over reef fronts and the high rates of water exchange involved, the actual water temperature, water quality, and solid substratum are likely essentially identical for all four forms. The typical form may receive the most light; the two slender forms, somewhat less; and the erect form with thin spatulate blades, the least light and water motion.

## Description of Other Species

*Betaphycus gelatinum* (Esper) comb. nov.

Basionym: *Fucus gelatinum* Esper, icones fucorum, Fasc. 4, p. 188, 1800.

Other Name: *Eucheuma gelatinae* (Esper) J. Agardh, Kongl. Vet.-Akad. Forhandl. 4:16, 1847.

Remarks: The type material for this species appears to be from an abundance of frond fragments found in the Esper collections housed in the Herbarium of Institut Allgemeine Botanik, Hamburg, Germany. However, a fragment (numbered 34697) in the Agardh Herbarium at the University of Lund, Lund, Sweden, appears to have come from this Esper collection. Physically, these fragments are poorly preserved, and like those in many other old collections of seaweeds, they will hardly stand conventional study, because they tend to disintegrate in cold water. However, they are accepted as isolectotypes. The specimen illustrated by Doty (1988, fig. 23A) is in the Hamburg herbarium and is selected as the lectotype.

Only Schmitz (1895) has reported that reproductory structures of *B. gelatinae* are on the upper surface. No male structures have been reported.

*Betaphycus speciosum* (Sonder) comb. nov.

Basionym: *Gigartina speciosa* Sonder, Bot. Zeit. 3, p. 55, 1845 (pages are not numbered on my copy).

Lectotype: Preiss No. 2565 as No. 34703 in the Agardh Herbarium of Lund University, Lund, Sweden.

Other name: *Eucheuma speciosum* (Sonder) J. Agardh, Kongl. Vet.-Akad. Forhandl. 4:16, 1847.

Remarks: The Preiss material was widely distributed to several herbaria, and some specimens are being labeled "holotype." Doty (1988, pp. 195–197, figs. 29–31) illustrates size and form as well as the uniquely advanced tetrasporangial morphology. Unlike *B. philippinensis* and *B. gelatinum*, this species has cystocarps laterally on upper axial segments (e.g., Doty 1988, fig. 24D). No spermatangia have been observed. This species is apparently restricted to Western Australia.

## Summary and Conclusions

Aside from its phycocolloids, *Betaphycus* has unique ecological and morphological features that distinguish it from other eucheumoids. Several have been mentioned here. In addition, beta-carrageenan accounts for a significant proportion of the phycocolloid in older cell walls of all three of its species, although prominent amounts of kappa- and gamma-carrageenans are present as well. *Betaphycus* is thus different from other eucheumoids, which usually have but one carrageenan prominent in the walls of their interior cells. Greer and Yaphe (l984) first reported that *B. gelatinum* produced beta- and kappa-carrageenan. Their determinations were made on disaccharide hydrolysates, and no physically discrete weighable amounts of beta-carrageenan were available. Santos (1989) was able to isolate beta-carrageenans in weighable amounts. She was working with both *B. philippinensis* and *B. speciosum*. The initial findings of Greer and Yaphe (1984) and of Santos have been extended recently (Renn et al. 1993).

The consistent presence of beta- and kappa-carrageenan in the three *Betaphycus* species named here has been a prime reason for taxonomic distinction of this genus. Only the tetrasporangial contents have been studied. Most of the fronds examined have been tetrasporic. The cystocarpic stages are essentially rare, seen in less than 0.5% of the more than 1000 thalli of the type species studied in this respect. When seen, cystocarps have always been initially subterminal on ventral or marginal proliferations and bearing one (the laterally displaced tip of the original supporting proliferation) or more denticulations positioned equatorially. No male structure has been seen in any of the three species. The type of phycocolloid has been used (Liao et al. 1993, Doty 1988) in conjunction with morphological criteria to distinguish other taxonomic groups among the Gigartinales.

With publication of *Betaphycus*, the tribe Eucheumateae among the Gigartinales is expanded so that each of the three commercial phycocolloids obtained from its members comes from a different genus. These genera and their respective gels may now be referred to by the following scientific and common names and predominant cell wall component: *E. denticulatum* (common name "spinosum," produces iota-carrageenan), *Kappaphycus alvarezii* var. *tambalang* ("alvarezii" or "tambalang," kappa-carrageenan), and *B. gelatinum* ("gelatinum," beta-carrageenan). *Kappaphycus cottonii* does not appear in commercial quantities.

## Acknowledgments

Financial support from the University of Hawaii Sea Grant College Program, the University of Hawaii Botany Department, and FMC Corporation is gratefully acknowledged. Provision of the Latin by Meng Sung Doty is appreciated. Clerical, curatorial, and nomenclatural assistance were provided by Beverly J. Cook, Jack R. Fisher, and Dr. Paul Silva, respectively, and many specimens were received from Vicente B. Alvarez and Dr. Gerald T. Kraft; all were most generous of their time and skills.

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# Section V. Taxonomic Index