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TAXONOMY OF ECONOMIC SEAWEEDS

With reference to some Pacific and Western Atlantic species

Volume III

Isabella A. Abbott, Editor

A Publication of the
California Sea Grant College

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Rosemary Amidei
Communications Coordinator

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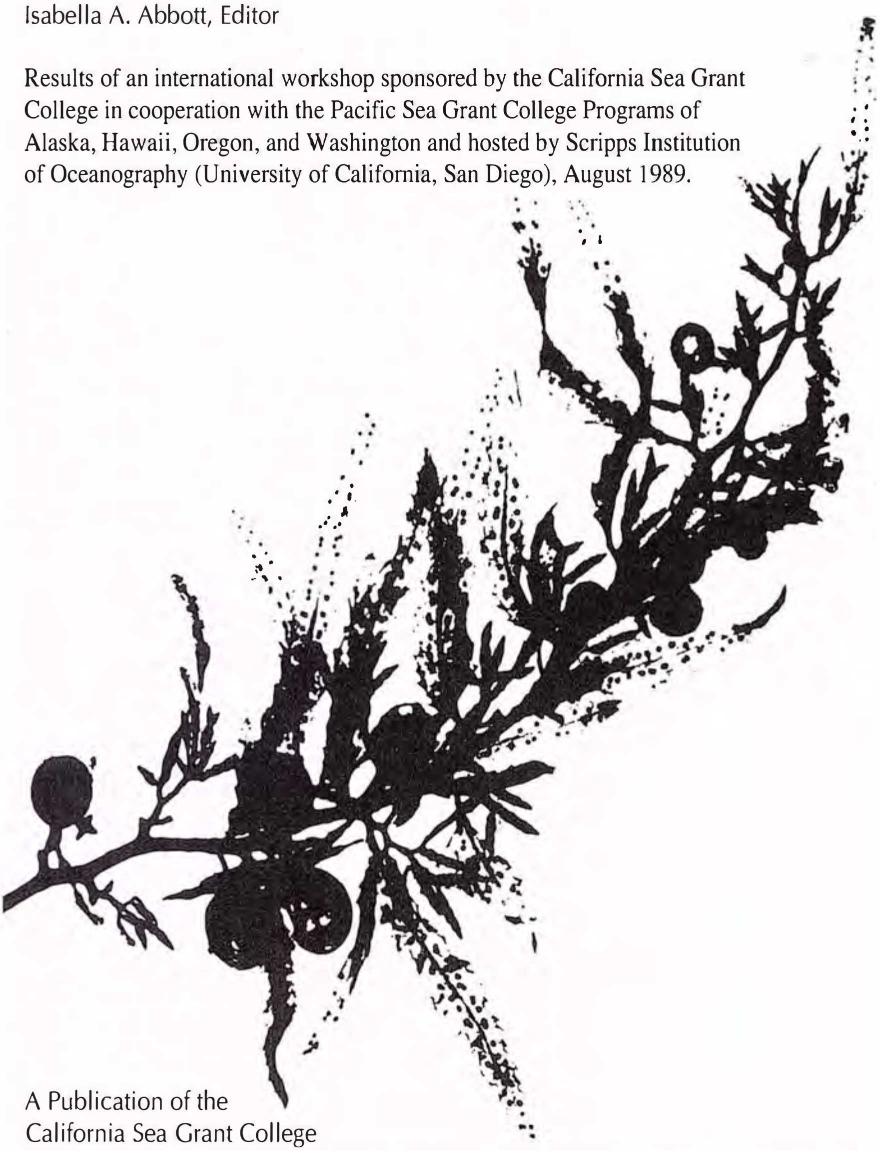
Results of an international workshop sponsored by the California Sea Grant College in cooperation with the Pacific Sea Grant College Programs of Alaska, Hawaii, Oregon, and Washington and hosted by Scripps Institution of Oceanography (University of California, San Diego), August 1989.



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UNIVERSITY OF HAWAII AT MANOA
SEA GRANT COLLEGE PROGRAM
2525 CORREA ROAD, HIG 238
HONOLULU, HAWAII 96822

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Table of Contents

Section I. Part II. *Sargassum* Subgenus *Bactrophycus*

Section II. Gelidiales

Section III. *Gracilaria*

Section IV. *Eucheuma*

Preface

James J. Sullivan
Director, California Sea Grant College

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

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

That point was underscored by an example offered by Isabella A. Abbott, of the University of Hawaii, who cited *Gracilaria* as one example of the importance to industry of proper identification of species. Of two Hawaiian species of *Gracilaria*, she noted, one provides three to four times better gel strength in agar than does the other.

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

Introduction

Isabella A. Abbott, Workshop Convener and Editor

The workshop held at the Scripps Institution of Oceanography (part of the University of California, San Diego) in La Jolla, California, in August 1989 attracted systematists from China, Japan, Korea, Taiwan, the Philippines, Vietnam, Chile, South Africa, Portugal, and several places in the United States (Washington, D.C., Florida, California, and Hawaii). It was the most international of the three algal systematics workshops, and in some ways our most successful in terms of making friends and sharing ideas as well as specimens.

The workshop was dominated by the number of scientists (eight) working on the brown alga *Sargassum*; specimens of this alga took over every spare tabletop and all available floor space, making it necessary for some scientists to defend steadfastly their desk space for their own few specimens. The result of all this interest and activity is that Sargassum has the lion's share of papers in this workshop volume.

Five taxonomists devoted themselves to *Gracilaria* and its relatives, and four to *Gelidium* and its relatives. In addition, Dr. Yoshida turned in a paper on a poorly known species of *Eucheuma*, a red alga of great commercial importance in the Philippines.

Workshop participants reviewed some of the papers in this volume, and other colleagues read others. As editor, I protected the opinions of the writers who did not have English as their first language; any changes that were suggested were carefully examined so that meanings were not inadvertently changed. Several papers had to be rewritten to make their content unambiguous. In order to make this workshop thoroughly international, it was necessary to respect the opinions and integrity of all and to make certain that each participant was able to make a contribution within the context of his or her own background, knowledge, and horizons. Fortunately, most of the participants could handle English passably, and those for whom English was not the primary tongue were certainly better linguists than were those of us who spoke only English.

Despite the many contributions on *Sargassum*, the *Sargassum* specialists are only now beginning to understand the genus; they may soon be able to move from a "local flora" base to a regional, and perhaps Pacific, base. However, we must first examine the numerous "old" Pacific species and varieties in order to eliminate redundant and superfluous names and to refashion the classification scheme along more modern and more realistic lines.

Because of editorial delays, two papers were removed from this volume and published elsewhere. One of them was on *Pterocladia* from the Gelidiales group (B. Santelices), and the other was on *Gracilaria* (I. Abbott, Zhang Junfu, and Xia Bangmei). Both papers appeared in *Pacific Science*, vol. 45, 1991.

Speaking for myself, I would never have believed how much interest I was to develop in the brown alga *Sargassum*. In fact, I have probably devoted as much time to *Sargassum* as I have to the red alga *Gracilaria*, which is to say, weeks. The genus *Sargassum* well illustrates every aspect of the problems in systematics (of any group of organisms): I strongly recommend it to anyone who lives near areas where species or populations are abundant. You will never run out of problems to work on, and you are assured of making interesting contributions to our understanding of the group. No group of marine algae could be more challenging.

A final reminder about how Chinese surnames and first names are used in this volume. Unless the authors requested otherwise, surnames are listed first (e.g., Lu Baoren: Baoren is the author's first name, and Lu is his family name). In the bibliography for the Chinese papers, then, the names are listed "Xia Bangmei," without a comma after Xia. We do this (as does *Taxon*, the international journal for nomenclature and taxonomy) as a courtesy to our Chinese colleagues, who themselves recently have had the spelling of their names changed (which accounts for Zhang Junfu, who was formerly known as C. F. Chang).

Finally, following the examples given in the "Berlin Code" of the International Code of Botanical Nomenclature (1988), reference to *place* of publication follows author name(s) whenever nomenclature (i.e., the name or status of the species or other taxonomic category) is concerned. In these instances, the publication is *not* included in Literature Cited. However, if the citation of a name has to do not with nomenclature but with someone's recognition of the species—that is, it is a report of the species—the place of publication appears in the Literature Cited. In part, this change was made to avoid the extremely lengthy literature lists that usually follow nomenclature papers. As editor, I have tried to observe these new rules, but admittedly have not always been consistent as a result of my incomplete understanding of the rules. I trust readers will be tolerant of any inconsistencies.

Acknowledgments

The California Sea Grant College, which is headquartered at Scripps Institution of Oceanography (part of the University of California, San Diego), received our highest marks at the workshop for support and cooperation. No request was too small, no problem insurmountable. We thank Sea Grant's director, Dr. James J. Sullivan, and his staff for making our visit memorable, smooth, and thoroughly enjoyable.

The University had condominium units in which participants lived; and in some instances, we shared the cooking. What a thrill it was for our guests from overseas to purchase, cook, and eat "American food," even though it might only be California rice and tofu. The food we had in China will never be surpassed in quantity or quality, but I believe that the participants found the La Jolla experience memorable for their enjoyment in sharing the agricultural wealth of America. Dr. Sullivan did a great job of showing the group the meaning of Western hospitality.

We also want to thank Dr. Joan G. Stewart of Scripps for serving as our on-the-spot contact and for helping us in so many ways every day.

As convener of the workshop, I thank Dr. Sullivan and the Sea Grant staff for adding the workshop to their already busy schedule and the administration of Scripps for making us welcome. I also thank the Sea Grant directors of Alaska, Washington, Oregon, and Hawaii for funds that helped to defray transportation costs.

As editor, I thank Rosemary Amidei, Communications Coordinator of the California Sea Grant College, and the communications staff for past and present cooperation in the preparation of these workshop publications. The professional appearance and scholarly contributions of these publications make us phycologists the envy of our colleagues.

Participants

The *Sargassum* Group

Tetsuo Ajisaka
Division of Tropical Agriculture
Faculty of Agriculture
Kyoto University
Kyoto, Japan

Young-Meng Chiang
Institute of Oceanography
National Taiwan University
P. O. Box 23-13
Taipei, Taiwan

John A. Kilar
Mote Marine Laboratory
1600 City Island Park
Sarasota, Florida
(Present address: 516 Mast Rd.,
Goffstown, New Hampshire 03045)

In Kyu Lee
Department of Botany
Seoul National University
Seoul, Korea

Lu Baoren
Institute of Oceanology
Academia Sinica
7 Nan Hai Road
Qingdao, People's Republic of China

Tseng C. K.
Institute of Oceanology
Academia Sinica
7 Nan Hai Road
Qingdao, People's Republic of China

Gavino Trono, Jr.
Marine Science Institute
University of the Philippines
Diliman, Quezon City
Philippines

Tadao Yoshida
Department of Botany
Faculty of Science
Hokkaido University
Sapporo, Japan

The *Gelidiales* Group

Ricardo A. Melo
Department of Biological Sciences
University of California
Santa Barbara, Calif. 93106
(Present address: Departamento
de Biologia Vegetal, Faculdade de
Ciencias, Universidade de Lisboa,
Bloco C-2, Piso 4, 1700 Lisbon, Portugal)

Richard E. Norris
Kirstenbosch Botanical Garden
Private Bag x7
Cape Town 7735, South Africa
(Present address:
Department of Botany
University of Hawaii
Honolulu, Hawaii 96822)

Bernabe Santelices
Pontificia Universidad Catolica de Chile
Casilla 114-D
Santiago, Chile

Joan G. Stewart
A-002
Scripps Institution of Oceanography
University of California, San Diego
La Jolla, California 92093

The *Gracilaria* Group

Isabella A. Abbott
Department of Botany
University of Hawaii
Honolulu, Hawaii 96822

Nguyen Hun Dinh
Center for Science/Production
of Seaweed
24 Hung Zong
Nha Trang, Vietnam

James N. Norris
Department of Botany
NHB 166
Smithsonian Institution
Washington, D. C. 20560

Xia Bangmei
Institute of Oceanology
Academia Sinica
7 Nan Hai Road
Qingdao, People's Republic of China

Zhang Junfu
Institute of Oceanology
Academia Sinica
7 Nan Hai Road
Qingdao, People's Republic of China

Eucheuma

Tadao Yoshida
Department of Botany
Faculty of Science
Hokkaido University
Sapporo, Japan

Section I. *Sargassum*

INTRODUCTION

Isabella A. Abbott

The *Sargassum* contributions in this volume differ from those in earlier volumes and show that in some cases large strides have been made as a result of the studies in the previous two workshops. Only the eldest of us, Professor C. K. Tseng of China, had the vision during those beginning efforts in Guam (1985) to see that valid contributions could be made to this genus. So, two subgenera and more than 120 species later, where are we?

First, we are still in the western Pacific and adjacent warm-water areas. We have not investigated all of this geographical area, but we are making headway. In this volume, we add species from Korea and the Philippines and look forward to future contributions from Vietnam, and perhaps Thailand and Indonesia.

Second, we are beginning to compare western Pacific species with some from the Caribbean. We have found species of similar appearance for which statistical analyses were required to show that although species strongly resemble each other, they are different species that have probably evolved along similar pathways, isolated by distance, water temperature, and land masses. It is clear to me that the techniques of enzyme chemistry can be used to help resolve systematic problems. *Sargassum*, for example, is waiting for sophisticated chemistry to overcome the difficulties of phenolics and other refractory compounds like alginates. It will be much easier for the chemical evolutionists to start off with named taxa: that in itself will be one great contribution from the "*Sargassum* group."

The previous workshop, held in Qingdao, China, was hampered by restrictions in time and by the limited numbers of assembled specimens, so "local" *Sargassum* floras were described. Hawaiian (Magruder), Micronesian (Tsuda), Japanese and Taiwanese (Yoshida), and Chinese (Tseng and Lu) specimens were treated separately. We are not yet able to overcome this geographical provincialism despite the fact that we have all seen many more specimens than we had previously. However, our horizons have expanded. Those of us who live in the western Pacific were treated to a large number of specimens from the Caribbean brought by John Kilar and James Norris (United States), and we could easily see that the problems we face in one part of the world are problems in other parts as well. Among the numerous specimens brought by Drs. Ajisaka, Trono, and Chiang, we could recognize variants of species we have in our own flora. We want especially to encourage Dr. Nguyen to look for the *Sargassum* species that were described earlier from Vietnam, and we further encourage him to assemble a large collection for the next workshop so we can follow the distribution of the species we know and come to recognize taxa that may be outside our present range.

And what of *Sargassum* subgenus *Bactrophycus* from Korea? Why do all Korean *Sargassum* species belong to this subgenus (which is endemic to the coasts of China and Japan, but which is not nearly as numerous in species as is subgenus *Sargassum*)? Are the waters off Korea really testing the limits of species of *Sargassum*? Are there other places in the world where conditions promote this kind of evolution?

The *Sargassum* papers in this volume express the state of systematics and taxonomy in the algae. They range from the conservative approach of qualitative morphological description of species to the statistical treatment of populations of species. They are the product of examining specimens and trying to make them "fit" into a previously described system. Our strategy can be compared to that of assembling a jigsaw puzzle in which the edges of the pieces do not quite fit. We may persist nonetheless in laying the pieces next to each other until the total picture emerges. Then we can "fix" the pieces. This is the method of taxonomists who are compelled to put the best name they can on an herbarium specimen so that it can be filed, and so that the name can be used. Another school of taxonomists collects a lot of specimens, takes measurements and means, and presents a quantitative picture of the species (this approach is frequently used when no one specimen qualifies as an absolute representative of the species). Some specimens of *Sargassum* could be treated in either way, probably satisfactorily.

Despite strenuous efforts to make substantial progress in *Sargassum* taxonomy, the *Sargassum* group appears to want more: more specimens, more time, and more colleagues to join them. By these additions, they think that they will eventually make a useful contribution.

The entire system of classification for *Sargassum* is confused, and in places it is too vague to be useful. For example, the choice of rank within a subgenus is understood to mean that certain species can be grouped together in some fashion that includes all of the generic-level features, but that some other features, perhaps of a minor nature, can be recognized as forming a grouping between genus and species. Thus, the two subgenera that we have studied in the western Pacific, *Sargassum* subgenus *Sargassum* (Tseng and Lu 1988; Abbott et al. 1988; Yoshida 1988) and *Sargassum* subgenus *Bactrophycus* (Tseng et al. 1985), are distinguished from each other primarily by the shape of their axes. In subgenus *Bactrophycus*, axes are compressed, with the two edges expanded and varying from that to angular; in subgenus *Sargassum* (Setchell 1931), axes are cylindrical, compressed, or flattened. It can be seen that even at this first-level key character, the taxa probably do not clearly fall into one *or* the other category. To discard the subgeneric level before the constituents of this level are assembled, studied, and understood, however, would be to effect a piecemeal kind of correction that would not solve the difficulties. If a fresh approach does not develop, the two approaches that we use here—specimen and population biology—will continue to shed light a little at a time on the complex that is *Sargassum*.

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Part I. *Sargassum* Subgenus *Sargassum*

STUDIES ON THE MALACOCARPIC *SARGASSUM* OF CHINA
I. *FRUTICULIFERAE* J. AGARDH

Tseng C. K. and Lu Baoren

Abstract

The Chinese species of the subsection *Fruticuliferae* of the malacocarpic *Sargassum* are reviewed. This subsection of the subgenus *Sargassum* is characterized by species with smooth receptacles arranged in bristly (squarrose) cymes that are pedicellate, but with both axes and branches merging with receptacular tissue. Of the 10 species assigned by J. G. Agardh to this group, only two have been accepted. In China, a striking species with spinous branches and very crowded leaves that are mostly pinnatifid, *S. polyporum* Montagne, was assigned to *Fruticuliferae*. A new species was recently added, namely, *S. longicaulis* Tseng et Lu, which has smooth axes and branches; very elongated axis; and very elongated, pinnatifid lower leaves.

Introduction

The malacocarpic *Sargassum* are species of the section *Malacocarpicae* of the subgenus *Sargassum*, with smooth, non-spinous receptacles arranged cymosely or racemosely. The *Malacocarpicae* formed the second of two "series" of J. G. Agardh (the first was the series *Acanthocarpicae*), and both series were elevated, following the International Code of Botanical Nomenclature (Voss et al. 1983), to the rank of section by Abbott et al. (1988). Within the section *Malacocarpicae*, the rank of tribe was used by J. G. Agardh (1889), DeToni (1895), and Grunow (1916a) for the recognition of three groups of taxa: tribe IV of J. G. Agardh (1889), *Fruticuliferae*; tribe V of J. G. Agardh (1889), *Cymosae*; and tribe VI of J. G. Agardh (1889), *Racemosae.* Article 4.1 of the Code restricts the use of the rank "tribe" for family-level categories; a new rank must therefore be proposed for these intrageneric groups since we accept them.

The rank **subsection** in *Sargassum* subgenus *Sargassum* has never been used, and therefore no confusion will be created if we transfer these three taxa to the rank of subsection as follows:

1. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* **subsection** *Fruticuliferae* (J. G. Agardh) Tseng et Lu, stat. nov.

Basionym: *Sargassum* subgenus *Sargassum* (=*Eusargassum*) section *Malacocarpicae* (=series II *Malacocarpicae*) tribe *Fruticuliferae* J. Agardh (J. G. Agardh, Kgl. Sv. Vet.-Ak. Handl. 23(3) p. 34, pl. 29, fig. 1, 1889).

2. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* **subsection** *Cymosae* (J. Agardh) Tseng et Lu, stat. nov.

Basionym: *Sargassum* subgenus *Sargassum* (=*Eusargassum*) section *Malacocarpicae* (=series II *Malacocarpicae*) tribe *Cymosae* J. Agardh (J. G. Agardh, Kgl. Sv. Vet.-Ak. Handl. 23(3) p. 34, pl. 29, figs 2–5, 1889).

3. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* **subsection** *Racemosae* (J. Agardh) Tseng et Lu, stat. nov.

Basionym: *Sargassum* subgenus *Sargassum* (=*Eusargassum*) section *Malacocarpicae* (=series II *Malacocarpicae*) tribe *Racemosae* J. Agardh (J. G. Agardh, Kgl. Sv. Vet.-Ak. Handl. 23(3) p. 34, pls. 10, 12, 30, 31, 1889).

The *Fruticuliferae* were characterized by receptacles that form brushlike cymes that are pedicellate and without sterile axes or branches. The subsection contains 10 species. The *Cymosae* were characterized by their cymosely branched receptacles, where the branches are in fasciculate clusters, each with acuminate apices. At times, the branches were confluent with the fertile rachis, or more or less separated below. This subsection contains 16 species. The subsection *Racemosae* was characterized by receptacles arranged in a raceme, with individual receptacles or a receptacular branch, each with a sterile pedicel. When first formed, the receptacle or its branch may be subcymose, but on maturing, these become racemose, especially below (maturing in acropetal fashion). The subsection now has 21 species, and the Chinese species are described by us in this volume.

The *Fruticuliferae* were assigned 10 species by J. G. Agardh (1889), and Grunow (1916) recognized 17. Setchell (1936) accepted only two species for this group, *S. obtusifolium* J. Agardh from Hawaii, and *S. pachycarpum* J. G. Agardh from Tasmania. He believed that the remainder of J. G. Agardh's species were of antheridial predominance, belonging more properly to the series (now section) *Acanthocarpicae*, which is characterized by dentate or spiny receptacles. The two retained species differ from others placed in the section because both leaves and branches are clearly multifarious; the leaves especially are commonly cleft one to several times. A plant from Macao, China, with similar distinctive multifarious leaves is *S. polyporum* Montagne, which Setchell (1936) correctly added to the *Fruticuliferae*, having transferred it from the *Racemosae* where it had been placed by Grunow (1916).

In addition to *S. polyporum*, we have added a second species from China, *Sargassum longicaulis* Tseng et Lu, to the subsection *Fruticuliferae.*

Key to Chinese Species of fruticuliferous *Sargassum*

1. Axes and branches with hard protuberances, frequently with forked spines . . . . *S. polyporum*
1. Axes and branches completely smooth . . . . *S. longicaulis*

Description of the Species

Sargassum polyporum Montagne (Figs. 1, 3A–3C)

Montagne 1842, p. 20; J. G. Agardh 1848, p. 346; Grunow 1916, p. 173; Setchell 1936, p. 11, pls. 4–6; Tseng and Lu 1991.

Fronds dark brown, attaining a height of 23 cm, commonly with encrusting coralline algae on the branches and leaves. Holdfast discoid to subconical (Fig. 3A), 1.5 cm in diameter, giving rise caespitosely to four to six main axes. Main axis warty (with hard protuberances), cylindrical, 1.5–2 mm in diameter, giving rise to two to three subcylindrical or compressed primary branches, 20 cm long, 1.5 mm in diameter, protuberances often with sharp spines, particularly in the upper part of the branches (Fig. 3B); secondary branches very short, subequal, about 1.5–2 cm long, very muriculate, densely spirally alternately arranged at intervals of 0.5–1 cm. Leaves dark brown, usually twisted, densely disposed, two kinds, one pinnatifid, laciniate with the division linear, entire, or wavy at the margins, lower part irregularly dentate at margins, 4–5 cm long, 8–10 mm wide, and the other oblong, bipinnatifid, 1.5 cm long, 6–8 mm wide, obtuse at the apex, entire or wavy at the margins, both kinds of leaves with cuneate, asymmetrical base and cylindrical petiole, 1 mm long, conspicuous percurrent midrib and irregularly scattered cryptostomata. Our

1

2

Fig. 1. ***Sargassum polyporum*** **Montagne (AST 55-1432).**
Fig. 2. ***Sargassum longicaulis*** **Tseng et Lu (AST 55-1434).**

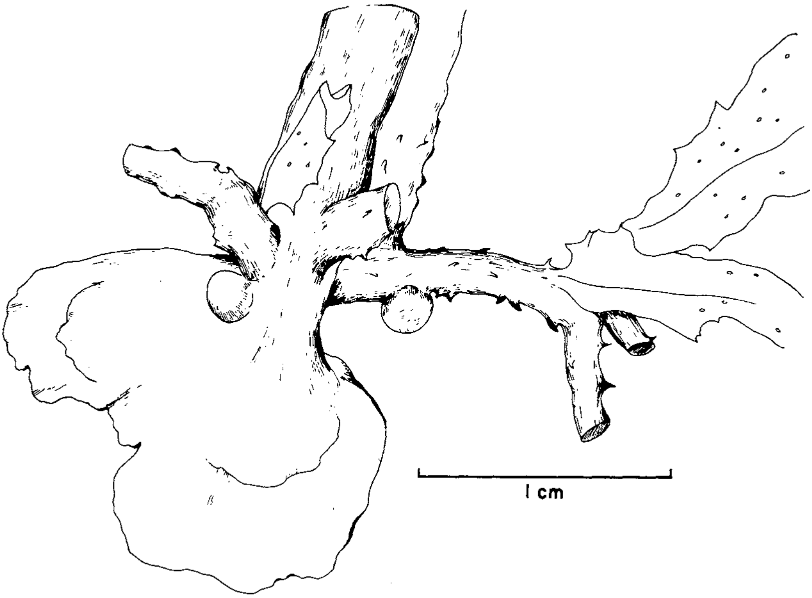
specimens are without vesicles.

Plants dioecious. Female receptacles (Fig. 3C) subcylindrical, compressed, branched, warty, obtuse at the apex, usually forked, 3–5 mm long, 0.8–1 mm in diameter, usually four to five receptacles cymosely arranged. Male plant not found.

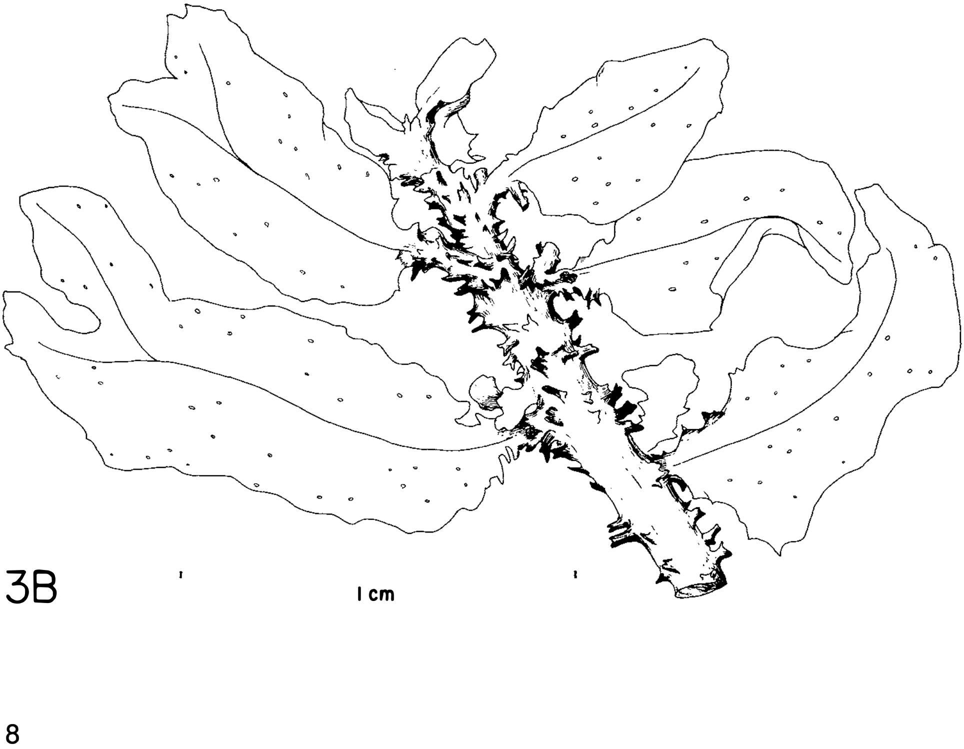
Habitat: Drifted ashore, Xuwen, Guangdong, in March (AST 55-1432) and growing in the lower intertidal pools, Dayawan Bay, Guangdong, in February (AST 56-2577).

Distribution: Endemic in Guangdong, China (Macao, type locality; Hong Kong; Xuwen; and Dayawan Bay).

Remarks: The type specimen was collected by Gaudichaud at Macao during the Voyage of *La Bonite.* Montagne (1842) described but did not illustrate this species, which is deposited in the herbarium of Montagne (Paris). According to Setchell (1936, p. 11), it seems to be an upper branch, or branchlets, of a mature plant, and he did not find anything like a well-developed inflorescence and did not investigate its sex. Our specimens seem to agree with the description of Grunow (1916) and figures of Setchell (1936), though our specimens have no vesicles. According to the description of Grunow, the vesicles of the type specimen are numerous, globular, 2–3 mm in diameter, muticous, and supported on a rather long and compressed stipe. According to our specimens collected at Xuwen, receptacles are often arranged cymosely on branchlets and are



3A



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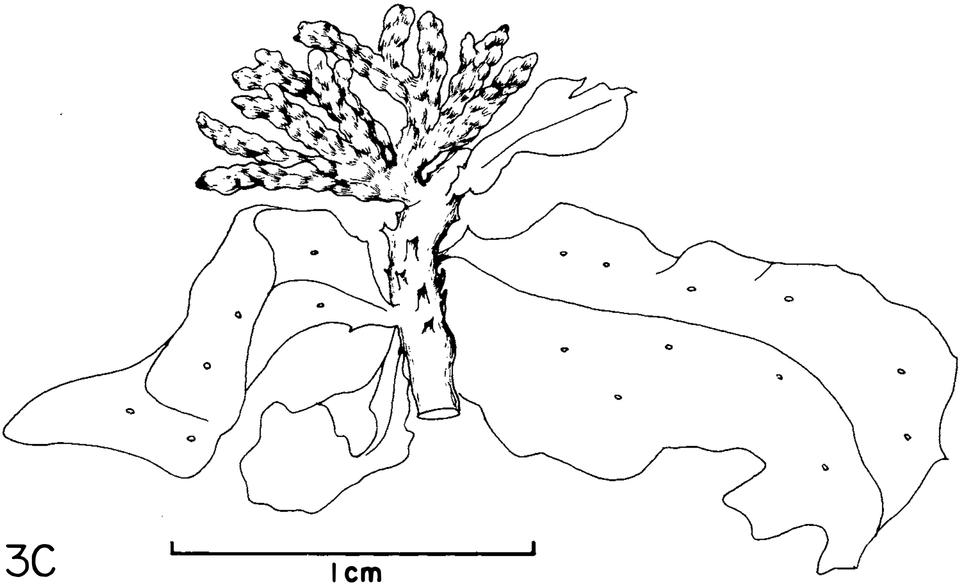

Fig. 3. *Sargassum polyporum* Montagne. *A*, Holdfast. *B*, Branchlet with biforked spines. *C*, Female receptacles.

female. Grunow (1916) described the receptacles as racemosely dichotomous filiform and subtorulose and probably male. It seems that we must wait until we obtain some good specimens before we can settle the problem of the receptacles. This is a species characterized by its spiny branches, the very crowded leaves, pinnately divided, and the short, crowded cymose receptacles.

Sargassum longicaulis Tseng et Lu (Figs. 2, 4)
Tseng and Lu 1990.

Frond dark brown, coarse, attaining a height of 20 cm. Holdfasts discoid, giving rise to long, terete, main axes, up to 6 cm in height, 3 mm in diameter, with numerous stumps on the surface. Primary branches smooth, subcylindrical, compressed, 2–2.5 mm in diameter; secondary branches shorter, beset with fructiferous branchlets. Basal leaves very long, to 21 cm, 13 mm wide, thick and hard, deeply pinnately divided at the margins, midrib conspicuous, raised, percurrent, entire or wavy at the margins, cryptostomata nearly absent; middle and upper leaves oblong or lanceolate, 5–6 cm long, 6–7 mm wide, obtuse or acute apices, entire at the margins, cryptostomata nearly absent. Vesicles spherical, rounded at the tips, 5–6 mm in diameter, cryptostomata nearly absent, pedicels terete, 4 mm long.

Plants dioecious. Male receptacles terete, forked two to three times, smooth on the surface, up to 12 mm long, 1 mm in diameter, roughly cymose; no sterile axes or sterile bases to the branches. Female plants not seen.

Habitat: Growing in lower intertidal pools, Xuwen county (AST 55-1434, 55-1458), Haifeng (AST 56-3200, 56-3256, 56-3328), all Guangdong, in March.

Distribution: Endemic in Guangdong, China (Xuwen, type locality; and Haifeng).

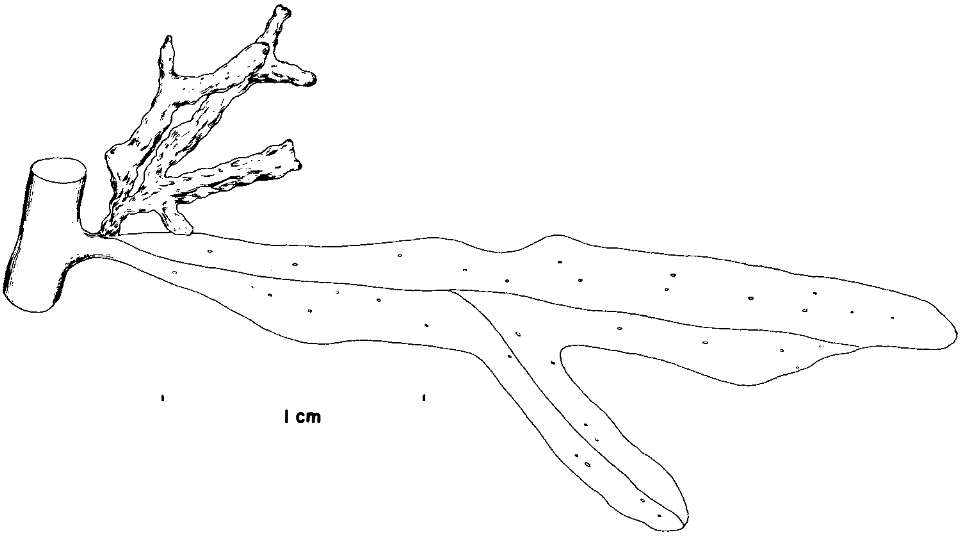

Fig. 4. ***Sargassum longicaulis*** **Tseng et Lu. Male receptacle with forked leaf.**

Remarks: This species is characterized by its very long main axes (to 6 cm), very long (to 21 cm) deeply pinnately divided primary leaves, its male receptacles forked two to three times, cymosely arranged without any sterile axes or sterile bases. It is related to *S. polyporum* Montagne, differing in its smooth branches and very long basal leaves.

Acknowledgments

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STUDIES ON THE MALACOCARPIC *SARGASSUM* OF CHINA:
II. *RACEMOSAE* J. AGARDH

Tseng C. K. and Lu Baoren

Abstract

The Chinese species of the subsection *Racemosae* (Tseng and Lu this volume) of the malacocarpic *Sargassum* are reviewed. This subsection is characterized by smooth receptacles arranged racemosely. Of a total of 21 species, six have previously been credited to China, among which four species are represented in our collections. Additionally, one new record of an old species and eight newly described species are listed, thus making a total of 13 species for China. Three species, including two recently described, belong to the series *Glandulariae* (stat. nov.), characterized by short axillary and glandular fertile branches. Ten species, including six recently described taxa, belong to the series *Siliquosae* (stat. nov.), characterized by comparatively longer fertile branches and generally nonglandular branchlets.

Introduction

The subsection *Racemosae* is a group of *Sargassum* with smooth receptacles arranged racemosely. It consists of 21 species according to J. G. Agardh (1889) and 30 species according to Grumnow (1916). J. Agardh divided the subsection *Racemosae* into three subseries. The first, *Acinariae*, consisting of eight species, has very short axillary fertile branches and lanceolate-conical receptacles. The second of the series, also consisting of eight species, is *Glandulariae*, with short, axillary glandular fertile branches. The third and last series, *Siliquosae*, shows eventually elongated fertile branches and pedicellate, cylindrical, siliquous (narrow-elongate) receptacles that are pinched in here and there, alternately placed on an axis. Grunow (1916) increased the number of *Racemosae* to 30: 11 *Acinariae*, 9 *Glandulariae*, and 10 *Siliquosae*.

J. G. Agardh (1889) listed only two species from China, *S. siliquosum* and *S. henslowianum* of the *Siliquosae*, no *Acinariae*, and no *Glandulariae*. Grunow (1916) added four more species for China: *S. acinaria* C. Agardh var. *crassicescula* (*Acinariae*), *S. concinum* Greville var. *natuanensis* Grunow (*Glandulariae*), and *S. polyporum* Montagne (*Racemosae*). Another species, *S. baccularia* (Mertens) C. Agardh var. *lantowensis*, was listed by Grunow in *Parvifolia* of section *Acanthocarpicae*, but later it was moved by Setchell (1936) to *Racemosae*. Setchell (1936) credited three species to the Chinese *Racemosae*: *S. baccularia* (Mert.) C. Agardh var. *lantowensis* Grunow; *S. henslowianum* C. Agardh, including var. *bellonae* Grunow; and *S. kuetzingii* Setchell. He also removed *S. polyporum* to subsection (formerly tribe) *Fruticuliferae*.

For China, among the *Racemosae* of the section *Malacocarpicae*, six species are recorded: *S. acinaria* of *Acinariae*, *S. baccularia* and *S. concinum* of *Glandulariae*; and *S. siliquosum*, *S. henslowianum*, and *S. kuetzingii* of *Siliquosae*. *Of these, we have found only S. baccularia, S. siliquosum, S. henslowianum*, and *S. kuetzingii*. The status of *S. acinaria* var. crassiuscula and *S. concinum* var. *natuanensis* is still unknown. However, we have found *S. paniculatum* (*Siliquosae*), previously known from the Indian Ocean, and have named eight new species: *S. agaviforme, S. capilliforme, S. frutescens, S. fruticulosum, S. guangdongii, S. leizhouense, S. qinzhouense*, and *S. shangchuanii* (Tseng and Lu, 1990b). There are altogether 13 species of Chinese *Racemosae*.

In the previous paper (Tseng and Lu this volume), we assigned subsection status to *Racemosae*, changing from the tribe designation given by J. G. Agardh (1889) and used by subsequent workers. Here, we give the category **series** to what are now J. G. Agardh's (1889) subtribes *Acinariae*, *Glandulariae*, and *Siliquosae*:

1. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* **series** *Acinariae* (J. Agardh) Tseng et Lu, stat. nov.

   Basionym: *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* subtribe *Acinariae* J. Agardh (J. G. Agardh, Kgl. Sv. Vetensk.-Ak. Handl. 23, p. 39, 1889).
2. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* **series** *Glandulariae* (J. Agardh) Tseng et Lu, stat. nov.

   Basionym: *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* subtribe *Glandulariae* J. Agardh (J. G. Agardh, Kgl. Sv. Vetensk.-Ak. Handl. 23, p. 39, 1889).
3. *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* **series** *Siliquosae* (J. Agardh) Tseng et Lu, stat. nov.

   Basionym: *Sargassum* subgenus *Sargassum* section *Malacocarpicae* subsection *Racemosae* subtribe *Siliquosae* J. Agardh (J. G. Agardh, Kgl. Sv. Vetensk.-Ak. Handl. 23, p. 39, 1889).

Key to Chinese Species of Racemose *Sargassum*

1. Branchlets glandular 2
1. Branchlets smooth, not glandular 6

    2. Leaves needlelike . . . . *S. capilliforme*
    2. Leaves lanceolate 3

3. Primary branches flattened below . . . . *S. fruticulosum*
3. Primary branches terete 4

    4. Leaves less than 2 cm long, and vesicles small, less than 2 mm in diameter . . . . *S. baccularia*
    4. Leaves more than 2.5 cm long and vesicles large, more than 6 mm in diameter generally 5

5. Branchlets elevatedly glandular, leaves with less oblique base . . . . *S. qinzhouense*
5. Branchlets glandular but not elevated, leaves with strongly asymmetrical oblique base . . . . *S. siliquosum*

    6. Leaves on the basal and other parts often dissected 7
    6. Leaves not dissected 9

7. Frond agave-like with long basal leaves . . . . *S. agaviforme*
7. Frond not agave-like 8

    8. Holdfast discoid, fronds not bushy . . . . *S. leizhouense*
    8. Holdfast conical, whole frond bushy . . . . *S. frutescens*

9. Primary branches stout, flattened below, female receptacles compressed . . . . *S. shangchuanii*
9. Primary branches compressed to terete, receptacles terete 10

    10. Frond slender and soft, vesicles usually with a very long stipe (to 10 times their diameter) . . . . *S. kuetzingii*
    10. Frond coarse, vesicles with comparatively short stipe 11

11. Receptacles racemosely arranged 12
11. Receptacles paniculately arranged . . . . *S. paniculatum*

    12. Primary branches compressed below, absence of juvenile receptacles in elongate axes . . . . *S. guangdongii*
    12. Primary branches cylindrical below, with juvenile receptacles in elongate axes . . . . *S. henslowianum*

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Fig. 1. ***Sargassum baccularia*** **C. Agardh (AST 56-1616).**
Fig. 2. ***Sargassum capilliforme*** **Tseng et Lu (AST 55-2259).**
Fig. 3. ***Sargassum qinzhouense*** **Tseng et Lu (AST 55-1987).**
Fig. 4. ***Sargassum siliquosum*** **J. Agardh (AST 87-1392).**

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Fig. 5. *Sargassum shangchuanii* Tseng et Lu (AST 55-3641).
Fig. 6. *Sargassum frutescens* Tseng et Lu (AST 55-3069).
Fig. 7. *Sargassum fruticulosum* Tseng et Lu (AST 55-2253).
Fig. 8. *Sargassum guangdongii* Tseng et Lu (AST 55-1191).

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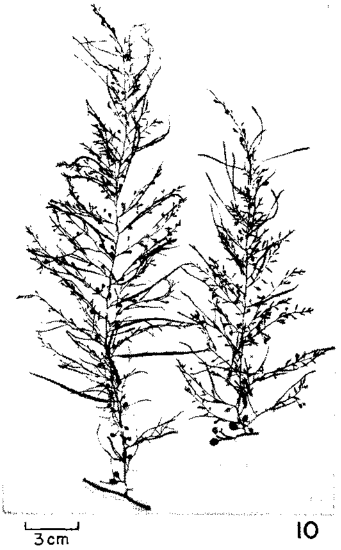

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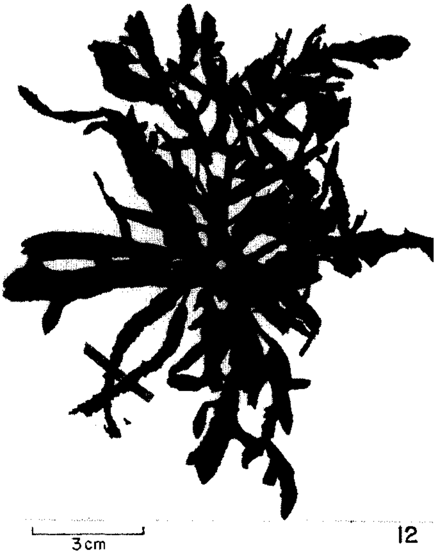

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Figs. 9 and 10. *Sargassum henslowianum* C. Agardh (Tseng 489, 639).
Figs. 11 and 12. *Sargassum agaviforme* Tseng et Lu (AST 555-1705).

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Fig. 13. ***Sargassum kuetzingii*** **Setchell (Tseng 2775).**

Figs. 14 and 15. ***Sargassum paniculatum*** **J. Agardh (AST 62-1543).**

Fig. 16. ***Sargassum leizhouense*** **Tseng et Lu (AST 87-1358a).**

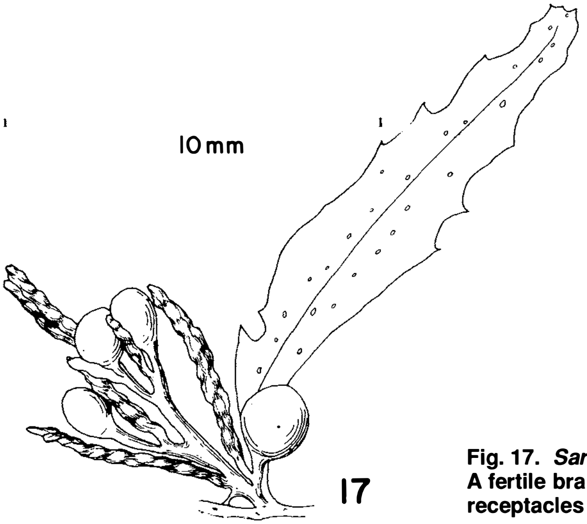

Fig. 17. ***Sargassum baccularia*** **C. Agardh. A fertile branchlet bearing male receptacles and vesicles.**

SERIES *GLANDULARIAE*

Sargassum baccularia (Mertens) C. Agardh (Figs. 1, 17)

C. A. Agardh 1824, p. 304; J. G. Agardh 1848, p. 307; 1889, p. 119, tab. 31, fig. 4; Reinbold 1913, p. 171; Grunow 1916, p. 12; Setchell 1936, p. 12, pl. 2, figs. 4–7, pl. 3, figs. 1–5.

Synonym: *Fucus baccularia* Mertens, Mém. Mus. d'Hist. Nat. 5, p. 6, 1819.

Primary branches cylindrical, smooth, to 36 cm long, 2 mm in diameter; secondary branches cylindrical, shorter, to 18 cm long, about 1 mm in diameter, smooth, arising at or near right angle of divergence, and alternate at intervals of 2–4 cm; branchlets filiform, glandular, beset with receptacles, leaves, and vesicles. Leaves on secondary branches and branchlets lanceolate, 1–2 cm long, 2–4 mm wide, dentate at the margins, obtuse or acute at the apices, and slightly oblique at bases, with midrib vanishing at their upper parts, and cryptostomata slightly elevated, scattered at both sides. Vesicles very small, obovate or spherical, densely and abundantly grouped at the bases of the receptacular branchlets, rounded or acute at the apices, 1–2 mm in diameter, with a few elevated cryptostomata, sometimes biauriculate, pedicels terete or flattened, 2–2.5 mm long.

Plants diecious. Male receptacles cylindrical, slender, smooth, 4–6 mm long, 0.4–0.5 mm in diameter, simple or two to four racemosely arranged, intermixed with vesicles on the axils of the branches. Female plants not found.

Habitat: Drifted ashore, Qionghai, Hainan, in March (AST 80-2702); Xisha Islands in November (AST 56-1616).

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

Remarks: The two aforementioned specimens (see Habitat) are undoubtedly members of *S. baccularia*. The one from Xisha Islands fits quite well the description of the var. *subcompressa* by Grunow (1916, p. 12), and the other, collected from Qionghai, Hainan, fits quite well that of the var. *lantowensis* by Grunow (1916, p. 12). Both have characteristically many small vesicles, but because only two specimens are available for this study, we have refrained from separating them into two varieties.

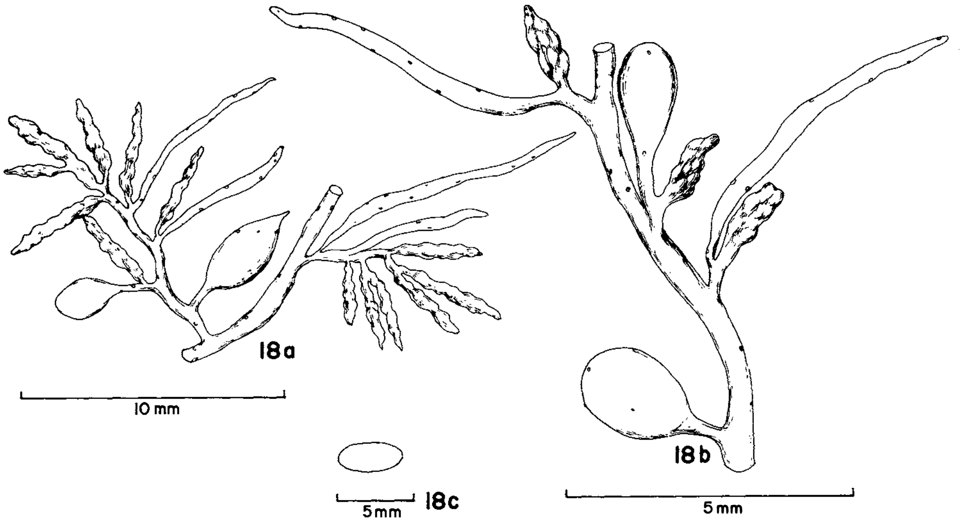

Fig. 18. *Sargassum capilliforme* Tseng et Lu. a, Fertile branchlet bearing male receptacles and vesicles. b, Fertile branchlet with female receptacles, vesicles, and leaf. c, Section of the leaf.

Sargassum capilliforme Tseng et Lu (Figs. 2, 18)
Tseng and Lu 1990b.

Frond dark brown, slender, attaining a height of 40 cm. Holdfast discoid, 3 mm in diameter, main axes very short, 3 mm in height, cylindrical, smooth, 2 mm in diameter. Primary branches smooth, cylindrical, 1 mm in diameter; secondary branches slender, glandular, cylindrical, 1 mm in diameter, arising at intervals of 1.5–2 cm, branchlets. Leaves on primary branches fleshy, linear, elliptic in section, 1.5 mm wide, 2 cm long, generally 13 times, sometimes 60 times as long as wide, entire or wavy at the margins, without midrib, with a few cryptostomata and blunt apices; leaves on the secondary branches linear, 1 mm wide, 1.5 cm long, usually 15 times as long as wide, entire at the margins, without midribs, with acute apices. Vesicles ovate to fusiform, 2 mm long, 1.5 mm in diameter, with a few cryptostoma, rounded or provided with a sharp point at the apex, pedicels cylindrical, sometimes flattened, to 3 mm long.

Plants dioecious. Male receptacles cylindrical, smooth, sometimes branched, 3–4 mm long, 0.5 mm in diameter; female receptacles conical, smooth, 1–1.5 mm long, 0.5–0.8 mm in diameter, usually simple; both male and female receptacles racemosely arranged.

Habitat: Growing on lower intertidal rocks, Naozhou Island, Guangdong, in May (AST 55-2254, 55-2258, 55-2259, 55-2262a, 55-2264, 55-2267, 62-2380, 62-2429).

Distribution: Endemic in China (Naozhou Island, Guangdon, type locality).

Remarks: *S. capilliforme* is characterized by its filiform leaves, entire at the margins, without midrib; glandular branchlets; and both male and female receptacles shortly racemosely arranged, belonging to *Racemosae* of J. G. Agardh. The species is most closely related to *S. filifolium* C. Agardh (Grunow 1915, p. 2) and *S. filliforme* Montagne (Grunow, 1916, p. 14), both belonging to *Parvifoliae* J. Agardh of section *Acanthocarpicae*. The present species has, however, nondenticulate female receptacles.

Fig. 19. ***Sargassum qinzhouense*** **Tseng et Lu. A fertile branchlet bearing male receptacles with vesicle.**

Sargassum qinzhouense sp. nov. (Figs. 3, 19)
Tseng and Lu 1990b.

Fronds yellow-brown, attaining a height of 60 cm, arising from scutate discoid holdfasts, 5 mm in diameter. Main axes terete, smooth, very short, 4 mm in height, 2 mm in diameter. Primary branches cylindrical, smooth, 1.5 mm in diameter; secondary branches 8–10 cm long, alternate at intervals of 2–2.5 cm, near right angle of divergence; branchlets glandular. Basal leaves oblong, 2.5 cm long, 8 mm wide, entire to slightly dentate at the margins, midrib percurrent; leaves on the primary branches lanceolate, 4.5 cm long, 6 mm wide, sharply dentate at the margins, midrib percurrent with prominently elevated cryptostomata, irregularly scattered on both sides, wtih acute apices and lightly oblique cuneate bases; leaves on the secondary branches similar to primary branch leaves but smaller, 2.5–3 cm long, 3–4 mm wide. Vesicles spherical or ovate, to 6 mm in diameter, generally rounded at the apices, a few with sharp points, with a few cryptostomata on the surface, and cylindrical, sometimes flattened pedicels, about 3 mm long.

Plants dioecious. Male receptacles cylindrical, smooth, to 8 mm long, 0.5 mm in diameter, usually branched, three to four receptacles racemosely arranged at the axils of the branchlets, intermingled with vesicles. The central receptacle of a branchlet appears to have retained apical growth ability and keeps on giving rise to a certain number of receptacles. Female plants not found.

Habitat: Growing on lower intertidal rocks, Qingzhou, Guangxi, in May (AST 55-1987).

Distribution: Endemic in China (Qingzhou, Guangxi, type locality).

Remarks: This species is characterized by its prominently elevated glandular branchlets and its racemosely branched, cylindrical, smooth, male receptacles, the central receptacle of the branchlet retaining apical growth, continuing to give rise to new receptacles. It is closely related to *S. siliquosum*, differing in its smaller, less oblique basal part of the leaf and continued apical growth of the central receptacle.

SERIES *SILIQUOSAE*

Sargassum siliquosum J. Agardh (Figs. 4, 20)

J. G. Agardh 1848, p. 316; 1889, p. 121, pl. 10; Reinbold 1913, p. 154; Grunow 1916, p. 173; Yamada 1942b, p. 503, fig. 9; Yoshida 1988, p. 18, fig. 17.

Fronds dark brown, attaining a height of 60 cm, with discoid holdfasts, 1 cm in diameter. Main axes terete, 3–5 mm in height, 2 mm in diameter, nearly smooth on the surface. Primary branches terete, smooth, 2 mm in diameter; secondary branches alternate at intervals of 2–3 cm, somewhat glandulate in upper branches. Leaves on primary branches elongated-elliptical lanceolate, generally 4–5 cm, but up to 12 cm long, 8–12 mm wide, wavy or shallowly irregularly dentate at the margins, apices obtuse, midribs vanishing below the apices, with an oblique asymmetrical cuneate base, irregularly scattered cryptostomata; leaves on the secondary branches lanceolate, 3–4 cm long, 3–4 mm wide. Vesicles spherical, obovoid, round, or sharply pointed at the apices, 5 mm in diameter, up to 6 mm long, cryptostomata rarely present on the surface, pedicels cylindrical or flattened, shorter than the vesicle.

Plants dioecious. Male receptacles terete, smooth, to 15 mm long, 1 mm in diameter, simple or branched, three to five racemosely arranged on the branchlets, usually with vesicles. Female plants not seen.

Habitat: Growing on lower intertidal rocks, Naozhou island, Guangdong, in April (AST 55-1589, 55-1698, 87-1033, 87-1093, 87-1095, 87-1392), Guannan, Wenchang, and Hainan in June (Tseng 441), Zhanqiao, Qingdao, in November (AST 51-1286), Xiaoqingdao, Qingdao, in August (AST 49-0002).

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

Remarks: This species is characterized by its large elliptic to lanceolate leaves on the primary branches, with strongly asymmetrical oblique bases and obtuse apices and leaves on the secondary branches, with less oblique bases and receptacle smooth, cylindrical in racemose inflorescence. We have a specimen collected from Hainan in 1933 and identified by Setchell as *S. siliquosum* var. *bicornuta* Grunow, with small leaves 1.0–1.5 cm long and 0.3 cm wide, but the vesicles are not "subalatis saepe bicornutis." It is a fragment of the tip, and similar plants of small upper leaves also are found. The Qingdao specimens are very large in the leaves and more obliquely asymmetrical than the others. At first, we put them in this species as a new variety, but after careful studies, we could find only minor difference in the size of the leaves. We finally decided that this widely distributed species is quite variable in size, and therefore we consider the small-leaf form from Hainan and the large-leaf form from Qingdao as a single species.

The glandular branches and branchlets make us hesitate to name the species as *S. siliquosum*, for which no mention has been made previously of its glandular occurrence. However, the other parts agree so well with *S. siliquosum* that we think the identification is correct.

Chou and Chiang (1981) reported this species from Nanwan and Chuanfanshih, Taiwan, with elliptical, duplicated leaves (pl. 1, fig. 7). We think, on the basis of the sketch, that it cannot be the present species, although we are quite sure that *S. siliquosum* does grow in Taiwan.

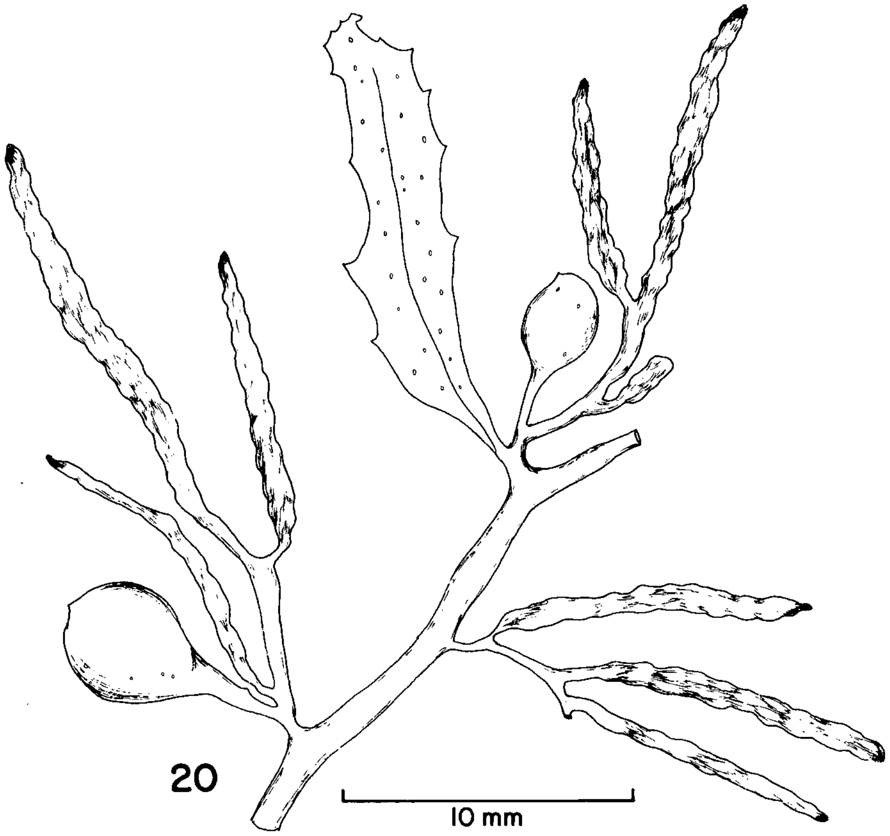

Fig. 20. *Sargassum siiliquosum* J. Agardh. A fertile branchlet bearing male receptacles with vesicles.

Sargassum shangchuanii Tseng et Lu (Figs. 5, 21)
Tseng and Lu 1990a.

Frond dark brown, attaining a height of about 40 cm. Holdfast dscoid, 1.5 cm in diameter, giving rise to terete, warty main axes, about 2 cm in height. Primary branches stout, flattened below and cylindrical upwards, 2 mm wide; secondary branches cylindrical, 20 cm long or more; branchlets very short, 2–3 cm long, arising at intervals of 2–4 cm. Basal leaves rather thick, coriaceous, very narrow, to 4 cm long, 3 mm wide, entire to shallowly toothed at the margins, midrib percurrent, and a few scattered cryptostomata; middle leaves asymmetrical lanceolate or irregular, 2–3 cm long, 4–5 mm wide, wavy or, rarely, shallowly dentate at the margins, midribs percurrent with a few cryptostomata; leaves on the branchlets linear, asymmetrical, often upper part of the leaves wider than lower parts, 2–4 cm long, 1–2 mm wide, entire at the margins, midrib near the apex, without cryptostomata. Vesicles spherical, ovate, rounded, or with sharp point at the apex, without cryptostomata, to almost 7 mm in diameter, pedicels cylindrical, 5–7 mm long, sometimes flattened, foliose, single, occasionally with double vesicles.

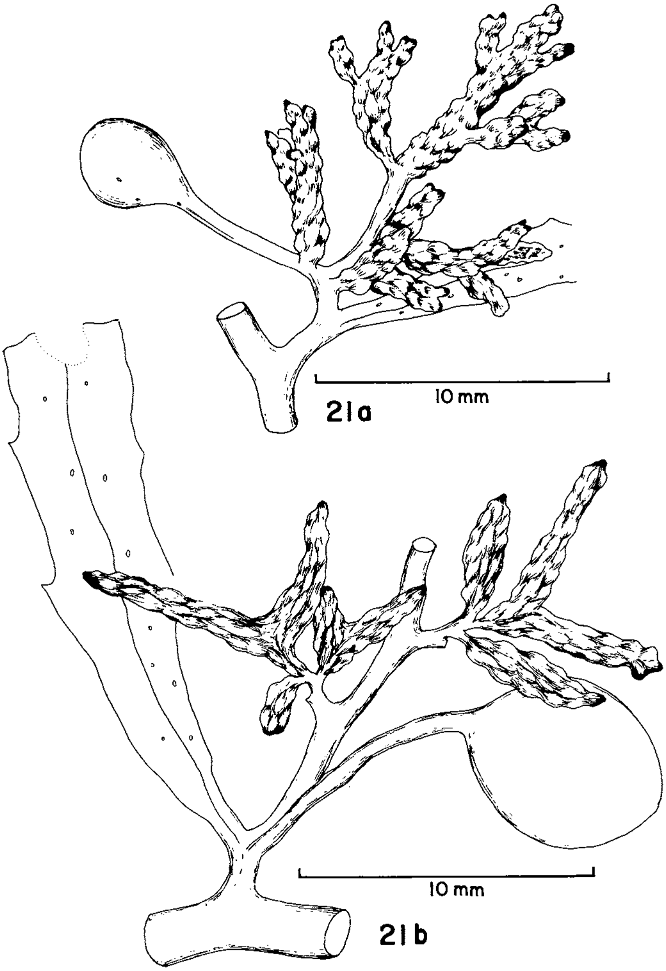

Fig. 21. ***Sargassum shangchuanii*** **Tseng et Lu. a, Fertile branchlet bearing female receptacles with vesicle. b, Fertile branchlet bearing male receptacles and vesicle.**

Plants dioecious. Male receptacles terete, smooth, simple or bifurcate, 8–10 mm long, 1–1.2 mm in diameter; female receptacles shorter, compressed, two to three times forked, usually bifurcate at the apex, 6 mm long, 1.5–2 mm wide, very complex, two to three or more male or female receptacles racemosely arranged at the fructiferous branchlets.

Habitat: Growing on the middle intertidal region and deep rock pools, Shangchuan Island, Guangdong, in December (AST 55-3641, 55-3642) and February (AST 55-1063).

Distribution: Endemic in China (Shangchuan Island, Guangdong, type locality).

Remarks: This species is characterized by its stout primary branches, flattened below and cylindrical above; very narrow leaves, generally entire at the margins; and female receptacles compressed and two to three times bifurcate.

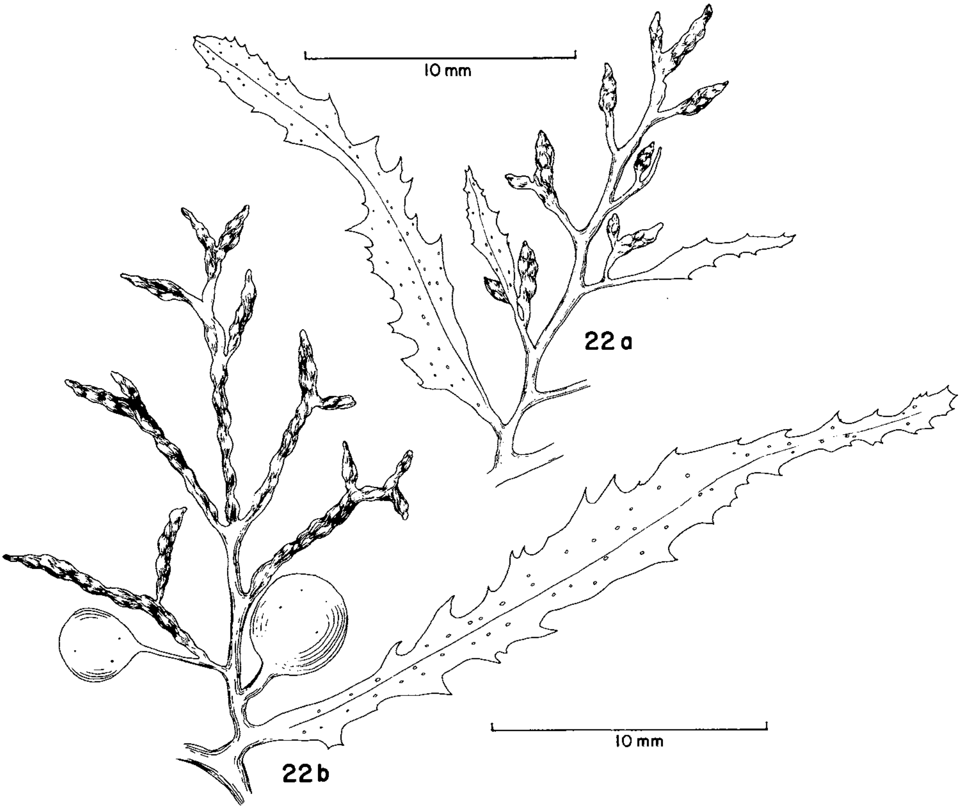

Fig. 22. *Sargassum frutescens* Tseng et Lu. a, Fertile branchlet bearing female receptacles. b, Fertile branchlet bearing male receptacles and vesicles.

Sargassum frutescens Tseng et Lu (Figs. 6, 22)

Tseng and Lu 1990a.

Fronds dark brown, frutescent, attaining a height of 26 cm. Holdfast conical, 1.5 cm in diameter, giving rise to four to eight caespitose main axes. Main axes terete, 1.5–2.5 cm in height, 2 mm in diameter, each giving rise to one to three primary branches. Primary branches cylindrical, smooth, 1–2 mm in diameter, dense, nearly equal; secondary branches alternate at intervals of 0.5–1 cm, short, 4–6 cm long, 0.5 mm in diameter, beset with fructiferous branchlets with abundant vesicles and leaves, thus giving the whole frond a characteristic bushy appearance. Basal leaves thicker, larger, some forked, elongated lanceolate, 4–5 cm long, 5–6 mm wide, entire, wavy or shallowly dentate at the margins, midribs conspicuous, percurrent, cryptostomata irregularly arranged on both sides of the midrib with blunt apices and cuneate bases. Middle and upper leaves similar to the basal leaves but thinner and smaller, 2–2.5 cm long, 4–5 mm wide, and with acute apices. Vesicles spherical or ovate, 3 mm in diameter, rounded or sharp point at apices, with a few cryptostomata on the surface, pedicels cylindrical, sometimes flattened to foliose, with midrib and dentate at margins, 4–7 mm long.

Plants dioecious. Receptacles racemosely or paniculately arranged on the fructiferous branchlets, elongated in growth, usually male receptacles arranged mainly in panicle, female receptacles arranged mainly in raceme. Male receptacles cylindrical, branched, smooth on the surface, usually forked at the upper parts, 4–5 mm long, 0.3–0.4 mm in diameter; female receptacles smooth, subcylindrical to fusiform, shorter, 2–3 mm long, 0.7–0.8 mm in diameter.

Habitat: Growing on lower intertidal rocks, Fangcheng, Guangxi, in November (AST 55-3068, 55-3069, 55-3075).

Distribution: Endemic in China (Fangcheng, Guangxi, type locality).

Remarks: This is a characteristic species, with conical holdfast giving rise to four to eight caespitose main axes, each main axis giving rise to one to three primary branches, each primary branch giving rise to numerous nearly equal secondary branches, thus giving the whole frond a characteristic bushy appearance. Its small racemosely arranged receptacles are also characteristic.

Sargassum fruticulosum Tseng et Lu (Figs. 7, 23)

Tseng and Lu 1990a.

Fronds dark brown, attaining a height of 35 cm. Holdfasts discoid, about 1 cm in diameter, with usually one to three warty cylindrical main axes, 1–1.5 cm in height, 2–3 mm in diameter. Primary branches smooth, complanate below, 2 mm wide, cylindrical above, 1 mm in diameter; secondary branches shorter, about 15 cm long, cylindrical, smooth, about 1 mm in diameter, beset with filiform glandular branchlets. Basal leaves somewhat coriaceous, lanceolate, 4–5 cm long, 5–6 mm wide, entire at the margins, with cuneate bases and acute apices, conspicuous percurrent midribs, without cryptostomata; middle and upper leaves on the primary branches smaller, with a few cryptostomata on both sides of the midrib, and dentate at the margins; leaves on the secondary branches very narrow, linear, 2.5–3.5 cm long, 2–3 mm wide, with conspicuous percurrent midribs, and a few cryptostomata; entire, rarely dentate at the margins. Vesicles spherical or ovate, 3–5 mm in diameter, rounded at the apices, generally without cryptostomata, occasionally with one to two cryptostomata, pedicels cylindrical, about 4–5 mm long.

Plants dioecious. Male and female receptacles cylindrical, usually furcate or bifurcate at their upper parts, warty at surface, without spines, racemosely arranged. Female receptacles to 4 mm long, 0.5–0.8 mm in diameter; male receptacles to 6 mm long, 0.5 mm in diameter, usually four to five or more paniculately arranged on the receptacular branchlets. Receptacles cymosely arranged when young.

Habitat: Growing on lower intertidal and subtidal rocks, Naozhou Island, Guangdong, in May (AST 55-2253, 55-2262).

Distribution: Endemic in China (Naozhou Island, Guangdong, type locality).

Remarks: This species is characterized by its frond, with complanate primary branches, glandular branchlets, and receptacles that are warty, cylindrical, and profusely paniculately arranged on the branchlets. In the plants as a whole, the present species appears to be related to the *S. acinaria* (Turner) C. Agardh group, especially in the report by Grunow of *S. acinaria* var. *crassiuscula* Grunow in the China Sea (Grunow 1915, p. 155). In the arrangement of the receptacles, however, the present species has a typical racemose to subpaniculate inflorescence and is thus a member of *Racemosae*. These are complicated by the inflorescence in its younger stage, which is cymosely arranged; this also is found in some other species. Possibly this species has been described before but presented inaccurately. For the time being, however, it seems best to give it a new name.

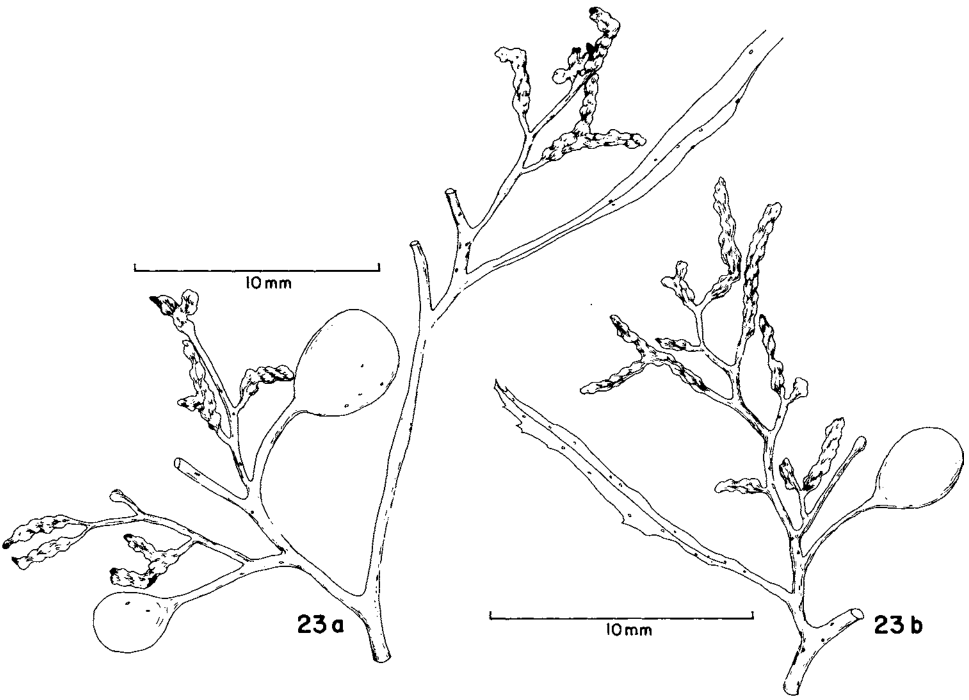

Fig. 23. *Sargassum fruticulosum* Tseng et Lu. a, Fertile branchlet bearing female receptacles with vesicles. b, Fertile branchlet bearing male receptacles with vesicles.

Sargassum guangdongii Tseng et Lu (Figs. 8, 24)

Tseng and Lu 1990a.

Fronds coarse, loosely branched, with internodes to about 10 cm long, attaining a height of about 1 m. Holdfasts discoid, 2 cm in diameter, giving rise to several caespitose terete main axes, up to 2 cm in height, 2 mm in diameter. Primary branches smooth, compressed below, terete above, 2 mm wide; secondary branches terete, usually 7–17 cm long, 1 mm in diameter. Leaves lanceolate, dentate at the margin, with oblique, cuneate bases, few cryptostomata, with percurrent midrib. Basal leaves up to 9 cm long, 15 mm wide, wavy, irregularly dentate at the margins, obtuse at apices; upper leaves narrower, 6–7 cm long, 4–6 mm wide, coarsely dentate; leaves on the secondary branches very narrow, nearly linear, up to 4 cm long, 2–3 mm wide, shallowly dentate at the margins. Vesicles spherical or ovate, rounded at apices, young ones sharply pointed, 4–7 mm in diameter, with very few cryptostomata on the surface, pedicels terete, 4–6 mm long, 0.4–0.5 mm in diameter, single, but occasionally two from the same node.

Plants dioecious. Receptacles cylindrical, smooth, usually forked at their upper parts, racemosely arranged in fructiferous branchlets. Male receptacles slender, 10 mm long, 1 mm in diameter; female ones shorter and broader, 5–7 mm long, 1.2 mm in diameter.

Habitat: Growing on subtidal rocks, Shangchuan Island, Guangdong, in February to March (AST 55-1027, 55-1191, 55-1193, 55-1202).

Distribution: Endemic in China (Shangchuan Island, Guangdong, type locality).

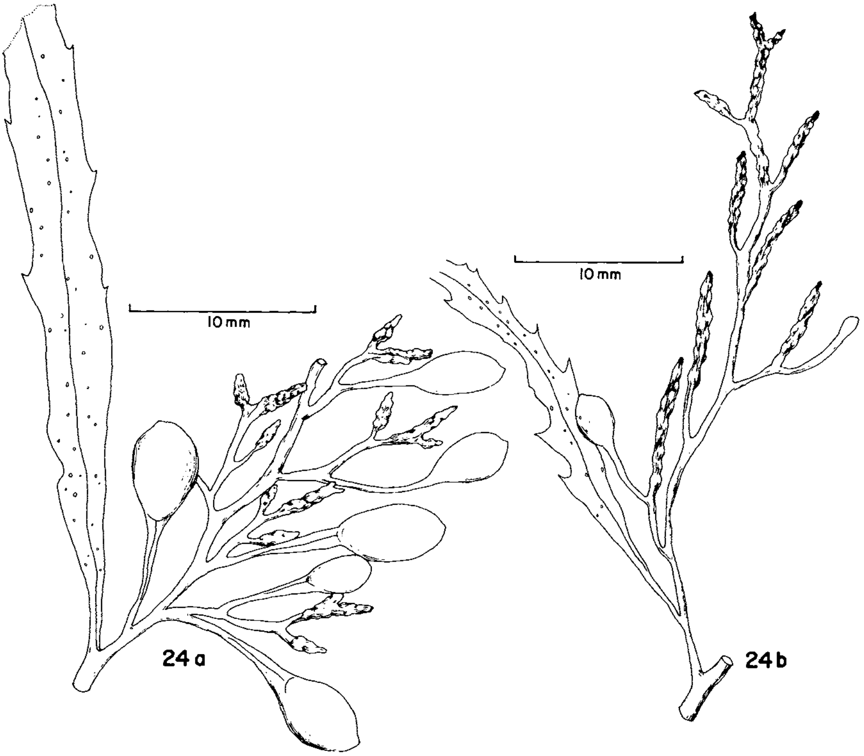

Fig. 24. *Sargassum guangdongii* Tseng et Lu. a, Fertile branchlet bearing female receptacles with vesicles. b, Fertile branchlet bearing male receptacles with vesicles.

Remarks: *Sargassum guangdongii* is closely related to *S. henslowianum* C. Agardh. It differs in its looser habit, primary branches compressed below, much larger lower leaves, shorter receptacular branchlets, and absence of young receptacles on elongated axes.

Sargassum henslowianum C. Agardh (Figs. 9, 10)

J. G. Agardh 1848, p. 315; 1889, p. 121, pl. 11; Grunow 1916, p. 176; Setchell 1936, p. 14, pls. 7–8, figs. 1–4; Pham-Hoang 1967, p. 320, fig. 29; Lu and Tseng 1983, p. 230, pl. 116, fig. 2.

Fronds dark brown, coarse, attaining a height of about 1 m; holdfasts discoid, about 1–1.5 cm in diameter, giving rise to one or two main axes. Main axes short, terete, 1–1.5 cm in height, 2–3 mm in diameter, with somewhat warty surface, giving rise to several cylindrical to subcylindrical smooth primary branches, about 1 m in height, 1–2 mm in diameter; secondary branches shorter, cylindrical, smooth, 30–40 cm high, 0.5–1 mm in diameter, beset with filiform fructiferous branchlets. Lower leaves on primary branches thicker, lanceolate, with oblique cuneate bases and acute apices, distinct percurrent midrib, to 8 cm long, 1 cm wide, with some shallow teeth at the margins, cryptostomata scattered over two sides of the midrib; upper leaves narrow-lanceolate, similar to lower leaves but narrower, 5–7 cm long, 4–5 mm wide; leaves on secondary branches narrow-lanceolate or linear, acute or blunt at their apices, with oblique cuneate bases, 5–6 cm long, 2–3 mm wide, sharply dentate at the margins. Vesicles usually spherical or subspherical, 5–7 mm in diameter, rounded at the apices, without cryptostomata, ovate sometimes, with a sharp tip when young, with slender terete stipes, about 6–10 mm long, sometimes foliaceous.

Plants dioecious. Receptacular branches elongated when still very young, with juvenile receptacles racemosely arranged and eventually becoming longer than the elongated bracteal leaves when mature. Male receptacles smooth, cylindrical, mostly simple, sometimes forked in the upper parts, attaining 1.5 cm in length and 1 mm in diameter; when mature, blunt at the apices, with a short cylindrical stipe at the base. Female receptacles fusiform, simple, sometimes forked in the upper parts, smooth, about 4–8 mm long, 1–1.5 mm in diameter, blunt at the apices, with a small stipe at the base.

Habitat: Growing on subtidal rocks, Hong Kong in January to April (Herklots 85, 113, 132, 136, 168, 180, 181; McClure 692, 85; Tseng 52, 277, 489, 639, 2182); Shantou in March (AST 54-4629, 54-4686); Shangchuan Island in February (AST 55-1026); Zhapo in December (AST 55-3461); Huiyang in February (AST 56-2374, 56-2402); and Naozhou island in April (AST 87-1026), all from Guangdong Province; Putian in May and Pingtan in June in Fujian Province.

Distribution: China (Macao, type locality; Hong Kong; widely distributed in Guangdong, Fujian, and Taiwan) and Vietnam.

Remarks: *Sargassum henslowianum* is a coarse species that varies greatly in the size of the frond. This species is characterized by (1) the elongated juvenile receptacular branchlets, which grow to about 6 cm long, in contrast to most other *Sargassum* in which the growth of receptacular branchlets occurs at a later stage, and (2) the copious leaves, much larger on the lower part and narrower on the upward part.

A description of *S. henslowianum* was first published by J. G. Agardh (1848), with the type locality placed in Macao. It is abundant in, and quite characteristic of, the Hong Kong area. In its vegetative stage, it is easily confused with *S. graminifolium* and *S. vachellianum* because of its large leaves and general habit. The branches are cylindrical and subcylindrical in *S. henslowianum*, whereas they are flattened in the two other species. It can also be differentiated from these species by the presence of very young receptacles on elongated receptacular branchlets (Fig. 10). This is a widely distributed species in the South China Sea and the southern part of the East China Sea and is also quite a variable species. The aforementioned facts and the lanceolate toothed leaves that are broader below and narrower above help characterize this species.

In our specimens, parts of the fruiting materials have extremely narrow leaves and perhaps could be identified with var. *bellonae* Grunow (1916). it seems too early to separate some of the Hong Kong specimens from each other; at least, we find it difficult to do so now. For the time being, therefore, we are treating all of our specimens as *S. henslowianum* disregarding the variety *bellonae.*

Sargassum kuetzingii Setchell (Figs. 13, 25)

Setchell 1931, p. 249, fig. 38; 1936, p. 15, pl. 8, figs. 5–6; Pham-Hoang 1967, p. 323, fig. 31; Tseng and Lu 1978, p. 8, pl. 5, fig. 7; Lu and Tseng 1983, p. 233, pl. 117, fig. 2; Chou and Chiang 1981, p. 147, pl. 3, fig. 5.

Synonym: *Stichophora debilis* Kuetzing 1849, p. 26, pl. 71b, *non Sargassum debile* Grev. Ann. Mag. Nat. Hist. Ser. 2, 2: 276, 1849.

Fronds slender, yellowish-brown, soft, attaining a height of 50 cm; holdfast discoid, up

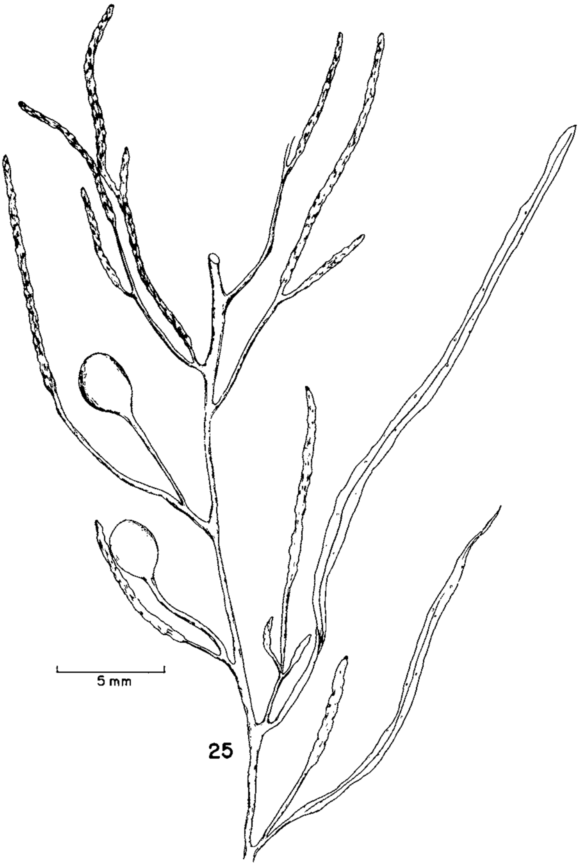

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Fig. 25. ***Sargassum kuetzingii*** **Setchell. A fertile branchlet bearing male receptacles with vesicles.**

to 10–12 mm in diameter. Main axes slender, cylindrical up to 10 mm in height, 2 mm in diameter, giving rise to primary branches, cylindrical and slender, 40–50 cm long, 0.4–0.8 mm in diameter; secondary branches to 20 cm long and about 0.4 mm in diameter, branchlets to 10 cm below and decreasing to about 2 cm above. Basal and lower leaves elongated-lanceolate, up to 5 cm long, 4–5 mm wide, dentate at the margins, with acute apices, conspicuous, percurrent midrib, with one row of cryptostomata on both sides of the midrib, cuneate base with short cylindrical stipe, 2 mm long; middle and upper leaves similar to basal leaves but slenderer, 4–5 cm long, 2–3 mm wide; leaves on the branchlets very slender, linear-lanceolate, 2.5–3 cm long, 0.4–1 mm wide, entire or very slightly dentate at the margin, with conspicuous midribs, acute apices, cuneate bases, and filiform stipes. Vesicles subspherical, oval, 2–3 mm in diameter, with rounded apices, a few cryptostomata, and cylindrical or foliose stipes, generally about twice their diameters but sometimes reaching a length of about 3 cm, more than 10 times its diameter, which makes the species easily recognizable.

Plants dioecious. Receptacles racemose, smooth and cylindrical, blunt at the apices, simple when young and racemose when old, each with a filiform stipe 6–10 mm long. Male receptacles characteristically very slender, up to 14 mm long, 0.2–0.5 mm in diameter; female receptacles shorter but broader, 4–6 mm long, 0.9–1 mm in diameter.

Habitat: Growing on lower tidal rocks and drifted ashore, Qingzhou Bay, Guangxi, in May (AST 55-2057), Hong Kong in May (Tseng 2775, McClure 71d), Xisha Islands in May (AST 75-1299, 75-1304a, 75-1305e).

Distribution: China (Macao, type locality; Hong Kong; Qinzhou Bay; and Xisha Islands) and Vietnam.

Remarks: This is a little-known species. The original description was of a specimen from Macao in the South China Sea identified as *Stichophora debilis* Kützing, characterized by its very delicate fronds with cylindrical smooth receptacles arranged on elongated racemes. Grunow made it a synonym of the better known *S. henslowianum.* Setchell was right in separating the two species, placing the Macao plant in the genus *Sargassum* and renaming it *S. kuetzingii,* because the name *S. debilis* had already been used by Greville for another totally different plant. This species is characterized by its extremely delicate yellowish-brown fronds with elongated vesicular stipes (sometimes to 10 times their diameter) and its very delicate (as slender as 0.2 mm) racemosely branched male receptacles when mature.

Sargassum agaviforme Tseng et Lu (Figs. 11, 12, 26)

Tseng and Lu 1990a.

Fronds arising from a central base, crowded, coarse (*Agave*-like), dark brown, medium size, to about 35 cm in height. Two to several main axes arising from a small discoid holdfast, about 5 mm in diameter. Main axes cylindrical, warty, 12 mm in height, 2 mm in diameter. Primary branches smooth, subcylindrical, to about 35 cm high, 1–1.5 mm in diameter below, cylindrical upward, less than 1 mm in diameter; secondary branches smooth, arising at intervals of 1–2 cm, shorter to about 10 cm long, beset with similar branchlets. Basal leaves pinnatifid or forked to about 6 cm long, 6 mm wide, with toothed margins and cuneate bases, blunt at apices, midribs conspicuous, generally percurrent, with cryptostomata irregularly scattered on both sides of the midrib. Leaves on the primary branches lanceolate or linear, simple or forked, 3–5 cm long, 1.5–2.5 mm wide with sharply toothed margins and cuneate bases, percurrent midribs, and irregularly scattered cryptostomata. Leaves on the secondary branches and branchlets linear or filiform, 2–3 cm long, 1–2 mm wide, midribs delicate, sharply toothed in margins. Vesicles spherical, to 2.5 mm in diameter, rounded at apices, with a long pedicel about 4–5 mm long.

Plants dioecious. Inflorescence characteristically repeatedly racemose and very well developed. Male receptacles slender, cylindrical, smooth, usually branched one or two times on the upper parts of the receptacles, sometimes forked at the apices, 4–5 mm long, 0.4–0.5 mm in diameter, each with a short pedicel. Female receptacles cylindrical or conical, smooth, branched one or two times, 3–5 mm long, 0.6–0.7 mm in diameter, usually forked at the apices. Both female and male receptacles racemosely or often paniculately arranged on receptacular branchlets.

Habitat: Growing on lower intertidal and subtidal rocks, Naozhou Island, Guangdong, in April (AST 55-1653, 55-1705, 55-1706, 55-1709); Qinzhou and Fangcheng, Guangxi, in May (AST 55-2037, 55-2038, 55-2114, 55-2115, 55-2116, 55-2148, 55-2153, 55-2180).

Distribution: Endemic to China (Naozhou Island, Guangdong, type locality; Qinzhou

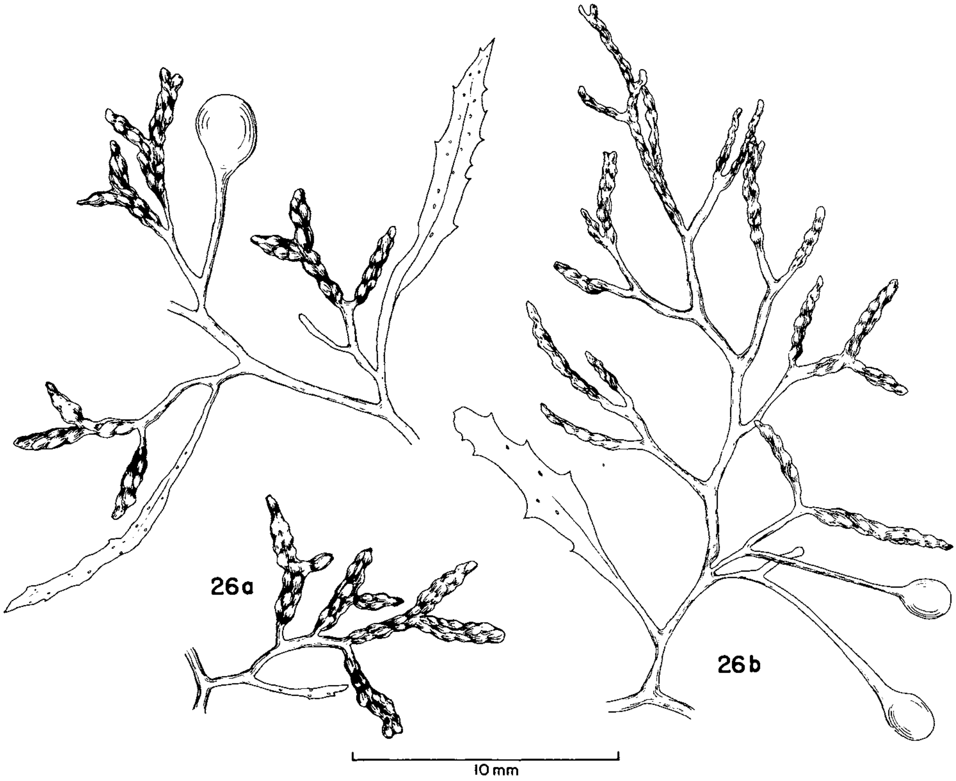

Fig. 26. ***Sargassum agaviforme*** **Tseng et Lu. a, Fertile branchlet bearing female receptacles with vesicles. b, Fertile branchlets bearing male receptacles with vesicles (upper left, right).**

and Fangcheng, Guangxi).

Remarks: The primary branches arising from the basal axes and full of receptacular branchlets look just like the land plant *Agave* with its flowering branches; hence the name "agaviforme." The young basal leaves are commonly pinnatifid or forked. The vesicle has a slender, long stalk similar to that of *S. kuetzingii*, but never as long. These three characteristics make it easy to differentiate this species from other closely related species such as *S. kuetzingii.*

Sargassum paniculatum J. Agardh (Figs. 14, 15, 27)

J. G. Agardh 1848, p. 315; 1889, p. 122, pl. 12, figs. 1–3; Kützing 1849, p. 619; Reinbold 1913, p. 163; Grunow 1916, p. 177.

Holdfast and axis not available. Primary branches glaucescent, cylindrical, smooth, about 50 cm in height, 1.5 mm in diameter; secondary branches arising from the axils of the primary leaves, alternate at intervals of 3–5 cm, cylindrical and smooth, about 20 cm in height, 1 mm in diameter; branchlets short, beset with vesicles and receptacles. Leaves lanceolate, with oblique cuneate bases and acute apices, midribs conspicuous, percurrent,

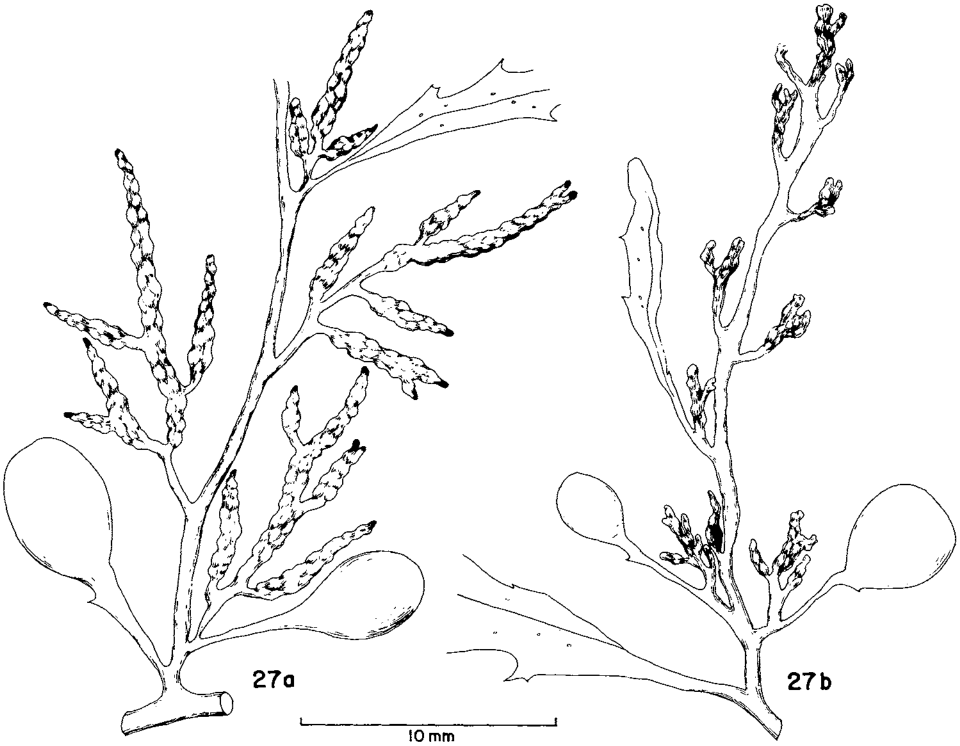

Fig. 27. ***Sargassum paniculatum*** **J. Agardh. a, Fertile branchlet bearing female receptacles with vesicles. b, Fertile branchlet bearing male receptacles.**

cryptostomata irregularly scattered on both sides, sharply or shallowly dentate at the margins; primary leaves longer and broader, up to 11 cm long, 1 cm wide; secondary leaves shorter and narrower, up to 6 cm long, 4 mm wide. Vesicles spherical or obovate with a few cryptostomata, up to 8 mm in diameter, rounded at apices, young ones with sharp points at apices, pedicels terete or foliaceous, up to 18 mm long, 2 mm wide.

Plants dioecious. Male receptacles terete, usually branched on the upper parts, up to 20 mm long, 2 mm in diameter. Female receptacles conical, up to 11 mm long, 1 mm in diameter. Both usually forked at the apices, paniculately arranged in lower parts of the branchlets, but usually racemosely arranged in younger upper parts.

Habitat: Growing on subtidal rocks, Huilai in March (AST 89-0002), Naozhou Island in July (AST 62-1543), both from Guangdong.

Distribution: Indian Ocean and China.

Remarks: This species resembles *S. henslowianum* very much but differs in its more compact growth with subpaniculate and paniculate receptacular branchlets. Our plants are still quite young, and the receptacles are mostly subpaniculately arranged. The species is newly reported from China.

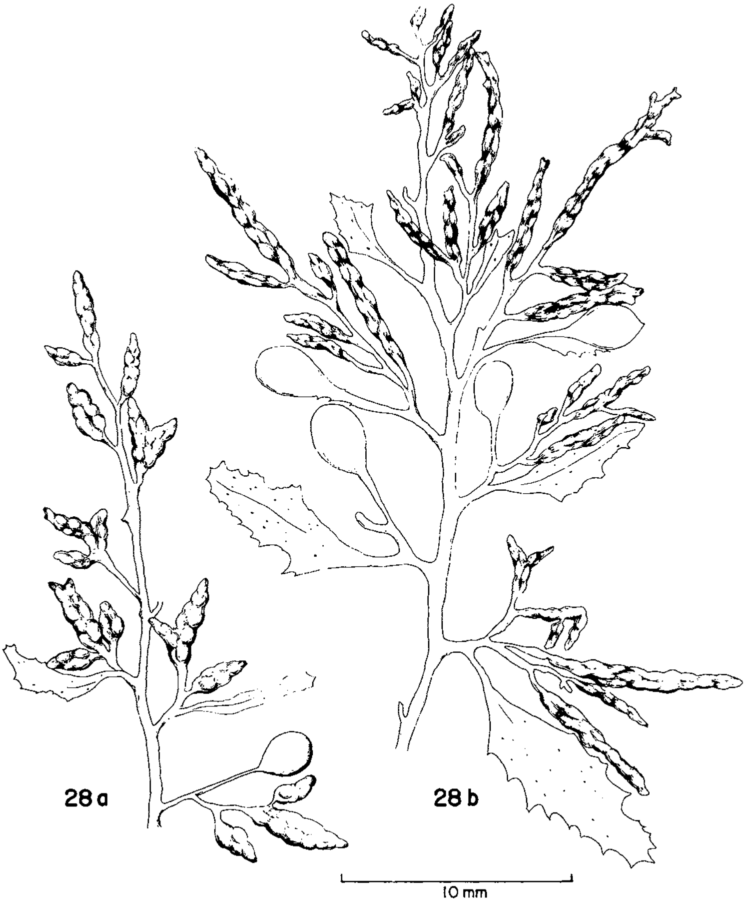

Fig. 28. *Sargassum leizhouense* Tseng et Lu. a, Fertile branchlet bearing female receptacles with vesicles. b, Fertile branchlet bearing male receptacles with vesicles.

Sargassum leizhouense Tseng et Lu (Figs. 16, 28)
Tseng and Lu 1990a.

Fronds dark brown, coarse, attaining a height of 50 cm. Holdfasts discoid, subconical, 1–1.5 cm in diameter, sometimes two or three main axes arising from a holdfast. Main axes warty, terete, up to 2 cm in height, 1–2 mm in diameter. Primary branches and some budlike structures often arising from the upper part of the axes; budlike structures short, about 1 cm in height, 3–5 mm in diameter; primary branches smooth, subcylindrical, compressed below, cylindrical above, 1.5–2 mm in diameter; secondary branches shorter, 5–10 cm in height, similar to primary branches in habit, alternate at intervals of 2–4 cm, giving rise to branchlets beset with leaves and receptacles. Leaves with percurrent midribs, scattered cryptostomata, dentate margins, obtuse at tips, and cuneate at bases. Basal leaves thick, large, usually dissected, lanceolate, 5–7 cm long, 9–10 mm wide. Upper leaves lanceolate, nearly equal in length, 4–5 cm long, 4–5 mm wide, usually undissected. Vesicles spherical, smooth, rounded at the apex, 3–4 mm in diameter, cryptostomata rare on the surface, pedicels cylindrical, 2–3 mm long, usually shorter than vesicles.

Plants dioecious. Receptacles cylindrical, smooth, subpaniculately arranged on fructiferous branchlets. Male receptacles elongated, sometimes branched, usually forked at apices, 7–15 mm long, 0.7–0.8 mm in diameter. Female receptacles branched, 4–5 mm long, 0.8–1 mm in diameter, often forked at the apex, occasionally forked three to four times.

Habitat: Growing on the lower intertidal and subtidal rocks, Naozhou Island, Guangdong, in April to May (AST 87-1030, 87-1068, 87-1358a, 87-1364, 87-1387, 87-1388, 73-0538, 86-1244, 86-1256).

Distribution: Endemic in China (Naozhou Island, Guangdong, type locality).

Remarks: This species is characterized by the following: (1) It has large, basal dissected leaves; the upper leaves are usually equal in length. (2) The receptacles are subpaniculately arranged; the male ones are elongated and warty. (3) Budlike structures arise from the upper parts of the main axes. It is closely related to *S. paniculatum* but differs in its dissected lower leaves, its copiously branched frond, and its compressed lower parts of the primary branches.

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DISTRIBUTION AND VARIATION IN *SARGASSUM POLYCYSTUM* C. A. AGARDH (FUCALES, PHAEOPHYTA)

Young-Meng Chiang, Tadao Yoshida, Tetsuro Ajisaka,
Gavino Trono, Jr., Tseng C. K., and Lu Baoren

Abstract

Sargassum (subgenus *Sargassum*) *polycystum* C. A. Agardh appears to be a common species in the western Pacific and the eastern Indian Ocean, occurring approximately between 23° N and 23° S and between 80° E and 180° E (except for Okinawa, which is near 26° N). A number of features appear to be characteristic of the species, and we have verified them by examination of many specimens from a wide geographical range. These are the possession of branched stolons in the mature plant; highly elevated protuberances on the surfaces of stems and branches, formed by the elevation of cryptostomata; and the presence of large numbers of small vesicles in the mature plants. In the process of studying specimens, we recognized new records from Fiji, Tonga, and New Caledonia in the central south Pacific.

It was possible to compare tank- vs ocean-grown plants in which the following differences were noted. Cryptostomata and superficial protuberances were more numerous and more dense and prominent on tank-grown plants than on ocean-grown plants. Stolons were smooth or with few protuberances on ocean-growing plants and were more densely covered with protuberances on tank-grown material. Although characteristic of adult plants, stolons were not present when the plants were young.

Introduction

Plants of *Sargassum* subgenus *Sargassum* are among the most dominant and abundant marine algae in shallow waters of the subtropics and tropics. Their widespread distribution and high degree of morphological variation make the specific determination of the subgenus difficult (Soe-Htun and Yoshida 1986; Kilar and Hanisak 1988, 1989). Soe-Htun and Yoshida (1986) found a certain regularity in morphological changes of branches, leaves, and vesicles according to ages, developmental stages, and habitats of the plants of *Sargassum*. Yoshida (1988a, 1988b) emphasized that an understanding of the changes in and the variability of conceptacles, cauline leaves, and other morphology during development is needed and that this should be combined with ecologically and phenologically induced features in order to identify species. Such data are recorded for only a few species (Terawaki et al. 1982, 1983a, 1983b, 1983c, 1984; Soe-Htun and Yoshida 1986; Kilar and Hanisak 1988, 1989).

During this study, we were able to examine a large number of herbarium specimens of many species of this subgenus collected from various parts of the Indo-Pacific regions. Among these specimens, those with stolons as well as protuberances that arise from the surface of the stem and branch were designated as *S. polycystum* irrespective of other features. The range of the morphological variations of these features needs to be established. We analyze a few of these variations in this paper.

The description is based mainly on specimens collected from Taiwan, but specimens from Okinawa, Xisha Islands (China), Vietnam, Philippines, Fiji, Guam, New Caledonia, Tonga, Saipan, Java, Heron Island (Australia), and India (Table 1) were also used. Descriptions given by Chou and Chiang (1981), Yoshida (1988a, 1988b), Tseng and Lu (1988), and Tsuda (1988) for *S. polycystum* were carefully studied and compared.

Materials and Methods

The materials were collected from various regions (Table 1) and brought to La Jolla, California, during the workshop. Liquid-preserved specimens of whole plants collected from southern Taiwan were used for drawings. Plants collected at Nanwan, Ping-tong Hsien, in southern Taiwan and transplanted to Fulung, Taipei Hsien, in northern Taiwan were also used for observations and comparisons. The transplanted plants were grown in a concrete tank (4 m x 2 m x 1.5 m) with continuously running natural seawater from 30 September 1989 through 5 January 1990.

Description of the Species

Sargassum polycystum C. A. Agardh (Figs. 1–4)

C. A. Agardh 1824, p. 304.

Synonym: *S. microphyllum non* C. Agardh (C. A. Agardh, 1824, p. 306; Yendo 1907, p. 137; Okamura 1931, p. 108; Yamada 1925, p. 247).

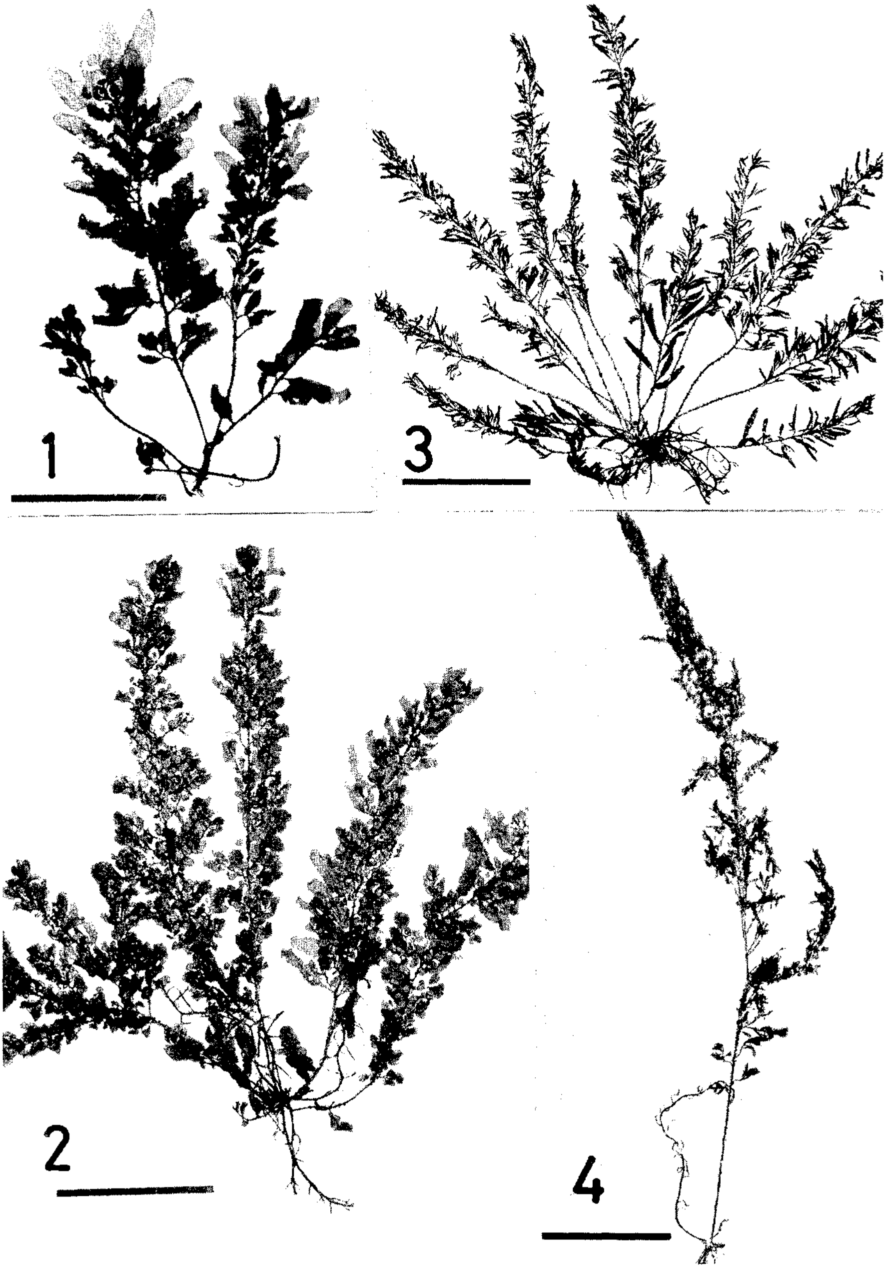
Application of This Name: Yamada 1942, p. 376, figs. 5, 6; 1950, p. 193; Tseng et al. 1962, p. 92, pl. 5, fig. 36; Tseng and Lu 1978, p. 6, pl. 4, fig. 6; Pham-Hoang 1967, p. 306, fig. 21; Chou and Chiang 1981, p. 134, pl. 2, figs. 1, 2; Lu and Tseng 1983, p. 236, pl. 119, fig. 1; Tseng and Lu 1988, p. 47, figs. 13, 26, 27; Tsuda 1988, p. 62, fig. 4; Yoshida 1988b, p. 17, fig. 14.

Thallus yellowish brown, up to 2 m long; attached to substratum with a discoid holdfast (Fig. 5) or rhizoidal system that gives rise to a main axis. Main axes (Fig. 5) cylindrical or terete, 4–11 mm in height, 1.5–2 mm in diameter, giving rise to cauline leaves, primary branches as well as branched stolons. Cauline leaves (Fig. 6) oblanceolate, lanceolate, vertically or horizontally oriented, 10–25 mm long, 3–5 mm wide, with many cryptostomata randomly distributed on both sides of the midrib, dentate or undulate at the margins; midrib usually extending up to the apex of leaves, which are obtuse or somewhat acute at the tips, sessile or with short petiole, 1.5–2 mm long. After a cauline leaf is shed, a prominent circular scar is left on the axis (Fig. 5). Stolons (Fig. 7) cylindrical or terete, 1–2 mm in diameter, surface smooth or with pointed spines, and short branches issued alternately or pinnately; apex with buds formed distichously (Fig. 7); terminal part of some branches forming secondary attachment discs (Fig. 7). Both primary and secondary branches and branchlets show many to a few cryptostomata, which are elevated to form protuberances, 1–2 mm in height, Y- or trumpet-shaped (Fig. 8). Leaves (Fig. 9) on primary and secondary branches and on branchlets sessile or with short petiole, usually ovate, oblong elliptic or sometimes oblanceolate, lanceolate, 1.5–6 cm long, 8–12 mm wide, decreasing in size to about 1 cm long and 4 mm wide on more mature terminal branchlets. Margin usually dentate, serrate, slightly or deeply incised, wavy or nearly entire. Midrib usually present, but absent in leaves of secondary branches and branchlets, slightly or not raised above leaf surface, usually vanishing below the apices or middle part of leaves, which are rounded or pointed at the tips. Cryptostomata prominent, slightly raised above leaf surface, distributed in one to four regular or irregular rows on each side of midrib, with circular to narrowly elliptic opening, 0.3–0.6 mm in diameter, with long hairs issuing from the opening. Vesicles (Fig. 10) small, spherical to ovate, 1.5–2 mm in diameter, usually crowned with one to a few leaflets or a sharp tip, with cryptostomata randomly scattered on the surface of the vesicles and more or less raised from it. Stalks of the vesicle terete, shorter than the vesicle or almost the same length, with or without cryptostomata. In some cases, terminal portion of mature thalli

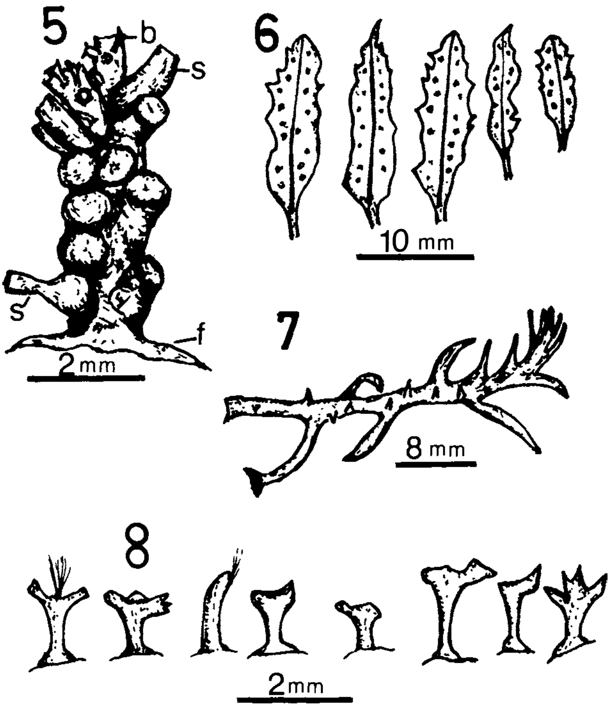
Table 1. Herbarium Specimens of *Sargassum polycystum* Examined

Locality	Date of Collection	Source
Ikei Island, Okinawa	June 27, 1982	Ajisaka Herbarium
Miyako Island, Okinawa	April 10, 19--	Ajisaka Herbarium
Xisha Island, China	Jan. 23, 1976	Tseng Herbarium
Nha Trang, Vietnam	Jan. 30, 1953	
Palawan Island, Philippines	May 22, 1978	Trono Herbarium
Fiji	Oct. 11, 1985	Ajisaka Herbarium
Agana Bay, Guam	March 20, 1945	Ajisaka Herbarium
New Caledonia	Dec. 20, 1987	
Tonga	Dec. 16, 1987	
Saipan	---	
Pulau Ketor, Java	April 27, 1954	
Mhanchye, Burma	Jan. 28, 1982	
Heron Island, Australia	Aug. 1988	
Vishakapatna, India	Dec. 19, 1979	
Siaoliuchiu, Taiwan		Chiang Herbarium
Chiang 73064	April 3, 1973	
Maopito, Taiwan		Chiang Herbarium
Chiang 76901	Nov. 19, 1972	
Chiang 73116	April 3, 1973	
Chiang 78056	March 12, 1978	
Haikou, Taiwan		Chiang Herbarium
Chiang 76901	Sept. 12, 1976	
Nanwan, Taiwan		Chiang Herbarium
Chiang 76301	Feb. 19, 1976	
Chiang 890429	April 29, 1989	
Chialoshui, Taiwan		Chiang Herbarium
Chiang 770109	Jan. 19, 1977	
Lanyu, Taiwan		Chiang Herbarium
Chiang 77102	Oct. 2, 1977	
Tungsha, Taiwan		Chiang Herbarium
Chiang 75060	March 29, 1975	
Chuanfanshi, Taiwan		Chiang Herbarium
Chiang 84006	Dec. 18, 1984	

consists of leafless secondary branches bearing numerous receptacles and minute spherical vesicles (Fig. 4).



Figs. 1–4. ***Sargassum polycystum*** **C. A. Agardh. Scale bars = 5 cm. Fig. 1, Young plant, Chiang 77102. Fig. 2, Chiang 840046. Fig. 3, Chiang 770109. Fig. 4, Mature plant, Chiang 890429.**



Figs. 5–8. *Sargassum polycystum* C. A. Agardh. Fig. 5, Basal portion showing discoid holdfast (f), stolons (s), and branches (b) growing from axis. Fig. 6, Cauline leaves showing morphological variations. Fig. 7, Terminal part of a stolon, showing distichus bud, branches, and attachment disc at the tip of a branch. Fig. 8, Protuberances showing morphological variations.

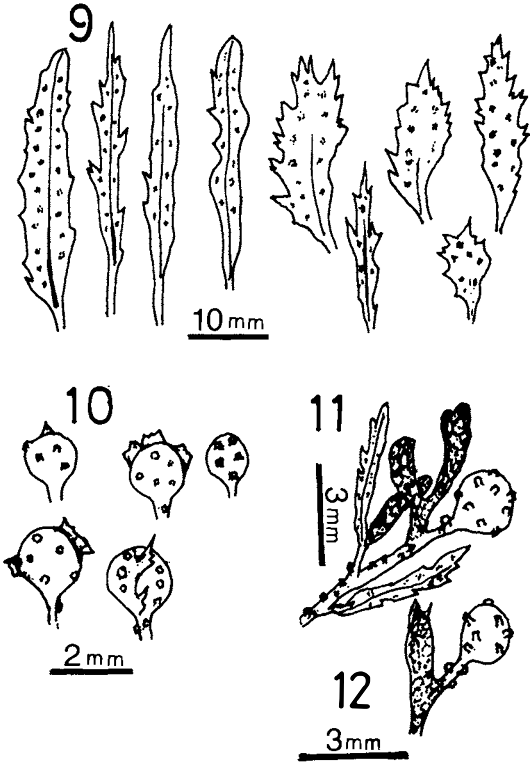
Plants dioecious. Male receptacle (Fig. 11) smooth, cylindrical or terete, up to 1 cm long, less than 1 mm in diameter, branching from an ultimate branchlet, paniculate or racemose. Female receptacle (Fig. 12) compressed, often forked, with tooth at apex, up to 3 mm long, 0.2–1 mm wide, with spines along the margin, sometimes bearing small leaflets or vesicles, solitary or arranged in racemes. Receptacles carpophyllous (of mixed branchlets; see Tseng and Lu 1988, p. 25).

Habitat: Common in midintertidal to shallow subtidal rocks and in supratidal pools that have coral-fragment bottoms. In Taiwan, it appears year-round but is most abundant in February to May; in Guam, perennial (Tsuda 1988); in Hainan and Xisha Islands (Tseng and Lu 1988), from February to June and January to June, respectively.

Distribution: Sunda Island, Indonesia (type locality); Okinawa; Taiwan; Hainan Island and Xisha Islands, China; Philippines; Vietnam; Fiji; Guam; Saipan; Tonga; Heron Island, Australia; Burma; New Caledonia; Sri Lanka; and India.

Discussion

From examination of specimens and the data available, we found that the range of distribution of *S. polycystum* is in the warm-water regions of the mid and western Pacific



Figs. 9–12. *Sargassum polycystum* C. A. Agardh. Fig. 9, Leaves of primary and secondary branches and branchlets. Fig. 10, Vesicles. Fig. 11, Male receptacle with leaf and vesicle. Fig. 12, Female receptacle with vesicle.

and the eastern Indian Ocean; that is, approximately between 23° N to 23° S, 80° to 180° E, with the exception of Okinawa, which is located farther north than 23° N. Many tropical species of seaweeds can be found in Okinawa because of the warm-water current (Kuroshio) that passes through the area (Taniguti 1987).

In many species, such as *S. crispifolium* (Terawaki et al. 1983c) and *S. cristaefolium* (Soe-Htun and Yoshida 1986), the morphology and size of cauline leaves are quite different from those of primary branches, but in *S. polycystum*, both kinds of leaves are quite similar morphologically and in size. Primary branches and stolons are produced from almost the same place on the main stem, but stolons are issued at a later stage of development of the thallus, and therefore, in some young plants, no stolons are formed. Primary branches produce many cryptostomata, which are raised to form Y-shaped or trumpet-like protuberances (Fig. 8). [Ed. note: In *Sargassum* literature, these elevations are referred to as muricate (=hard excrescences), verrucose (=warty), and, occasionally, as spines, although lacking a sharp point.] The number of cryptostomata and the height of the protuberances depend on habitat conditions. In some thalli, some branches have many cryptostomata, whereas other branches have fewer. We also found that the branches of the transplanted plants that were grown floating in the tank produced cryptostomata distributed densely on the branch and raised higher than those found on plants growing in natural habitats. The surface of the stolons is smooth, or with a few pointed protuberances, but stolons of the transplanted thalli, like primary branches, are covered densely with many Y-shaped protuberances of cryptostomatal origin. As in many other species of *Sargassum*, the morphology and size of the leaves are quite variable (Fig. 9). Those growing on mature plants or on the upper part of the thallus are smaller than those found on immature plants or on the lower part of the thallus. In some species, such as *S. echinocarpum* J. Agardh (Magruder 1988, fig. 12), the size and morphology of vesicles are quite variable, but in *S. polycystum*, vesicles are usually circular and 1.5 to 2 mm in diameter no matter where they grow or on which part of the plant. However, vesicles of transplanted thalli have more cryptostomata and crowned leaflets than vesicles of thalli on plants growing in natural conditions do. The carpophyllous nature of the female receptacles of this plant is noted (Tseng and Lu 1988). In conclusion, *S. polycystum* can be identified easily on the basis of its prominent Y-shaped or trumpet-like protuberances on the surface of stems and branches and the presence of branched stolons from the main stem. The combination of these two features is unique among the *Sargassum*. In addition, the presence of numerous small vesicles on mature plants makes this species a distinct taxon. Among the species of *Sargassum, S. herporhizum* Setchell and Gardner, which was reported from the Gulf of California (Setchell and Gardner 1924), is also characterized by the presence of branched stolons. However, it has no protuberances on the surface of stems and branches. As mentioned before, the number of protuberances could be influenced by habitat. If so, *S. herporhizum* should be studied further.

Acknowledgments

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THE GENUS *SARGASSUM* IN THE PHILIPPINES

Gavino C. Trono, Jr.

Abstract

Although the Philippines reportedly have one of the largest assemblages of *Sargassum* species in the Pacific, 70 recorded taxa, the species are poorly known, and a great deal of work will have to be done to sort out the older records from the new. Moreover, the range of morphological variation will have to be understood before any permanent progress can be made in the taxonomy of the genus for this geographical region.

Twenty-eight taxa are recognized in this paper, although 13 of them were not assigned specific names. Some of the latter may be new species, but, more importantly, some may be taxa that have been described previously but because of insufficient material or poor descriptions cannot be readily matched with the newer material.

Five species have been added to the recently compiled catalog of Philippine algae. They are *S. crassifolium* J. Agardh, *S. feldmannii* Pham-Hoang, *S. gracillimum* Reinbold, *S. kushimotense* Yendo, and *S. turbinarioides* Grunow. Of these, *S. crassifolium* is the most widely distributed and recognized throughout the warm western Pacific. Range extensions are made for the remaining taxa, which are not as well known.

Introduction

Sargassum is the most common genus richly represented in the marine macrobenthic algal flora of the Philippines, but it is the least studied. More than 70 species have been listed in the most recent catalog of benthic marine algae in the country (Silva et al. 1987), but the certainty of most of these records is questionable. The difficulty in the correct identification of the various taxa stems mainly from the polymorphic nature of the species. The morphological variability has been shown to be closely associated with the different growth stages of the species (Ang and Trono 1987). Most of the early reports are merely listings or may include only brief and incomplete information. Moreover, most of these reports have been based on dried fragmented and incomplete materials, which could have represented parts of the same species. The taxonomic report on the genus *Sargassum* from Calatagan, Batangas (Ang and Trono 1987), although geographically limited in scope, is the first comprehensive paper on the genus incorporating information on the changes in morphology of the different growth stages.

Thus, little usable information on the taxonomy of the genus is available to date. This paper is my first attempt to do detailed taxonomic studies on the genus by using materials collected from all parts of the Philippines. Except for one species in which the morphology of the vegetative materials is quite distinctive, only the reproductive or fertile materials were used for morphological studies. Characters used in discriminating one taxon from the other are the type of holdfast; the nature and shape of the cross section of the stem and branches; the morphology of the leaves on the different branch orders; the nature, form, and distribution of the cryptostomata; the sexuality of the plants; the structure and shape of the vesicles; and the nature and form of the receptacles.

A total of 28 taxa are reported in this paper, 13 of which were not assigned specific epithets. These taxa appear to be undescribed entities and are included here as *Sargassum* species for the present to make this report more complete.

Many more materials in the G. T. Velasquez Phycological Herbarium at the Marine Science Institute, College of Science, University of the Philippines at Quezon City, remain to be studied.

Key to Philippine Species of *Sargassum*

1. Thallus with ramifying rhizoidal holdfast 2
1. Thallus without ramifying rhizoidal holdfast 4

  2. Branches muricate (lumpy) with many simple or branched protuberances (elevated cryptostomata) . . . . *S. polycystum*
  2. Branches smooth without protuberances 3

3. Leaves of secondary and terminal branches linear-lanceolate to oblanceolate with slightly asymmetrical acute base . . . . *Sargassum* sp. No. 3
3. Leaves of secondary and terminal branches obovate to oblanceolate with distinctly asymmetrical base . . . . *S. hemiphyllum*

  4. Leaves of primary and secondary branches, especially of fertile thalli, broad, ovate, oblong, elliptical, obovate 5
  4. Leaves of primary and secondary branches, especially of fertile thalli, narrow, linear to linear-lanceolate 16

5. Leaves with "duplicated" margins or margins and portion of blade 6
5. Leaves without duplicated margins or portion of blade 9

  6. Leaves vertically attached with duplicated or doubled margins . . . . *S. crassifolium*
  6. Leaves horizontally attached with duplicated margins or duplicated margin and portion of blade 7

7. Leaves small, up to 1 cm long, obovate, turbinaroid; vesicles elliptical . . . . *S. turbinarioides*
7. Leaves large, up to 2.5 cm long, broadly oblong-oblanceolate 8

  8. Vesicles mainly as phyllocysts (leafy vesicles), oblong-elliptical . . . . *S. feldmannii*
  8. Vesicles not in form of leafy vesicles, spherical . . . . *S. cristaefolium*

9. Holdfast scutate 10
9. Holdfast discoid-lobed 13

  10. Leaves oblong, large, more than 15 mm wide, thin membranous; vesicles large (>4 mm in diameter) with short, flattened stalk . . . . *Sargassum* sp. No. 12
  10. Leaves variable in shape, small, less than 10 mm wide, thick; vesicles small, less than 4 mm in diameter 11

11. Vesicles few, oblong-elliptical, winged, toothed, or with coronal leaf with flattened stalk as long as vesicle . . . . *Sargassum* sp. No. 10
11. Vesicles numerous, small, variable in shape; stalk short, less than one-half the length of vesicle 12

  12. Vesicle smooth; female receptacular branch compressed at base, triquetrous and twisted . . . . *S. siliquosum*
  12. Vesicle lumpy due to elevated cryptostomata; female receptacular branch compressed at base, triquetrous toward tip but not twisted . . . . *S. baccularia*

13. Branches lumpy, with simple or branched protuberances 14
13. Branches smooth, without protuberances 15

  14. Leaves glaucescent, cryptostomata mostly arranged along/near margin; receptacular branches terete at base and compressed to triquetrous toward lobed tips, twisted . . . . *Sargassum* sp. No. 7
  14. Leaves not glaucescent, cryptostomata scattered; receptacular branch terete . . . . *Sargassum* sp. No. 6

15. Leaves of primary and secondary branches oblong to lanceolate; midrib evanescent; base not winged; leaves of upper order branches modified into phyllocysts; triquetrous receptacular branches foliaceous . . . . *Sargassum* sp. No. 2.
15. Leaves of primary and secondary orders elliptical-oblong; midrib distinct, winged near base, evanescent at tip; phyllocysts absent; receptacular branch trigonous, not foliaceous . . . . *Sargassum ilicifolium*

16. Primary and secondary branches distinctly flattened or compressed throughout 17
16. Primary and secondary branches terete, or bases of primary branch slightly compressed but upper portion and secondary branches terete 20

17. Leaves linear to linear-lanceolate, up to 8 cm long, more than 10 times longer than wide; margin entire, slightly dentate, undulate 18
17. Leaves mainly lanceolate, not more than 5 cm long, less than 10 times longer than wide; margin sharply serrate/dentate 19

18. Vesicles elliptical to slightly fusiform with flattened stalk three or more times longer than vesicle . . . . *S. binderi*
18. Vesicles spherical; stalk short, terete or slightly flattened, shorter than the vesicle . . . . *S. oligocystum*

19. Entire margin of leaves serrate/dentate; vesicle elliptical to slightly fusiform; stalk flat, more than three times longer than vesicle . . . . *Sargassum* sp. No. 8
19. Basal portion of leaf margins entire; vesicle elliptical to obovate; stalk terete or slightly flattened, not more than twice as long as vesicle . . . . *S. kushimotense*

20. Primary branches slightly compressed near base; terete at upper portions 21
20. Primary branches fully terete 23

21. Branches lumpy due to simple to branched protuberances; leaves linear, very long, more than 10 times longer than wide . . . . *Sargassum* sp. No. 13
21. Branches smooth; leaves linear or linear-lanceolate, not more than eight times longer than wide 22

22. Margins of leaves of fertile secondary branches entire at attenuated basal half, serrate at distal portion; vesicles numerous, closely associated with receptacles (zygocarpic), spherical to obovate with plain tip; short terete stalk less than half length of vesicle . . . . *Sargassum* sp. No. 5.
22. Margins of leaves of fertile secondary branches fully serrated; vesicles few, oblong-obovate to slightly fusiform, tip plain or with a spine; stalk terete or flattened, more than half the length of vesicle . . . . *Sargassum* sp. No. 4

23. Leaves small, less than 20 mm long in fertile thalli; branches filiform 24
23. Leaves larger, more than 20 mm long in fertile thalli; branches coarse, not filiform 25

24. Leaves associated with receptacle mainly linear to linear-oblanceolate; leaves, vesicles, and receptacular branches closely associated (zygocarpic) . . . . *S. gracillimum*
24. Leaves associated with receptacle mainly filiform; receptacle subtended by float or leaf; not zygocarpic . . . . *Sargassum* sp. No. 11

25. Leaves highly glaucescent, silver-gray; female receptacle zygocarpic, receptacular branch compressed or trigonous at tip . . . . *Sargassum* sp. No. 9
25. Leaves not glaucescent 26

26. Leaves with entire or sparsely and lightly dentate margin; vesicles slightly compressed, distinctly fusiform, plain, ribbed or winged, top often with a spine or crown . . . . *Sargassum* sp. No. 1
26. Leaves with distinctly serrate or dentate margins; vesicle spherical, obovate, or oblong 27

27. Leaf margin serrate; vesicles spherical or obovate; blunt; base commonly ear-like . . . . *S. paniculatum*
27. Leaf margins denticulate; vesicles oblong, slightly compressed, commonly with apiculate tip . . . . *S. cinctum*

Description of the Species

Sargassum baccularia (Mertens) C. A. Agardh (Fig. 93)

C. A. Agardh, 1824, Syst. alg., p. 304; J. G. Agardh 1848, p. 307; Reinbold 1913, p. 171; Pham-Hoang 1967, p. 314; Ang and Trono 1987, p. 389, fig. 1A.

Holdfast shield-shaped; stem short, terete, verrucose, up to 15 mm long; primary branches compressed at base and terete toward upper portions; secondary branches terete; terminal branchlets with short, hard lumps due to elevated cryptostomata. Leaves of primary branches ovate to ovate-lanceolate or narrow elliptical, up to 60 mm long, 20 mm wide; base slightly asymmetrical, obtuse; margin entire to dentate-serrate; midrib distinct up to tip; cryptostomata numerous, distinct, slightly elevated, irregularly scattered. Leaves of secondary branches narrow elliptical to lanceolate, up to 35 mm long, 8 mm wide; base acute, shortly stalked; margin coarsely and irregularly serrate; tip acute; midrib distinct; cryptostomata slightly elevated. Leaves of terminal branchlets lanceolate, up to 17 mm long, 3 mm wide; midrib disappearing; cryptostomata distinct, slightly elevated, arranged in single row at each side of midrib. Vesicles spherical to oblong-obovate, few in fertile materials, up to 3 mm in diameter; stalk short, less than one-half the length of vesicle; cryptostomata many, elevated, giving it a lumpy appearance.

Plant dioecious. Receptacles a cyme or raceme. Female receptacular branch up to 5 mm long, compressed at base to triquetrous at the distal portion with teeth along edges. Male receptacular branch terete, verrucose, up to 12 mm long, 0.75 mm in diameter, simple to branched.

Local Distribution: Calatagan, Batangas.

Geographical Distribution: Philippines, Taiwan, Vietnam, and Indonesia.

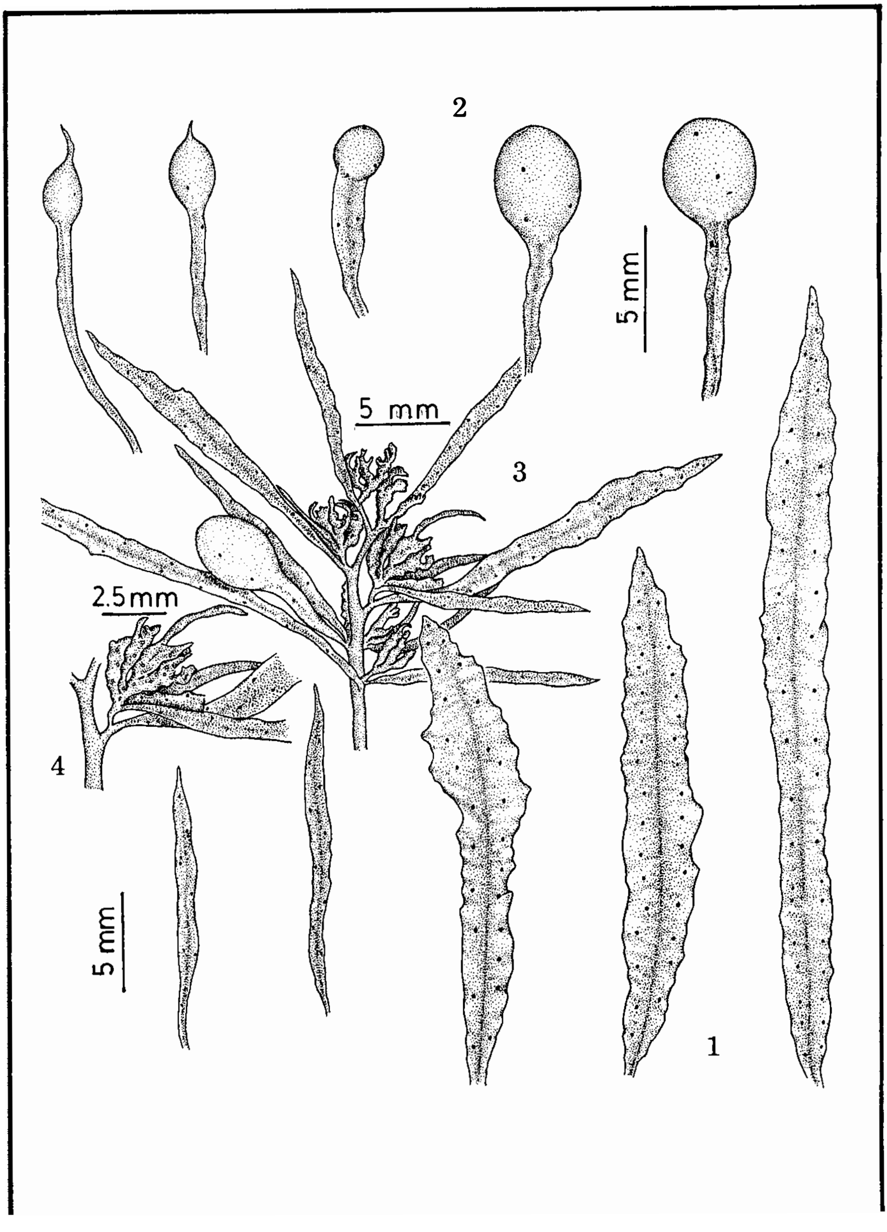
Remarks: This species has leaves with margins more regularly serrate with tapered tips than *S. paniculatum* does (Fig. 96). It can be differentiated from the latter because *S. baccularia* has distinctly elevated cryptostomata that give the vesicles and terminal branchlets a lumpy appearance. The female receptacular branch is mainly flat or compressed basally and has a triquetrous but nontwisting distal portion.

Sargassum binderi Sonder in J. G. Agardh (Figs. 1–4, 109)

J. G. Agardh, 1848, Sp. gen. ordines algarum, p. 328; Chou and Chiang 1981, p. 143; Yoshida 1988, p. 10.

All materials available lack a holdfast. Stem very short, 4 mm long, terete; primary branches distinctly compressed but terete toward distal portions, smooth, up to 3 mm wide; secondary branches terete, smooth, irregularly arranged at intervals of 2–5 cm along primary branch. Leaves of primary branches deciduous; those on secondary and tertiary branches uniformly linear to linear-lanceolate, up to 50 mm long, 3 mm wide, stalk short; base acute, margin entire or entire only at basal half to slightly serrate toward acuminate tip; cryptostomata quite distinct, slightly elevated, few, but with tendency to be arranged in rows along both sides of midrib; leaves of tertiary branchlets all linear, with margin entire or slightly serrate at distal ends with no recognizable midrib; cryptostomata arranged in two rows, at regular intervals along length of leaves. Vesicles oblong-elliptical, slightly compressed, few, up to 4 mm long, 3.2 mm wide, stalks terete to compressed, up to three times longer than vesicle; cryptostomata few, but large and slightly elevated. Tip of vesicle rounded, apiculate with a sharp spine or with filiform coronal leaf.

Receptacle axillary, dense cymes crowded on terminal laterals, zygocarpic, with reduced terete leaves associated with receptacular branches, which are terete, up to three



Figs. 1–4. ***Sargassum binderi*** **Sonder. Fig. 1, Leaves from different branch orders. Fig. 2, Forms of vesicles. Fig. 3, Portion of branch with receptacles. Fig. 4, Enlarged drawing of a receptacle.**

times branched, distal segments forming Y-shaped or forcipate tips.

All specimens are incomplete; thus, length of primary branches cannot be ascertained.

Local Distribution: Baler, Quezon.

Geographical Distribution: Philippines, Japan, Taiwan, Vietnam, Malaysia, Indonesia, and Sri Lanka.

Remarks: These materials resemble *S. oligocystum* reported by Ang and Trono (1987) from Calatagan, Batangas, Philippines, in the form of their flattened primary branches, but *S. oligocystum* is dioecious, and the lanceolate to narrowly ovate leaves are different from the mainly linear to linear-lanceolate leaves of *S. binderi.* The stalk of the vesicle is also very long in Philippine *S. binderi* as compared with the short stalk of the vesicle in *S. oligocystum* from Bolinao, Pangasinan (also reported in this paper), and identical with those from Calatagan.

Our materials resemble quite closely the specimens from Taiwan (Chou and Chiang, 1981) but differ on certain characters: the mainly linear to linear-lanceolate leaves, the very long terete or flat, smooth stalk of the vesicle, and the terete leaves associated with the receptacles. The materials also differ from the *S. binderi* as reported from Vietnam (Pham-Hoang 1967) in many characters. Chou and Chiang (1981) noted that the material of Pham-Hoang (1967) may be a different species.

Sargassum cinctum J. G. Agardh (Figs. 5–8, 110, 111)

J. G. Agardh, 1848, Sp. gen. ordines algarum, p. 324; Reinbold 1913, p. 161; Ang and Trono 1987, p. 389, figs. 1B, and 1C.

Thallus up to 60 cm tall; holdfast scutate, stem very short, although some up to 5.0 mm long; primary branches almost sessile on holdfast; primary and secondary branches terete, smooth. Leaves variable in shape: those of primary laterals mainly oblong to lanceolate, up to 30 mm long, 10 mm wide; those of secondary laterals linear-oblong to linear-lanceolate, very long, up to 80 mm, and 6 mm wide; those of terminal branchlets, oblong to narrowly oblong-ovate to linear-lanceolate; bases obtuse to acute, symmetrical to slightly asymmetrical in some, costate due to raised midrib, margin denticulate; apex acute to obtuse; cryptostomata distinct but not elevated, scattered although with tendency to form rows in narrow leaves. Vesicles variable in size: those on primary and secondary branches larger, 6–10 mm long and 4–8 mm in diameter, oblong; those on the terminal branches smaller, 1–3 mm long, 1–2 mm in diameter; mainly oblong-obovate, slightly compressed; apex plain or apiculate, laterally plane or narrowly winged or ribbed; stalk terete or flattened; cryptostomata generally absent.

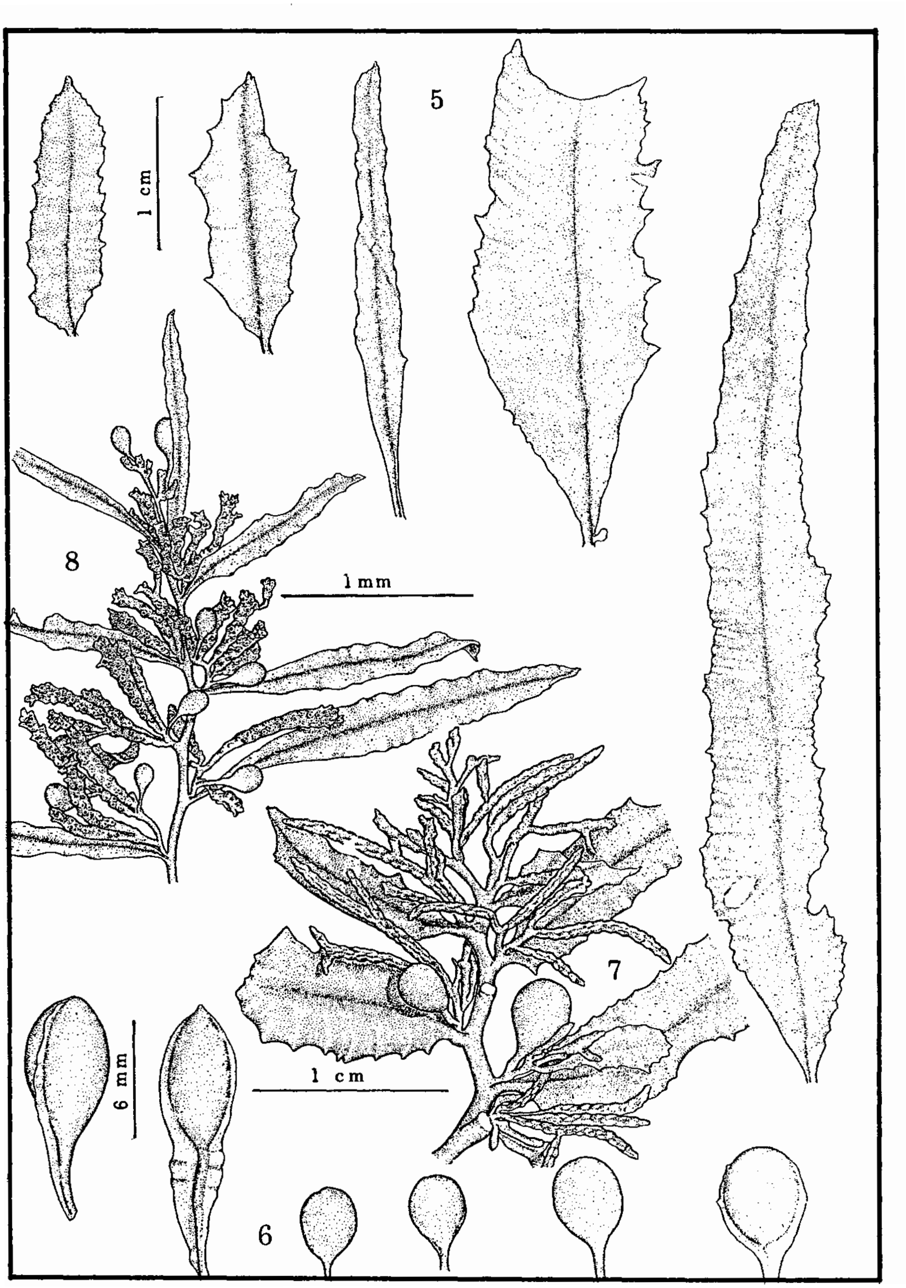
Plant dieocious. Male receptacle cymose to paniculate, receptacular branch simple or sometimes branched, terete, pinched in here or there, up to 11 mm long, 0.5 mm in diameter. Female receptacle cymose, receptacular branch terete near base, compressed toward distal end, with teeth at margin and apex.

Local Distribution: Calatagan, Batangas.

Geographical Distribution: Philippines, Japan, Indonesia, and Indian Ocean.

Remarks: This species is close to *S. paniculatum* but can be differentiated from it. *S. cinctum* has larger obovate to oblong vesicles, narrow linear-lanceolate leaves with finely denticulate margins, and distally compressed female receptacular branches.

Found growing attached to coralline rocks in wave-exposed, shallow, subtidal zone.



Figs. 5–8. ***Sargassum cinctum*** **J. G. Agardh. Fig. 5, Leaves from different branch orders. Fig. 6, Kinds of vesicles. Fig. 7, Portion of branch with male receptacles. Fig. 8, Portion of branch with female receptacles.**

Sargassum crassifolium J. G. Agardh (Figs. 9–11, 112)

J. G. Agardh, 1848, Sp. gen. ordines algarum, p. 326; Reinbold 1913, p. 158; Pham-Hoang 1967, p. 300, fig. 17; Ang and Trono 1987, p. 389, fig. 1D; Yoshida 1988, p. 12, fig. 6.

Holdfast discoid to sometimes shield-shaped; stem enlarged at base, terete, slightly pinched in here and there, up to 1 cm long. Primary branches slightly compressed, smooth, up to 50 cm long; secondary branches irregularly alternate on primary branches, slightly compressed, smooth, up to 12 cm long. Leaves thick, vertically attached, elliptical to elliptical-oblong, up to 30 mm long, 2 cm wide; base unequal; margin undulate, thickened, dentate or double dentate, tip obtuse to round; midrib disappearing toward tip; cryptostomata distinct, scattered, not elevated; leaves of higher order branches mainly elliptical-oval, up to 15 mm long, 10 mm wide; base unequal, obtuse; margin undulate, finely dentate, tip rounded; cryptostomata scattered. Vesicles of fertile materials small, 3–5 mm long, 2–3 mm wide, spherical to elliptical, slightly compressed, ribbed; margins sometimes with teeth or winged and toothed; some phyllocysts (Fig. 10) were observed; base flattened or winged; stalk short, less than one-third length of vesicle.

Receptacle a condensed cyme. Receptacular branch simple or shortly branched at the distal end, cylindrical to slightly compressed, slightly warty at the base, compressed to flattened toward distal half, with coarse teeth at margin, slightly twisted.

Local Distribution: Calatagan, Batangas; Bolinao, Pangasinan.

Geographical Distribution: Philippines, Japan, Taiwan, Vietnam, and Indonesia.

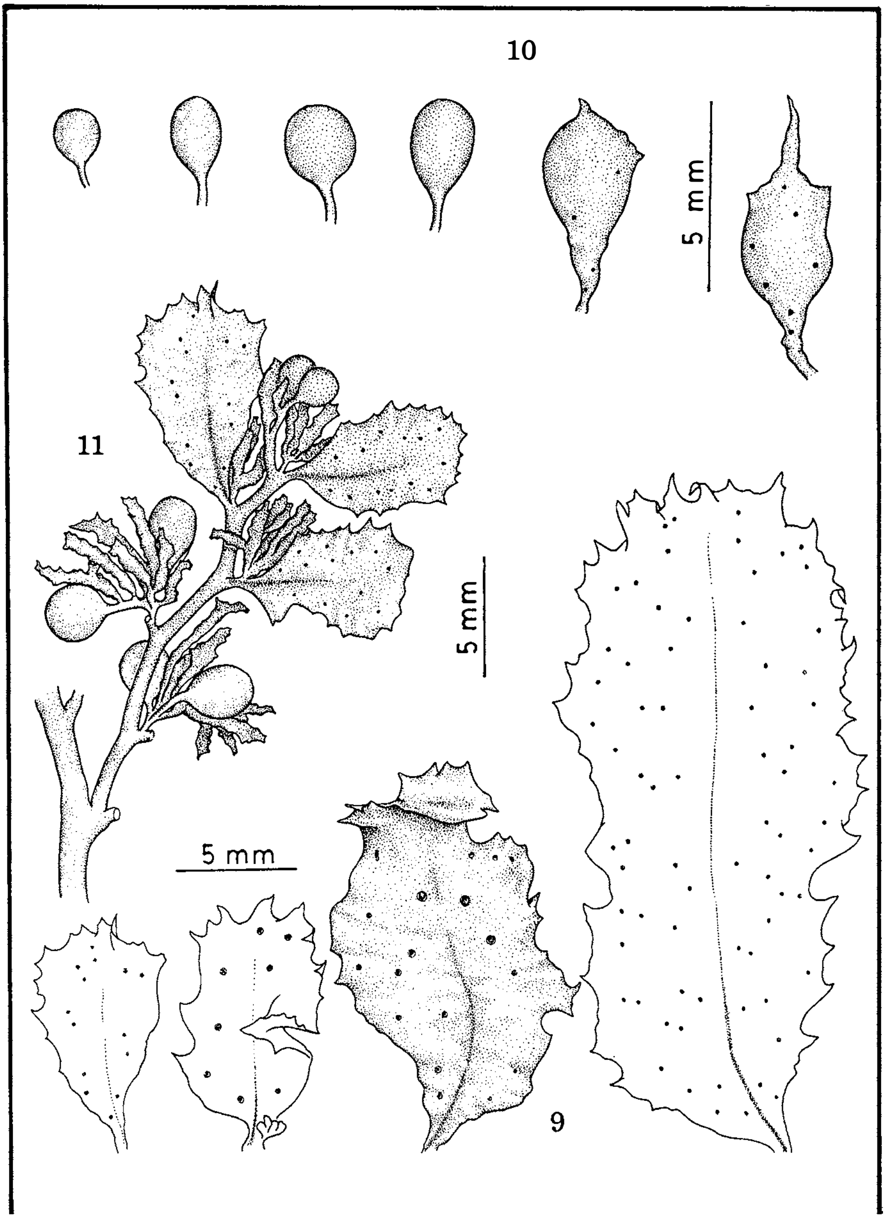
Remarks: The first report of this species in the Philippines was from Calatagan, Batangas (Ang and Trono 1987). It is highly possible that this species has been reported in the past as *S. cristaefolium* because of the "double" margin of the leaves. However, as pointed out by Ang and Trono (1987), the double margin of *S. crassifolium* involves only the double rows of the teeth of the margin of some leaves and does not involve the doubling of the blade as in *S. cristaefolium.* Also, the leaves of *S. crassifolium* are "vertical" in position in contrast to the horizontal position in *S. cristaefolium.*

Found growing on coralline rocks in wave-exposed, low intertidal to shallow subtidal zone.

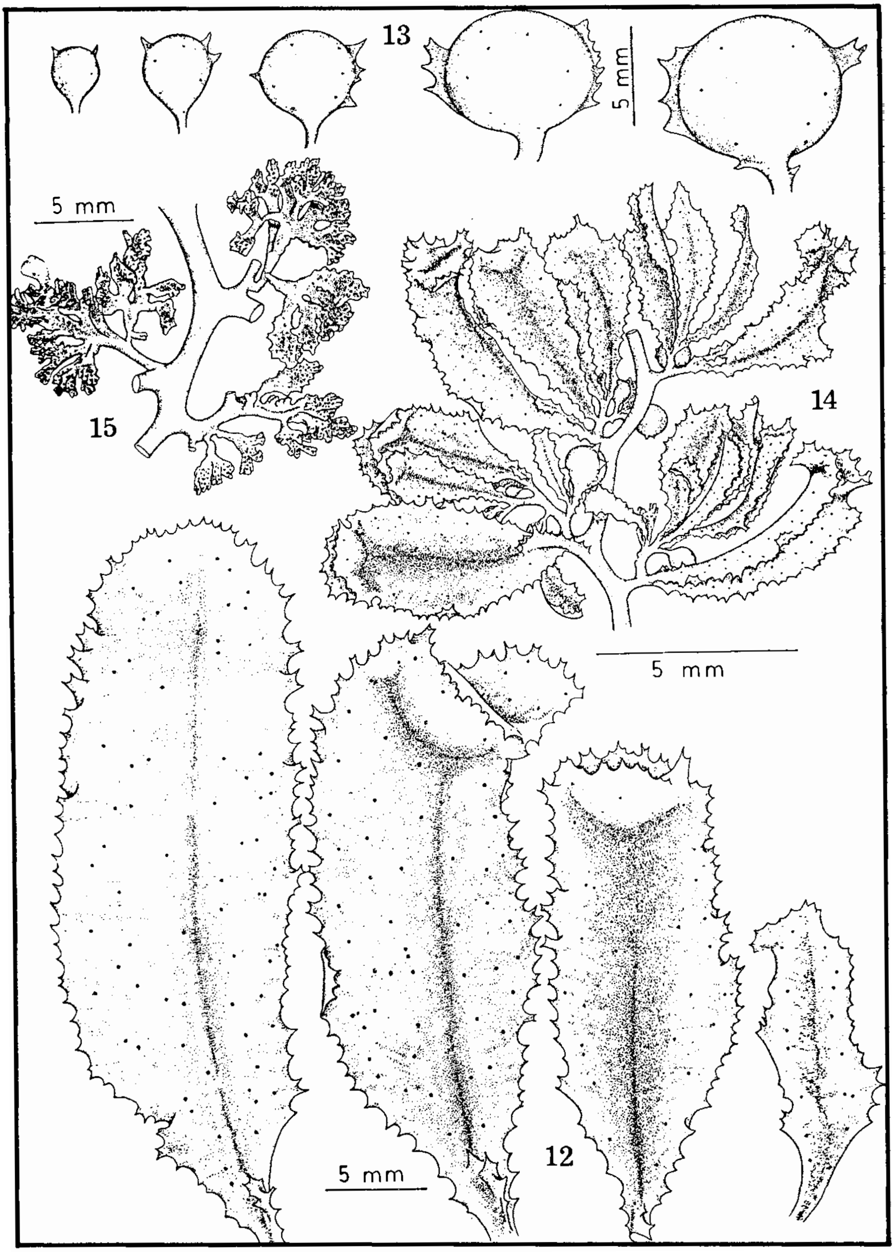
Sargassum cristaefolium C. A. Agardh (Figs. 12–15, 113)

C. A. Agardh, 1824, Syst. alg., p. 279; Reinbold 1913, p. 157, Pham-Hoang 1967, p. 299; Trono 1978, p. 12; Saraya and Trono 1980, p. 32; Chou and Chiang 1981, p. 136; Trono and de Lara 1981, p. 10; Trono and Ang 1982, p. 14. Tsuda 1988, p. 60; Yoshida 1988, p. 12.

Holdfast discoid; stem terete, short, 4–6 mm long; primary branches compressed to slightly flattened, smooth, up to 45 cm long; secondary branches irregularly alternately disposed at intervals of 1.5–2.0 cm along primary branches, generally short in nonfertile thalli, up to 3 cm long. Leaves thick and coriaceous, horizontally attached to branch; elliptical-obovate to broadly oblong-lanceolate, up to 2.0–2.5 cm long, 1.0–1.5 cm wide; base symmetrical to somewhat slightly asymmetrical in some, cuneate; stalk short with a row of two to three coarse spines at abaxial side; margin finely and irregularly serrate-dentate, some teeth duplicated; tip obtuse-rounded, mostly "duplicated," duplicated tips at right angle (Fig. 12) to plane of blade, in some leaves duplication extended about one-third along margin below tip; midrib only apparent up to basal half of leaf; cryptostomata distinct, numerous, irregularly scattered. Vesicles in nonfertile materials relatively large, few, spherical, 4–6 mm in diameter, plain, sometimes with spine or toothed wings along



Figs. 9–11. *Sargassum crassifolium* J. G. Agardh. Fig. 9, Leaves from different branch orders. Fig. 10, Forms of vesicles. Fig. 11, Portion of branch with receptacles.



Figs. 12–15. ***Sargassum cristaefolium*** **C. A. Agardh. Fig. 12, Leaves from different branch orders. Fig. 13, Forms of vesicles. Fig. 14, Portion of the branch with receptacles. Fig. 15, Detailed drawing of receptacles.**

sides; stalk short, terete to compressed, with teeth. Receptacle dense, simple to compound cyme, up to 5 mm long, with very short stalk; receptacular branch once or twice branched, compressed to flattened toward distal portion with teeth at tip and margin.

Local Distribution: Calatagan, Batangas; Bolinao, Pangasinan; Puerto Galera, Mindoro; Ilocos Norte, Quezon, Sorsogon, Samar, Siquijor, Zamboanga, Palawan, Batan.

Geographical Distribution: Philippines, Guam, Micronesia, Taiwan, Indonesia, Vietnam, Sri Lanka, and India.

Remarks: This species is differentiated from the other species with duplicated leaves by its horizontally attached leaves and spherical vesicles with toothed lateral wings. In *S. cristaefolium*, the duplicate portion of the leaf includes a portion of the blade; in *S. crassifolium*, the doubling is limited to the margin of the leaves only.

Found growing on rocky wave-exposed area from low intertidal to shallow subtidal zone.

Sargassum feldmannii Pham-Hoang (Figs. 16–22, 94)

Pham-Hoang, 1967, Ann. Fac. Sci. Saigon, p. 297, fig. 15; Noro 1989, p. 46, fig. 2C.

Holdfast discoid; stem short, 4 mm long, terete, smooth; primary branch up to 50 cm long, compressed throughout (soft and fleshy when soaked), smooth; secondary branches irregularly attached at intervals of 1–3 cm at lower portion of primary branch, those at upper portion arranged at alternating intervals of 1 cm (or less) and 2.5–7 cm apart, terete, smooth. Leaves of primary branch lacking (deciduous); those of secondary branches oblong, with short flattened stalk horizontally attached; base symmetrical, acute; margin finely dentate to double dentate (duplicated) toward upper margin and tip, rows of teeth pointing in opposite directions, tip rounded to obtuse; midrib lacking or not apparent; cryptostomata distinct, numerous, scattered, not elevated. Leaves of tertiary branchlets oblong to oblong-oblanceolate or spatulate, almost sessile; base symmetrical, acute; margin finely dentate, teeth pointing at various directions; tip mostly obtuse; many leaves in form of phyllocysts. Vesicles phyllocystic, oblong, elliptical, up to 8 mm long, 5 mm wide; margin of phyllocysts sharply dentate; cryptostomata present.

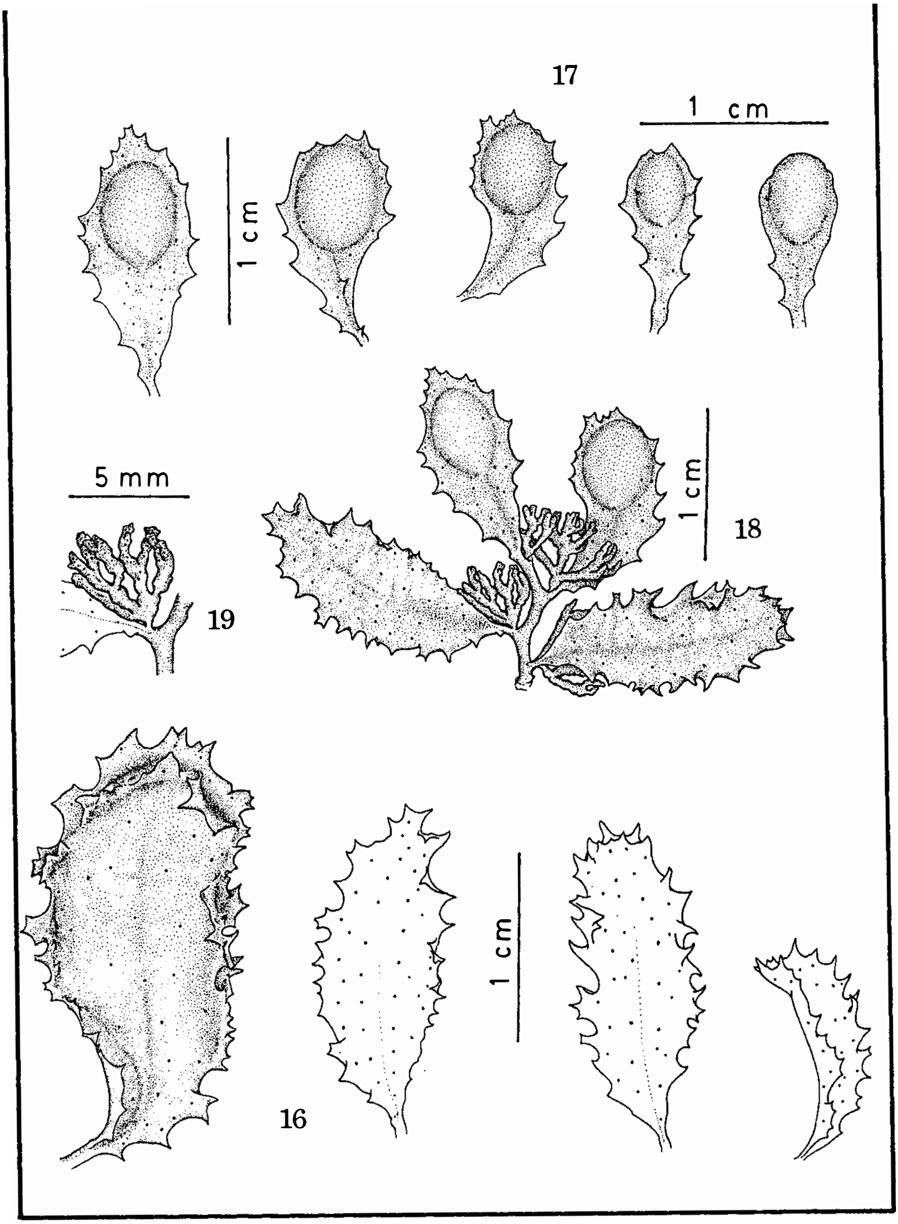
Receptacle a dense cyme or panicle; receptacular branches up to thrice branched; branches terete, slightly warty, generally ending in forcipate tips.

Local Distribution: Puerto Galera, Oriental Mindoro; Zamboanga.

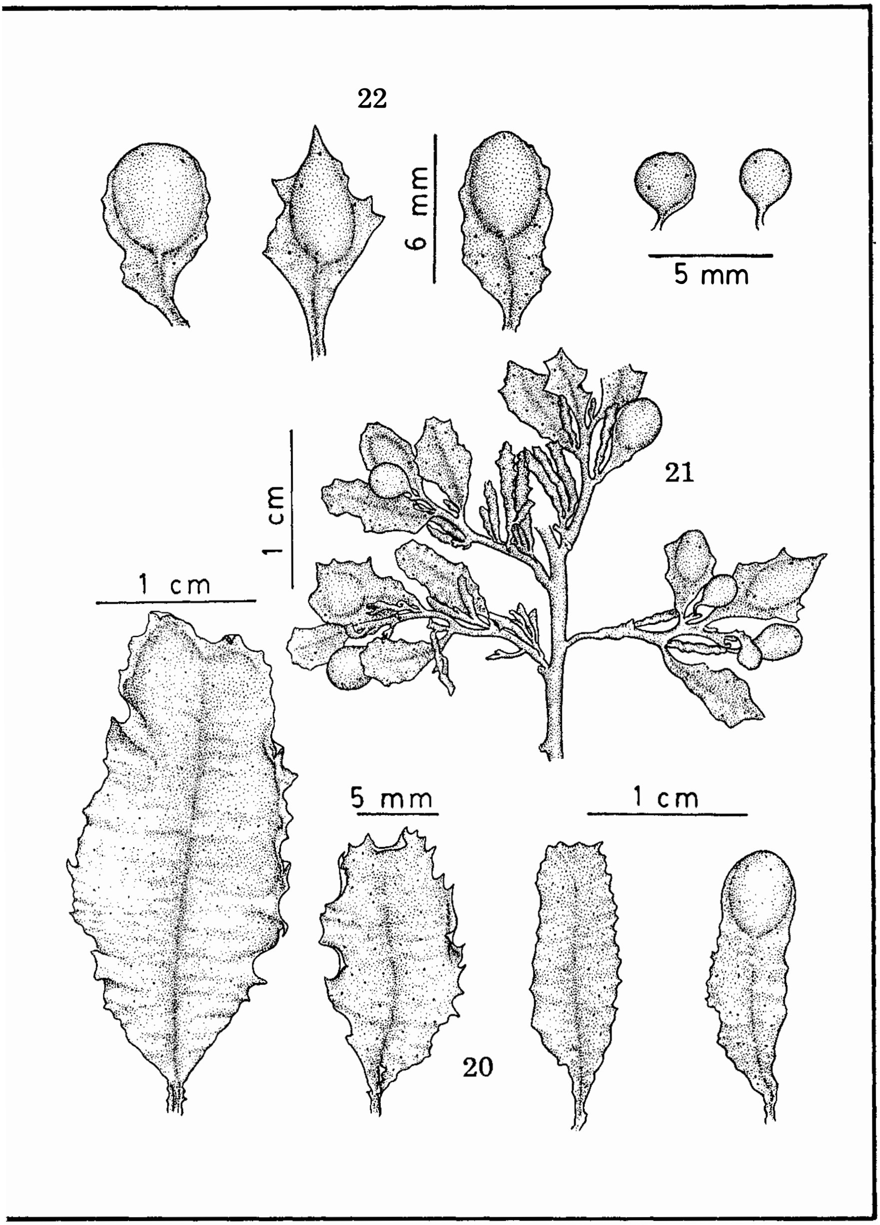
Geographical Distribution: Philippines and Vietnam.

Remarks: The specimen (T6611) resembles the material reported by Noro (1989) from Zamboanga in habit and those of Pham-Hoang (1967, fig. 15) from Vietnam, although the local material appears to lack the midrib in contrast to the type with disappearing midrib. The conspicuous phyllocysts in the species are matched in all specimens.

A whole specimen (1041.8) from Silaqui, Santiago Island, in Bolinao, with numerous phyllocysts (Fig. 22) is cited here. Almost all the vesicles are in the form of phyllocysts. However, the plant (Figs. 20–22) possesses a shield-shaped holdfast and a terete stem, strongly warty, up to 2 cm long. It differs from T6611 from Mindoro in several characters of the leaves: Leaves of the primary branch of 1041.8 are thinner, oblong, up to 20 mm long, 12 mm wide, vertically attached, with apparent midrib, and the margin does not possess double rows of teeth. Leaves of the secondary branches are much smaller than those in the primary branch and are mainly entirely or sparsely dentate. Almost all the leaves of the tertiary laterals directly associated with the receptacles are in the form of phyllocysts.



Figs. 16–19. ***Sargassum feldmannii*** **Pham-Hoang (a). Fig. 16, Leaves from different branch orders. Fig. 17, Forms of phyllocysts. Fig. 18, Portion of branch with receptacles. Fig. 19, Detailed drawing of receptacles.**



Figs. 20–22. ***Sargassum feldmannii*** **Pham-Hoang (b). Fig. 20, Leaves from different branch orders. Fig. 21, Portion of a branch with receptacles. Fig. 22, Forms of phyllocysts and vesicles.**

Sargassum gracillimum Reinbold (Figs. 23–27)

Reinbold, 1913, Siboga Exped. Monogr. 59A, p. 172.

Holdfast small, discoid; stem very short, mostly less than 1 mm long, terete; primary branches crowded at tip of stem, appearing almost sessile on holdfast, filiform, terete, up to 50 cm long; secondary and terminal branches terete, slightly to irregularly lumpy near their bases because of leaf scars, which are arranged alternately along primary branches at irregular intervals, farther apart near base and closer and crowded toward distal ends. Leaves on primary and secondary branches of younger thalli relatively longer than those at distal portions, generally obovate-oblanceolate, up to 12 mm long, 4 mm wide; base asymmetrical, acuminate to long and narrow, segment gradually grading, with stalk giving leaf a long-stalked appearance; margin of basal half of leaf generally entire, distal half coarsely and irregularly serrate; tip acute, obtuse to rounded; midrib apparent but disappearing below tip; cryptostomata distinctly elevated, scattered. Leaves of terminal branches and those associated with receptacles generally linear to linear-oblanceolate, appearing lumpy because of elevated cryptostomata; margin entire or with few teeth; midrib not apparent. Cryptostomata on leaves and floats marked by presence of hairs originating from opening (ostiole). Vesicles small, mainly obovate to sometimes oblong-obovate, less than 2 mm long, 1.5 mm wide, slightly compressed in some, lumpy in appearance because of presence of elevated cryptostomata; stalk short, less than one-half the length of vesicle; attached at base of receptacle or arising directly from the receptacular branch (zygocarpic); those attached to tip of receptacular branch appear long-stalked.

Plant dioecious, zygocarpic. Receptacle in dense panicles. Male receptacular branch terete, distinctly warty, simple or branched, up to 10 mm long. Female receptacular branch simple or branched, highly warty, terete near base and slightly compressed toward distal ends, with or without teeth.

Local Distribution: Puerto Galera, Oriental Mindoro.

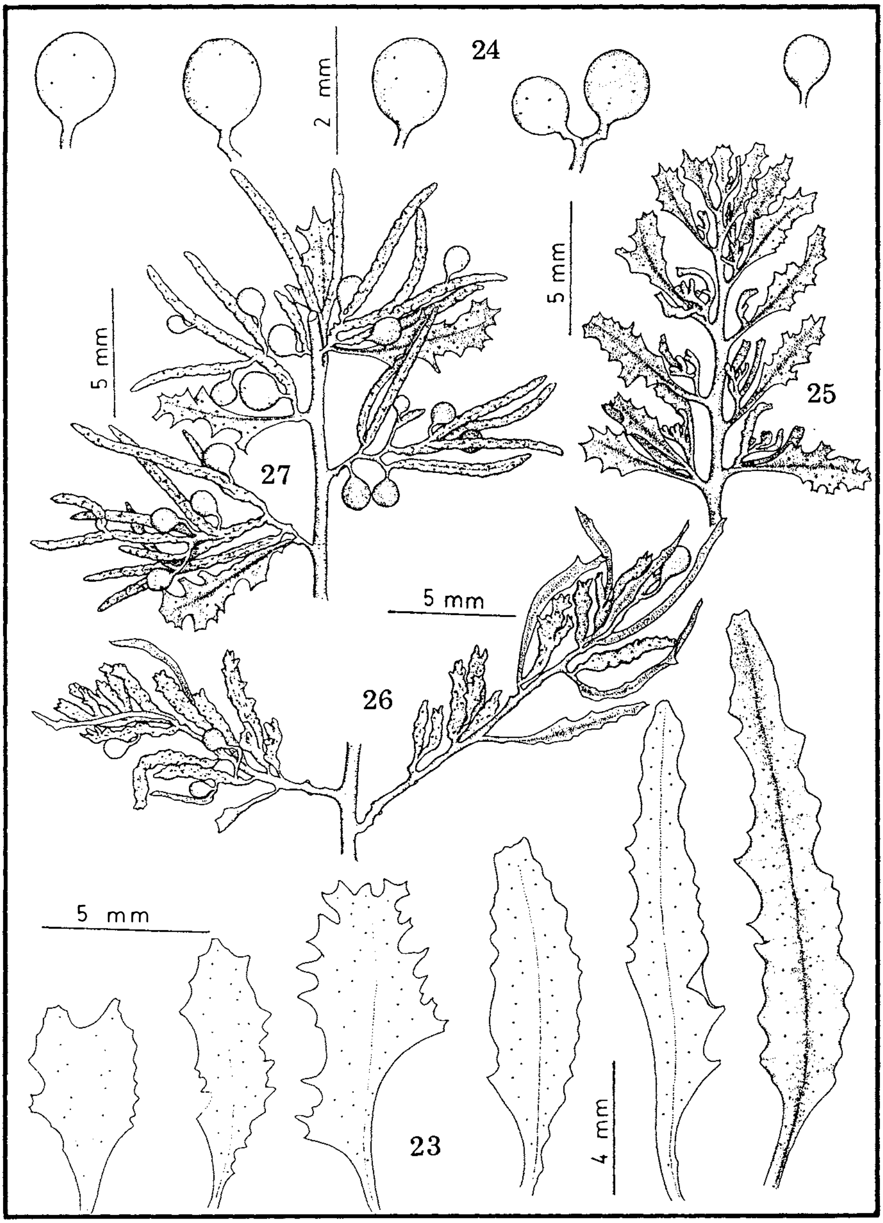
Geographical Distribution: Indonesia and Philippines.

Remarks: The specimens are identical with those of the materials described by Reinbold from the island of Kangeeng, except for some thalli, which are bigger, and for the dense and branched receptacular branches and longer stalks of vesicles.

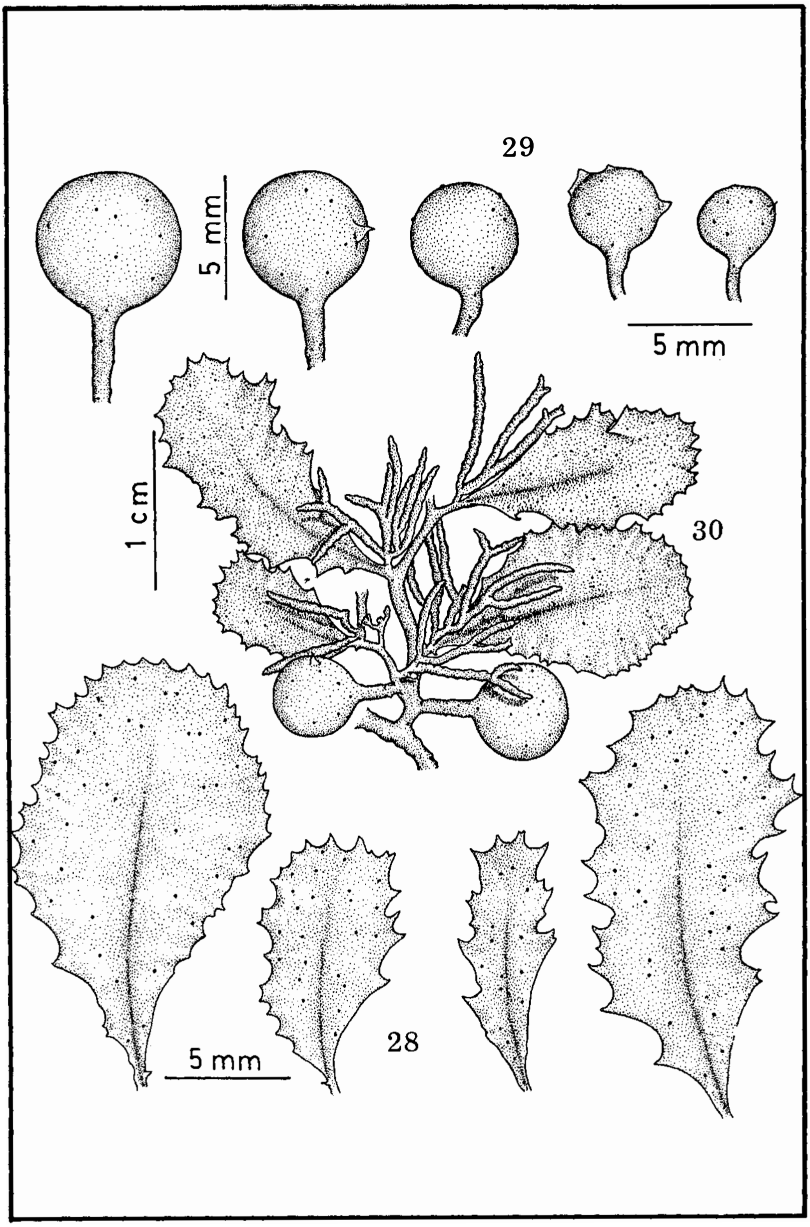
Sargassum hemiphyllum C. A. Agardh (Figs. 28–30, 114)

C. A. Agardh, 1824, Syst. alg., p. 307; Pham-Hoang 1967, p. 276, fig. 4; Chou and Chiang 1981, p. 134, pl. 2, fig. 3.

Holdfast small, discoid; very short stem, 1–2 mm long; ramifying rhizoidal holdfast issuing from tip of stem; primary branches filiform, slightly compressed at the bases, terete above, smooth, up to 80 cm long, 1 mm thick; secondary branches short, longest up to 6 cm long, terete, smooth; cryptostomata present on both secondary and tertiary branches. Leaves of primary and secondary branches horizontally attached, oblong-elliptical to oblong-obovate, up to 22 mm long, 15 mm wide; base generally symmetrical, obtuse; margin finely dentate; tip rounded; midrib absent or not apparent; cryptostomata many and distinct. Leaves of the terminal and tertiary branchlets generally smaller, vertically attached, mainly obovate-oblanceolate, up to 15 mm long, 9 mm wide; base distinctly asymmetrical, acute to acuminate, adaxial margin of base of blade entire and distinctly incurved toward axis, that of abaxial serrate or dentate, outwardly curved; margin dentate-serrate; tip obtuse or rounded; midrib absent; cryptostomata many, scattered, and apparent. Vesicles spherical-obovate, variable in size, largest up to 5 mm long, 4 mm in



Figs. 23–27. ***Sargassum gracillimum*** **Reinbold. Fig. 23, Leaves from different branch orders. Fig. 24, Forms of vesicles. Fig. 25, Portion of a young branch with receptacles. Fig. 26, Detailed drawing of female receptacle. Fig. 27, Detailed drawing of male receptacle.**



Figs. 28–30. ***Sargassum hemiphyllum*** **C. A. Agardh. Fig. 28, Leaves from different branch orders. Fig. 29, Forms of vesicles. Fig. 30, Portion of a branch with receptacles.**

diameter, small ones less than 1 mm in diameter, plain or slightly ribbed and with spines in some; cryptostomata prominent; stalk mainly terete or distinctly flattened in some, extending along side of vesicle as narrow wing or rib with teeth or spine, up to 5 mm long, from one-half to as long as length of vesicle.

Receptacle an axillary cyme, always arising from base of stalk of leaf or vesicle; receptacular branch slightly warty, simple or up to twice branched, straight, basal two-thirds always terete, with distal portion either terete in young or compressed with teeth or spines in mature ones.

Local Distribution: Puerto Galera, Oriental Mindoro.

Geographical Distribution: Philippines, Korea, Japan, China, Taiwan, Hong Kong, and Vietnam.

Remarks: The specimen is close or identical to those reported from Taiwan (Chou and Chiang 1981) in all aspects except for the presence of prominent cryptostomata on the leaves, vesicles, and terminal branches, making the last two structures slightly muricate. It differs from those reported by Tseng (1983) from China in the shape and margin of the leaves of the primary branches, the shape of the vesicles, and the presence of a rhizoidal holdfast.

Sargassum ilicifolium (Turner) C. A. Agardh

C. A. Agardh, 1820, Sp. alg., p. 11; C. A. Agardh, 1824, p. 296; J. G. Agardh 1848, p. 318; Reinbold 1913, p. 160; Pham-Hoang 1967, p. 306; Ang and Trono 1987, p. 393.

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

Holdfast discoid; stem short, terete, warty, 10–20 mm long; primary branches smooth, slightly compressed; secondary branches also slightly compressed, smooth, irregularly disposed on primary branch; determinate laterals terete, smooth. Leaves of primary branches elliptical-oblong, up to 31 mm long, 10 mm wide, smaller in fertile materials; margins irregularly dentate-serrate; tip mainly obtuse; base slightly asymmetrical, distinctly costate, attenuate toward a very short stalk; midrib distinct but disappearing toward tip; cryptostomata indistinct. Leaves of secondary laterals narrowly elliptical to lanceolate, linear-lanceolate, or obovate, up to 22 mm long (or longer), up to 5 mm wide; margin irregularly serrate-dentate; tip obtuse to acute; base equal to slightly unequal, slightly costate; stalk short; cryptostomata distinct and slightly elevated. Leaves of terminal branches narrowly elliptical to oblong-obovate or lanceolate; margin irregularly serrate; tip acute, obtuse, or round; base acute; midrib indistinct; cryptostomata irregularly placed or sometimes with tendency to form rows. Vesicles of fertile materials small, up to 2.5 mm long, 2.0 mm wide, numerous, spherical, oblong to obovate, slightly compressed in some, blunt, marginate, ear-like; apex smooth, apiculate or sometimes with one or two teeth; stalk very short, less than one-half the length of vesicle.

Plant dioecious. Receptacle racemose. Male receptacular branch terete, up to 12 mm long, 0.5–0.7 mm wide, pinched in here and there, tapered toward tip. Female receptacular branch compressed at base, generally triquetrous toward tip, dentate, up to 5.0 mm long, 1.8 mm wide.

Local Distribution: Batangas, Batanes, Ilocos Norte, Pangasinan, Mindoro, Samar, Cebu, Iloilo, Sulu, and Zamboanga.

Geographical Distribution: Philippines, Japan, Taiwan, Vietnam, Malaysia, Indonesia, Australia, Indian Ocean, and Sri Lanka.

Remarks: The species is differentiated from *S. siliquosum* and *S. paniculatum* by the more tapered leaves of its primary branches. In addition, the leaves of its secondary and tertiary branches are more elongated than those of the same order leaves of *S. siliquosum* but much shorter than those of *S. paniculatum*. The vesicles are more ear-like than those of *S. siliquosum*. The non-twisting triquetrous and bracteolated female receptacular branches also differentiate this species from *S. paniculatum* and *S. siliquosum*. The racemose male receptacle with terete receptacular branch differentiates the local material from materials with cymose or paniculate receptacles with flattened/compressed receptacular branches reported by Yoshida (1988).

Sargassum kushimotense Yendo (Figs. 31–34, 95)

Chou and Chiang 1981, p. 143, pl. 3, fig. 2.

Holdfast discoid to slightly conical; stem short, terete, smooth, up to 5 mm long; primary branches compressed, up to 4 mm wide, smooth, up to 30 cm long; secondary branches compressed, up to 20 cm long; determinate branches short, up to 3 cm, slightly compressed, alternately attached along primary and secondary branches at intervals of 1–2 cm, becoming closer toward tip; cryptostomata present. Leaves of primary branch deciduous; those of secondary branches linear-lanceolate, up to 45 mm long, 6 mm wide, membranous; stalk very short; base acute and slightly asymmetrical; sharply serrate margin; tip acute to acuminate; midrib percurrent up to tip; cryptostomata distinct, slightly elevated, with tendency to be in rows at both sides of midrib, those of determinate branchlets smaller and irregular in shape, bases sharply asymmetrical. Vesicles elliptical to elliptical-obovate, up to 11 mm long, 5 mm wide, tip smooth or with blunt teeth or apiculate; cryptostomata distinct; stalk variable in length, not more than twice length of vesicle, terete or flattened, winged, wings extending along side of vesicle as rib; cryptostomata distinct and elevated on flattened stalk.

Young receptacles cymose, subtended by a leaf consisting of two to four receptacular branches, short, up to 2 mm long, 0.5 mm in diameter, terete, segments oblong, slightly tapered to a blunt tip, in some with short, blunt spine.

Local Distribution: Lubang Island, Mindoro; Bolinao, Pangasinan.

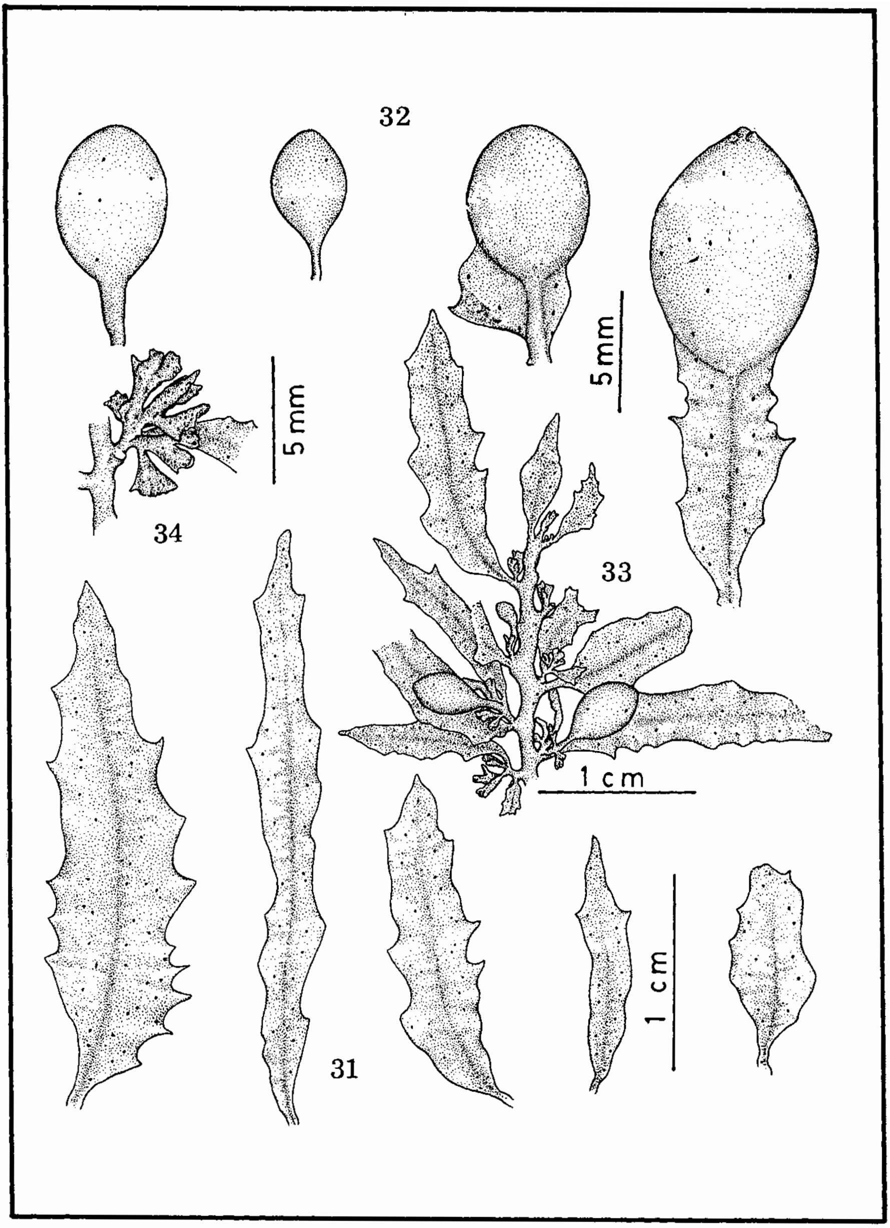
Geographical Distribution: Philippines, Japan, and Taiwan.

Remarks: The Philippine specimens match those from Taiwan, even though the latter are purely vegetative.

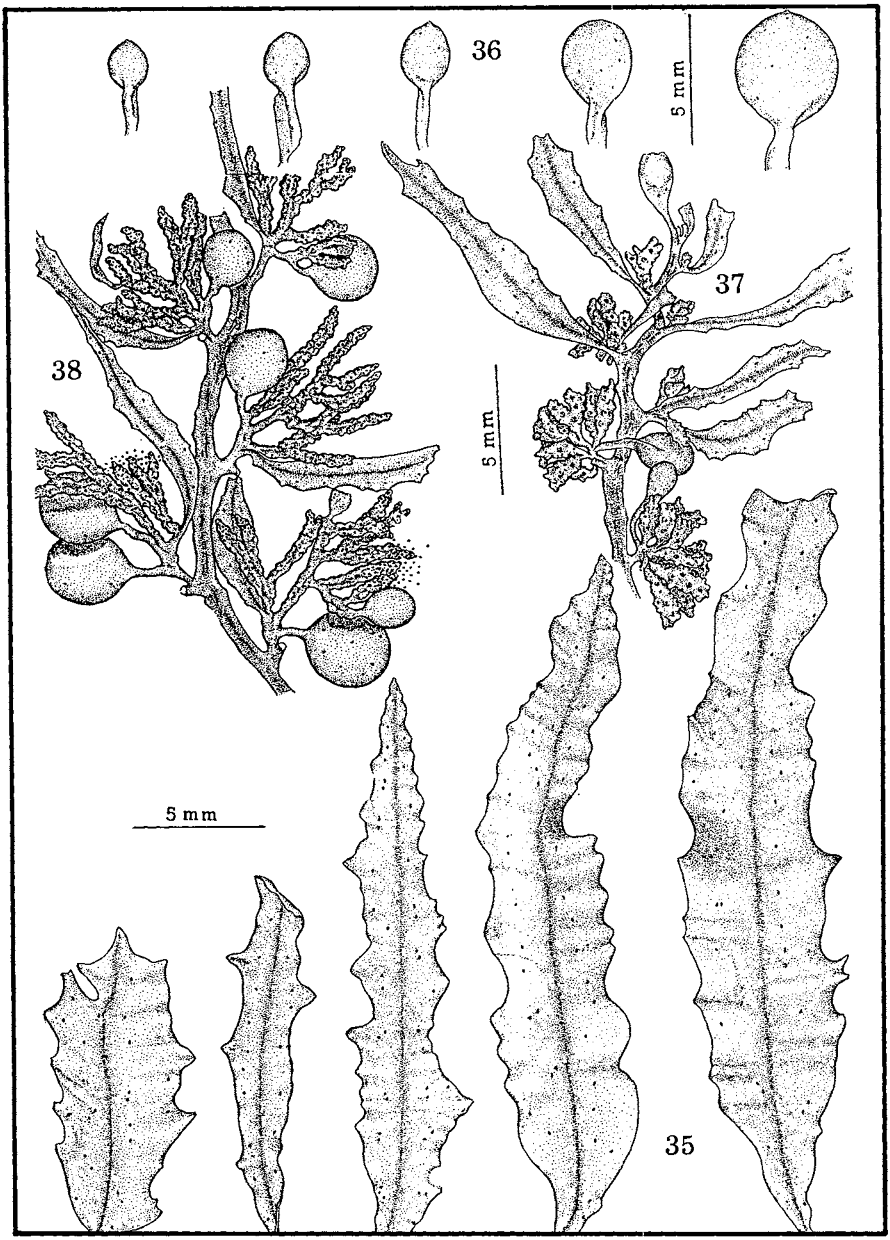
Sargassum oligocystum Montagne (Figs. 35–38, 115)

Montagne, 1845, Plantes cell., pp. 67–69; Ang and Trono 1987, p. 394.

Holdfast small, discoid; stem generally very short, about 5 mm long (but in one specimen, 30 mm long), cylindrical to slightly compressed, brownish, finely villose, simple or sometimes branched. Primary branches strongly flattened, especially at basal portions, 3–4 mm at broadest portions, smooth, up to 80 cm long; secondary laterals distichous, alternately arranged along primary branches, up to 18 cm long. Leaves of vegetative materials large, linear-lanceolate, up to 7.0 cm long, 1.2 cm wide, with very short stalks. Those of fertile materials much smaller and reduced, especially toward apical portions, linear to linear-lanceolate; base acute to cuneate; margin irregularly serrate-dentate; apex mainly obtuse to acute, those of the smaller leaves mainly acute; midrib distinct almost up to apex. Cryptostomata slightly elevated and scattered on blade, those on small leaves at terminal branches with tendency to form rows along both sides of midrib. Cryptostomata also present on vesicles. Those on vesicles of female receptacles more numerous and distinctly elevated, giving the receptacles a lumpy appearance. Vegetative plants with vesicles larger, from 2.5–7.5 mm long to 1.0–5.0 mm wide; those of fertile materials



Figs. 31–34. ***Sargassum kushimotense*** **Yendo. Fig. 31, Leaves from different branch orders. Fig. 32, Forms of vesicles. Fig. 33, Portion of branch with receptacles. Fig. 34, Detailed drawing of receptacular cluster.**



Figs. 35–38. ***Sargassum oligocystum*** **Montagne. Fig. 35, Leaves from different branch orders. Fig. 36, Forms of vesicles. Fig. 37, Portion of branch with female receptacles. Fig. 38, Portion of branch with male receptacles.**

smaller and variable in size, larger ones from 4–5 mm long by 2–3 mm wide, smaller ones 1.5 mm long by 1.0 mm wide; most vesicles with short cylindrical stalks, mainly 1 mm long, those on female plants longer (up to 4 mm) and stalks flattened; apices of vesicles mainly plain or occasionally with teeth or spine.

Plants dioecious. Male receptacles paniculate; receptacular branches up to three times unequally dichotomously branched, branches terete but highly warty. Female receptacles form dense cymes; receptacular branches simple or shortly branched, almost of same length, apices slightly compressed, margins and tips with few teeth or spines.

Local Distribution: Batangas, Pangasinan, Mindoro, Catanduanes, Sorsogon, Bohol, Cebu, Negros, Iloilo, Aklan, Palawan, Zamboanga, and Surigao.

Geographical Distribution: Philippines, Taiwan, Vietnam, Malaysia, and Sri Lanka.

Sargassum paniculatum J. G. Agardh (Figs. 39–41, 96)

J. G. Agardh, 1848, Sp. gen. ordines algarum, pp. 315–316; Reinbold 1913, p. 177; Cordero 1976, p. 24; Ang and Trono 1987, pp. 394–395.

Holdfast shield-shaped to discoid, massive in some where two or more thalli arise from a fused holdfast; stem up to 25 mm long, cylindrical, warty; primary branches terete, up to 80 (rarely to 175) cm long, smooth; secondary branches terete, irregularly alternately attached on primary branch, smooth.

Leaves of secondary branches of vegetative thallus mainly ovate-lanceolate to oblong to linear-lanceolate; base unequal; margin generally serrate, entire in some; apex generally obtuse to acute; midrib distinct but disappearing near apex; cryptostomata numerous, scattered. Leaves in fertile materials mainly linear to linear-lanceolate, some linear-oblanceolate, up to 40 mm long by 4–5 mm wide; base acute, slightly unequal; margin dentate-serrate, entire in some; apex narrowly acute; midrib distinct. Cryptostomata sparse in leaves of primary laterals, sparse and scattered in leaves of secondary laterals, but distinct and with tendency to be arranged in rows in narrow leaves of terminal branches. Vesicles numerous, spherical or obovate, blunt; base plain or ear-like or with narrow extended margin; mainly small in fertile materials; racemose; 1–2 mm long, with very short stalks, 1 or less than 1 mm long.

Plant dioecious. Male receptacle racemose, up to 15 mm long, pinched in here and there, 0.3–0.5 mm in diameter (in dried materials) with blunt tip. Female receptacle racemose, receptacular branches compressed to triquetrous, edges or margins finely serrate/dentate, up to 6 mm or sometimes longer in some, sometimes slightly twisted.

Local Distribution: Batan Island, Basco; Calatagan, Batangas.

Geographical Distribution: Philippines, Indonesia, Indian Ocean, and Pacific Coast of North America.

Remarks: Ang and Trono (1987) pointed out the overlapping size ranges of *S. paniculatum* and *S. siliquosum* leaves in young thalli of these species. The mainly linear and longer leaves and the compressed to three-sided and straight or, seldom, slightly twisted female receptacular branches of *S. paniculatum* are distinctive.

Found growing on coralline substrate at the low intertidal zone exposed only during extremely low tides.

Sargassum polycystum C. A. Agardh*

C. A. Agardh, 1824, Syst. alg., p. 304; Pham-Hoang 1967, p. 309, fig. 21; Trono 1976,

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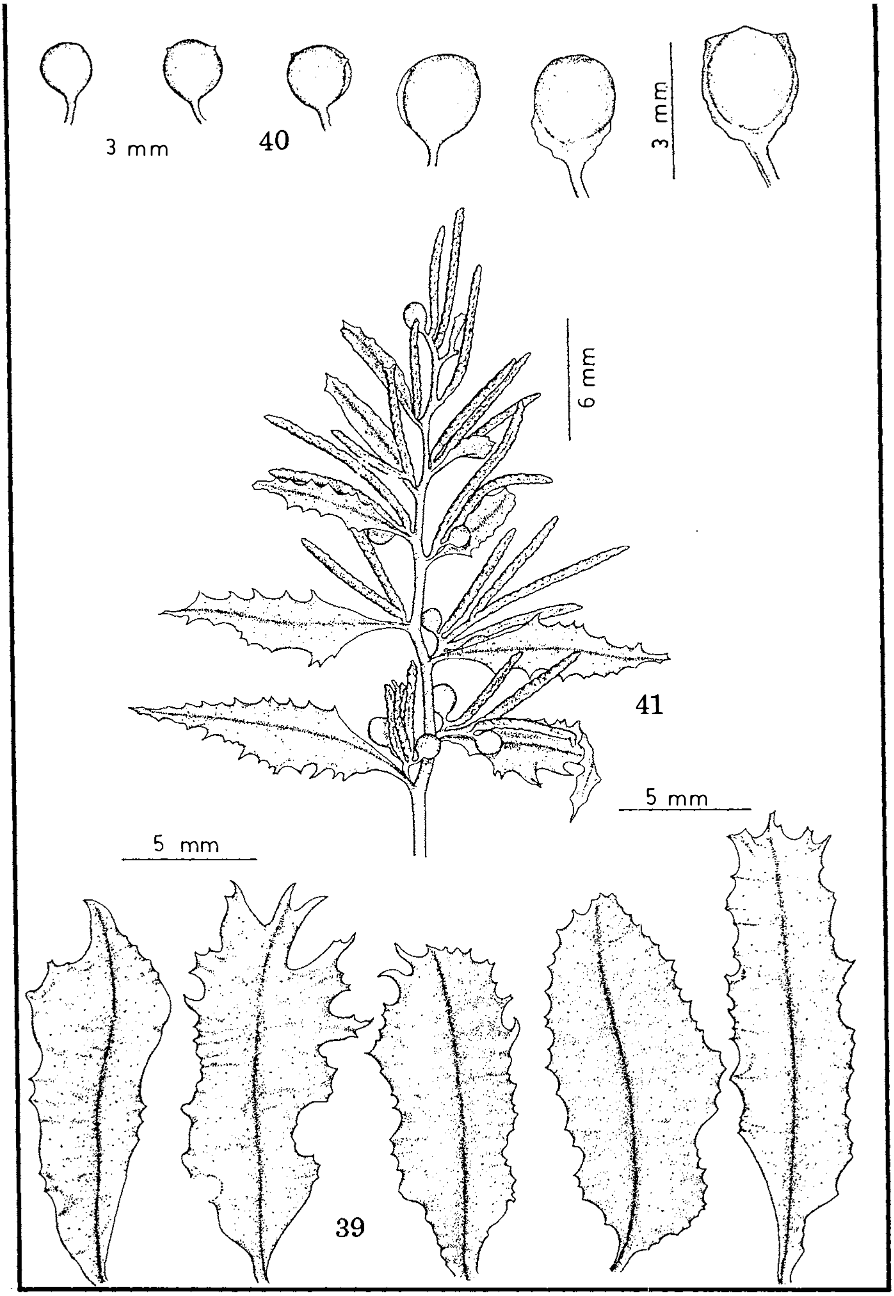
Ed. note: Illustrations for this species can be found in this volume in the chapters by Chiang et al., Tseng and Lu, Ajisaka, and Kilar et al.



Figs. 39–41. ***Sargassum paniculatum*** **J. G. Agardh. Fig. 39, Leaves from different branch orders. Fig. 40, Forms of vesicles. Fig. 41, Portion of branch with young male receptacles.**

p. 219; Trono 1978, p. 12; Trono and Ganzon-Fortes 1980, p. 49; Trono and de Lara 1981, p. 9; Yoshida 1988, pp. 17–18, fig. 14; Tseng and Lu 1988, pp. 47–48; Tsuda 1988, p. 62, fig. 4.

Thallus up to 90 cm tall; holdfast a small slightly elevated disk up to about 7 mm in diameter; stem brownish and finely villose, short, usually only 10 mm long, but in one specimen 20 mm long; primary branches crowded at distal end of stem, terete, lumpy, with many simple or Y-shaped short processes (elevated cryptostomata); several primary branches transformed into horizontal stolons, which are slightly compressed at basal portions, irregularly alternately branched, tip of some becoming transformed into attachment disks. Leaves on main branches of vegetative materials generally larger, up to 25 mm (30) to 6 (10) mm wide, broadly lanceolate to linear-lanceolate; in one specimen leaves at distal portion of branches ovate to broadly lanceolate; base of leaves asymmetrical; margin finely but irregularly serrate-dentate; apex obtuse to broadly acute to somewhat rounded in some; midrib distinct almost to apex of leaves. Cryptostomata numerous, distinct, and elevated (on processes on branches), scattered on leaves and vesicles. Vesicles numerous, very small, 1.5–2.5 mm long and 1.0–2.0 mm wide, mainly spherical-ovate to slightly elliptical; stalk terete, short; several floats may be borne on a single branchlet (raceme); apex smooth or with teeth or spine.

Plant dioecious. Male receptacle racemose to paniculate, receptacular branches terete, up to 5 mm long, warty. Female receptacle small, cymose, receptacular branches short, dense, compressed, slightly twisted, simple or forked with teeth or spines at margin and apices.

Local Distribution: Pangasinan, Palawan, Bataan, Ilocos Norte, Batangas, Mindoro, Quezon, Sorsogon, Samar, Biliran, Bohol, Cebu, Siquijor, and Zamboanga.

Geographical Distribution: Philippines, Guam, Taiwan, Japan, China, Vietnam, Indonesia, Singapore, Australia, Micronesia, Sri Lanka, and India.

Sargassum siliquosum J. G. Agardh (Fig. 97)

J. G. Agardh, 1848, Sp. gen. ordines algarum, p. 316; Reinbold 1913, p. 154; Cordero 1976, p. 24; Ang and Trono 1987, p. 395, fig. 2D.

Holdfast shield-shaped to massive and amorphous in old thalli; stem terete, warty, finely felted, up to 24 mm long; primary and secondary branches terete to slightly compressed, lumpy in young plants. Leaves of fertile plants variable in shape, lanceolate to oblong in secondary branches, up to 25 mm long, 8 mm wide; margin irregularly or finely serrate or dentate, entire or wavy; tip acute, obtuse, or rounded; base unequal, acute with short stalk; midrib disappearing toward tip; cryptostomata scattered. Leaves of upper order branches spatulate, clavate, or shortly lanceolate, up to 16 mm long, 7 mm wide; margin irregularly serrate at distal half, usually entire at basal half; tip round, obtuse, or truncate; base distinctly unequal; midrib indistinct; cryptostomata scattered. Vesicles also variable in shape, spherical, oblong, or obovate, some slightly compressed, slightly blunt, plain, apiculate, or ribbed, small, generally less than 2 mm in diameter, those of lower order branches bigger; stalk short, less than one-half diameter of vesicle, solitary, paired, or in short racemose cluster.

Plant dioecious. Receptacle racemose, receptacular branches simple or branched and stalked, forming panicles on receptacular branch. Male receptacle terete, pinched in here and there, tapered toward tip, up to 15 mm long, 0.5–0.75 mm in diameter, subtended by a vesicle or bracteole (leaf). Female receptacular branch compressed, triquetrous and twisted when mature, with serrate or dentate margin.

Local Distribution: Calatagan, Batangas, Ticao Island, Cavite, Ilocos Norte, La Union, Pangasinan, Quezon, Leyte, Samar, Biliran, Cebu, Mactan Siquijor, Iloilo, Aklan, Palawan, Misamis Occidental.

Geographical Distribution: Philippines, Japan, Vietnam, and Indonesia.

Remarks: This species is differentiated from *S. paniculatum* by its elliptical, lanceolate to oblanceolate leaves and the triquetrous strongly twisted female receptacles.

Sargassum turbinarioides Grunow (Figs. 42–45, 116)

Grunow, A. 1915, Verh. Zool. Bot. Ges. Wien, vol. 65, p. 395; Pham-Hoang 1967, p. 304, fig. 19.

Holdfast small, discoid; stem short, cylindrical, large at base, slightly tapered to tip, smooth or partly smooth and slightly warty; primary branches slightly compressed near base, becoming cylindrical toward upper portions, smooth, up to 50 cm long. Leaves coriaceous, obovate, 10 mm long, 8 mm wide; stalk very short, almost sessile, with coarse teeth; base (thick) acute, slightly asymmetrical in some; margin coarsely serrate, serration arranged in single or double rows; distal third of most leaves expanded into a cup-like structure, shape of cup-like structure mainly elliptical to oblong when viewed from top; margin coarsely toothed, teeth simple or divided, generally arranged in double rows; top view of leaf resembles that of *Turbinaria*; midrib not apparent even at base; cryptostomata scattered, very apparent, and slightly elevated. Vesicles many, some large, up to 12 mm long, 6 mm wide, generally elliptical-oblong or slightly oblong-obovate, stalk very short, less than one-fourth length of vesicle; irregularly lumpy because of cryptostomata; some slightly ribbed with or without coronal leaf, those without coronal leaf with a row of coarse spines on upper half.

Receptacle irregularly cymose with short stalk, once or twice branched, receptacular branch terete at lower half, slightly compressed toward distal half, with occasional teeth along the margin.

Local Distribution: First report for the Philippines: Puerto Galera, Oriental Mindoro.

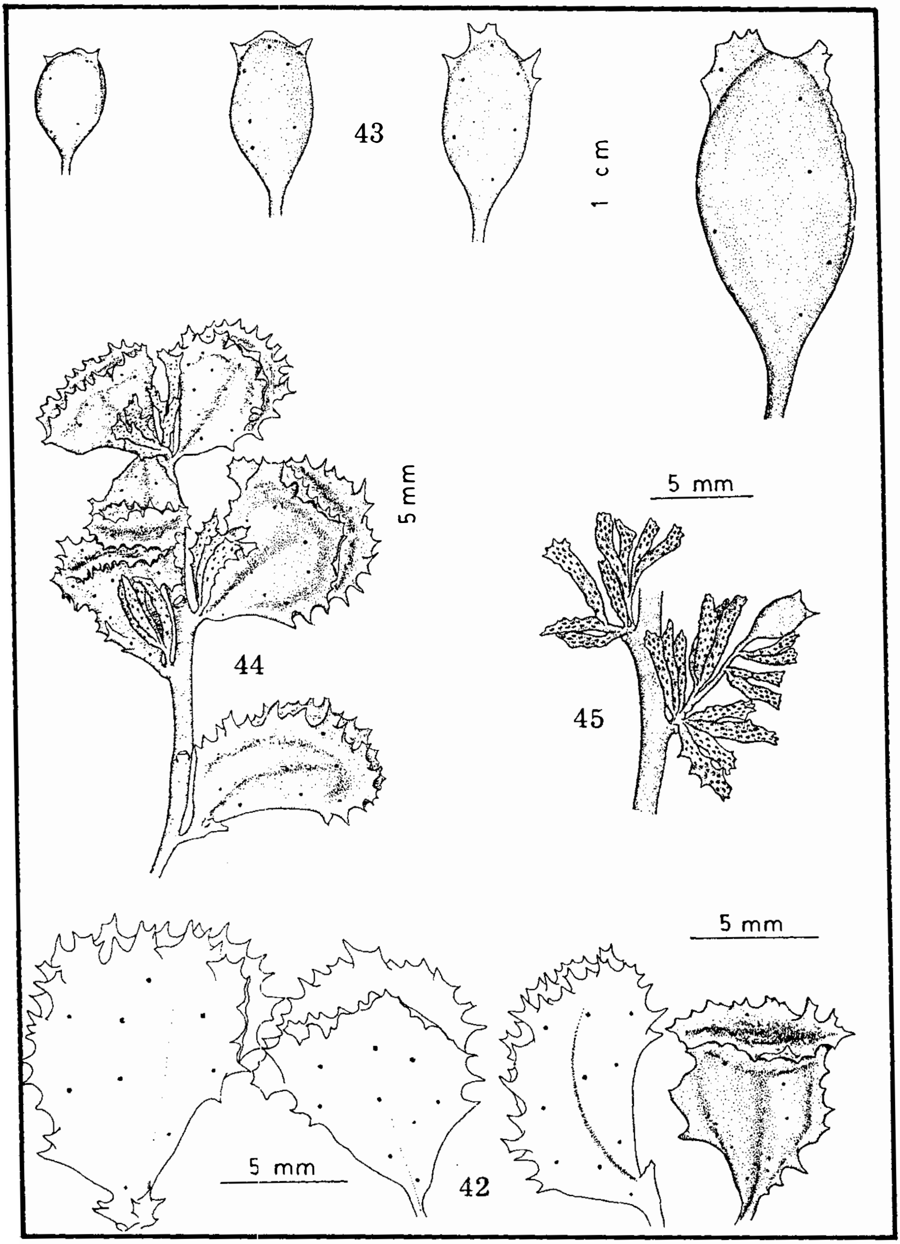
Geographical Distribution: Philippines, Vietnam, and New Caledonia.

Remarks: The "turbinaroid" distal half of the leaves, which forms a shallow depression at the top, and the very thick lower half are distinctly different from the duplicated leaves of *S. cristaefolium*. The oblong-elliptical vesicles and the terete receptacular branches with slightly compressed distal portion also are distinct from the spherical vesicles and flattened receptacular branches of *S. cristaefolium*.

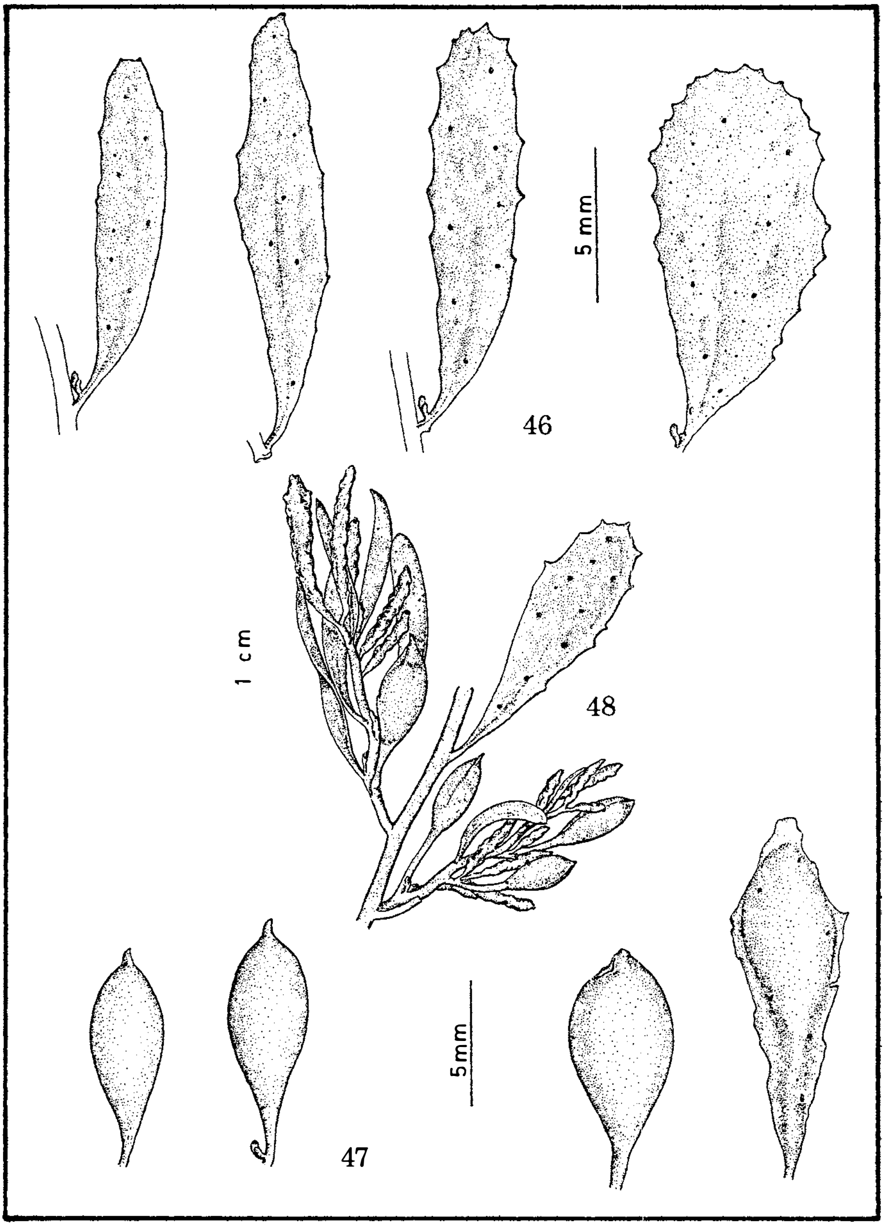
Sargassum sp. No. 1 (Figs. 46–48, 98)

Thallus up to 60 cm tall; holdfast incomplete but appears to be conical; stem very short, about 3 mm long; primary branches terete and smooth; secondary branches terete to slightly compressed, irregularly alternate along primary branch, up to 13 cm long. Leaves up to 25 mm long and 5 mm wide, obovate to linear-oblanceolate; stalk cylindrical or flattened; base symmetrical, acute; margin entire to finely dentate; apex obtuse to acute; midrib disappearing midway to apex; cryptostomata few, not distinct, irregularly scattered on blade. Vesicles distinctly spindle-shaped, slightly laterally compressed, up to 6.5 mm long, 3.0 mm thick, and 5.0 mm wide, with terete or flattened stalks; apex mucronate or expanded; some ribbed or with a narrow wing; surface smooth, with or without cryptostomata.

Receptacle a simple raceme or cyme, lax; receptacular branches few, terete, up to 8 mm long, 0.5–1.0 mm thick, pinched in here or there or warty.



Figs 42–45. *Sargassum turbinarioides* Grunow. Fig. 42, Leaves from different branch orders. Fig. 43, Forms of vesicles. Fig. 44, Portion of branch with receptacles. Fig. 45, Detailed drawing of receptacular clusters.



Figs. 46–48. ***Sargassum*** **sp. No. 1. Fig. 46, Leaves from different branch orders. Fig. 47, Forms of vesicles. Fig. 48, Detailed drawing of receptacles.**

Remarks: One specimen was available for examination. A cross section of the receptacular branch showed only male gametangia. The distinctly spindle-shaped and slightly laterally compressed vesicles and the linear to oblanceolate leaves with disappearing midrib are distinctive of this species. Nothing among the local materials or those reported by other authors from other countries comes close to this species.

The material (T6613) was collected by A. Cortez from Honduras, Puerto Galera, Oriental Mindoro, Philippines, on May 25, 1973.

Sargassum sp. No. 2 (Figs. 49–52, 99)

Holdfast discoid, 10–15 mm wide; stem short, 10–12 mm long, terete, smooth; primary branches slightly compressed, smooth, about 1.5 mm wide, up to 45 cm long; secondary branches slightly compressed, irregularly and alternately disposed at intervals of 1.0–3.0 cm along primary branches. Leaves of primary and secondary branches oblong-ovate to somewhat lanceolate, up to 2.5 cm long by 1.0 cm wide; stalk terete, short, about 1.0 mm long; base slightly asymmetrical, acute to obtuse; margin irregularly serrate; apex obtuse to acute; midrib faintly disappearing from about middle to apex. Cryptostomata few but apparent, not elevated. Leaves of higher order branches variable in shape, narrow-elliptical, lanceolate, or oblanceolate. Vesicles up to 6 mm long by 3 mm wide, narrowly elliptical to oblong, slightly compressed; stalk terete; apex acuminate to plain, mostly ribbed or winged with two or more teeth at apex and margin; most vesicles modified as phyllocysts.

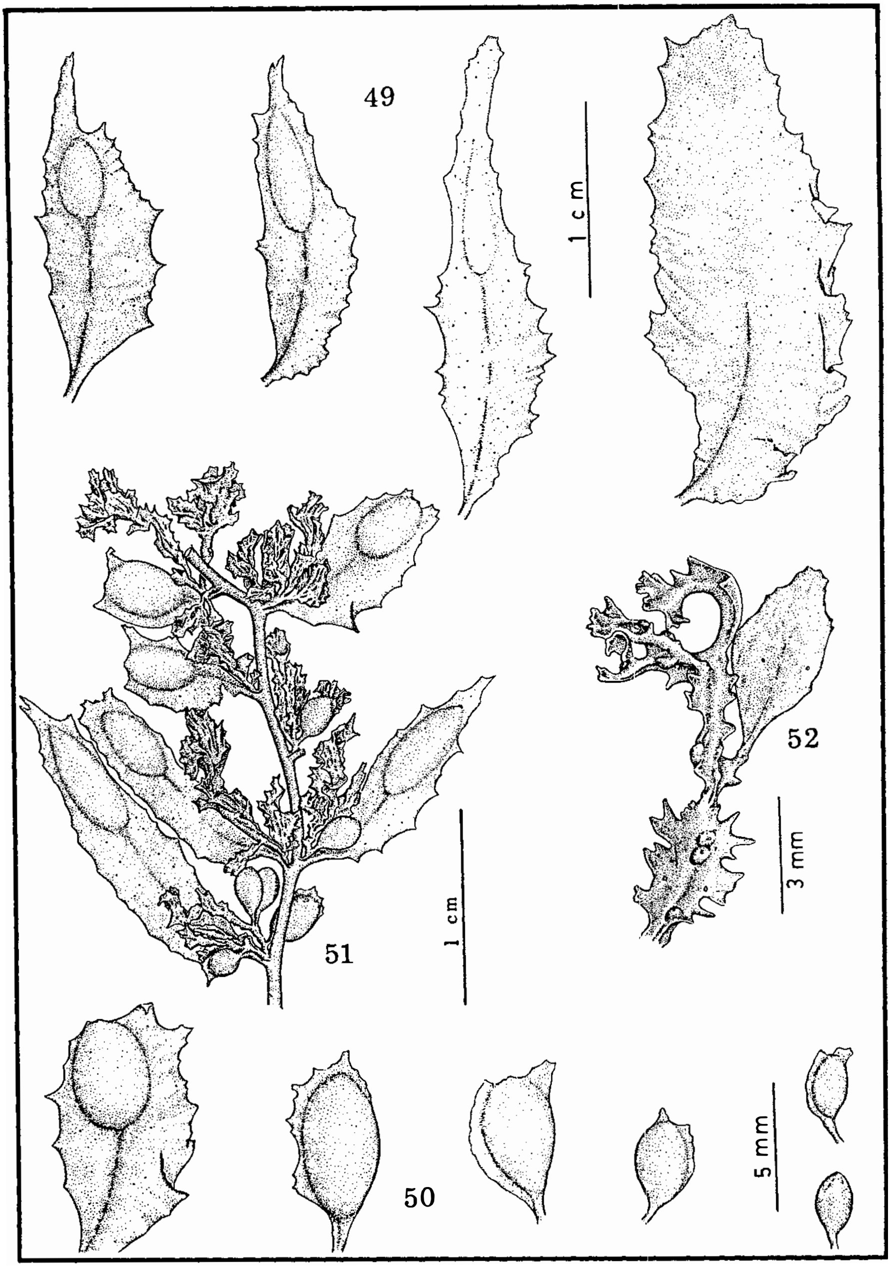
Old receptacles paniculate; receptacular branch simple or once branched, up to 30 mm long, 2 mm wide, branch distinctly three-angled, lateral wings or ridges foliaceous, slightly twisted, margin of ridges coarsely and irregularly serrate; conceptacles appear as mammillate bumps on surface of foliaceous ridges. Young receptacles forming a dense cyme, each cluster subtended by a phyllocyst; receptacular branch simple, flat to triquetrous, twisted, up to 6 mm long and 1.5–2.0 mm wide, expanded ridges foliaceous, well developed, and broad, their margins coarsely and irregularly serrate; conceptacles appear as dark bumps on flat surface of ridges; each receptacular branch subtended by a well-developed phyllocyst.

Remarks: Materials were collected from a reef in Borangan, Samar, on December 28, 1987, and January 29, 1988, respectively, by H. R. Montes and E. Colina.

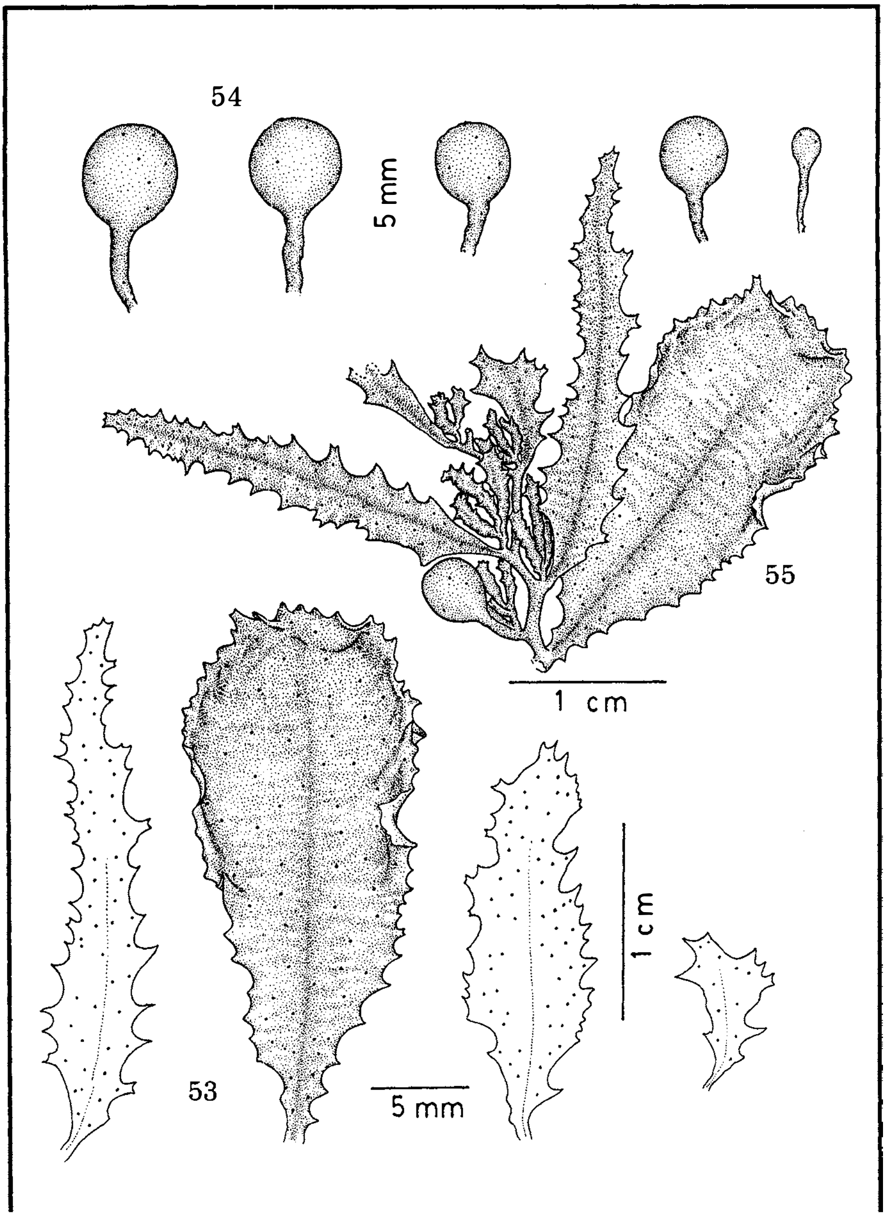
This species is distinguished by its long, foliaceous, three-angled, twisted receptacular branches; the presence of phyllocysts; and the form and shape of its vesicles.

Sargassum sp. No. 3 (Figs. 53–55, 100)

Only one specimen was available for examination, and its holdfast and the basal portion of the stem were missing. Primary branch up to 50 cm long, smooth, terete throughout; branched rhizoidal holdfast arising from base of primary branches; tips of some branches modified into attachment organs; secondary branches attached at intervals of 2–3 cm along primary branch, terete, longest at middle portion of thallus (up to 10 cm long), becoming shorter toward distal end; cryptostomata present. Leaves of secondary branches oblong-elliptical to oblong-lanceolate, up to 16 mm long, 10 mm wide; base slightly asymmetrical, acute; margin dentate to somewhat double dentate; tip rounded to obtuse; midrib very faint; cryptostomata numerous, scattered, distinct, slightly elevated. Leaves of tertiary or upper order branches oblong-oblanceolate to linear-oblanceolate or linear-lanceolate, up to 30 mm long, 3 mm wide; base acute to acuminate,



Figs. 49–52. ***Sargassum*** **sp. No. 2. Fig. 49, Leaves and phyllocysts from different branch orders. Fig. 50, Forms of vesicles. Fig. 51, Portion of branch with young receptacles. Fig. 52, Detailed drawing of a portion of an old receptacular branch.**



Figs. 53–55. *Sargassum* sp. No. 3. Fig. 53, Leaves from different branch orders. Fig. 54, Forms of vesicles. Fig. 55, Portion of branch with receptacles.

asymmetrical; margin irregularly serrate to somewhat double serrate (some teeth are divided); tip acuminate to obtuse; midrib also faint; cryptostomata numerous, scattered, slightly elevated. Vesicles obovate, slightly compressed, up to 4 mm long, 3 mm wide; stalk up to 4 mm long, terete to slightly compressed, distinctly flattened, some slightly ribbed or winged with one or more teeth; cryptostomata present.

Receptacle a loose cyme, axillary, attached to base of stalk of leaf or vesicle; consists of two or three receptacular branches terete at base and slightly compressed to flattened or slightly three-sided at distal portion; slightly warty, up to 3 mm long, 1 mm wide.

Local Distribution: San Isidro, Little Balatero, Baradero Bay, Puerto Galera, and Oriental Mindoro.

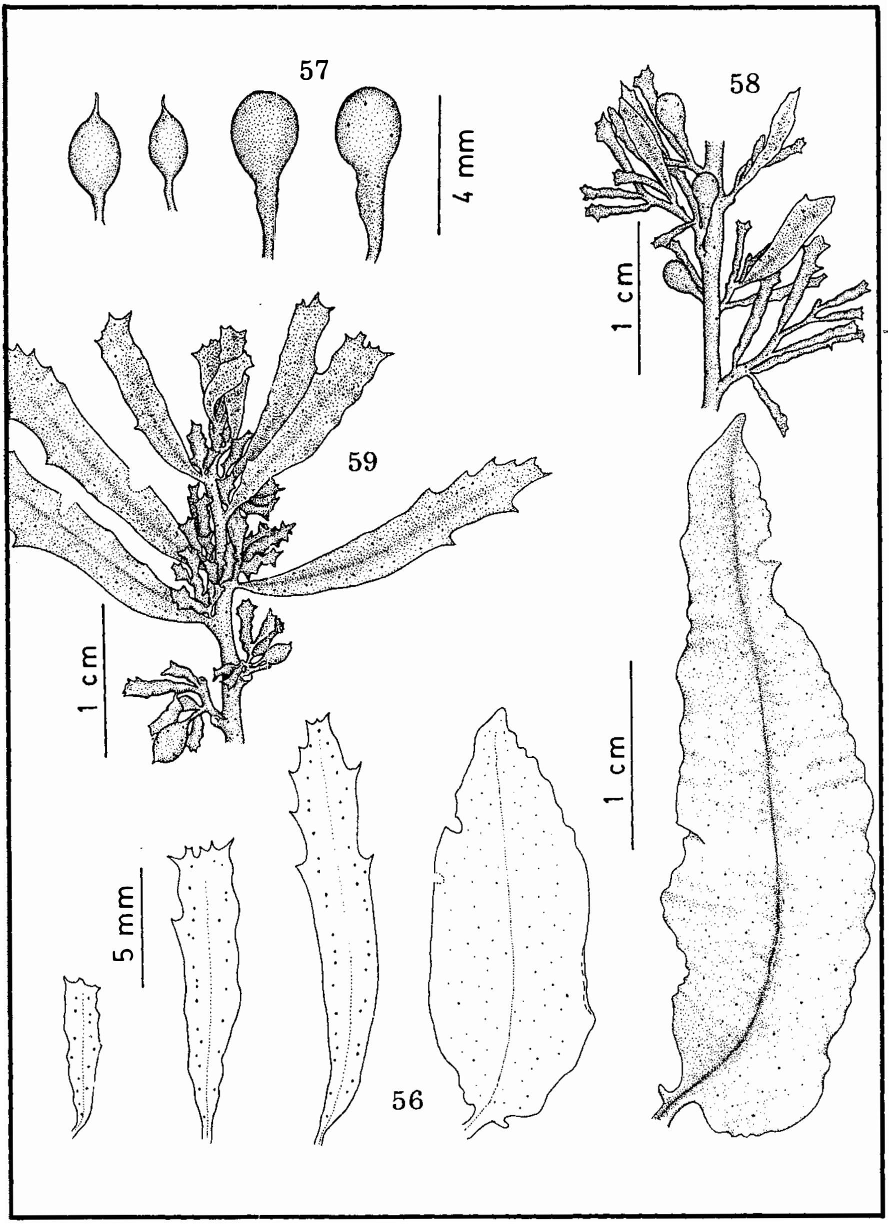
Remarks: The material distinctly belongs to the *Herporhizum* group of Dawson (1944) because of the presence of rhizoidal holdfast. It is, however, distinct from *S. herporhizum* Setchell et Gardner and *S. brandegeei* Setchell et Gardner from the Pacific Coast of North America in almost all other characteristics. It is nearer to *S. herporhizum* materials from Pangasinan, La Union, and Mindoro reported by Modelo (1988, p. 151), but it differs from these materials by its linear-lanceolate leaves of the upper order branches and the long stalk of the vesicle.

Sargassum sp. No. 4 (Figs. 56–59, 117)

Holdfast shield-shaped; stem up to 10 mm long, compressed, broader at smooth base, becoming narrow and slightly warty toward distal end. Primary branches crowded at distal end of stem, distinctly compressed at base, terete at upper portion, up to 45 cm long; secondary laterals terete, arranged alternately along primary branch, slightly lumpy because of cryptostomata, at intervals of 1–2 cm, up to 20 cm long, lower ones longer, becoming shorter toward tip of primary branch, giving shoot a conical shape. Leaves of young primary branches lanceolate to oblong-lanceolate, up to 38 mm long, 12 mm wide; base distinctly asymmetrical; short stalk; margin entire; tip obtuse; midrib apparent almost at tip; cryptostomata few to numerous, small, not elevated. Leaves of fertile secondary branches more or less uniformly lanceolate, to linear-lanceolate, up to 30 mm long, 5 mm wide; base acute, slightly asymmetrical, attached by short stalk with lateral spines; margin regularly serrate, in distal parts of blade, the basal portion of leaves of terminal branches entire; tip acute or blunt; cryptostomata numerous, very distinct, elevated, arranged in rows at both sides of midrib (especially in linear-lanceolate forms); midrib distinct but disappearing just below tip. Vesicles few, not apparent, oblong, obovate to slightly fusiform, up to 25 mm long; stalk terete or flattened; tip plain or with a sharp point; lumpy because of large elevated cryptostomata.

Plant dioecious. Male receptacle racemose to paniculate; receptacular branches simple or branched, terete at base, becoming compressed toward the tip, with few large teeth along the edges and tip, up to 12 mm long, 0.5 mm in diameter. Female receptacle a dense panicle; receptacular branches short, up to 2.5 mm long, 0.5 mm wide, some terete at base, becoming compressed toward distal portion, with a tendency to slightly twist at tip, coarse teeth present at edge and tip of branch.

Remarks: This particular species resembles *Sargassum* sp. No. 5 somewhat in habit and shape of the leaves, although species No. 5 has slightly broader leaves with simple serrate margins. Species No. 4 also has fewer oblong vesicles compared with the numerous spherical vesicles of species No. 5. The female receptacular branches of these two species are quite similar, but the terete male receptacular branches of species No. 5 differ markedly from the compressed male receptacular branches of species No. 4.



Figs. 56–59. *Sargassum* sp. No. 4. Fig. 56, Leaves from different branch orders. Fig. 57, Forms of vesicles. Fig. 58, Portion of branch with male receptacles. Fig. 59, Portion of branch with female receptacles.

Materials were collected from Barrio Pangil, Currimao, Ilocos Norte, Philippines, May 1983 by Ang Put, Jr.

Sargassum sp. No. 5 (Figs. 60–64, 101)

Holdfast shield-shaped, well developed, occasionally fused with neighboring holdfast; stem up to 30 mm long, warty; primary branches up to 40 cm long, compressed near base, terete at upper portions; secondary branches terete, up to 5 cm long, alternately disposed along primary branches, sparingly lumpy because of slightly elevated cryptostomata. Leaves of primary branches linear to linear-lanceolate, up to 40 mm long, 7 mm wide, short stalked to sessile; base asymmetrical with one or more spines, obtuse or acute; margin slightly undulate, irregularly serrate-dentate; tip acute to obtuse; midrib percurrent from base to tip; cryptostomata numerous, distinct, slightly elevated, scattered. Leaves of secondary branches linear to slightly linear-lanceolate, acuminate slightly asymmetrical; up to 22 mm long, 3 mm wide, very short stalked; base with spines; margin serrate to double serrate, teeth sharp; tip obtuse to acuminate; midrib apparent, almost up to tip; cryptostomata very distinct, numerous, and slightly elevated, with tendency to form rows along both sides of midrib. Vesicles numerous, closely associated with receptacles (zygocarpic), mainly spherical or obovate, up to 2 mm long, 1.5 mm broad, muricate because of elevated cryptostomata. In mature specimens vesicles and receptacles concentrated on basal four-fifths of secondary branch; leaves in this portion of branch fall off and only those near tip of the branch remain intact.

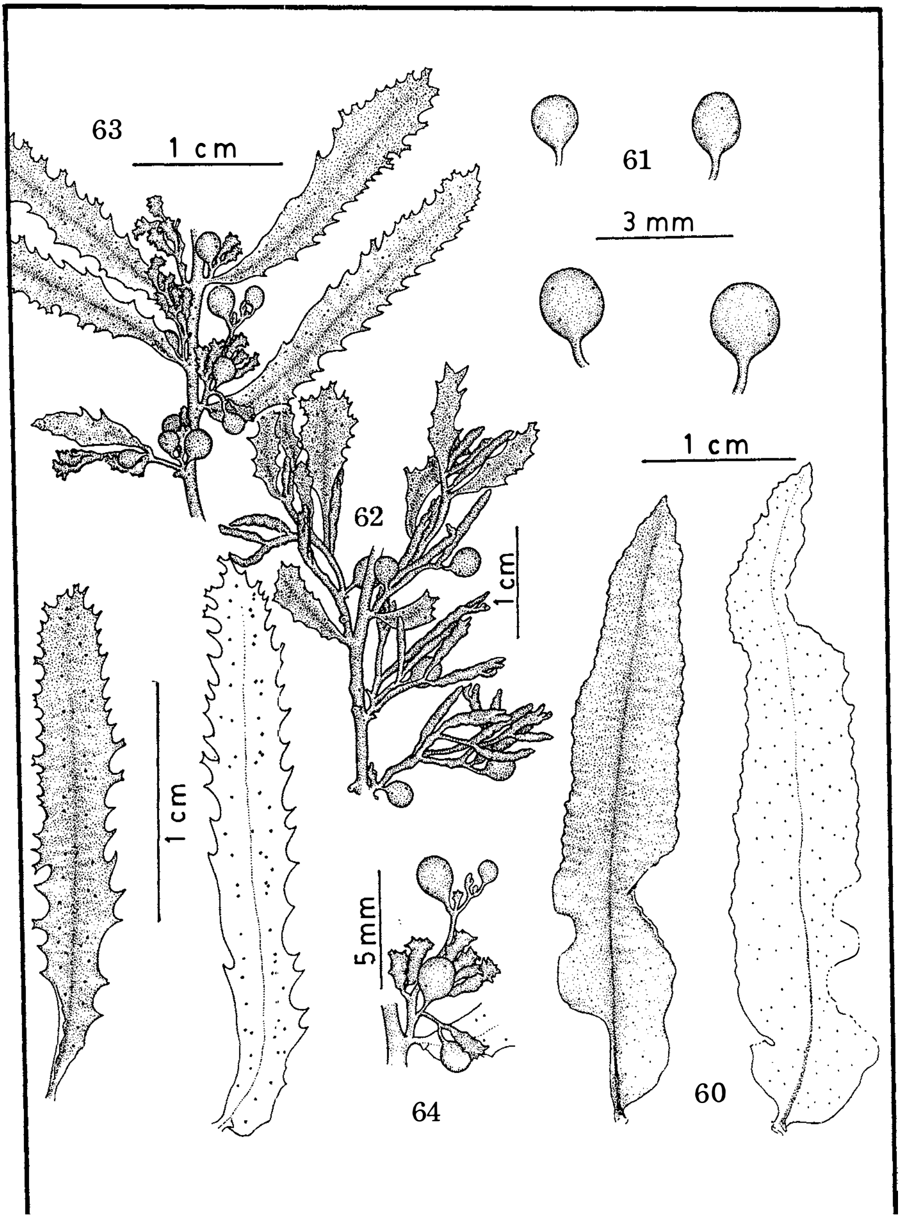
Plant dioecious. Receptacle cymose (young) or racemose (mature). Female receptacular branch short, compressed-flattened near base becoming three-sided at tip in well-developed ones, with teeth along margin and tip, up to 3 mm long, 1.2 mm wide. Male receptacular branch terete, warty, simple to twice branched, up to 7 mm long, 0.6 mm in diameter, tip blunt.

Remarks: This species is similar to *Sargassum* sp. No. 4 in habit but differs significantly. Species No. 5 has numerous, small spherical vesicles, and fhe forms of the male and female receptacular branches differ from those of species No. 4.

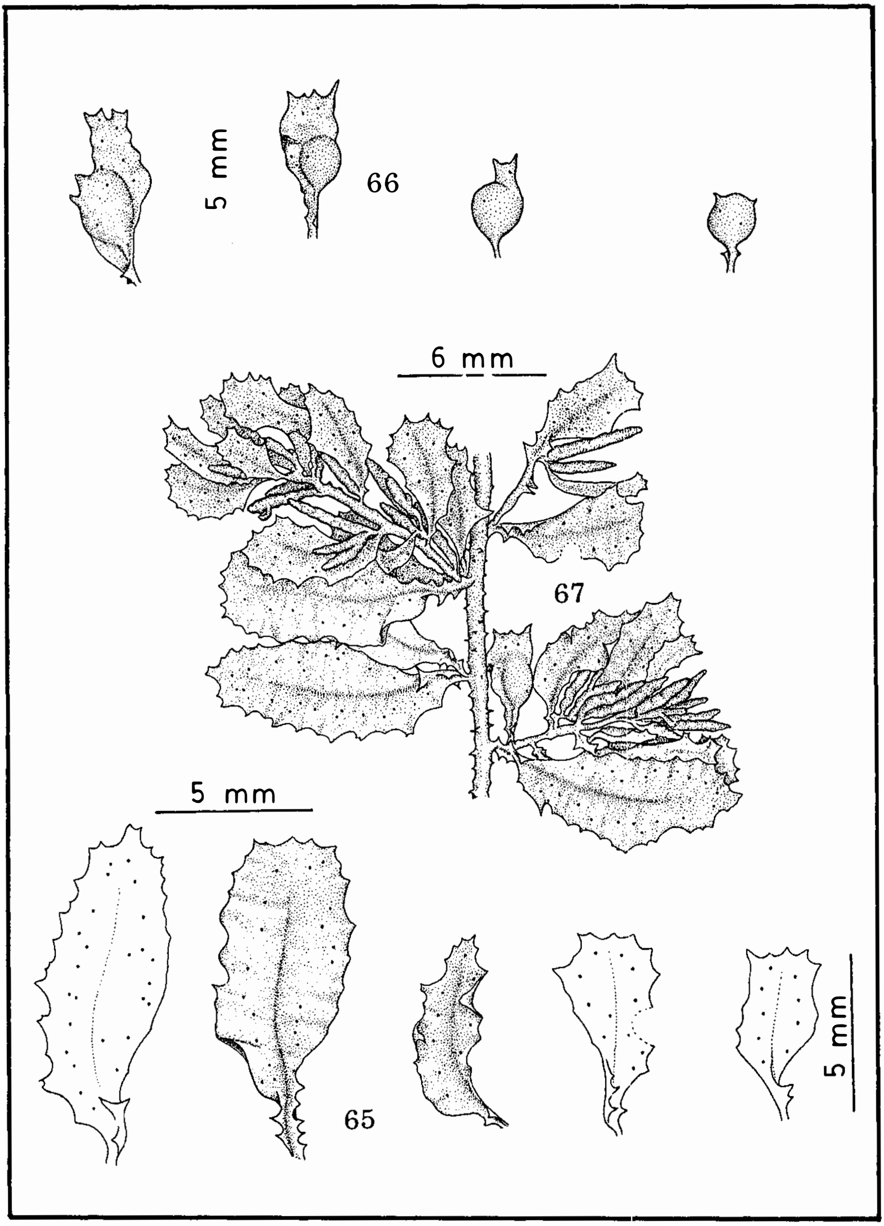
Materials were collected from Barrio Balingasay, Bolinao, Pangasinan, January 1983.

Sargassum sp. No. 6 (Figs. 65–67, 102)

Holdfast discoid, up to 1 cm wide; stem up to 30 mm long; base smooth, enlarged, tapering toward smaller, warty upper portion where bases of primary branches are crowded. Primary branches slightly compressed, highly muricate at their basal portions, up to 45 cm long, terete and slightly muricate in upper portions; secondary branches up to 7.5 cm long, regularly and alternately disposed at intervals of 1–2.5 cm along primary branch; terminal branches short, about 5–6 mm long near base, becoming shorter and attached at closer intervals toward distal end of secondary branch, densely covered with leaves and receptacles, giving secondary branches a distinctly lanceolate shape. Leaves coriaceous, those of the young and nonfertile lower branches distinctly oval-elliptical, up to 9 mm long, 5 mm wide, vertically attached by a short stalk; base asymmetrical, adaxial base of blade expanded laterally, margin with several teeth; plane of expansion at right angles to plane of blade; margin of blade entire; tip rounded; midrib disappearing; cryptostomata small, few, and not apparent. Leaves of upper fertile branches more variable in shape, oblong-obovate to broadly oblanceolate, up to 10 mm long, 4 mm wide; base more asymmetrical than those of young primary branches, adaxial part also laterally expanded with marginal teeth; margin of blade irregularly serrate; tip obtuse, acute, or



Figs. 60–64. ***Sargassum*** **sp. No. 5. Fig. 60, Leaves from different branch orders. Fig. 61, Forms of vesicles. Fig. 62, Portion of branch with male receptacles. Fig. 63, Portion of branch with female receptacles. Fig. 64, Detailed drawing of female receptacular cluster.**



Figs. 65–67. ***Sargassum*** **sp. No. 6. Fig. 65, Leaves from different branch orders. Fig. 66, Forms of vesicles. Fig. 67, Portion of branch with receptacles.**

rounded; midrib disappearing, not apparent; cryptostomata distinct, scattered, slightly elevated. Vesicles few, small, spherical, oval or obovate, up to 2 mm long, 1.8 mm in diameter, some appear to be slightly compressed; stalk short, terete, with or without spine, one-third or less than length of vesicle; tip with small spine or winged coronal leaf; lumpy in appearance because of cryptostomata.

Receptacle cymose; receptacular branch terete, simple or branched at tip, verrucose, up to 3 mm long, 0.4 mm in diameter, with blunt tips.

Remarks: The basal parts of the primary branches with hard excrescences; the distinctive base of the blade; the vesicles with coronal leaf; the distinctive shape of the secondary branch (or shoot); and the almost determinate tertiary laterals are distinctive of this species. The habit of this species resembles the habit of a certain fern.

Only one specimen was available. It was collected from Cabugao Bay, Virac, Catanduanes, February 22, 1962.

Sargassum sp. No. 7 (Figs. 68–70, 103)

Holdfast discoid, about 4 mm in diameter; stem very short, 5 mm long, terete, finely villose; primary branches crowded at tip of stem, compressed at base, terete above; primary, secondary, and terminal branches spinous, spines simple or branched. Leaves glaucescent, vertically attached, oblong-elliptical to elliptical, up to 10 mm long, 5 mm wide; stalk short; base distinctly asymmetrical, base of leaf at adaxial side expanded or winged with coarse teeth at margin, plane of expansion at right angles to plane of blade; margin entire, sometimes with one or more dull teeth; tip rounded to obtuse; midrib apparent near base but disappearing toward upper two-thirds of the leaf; cryptostomata few, inconspicuous, with tendency to be arranged in rows. Vesicles very few and small, presence not apparent, somewhat spherical to compressed, ribbed; stalk short, compressed; tip plain or acuminate; cryptostomata not apparent.

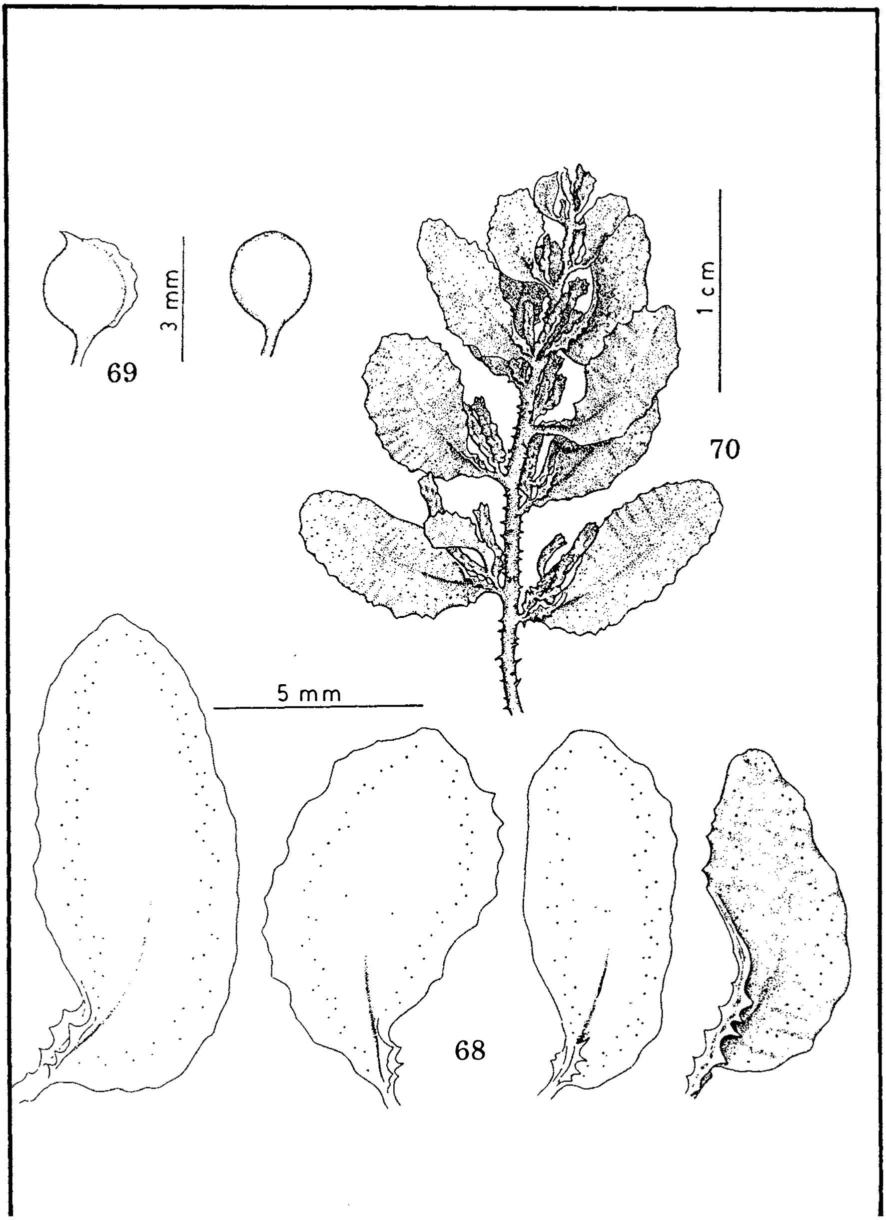
Receptacle a simple cyme with two forms. In young receptacles, receptacular branch may be simple or once branched, branches compressed and straight, slightly warty, margin with teeth or spines. In older receptacles, basal one-half or two-thirds terete to slightly compressed and highly warty, with or without teeth, their distal half compressed to flattened, with teeth, and slightly twisted. In others, distal portion becomes triquetrous and twisted, margins with teeth; in still others, two or more triquetrous segments develop at tip of old receptacular branches.

Remarks: This particular species differs from the other glaucous species by the more elliptical shape of its leaves with their very distinctive base; the spiny branches; flattened to three-sided receptacular branches; and very few, small vesicles.

Materials (T12202 and T12683) were collected from Tiwi Beach, Albay, February 5, 1962; T14853 was collected from Pulong Bakaw, Calatagan, Batangas, November 11, 1978.

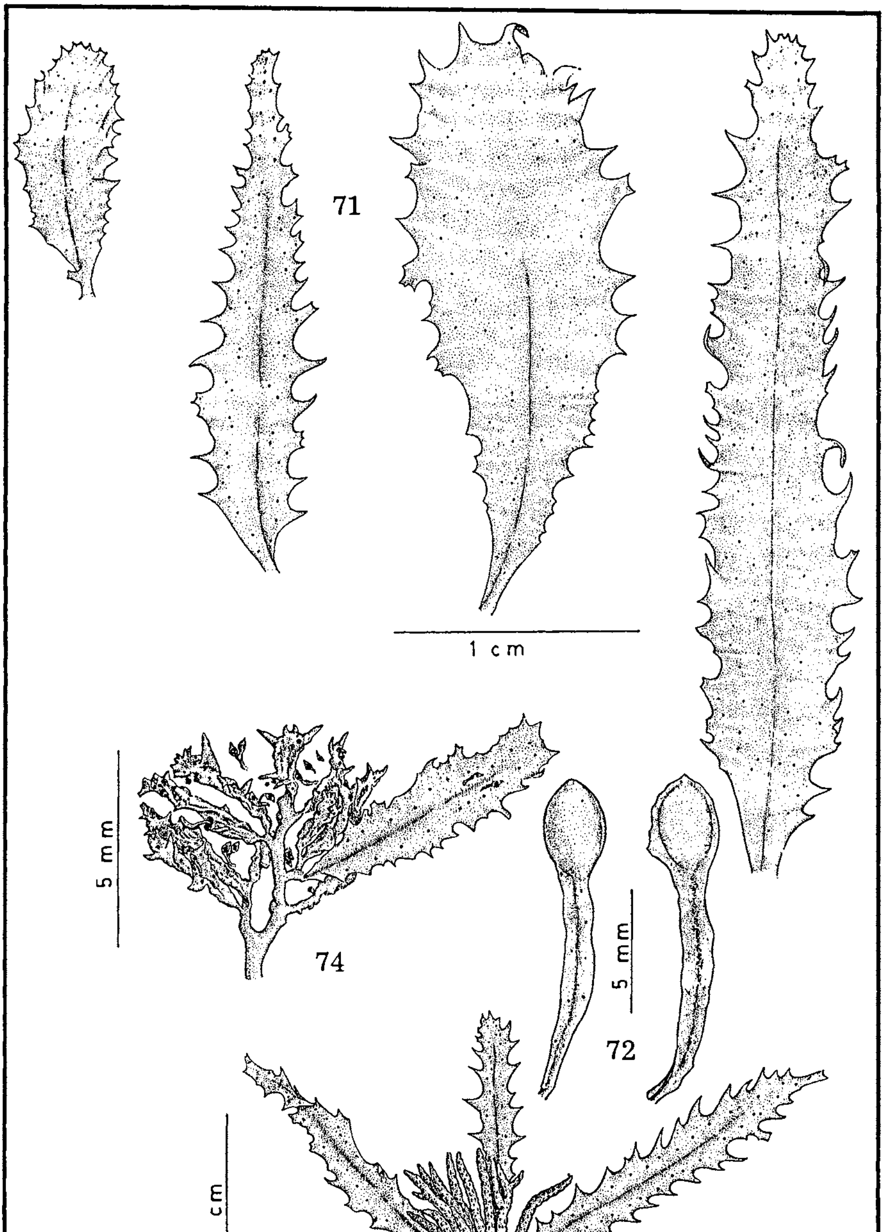
Sargassum sp. No. 8 (Figs. 71–74, 104)

Holdfast shield-shaped to discoid; stem very short, up to 5 mm long, terete, smooth. Primary branches strongly flattened at basal portion to compressed toward distal portion; secondary laterals compressed, pinnately-alternately arranged on primary branch, lower ones up to 50 mm long, becoming gradually shorter toward tip of primary branch, giving shoot a distinctly conical shape. Leaves of upper secondary laterals uniformly lanceolate to linear-lanceolate, up to 30 mm long, 5 mm wide; some on lower secondary laterals oblanceolate, up to 22 mm long, 10 mm wide; margin coarsely and deeply dentate-serrate;



Figs. 68–70. ***Sargassum*** **sp. No. 7. Fig. 68, Leaves from different branch orders. Fig. 69, Forms of vesicles. Fig. 70, Portion of branch with receptacles.**

Figs. 71–74. ***Sargassum*** **sp. No. 8. Fig. 71, Leaves from different branch orders. Fig. 72, Forms of vesicles. Fig. 73, Portion of branch with male receptacles. Fig. 74, Portion of branch with female receptacles.**


71
1 cm
74
5 mm
72
5 mm
73
1 cm

base acute; tip acute, rounded, or obtuse; midrib distinct but disappearing toward tip; cryptostomata distinct, elevated, scattered on broader leaves but with tendency to form rows on linear ones. Vesicles few, distinctly ellipsoidal, up to 5 mm long, 3 mm wide, entire or winged; tip obtuse; stalk flattened, very long, at least three times longer than length of vesicle; cryptostomata few.

Plants dioecious. Receptacle a cyme; receptacular branches simple or branched; male receptacular branch terete, slightly verrucose, up to 7 mm long, 0.5 mm in diameter, slightly tapered toward tip; female receptacular branch distinctly flattened and twisted toward distal half, up to 5 mm long, 1 mm wide; margin with large coarse teeth/spine.

Remarks: The only species that appears to be similar in habit and branching to *Sargassum* sp. No. 8 is *S. xishaense* Tseng et Lu. However, the flat branches, the coriaceous leaves with their markedly serrate-dentate margins, the flat and twisted female receptacles, and the dioecious plant of species No. 8 differentiate it from *S. xishaense*.

Materials were collected from Palawig, Zambales, Philippines, May 27, 1985.

Sargassum sp. No. 9 (Figs. 75–79, 105)

Holdfast discoid to conical; stem slightly compressed, up to 10 mm long; new laterals arising from holdfast or stem; primary branches many, crowded at tip of stem, terete, smooth or slightly lumpy at base, up to 40 cm long, filiform; secondary branches terete, smooth (or slightly lumpy because of leaf scar), up to 15 cm long, attached to primary branch at intervals of about 1 cm; terminal branches smooth, terete; cryptostomata sparse. Leaves highly glaucescent, thin, both surfaces of leaves silver-gray under low magnification, linear-oblong, oblanceolate or lanceolate, up to 40 mm long, 13 mm wide; those of secondary or fertile branches smaller, up to 15 mm long, 3 mm wide; stalk relatively short, terete, grading with acuminate, symmetrical base; margin entire or very slightly and sparsely denticulate, teeth small and hardly apparent under low magnification; tip rounded-obtuse to sometimes slightly apiculate, those associated with receptacles acute; midrib disappearing, not apparent; cryptostomata small, few, with tendency to be arranged in rows. Vesicles oblong-elliptical to oblong-obovate, up to 2–2.5 mm long, 1.5 mm wide, more numerous toward distal portions of branches; stalk short, less than one-third the length of vesicle; tip plain, apiculate, or with filiform coronal leaf, closely associated with receptacle; entire vesicle smooth; cryptostomata few, small, not very apparent.

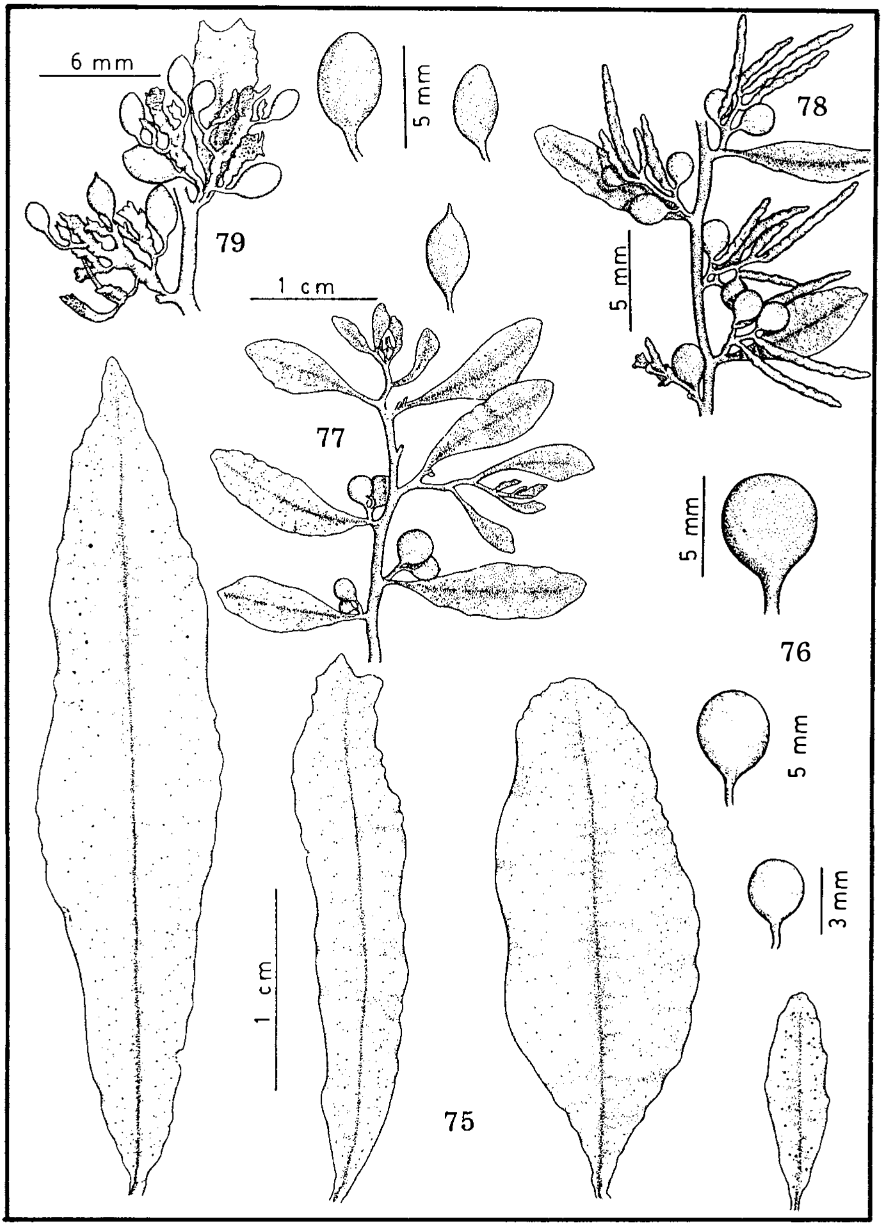
Plant dioecious. Male receptacle solitary or simple raceme, receptacular branch terete, torulose, always subtended by a leaf or vesicle. Female receptacle zygocarpic, a cyme or panicle, receptacular branch short, up to 4 mm long, 0.8 mm wide, terete, compressed near base or three-sided at tip with blunt teeth or spines, each receptacular branch always subtended by a leaf or vesicle, which may give rise to further vesicles or leaves.

Remarks: This species is one of the two taxa with distinctly glaucescent leaves. It differs from the other glaucescent species by its smooth terminal branches; linear-oblong to oblanceolate leaves; oblong to elliptical vesicles; and terete male receptacular branches and zygocarpic female receptacles, with compressed to trigonous branches.

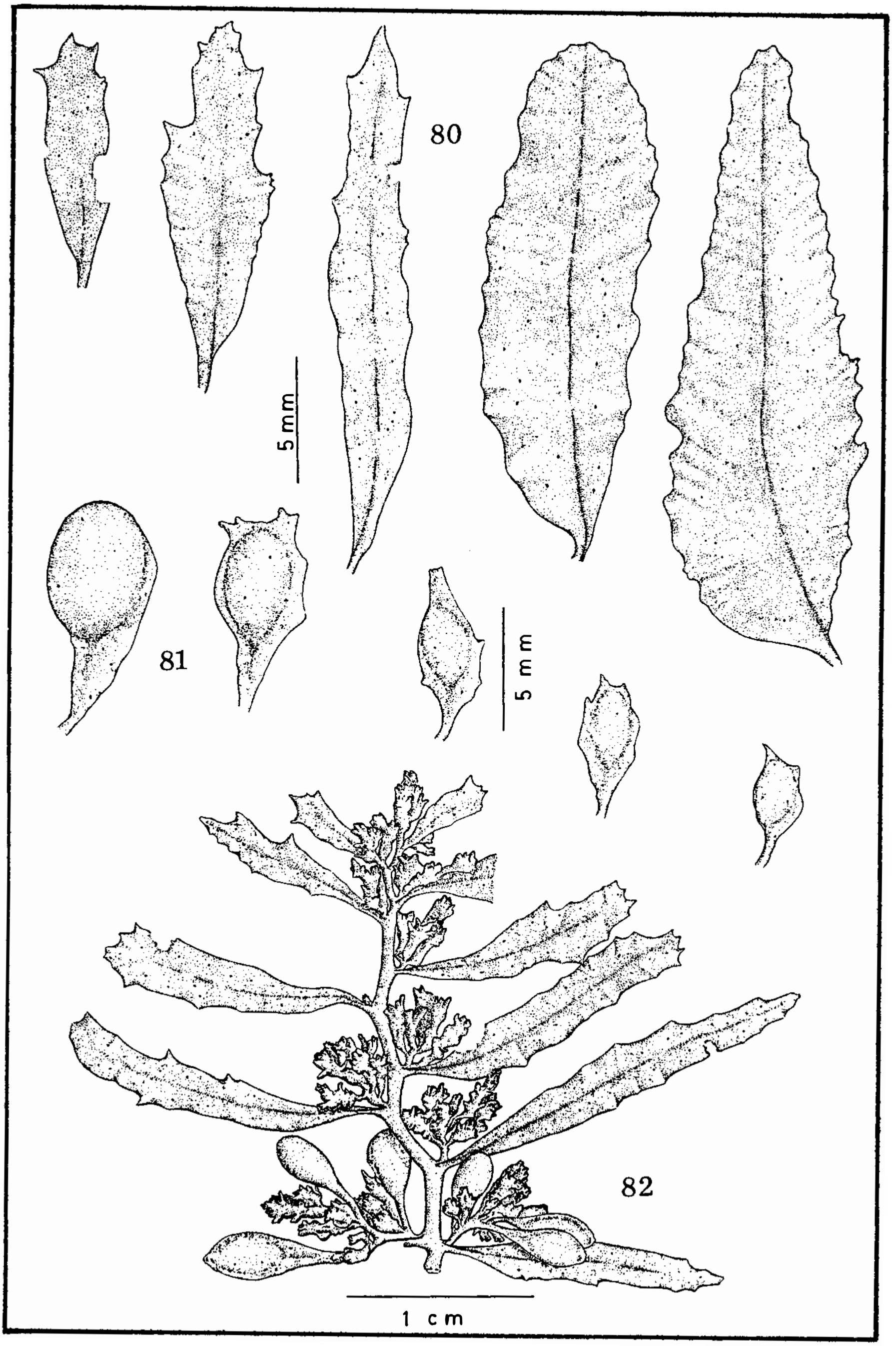
Materials (T12115 and T12114) were collected from Sitio Saay, Limay, and Puting Buhangin, Orion, both in Bataan, August 5, 1968.

Sargassum sp. No. 10 (Figs. 80–82, 106)

Holdfast shield-shaped; stem very short, about 5 mm long, terete, brownish, finely



Figs. 75–79. *Sargassum* sp. No. 9. Fig. 75, Leaves from different branch orders. Fig. 76, Forms of vesicles. Fig. 77, Portion of a young fertile branch. Fig. 78, Portion of branch with male receptacles. Fig. 79, Portion of branch with female receptacles.



Figs. 80–82. ***Sargassum*** **sp. No. 10. Fig. 80, Leaves from different branch orders. Fig. 81, Forms of vesicles. Fig. 82, Portion of branch showing receptacles.**

villous; primary and secondary branches compressed, smooth, up to 45 cm long; upper order branchlets terete and smooth; secondary branches alternate-pinnate on primary branch. Leaves of lower secondary laterals elliptical to oblong, obovate or oblong-lanceolate; base asymmetrical; margin entire or irregularly dentate; tip rounded to obtuse to sometimes emarginate; midrib disappearing near tip; cryptostomata sparse, scattered. Leaves on upper secondary branches mainly linear-lanceolate to narrowly oblong or oblanceolate, up to 25 mm long, 6 mm wide; bases slightly unequal, acute; margin slightly wavy, entire to irregularly dentate, or serrate toward acute to obtuse tip; midrib disappearing toward tip; margin of leaves at distal part of secondary laterals mainly entire and irregularly serrate toward tips; midrib indistinct; cryptostomata on leaves at tips of laterals distinct, with tendency to be arranged in rows. Vesicles few, elliptical to oblong or oblong-elliptical, slightly compressed, up to 5 mm long, 4 mm wide; stalk as long as or slightly shorter than vesicle, flattened, narrowly winged or ribbed; tip plain, mucronate, or with few teeth; cryptostomata few.

Receptacle densely cymose; receptacular branches once or twice branched, generally cuneate, up to 4 mm long, 1.5 mm at broadest portion, narrow and compressed at base or triquetrous becoming broader toward tip; tips coarsely toothed or lobed, center lobe twisted 90°.

Remarks: This appears to be an undescribed species. All the materials available appear to be female. This species is nearest to *S. baccularia* in the general form of the habit, the shield-shaped holdfast, the slightly compressed branches, and the linear-lanceolate leaves. However, species No. 10 is characterized by the short, terete, and smooth stem; the terete and smooth terminal branches; the slightly compressed oblong-oval to obovate vesicles with flattened stalks; and the cuneate or trigonous, toothed receptacular branches with distinctly twisted terminal lobes. In *S. baccularia*, *S. paniculatum*, and *S. siliquosum*, the compressed to trigonous female receptacular branches are more than twice as long and are not cuneate.

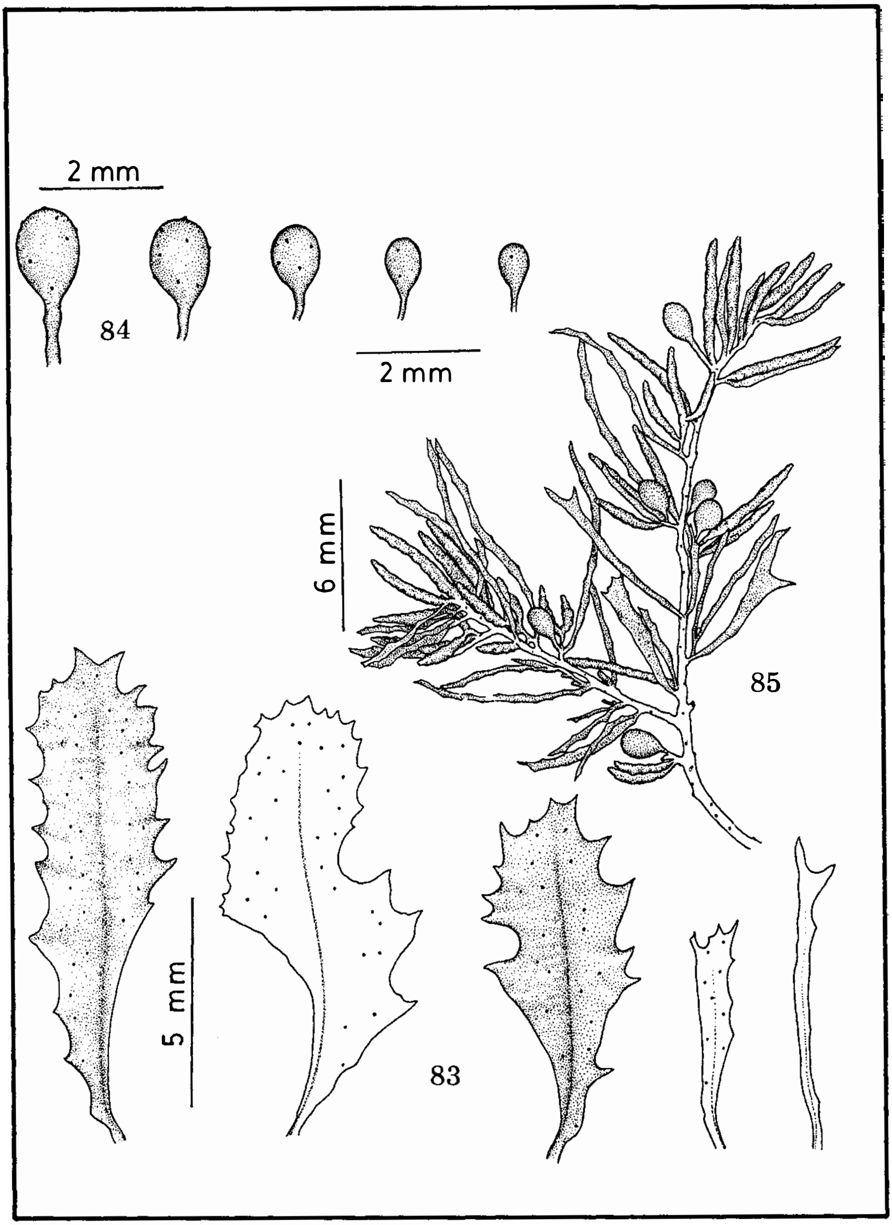
The materials were collected from a rocky, wave-exposed reef at Pangil, Currimao, Ilocos Norte, July 16, 1985, by G. C. Trono, Jr.

Sargassum sp. No. 11 (Figs. 83–85, 107)

Holdfast discoid and lobed; stem very short, less than 2 mm, slightly rugose, indistinct; primary branches originate from both stem and holdfast, somewhat compressed at base but terete above, up to 40 cm long, filiform, smooth; secondary and terminal branches slightly lumpy because of elevated cryptostomata. Secondary branches at distal half or third of primary branches attached at intervals of about 1–2 cm, with intervals becoming closer toward tip; length of secondary laterals about 30 cm, decreasing in length toward tip, producing a conical (pine-tree-like) shape. Leaves of young secondary branches small, linear-oblanceolate, up to 7 mm long, 1.5 mm wide at their broadest portion; stalk short; base acuminate; margin entire near base or coarsely serrate toward distal half; tip acuminate; midrib not apparent; cryptostomata distinctly elevated, giving leaves a spiny appearance. Leaves associated with receptacles linear, cylindrical, and filiform, up to 10 mm long, less than 0.5 mm in diameter, mainly cylindrical in cross section or some compressed toward distal half with few teeth; spiny in appearance because of dark, slightly elevated cryptostomata.

Vesicles numerous, muricate because of cryptostomata; oblong-elliptical, up to 2 mm long, 1 mm wide; stalk terete, relatively long, as long as or longer than length of vesicle.

Receptacle a lax raceme; receptacular branch simple or branched, branch terete and



Figs. 83–85. *Sargassum* sp. No. 11. Fig. 83, Leaves from different branch orders. Fig. 84, Forms of vesicles. Fig. 85, Portion of branch showing receptacles and filiform leaves.

pinched in here and there.

Remarks: *S. microceratium* is the only species that appears to be similar to species No. 11 in the form of the leaves. That is, filiform leaves are associated with the receptacles, but the leaves of the nonfertile branches are much longer. The oblong-elliptical, long-stalked vesicles and the spiny appearance of the terminal branches and vesicles due to elevated cryptostomata are distinct characters that differentiate species No. 11 from *S. microceratium*.

Materials (T12174 and T12209) were collected from Medio Island, Puerto Galera, Oriental Mindoro, May 1, 1955.

Sargassum sp. No. 12 (Fig. 108)

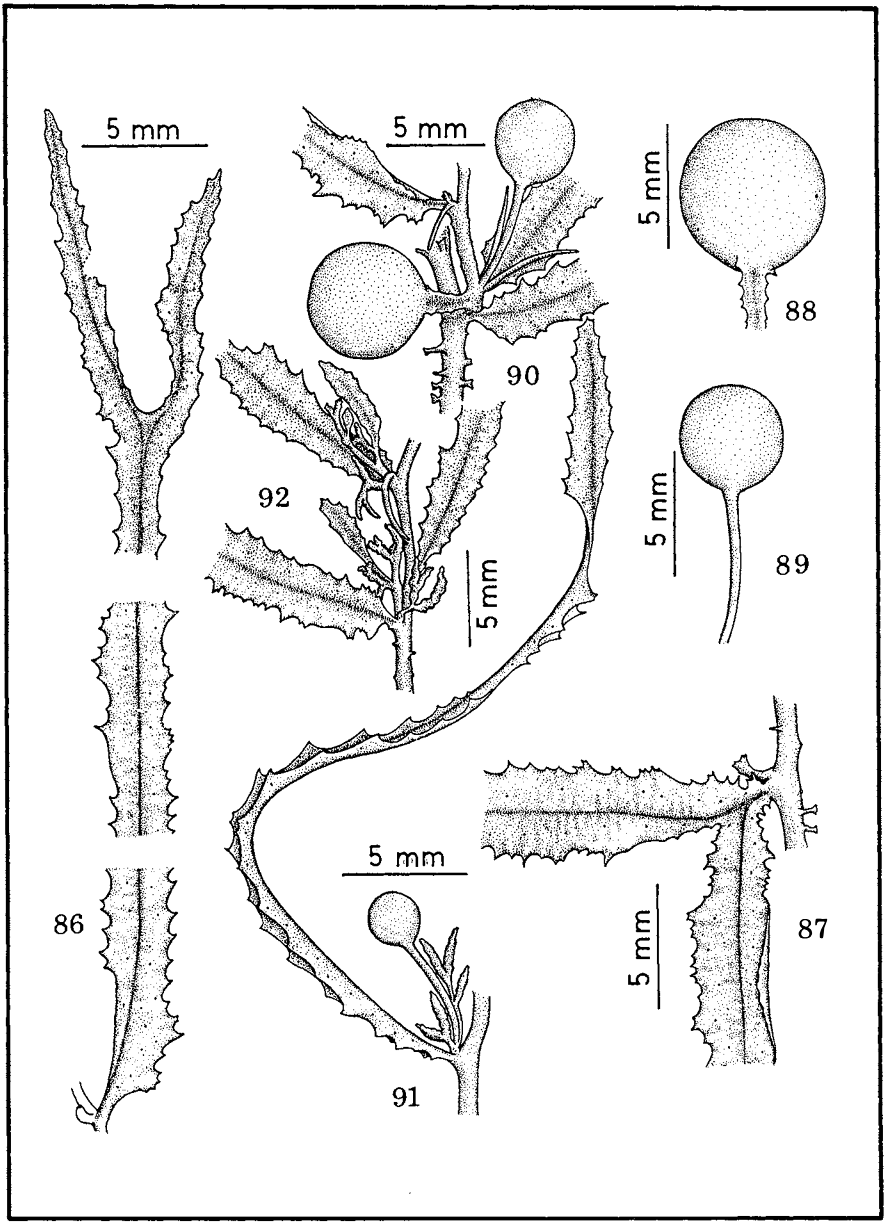
Holdfast shield-shaped, well developed; stem simple or branched, up to 4 cm long, terete, pinched in here or there; primary branches slightly compressed near base, terete at their distal portions, smooth; secondary branches short (in young thalli), up to 3 cm long, smooth, alternately arranged along primary axis at intervals of 1–4 cm. Leaves of primary and secondary laterals large, brown to slightly orange, thin and membranous, uniform in shape and form, mainly oblong to oblong-elliptical, 2–6 cm long, 1–2.5 cm wide; base asymmetrical, obtuse, sessile or with very short stalk; margin finely and regularly dentate, flat; tip rounded to obtuse; midrib distinct but evanescent below tip; cryptostomata distinct, numerous but small, scattered irregularly on blade. Vesicles few, spherical to slightly obovate, smooth, up to 8 mm long, 5 mm wide; stalk very short, generally less than one-third length of vesicle, flattened, winged, or sometimes triquetrous with teeth; cryptostomata numerous.

Remarks: All the materials available were vegetative. The large, membranous, brown to brown-orange, oblong to slightly oblong, elliptical leaves with very short stalks and the smooth and spherical vesicles of species No. 12 are distinctive among the many species included in this chapter. The lack of references has prevented me from assigning a binomial for species No. 12, but the materials seem to be nearest *S. latifolium* (Turner) C. A. Agardh.

Materials were collected from Romulo Island, Hundred Islands, Lucap, Pangasinan, July 20, 1985; T13109 was collected from El Salvador, Misamis Oriental, October 18, 1978.

Sargassum sp. No. 13 (Figs. 86–92, 118)

Materials lack holdfast and stem; primary branch slightly compressed at base but terete at upper parts, nonpercurrent, up to 35 cm long; secondary and terminal branchlets terete, spiny, processes simple or branched. Leaves of primary and secondary branches sessile, simple or some branched/divided at base or tip, coriaceous, horizontally attached, uniformly linear to linear-elongate, slightly tapering to tip, up to 50 mm long, 3–4 mm wide; base obtuse, with sharp spines; margin finely to irregularly dentate; tip obtuse to acute; midrib very distinct, elevated on ventral side and percurrent up to tip of leaf; leaves of terminal branchlets bearing receptacles with elongated cylindrical stalk grading into acuminate base; cryptostomata small, many, scattered on blade. Vesicles distinctly spherical, of two types; those arising from branch not associated with leaves or receptacle larger, up to 6 mm in diameter with short, flattened stalk; those associated with leaf or receptacle smaller, up to 4 mm in diameter and with long terete stalk, as long as or longer than vesicle. One curious character of the latter type is the development of the vesicle or the leaf associated with developing determinate laterals and the receptacle: The structure



Figs. 86–92. *Sargassum* sp. No. 13. Fig. 86, Leaf with apical portion of branch. Fig. 87, Leaf with branch portion. Fig. 88, Vesicle with short, flattened stalk. Fig. 89, Vesicle with long, terete stalk. Fig. 90, Portion of spinous branch showing the two types of vesicles. Fig. 91, Portion of branch showing a simple leaf, long-stalked vesicle, and receptacle. Fig. 92, Portion of branch showing young developing receptacles and stalk of vesicles.

FIG. 93

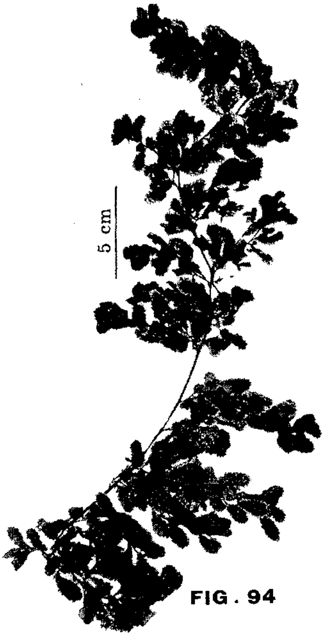


FIG. 94

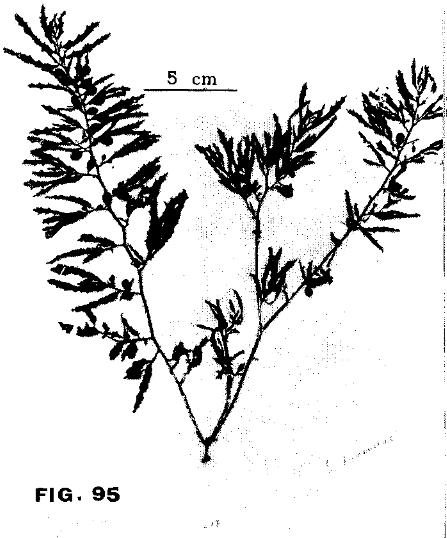


FIG. 95

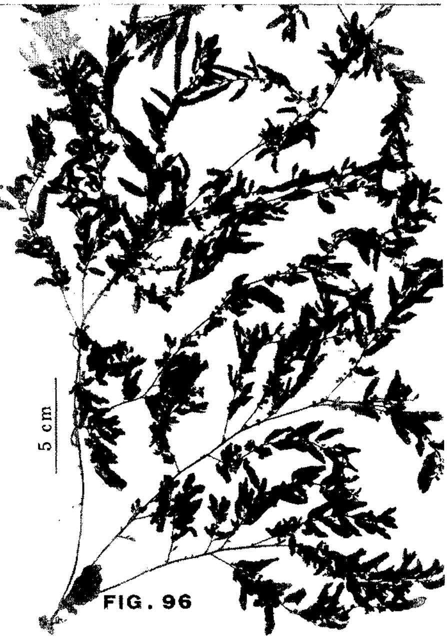


FIG. 96

Figs. 93–96. Fig. 93, *Sargassum baccularia*, habit of thallus. Fig. 94, *Sargassum feldmannii* Pham-Hoang, Habit. Fig. 95, *Sargassum kushimotense* Yendo. Habit. Fig. 96, *Sargassum paniculatum* J. G. Agardh. Habit of young thallus.

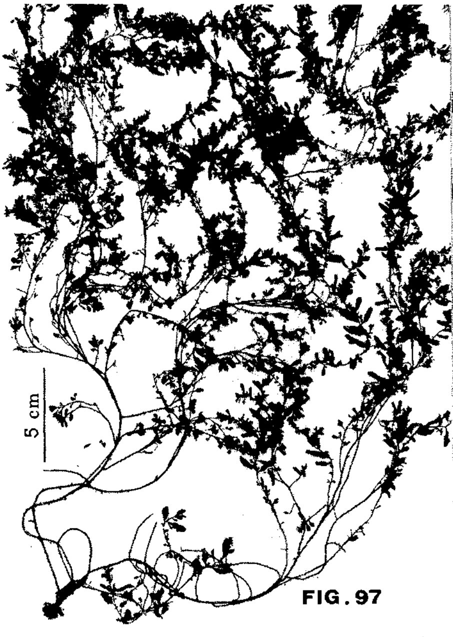


FIG. 97

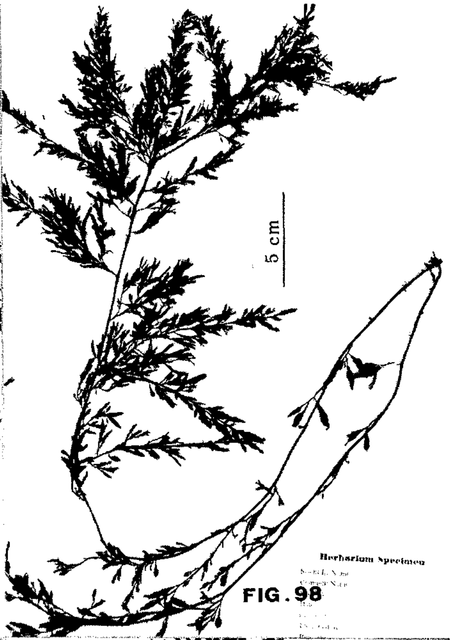


FIG. 98

FIG. 99

FIG. 100

Figs. 97–100. Fig. 97, *Sargassum siliquosum* J. G. Agardh. Habit of fertile thallus. Fig. 98, *Sargassum* sp. No. 1. Habit. Fig. 99, *Sargassum* sp. No. 2. Habit. Fig. 100, *Sargassum* sp. No. 3. Habit.

FIG. 101

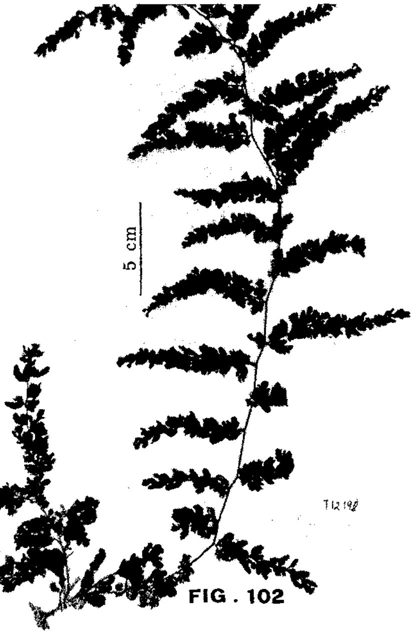


FIG. 102

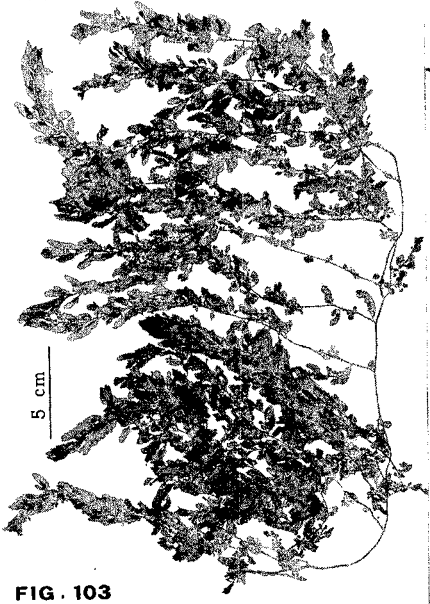


FIG. 103

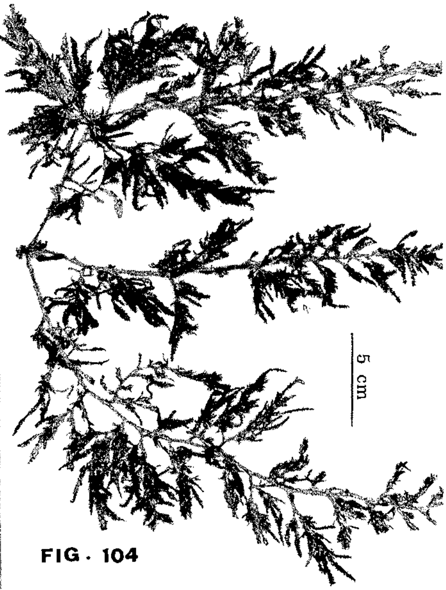


FIG. 104

Figs. 101–104. Fig. 101, *Sargassum* sp. No. 5. Habit. Fig. 102, *Sargassum* sp. No. 6. Habit. Fig. 103, *Sargassum* sp. No. 7. Habit. Fig. 104, *Sargassum* sp. No. 8. Habit.

FIG. 105

FIG. 106

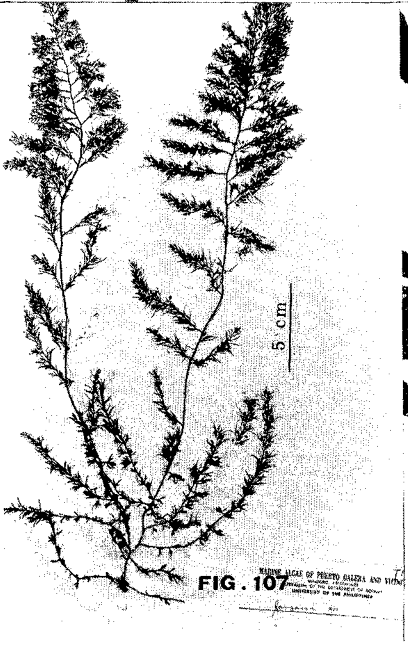


FIG. 107

FIG. 108

Figs. 105–108. Fig. 105, *Sargassum* sp. No. 9. Habit. Fig. 106, *Sargassum* sp. No. 10. Habit. Fig. 107, *Sargassum* sp. No. 11. Habit. Fig. 108, *Sargassum* sp. No. 12. Habit.

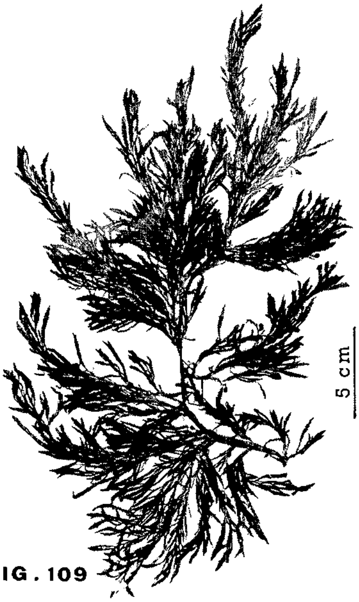


FIG. 109

FIG. 110

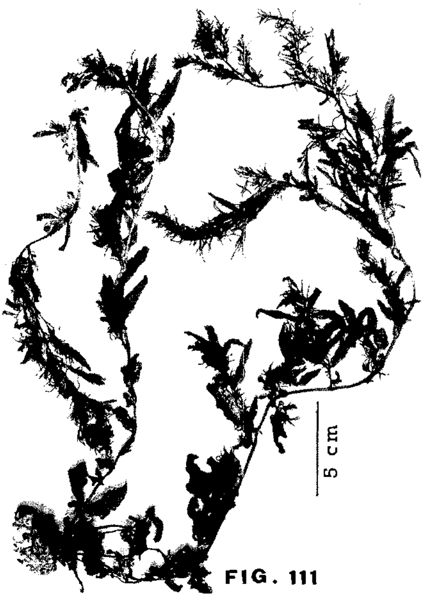


FIG. 111

FIG. 112

Figs. 109–112. Fig. 109, *Sargassum binderi* Sonder. Habit. Fig. 110, *Sargassum cinctum* J. G. Agardh. Habit of fertile female thallus. Fig. 111, *Sargassum cinctum* J. G. Agardh. Habit of fertile male thallus. Fig. 112, *Sargassum crassifolium* J. G. Agardh. Habit of fertile thallus.

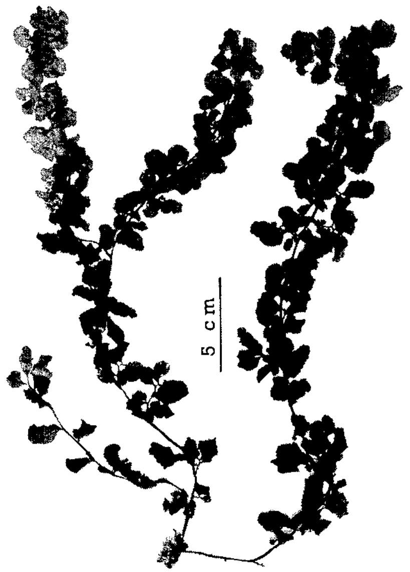


FIG. 113

FIG. 114

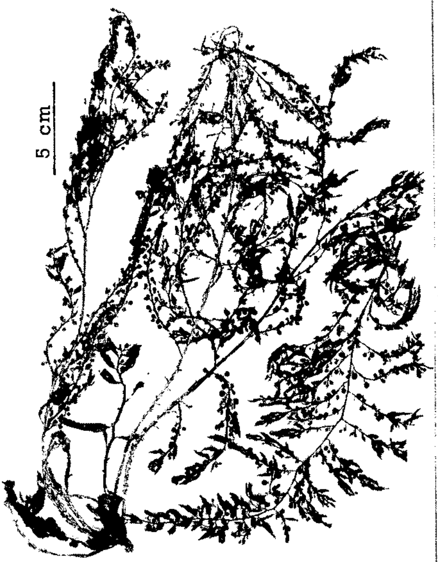


FIG 115

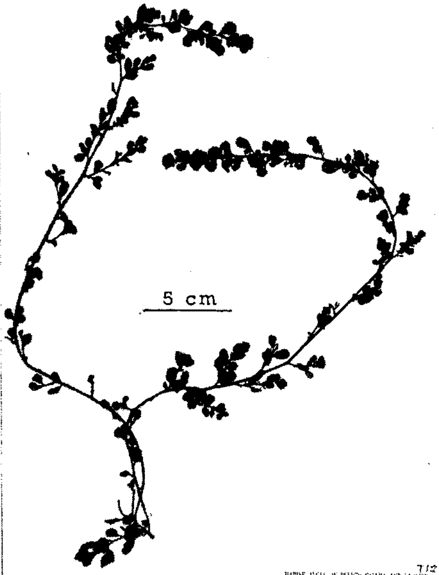


FIG. 116

Figs. 113–115. Fig. 113, *Sargassum cristaefolium* C. A. Agardh. Habit. Fig. 114, *Sargassum hemiphyllum* C. A. Agardh. Habit of fertile thallus. Fig. 115, *Sargassum oligocystum* Montagne. Habit of fertile thallus. Fig. 116, *Sargassum turbinarioides* Grunow. Habit.

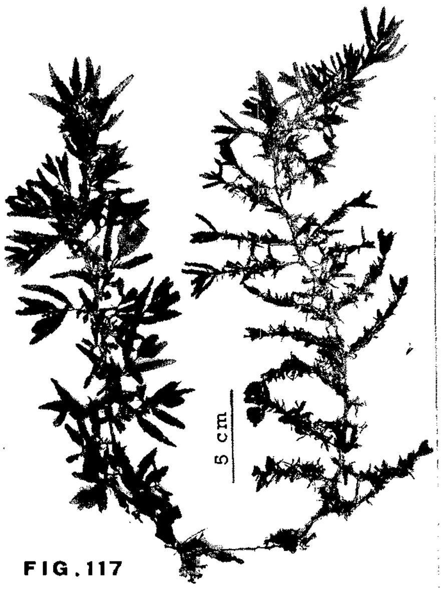


FIG.117

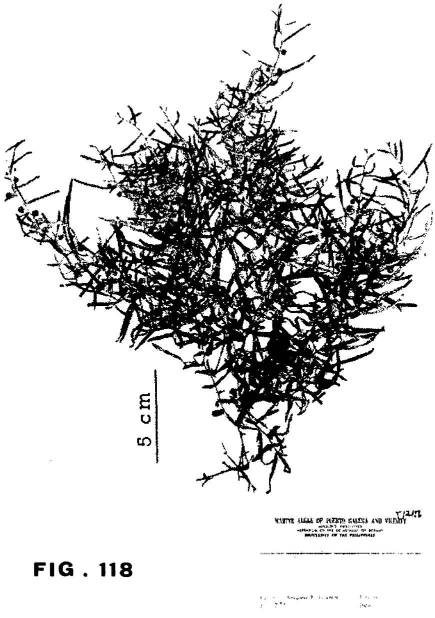


FIG . 118

Figs. 117–118. Fig. 117, *Sargassum* sp. No. 4. Habit of fertile thallus. Fig. 118, *Sargassum* sp. No. 13. Habit.

first develops as a simple, terete, straight, and highly pigmented (dark) branch from the base of the leaf on the primary or secondary branch, always subtending a young developing lateral; it differentiates into a leaf or vesicle after attaining a length of about 3–4 mm.

Receptacle a raceme; receptacular branch short, simple or branched, up to 2 mm long, 0.5 mm in diameter, warty, tapered to a blunt tip, segments cone-shaped.

Remarks: This species is close to *S. angustifolium* cited by Yoshida (1988) and by Tseng and Lu (1983), especially in its linear to linear-lanceolate leaves. It differs from the materials of Yoshida (1988) by having a percurrent midrib, some branched leaves, and two types of vesiclular stalk. It differs from the Chinese materials by having branched leaves and two types of vesicular stalk. The Philippine material is distinct in its spiny branches; the Japanese and Chinese materials have smooth branches.

Materials were collected from Balete Cove (T12158), April 21, 1948, and from Big Balaterio (T12156), May 10, 1947, Puerto Galera, Oriental Mindoro.

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ON THE EXPRESSION OF PHENOTYPIC VARIABILITY: WHY IS *SARGASSUM* SO TAXONOMICALLY DIFFICULT?

John A. Kilar, M. Dennis Hanisak, and Tadao Yoshida

Abstract

Anatomical and physiological variation is inherent in all living organisms, originating at both the genotypic and the phenotypic levels. In the morphologically complex phaeophyte *Sargassum*, characters exhibit variability on several scales: (1) temporal, (2) intraindividual, (3) interindividual, (4) environmental, and (5) interlocality (geographical). Taxonomic inconsistencies result from haphazard measurements of variation and from species descriptions that describe only part of the plant's anatomical range. Prominent features, such as blade shape and size, are used almost exclusively to distinguish taxa but are highly variable. Polymorphs increase between-plant variation and, in some cases, make species descriptions inadequate. The search for stable characters or suites of characters is further complicated by developmental cycles, low-occurrence traits, environmental variates (polymorphisms and polyphenisms), and genetic differences among populations. Variation at the phenotypic and genotypic levels must be understood before an acceptable species concept can be developed.

Introduction

Phycologists have long realized the functional role of the "biological species" but have often pondered its artificial nature, recognizing the difficulty in describing variability in a single, meaningful description. Some investigations have considered local populations, not the abstract species, to be the fundamental unit of nature, claiming that gene flow is rarely strong enough to unite populations into an integrated species (Ehrlich and Raven 1969). Although methods of reproduction and life history are important, vegetative organization plays a more significant role in delimiting marine algae (Papenfuss 1955). In the genus *Sargassum*, morphological features are highly differentiated, exhibiting temporal as well as within- and between-plant variability. In this paper, problems associated with the taxonomy of *Sargassum* are identified on the basis of observations of the Floridian and Bahamian floras and the published literature. Patterns in trait variation are elucidated, problems associated with haphazardly measuring such variations are listed, and a framework to resolve taxonomic inconsistencies is established.

Sargassum, with more than 400 described species, has the largest number of taxa in the Phaeophyta (Yoshida 1983) and occurs throughout most major oceans (the exception is the Antarctic [Nizamuddin 1970]). Its life history is typical of the Fucales, that is, haplobiontic; the organism is diploid in chromosome constitution. Asexual spore production is unknown, but free-floating pelagic species reproduce by thallus fragmentation. Annual (Tsuda 1972, Ang 1985), pseudoperennial (Ang and Trono 1987, Fletcher and Fletcher 1975a, De Wreede 1976, Prince and O'Neal 1979, Prince 1980), and perennial (Paula and Oliveira 1982, De Ruyther van Steveninck and Breeman 1987) life histories have been reported. *Sargassum* contributes significantly to coastal-zone biomass worldwide, fringing many temperate, subtropical, and tropical shores. The alga dominates many shallow-water habitats and is presently the deepest occurring brown alga: 200 m depth (*S. hawaiiensis* Doty et Newhouse [Magruder 1988]). Similar to the "kelps" in northern latitudes, nearshore and pelagic populations of *Sargassum* play critical roles in the life histories of many animal and plant species, providing them with a substratum, protection against predation, and a concentration of food (Mukai 1971, Dooley 1972). Two free-floating species, *S. fluitans* Bøgesen and *S. natans* (Linnaeus) J.

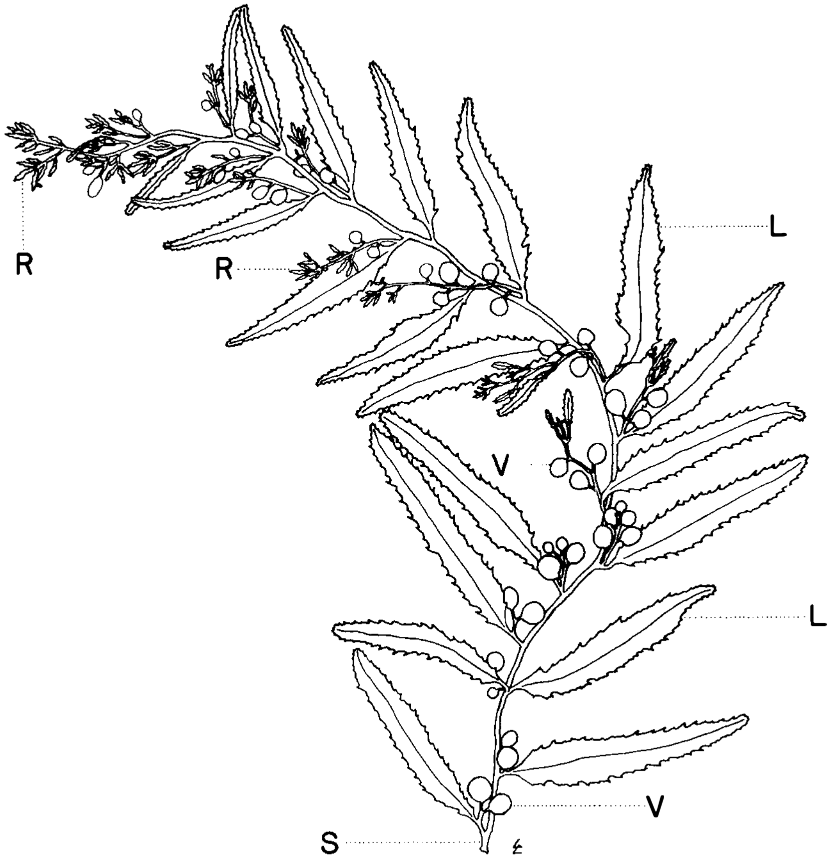

Fig. 1. Axis morphology of primary branches of *Sargassum*. V = vesicle; L = blade; R = receptacle; S = axis or stem.

Meyen, are the "keystone species" of the largest marine community in the world, the Sargasso Sea (Taylor [1975] recognizes a third species: *S. pusillum* Taylor). The questions of whether the derivation of these pelagic species is entirely a matter of past evolution and whether they should be dealt with as independent taxa or merely as phenotypic variations of a sessile species—one of the oldest questions in marine biology (Krümmel 1891, Winge 1923, Parr 1939, Ryther 1956)—are still unanswered since variation in their morphology is not well understood or documented.

In addition to its large number of described species, *Sargassum* is one of the most anatomically complex genera in the Phaeophyta. It consists of leaf-like blades, stems (axes), vesicles, fruiting branches, and a holdfast (Fig. 1). All features exhibit considerable latitude in form, size, or numbers. Blades are the principal light-harvesting organs in *Sargassum* (Fagerberg et al. 1979) and range from linear to lanceolate to ovate with entire, serrate, or highly dentate margins (Fig. 2). Furthermore, blades can be flat,

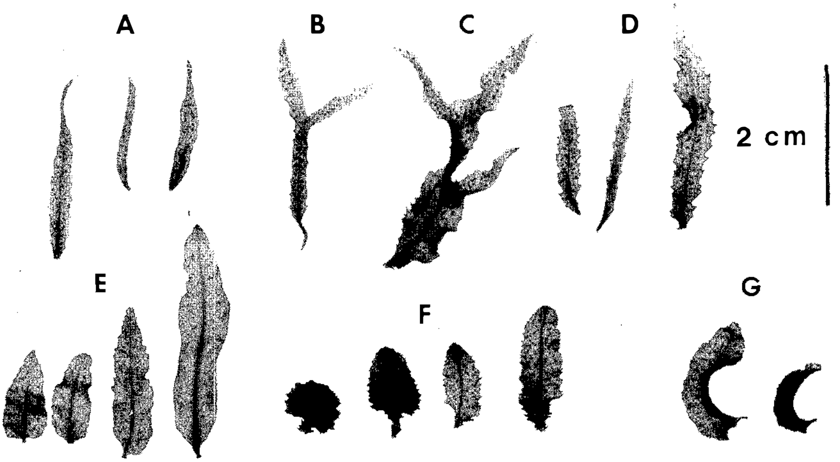

Fig. 2. Blade morphology of *Sargassum polyceratium*. A, Linear blades with nearly entire margins. B, Linear, bifurcated blade. C, Lanceolate, bifurcated blade. D, Linear blades with serrate margins. E, Linear-lanceolate blades. F, Ovate blades. G, Recurved, ovate blades.

recurved, undulate, or inflated. Such variability is understandable between taxa; however, it can occur within a single taxon (Howe 1920, Magruder 1988, Kilar and Hanisak 1989). Similar in appearance to the stomata on higher-plant leaves, cryptostomata occur on most plant features, and the arrangement and size of cryptostomata on blades are of taxonomic importance (e.g., *S. platycarpum* Montagne). In the western Atlantic, main axes are terete with or without acute spines that may be deciduous. Vesicles are common in these algae; their function is to support the thallus upright in the water column. Some of the features of the vesicle are among the most erratic and some others among the most stable: Alated (winged) vesicles exhibit a seasonal pattern, whereas the diameters of mature vesicles are nearly invariable (Ang and Trono 1987, Kilar and Hanisak 1988). Sexual structures are contained in modified blades called receptacles (Fritsch 1945), and their form and arrangement are as diverse as the somatic features are (Fig. 3). Although the number of different characters would seem to be sufficient to distinguish taxa, it is often exceedingly difficult to do so (Taylor 1960).

Phenotypic Expression

Temporal. Plant morphology changes with the age of the plant and its primary laterals. The number of laterals arising from the main or perennial stem (Jephson and Gray 1977, Umezaki 1986) and the degree of branching (Womersley 1954) are age-related characters. Blades of older plants, especially when reproductive, may have blades narrower than normal (Taylor 1960); studies of pseudoperennials, *S. polyceratium* Montagne (Kilar and Hanisak 1988) and *S. muticum* (Yendo) Fensholt (Kane and Chamberlain 1978, Critchley 1983a), and the annual *S. cristaefolium* C. Agardh (Soe-Htun

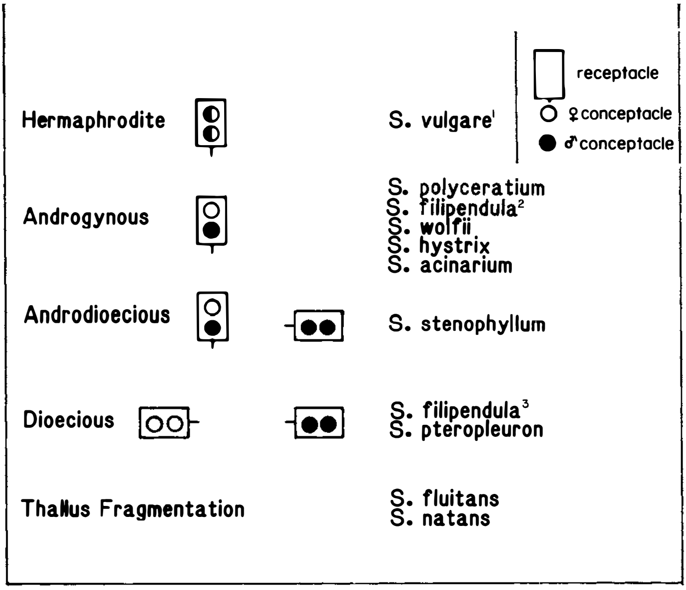

Fig. 3. Modes of reproduction and distribution of sex organs in Caribbean species of *Sargassum* (after Sawada 1958). With the exception of *Sargassum polyceratium*, all other androgynous species were determined from samples collected during a single month rather than over an annual growth cycle (Kilar and Hanisak, unpublished data). ¹From Paula (1978) as *Sargassum vulgare* var. *foliosissimum*. ²Collection site in the Indian River Lagoon. ³Collection site in the Homosassa River.

and Yoshida 1986) support this observation. In the perennial *S. stenophyllum* Martius, alterations in blade morphology are not as pronounced because laterals of similar morphology form throughout the year. Changes are more evident in annuals and pseudoperennials; newly produced blades become smaller in size and breadth as the frond matures, and older, broader blades are lost from the plant (Ang 1985, Soe-Htun and Yoshida 1986, Ang and Trono 1987, Kilar and Hanisak 1988). Blade senescence and loss are observed *in vitro* and *in situ* for many taxa (e.g., Norton 1977a, 1977b; Taniguchi and Yamada 1978; Terawaki et al. 1982, 1983a–d, 1984; Ang and Trono 1987).

Accompanying modifications in blade shape are changes in the size, number, and distribution of cryptostomata. In *S. polyceratium*, blades produced early in the season have more smaller-sized cryptostomata than do blades later in the season; the area (size) and numbers of cryptostomata are inversely related (Kilar and Hanisak 1988). The narrowing of the blade and the increased size of the cryptostomate modify the distribution of cryptostomata. Early in the season, cryptostomata occur randomly on the blade, whereas late in the season, they are arranged in roughly two rows. The arrangement of cryptostomata on the blade of *Sargassum* can take one or more forms: blades with cryptostomata (1) randomly arranged; (2) arranged in two rows, one on each side of the midrib; (3) confined by blade morphology to two rows, one on each side of the midrib; and (4) arranged in two rows but with cryptostomata randomly arranged within the row (Fig. 4). Distinguishing taxa by cryptostomata becomes difficult without previous knowledge of

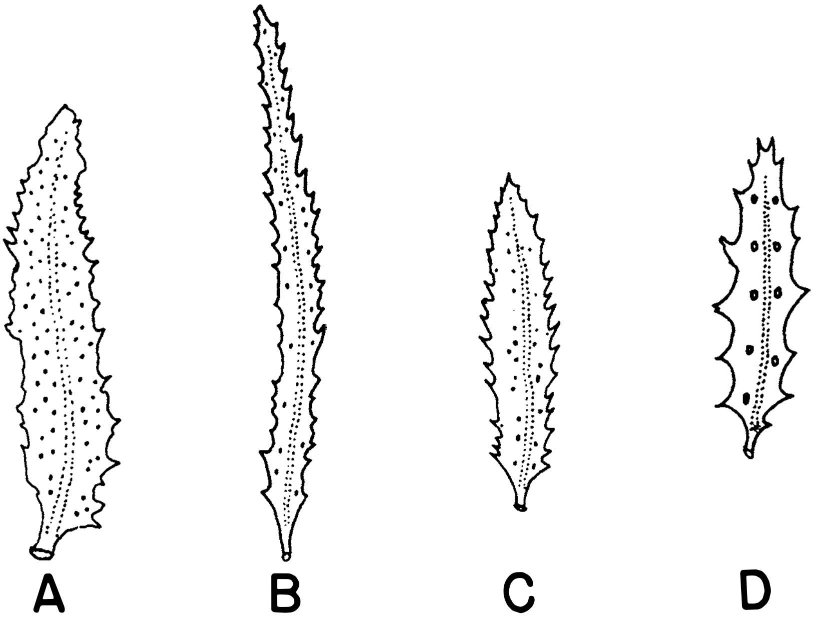

Fig. 4. Distribution of cryptostomata. A, Random distribution. B, Confined by morphology to two rows, one on each side of the midrib. C, Randomly arranged within two rows, one on each side of the midrib. D, In two rows, one on each side, close to the midrib.

seasonal modifications and interspecific ranges. Ontogenetic changes in the size, number, and arrangement of cryptostomata are poorly documented and appear widespread within *Sargassum*.

The number of vesicles is related to the size of the primary laterals. However, in some species vesicles form only on the upper ramuli, usually before receptacles develop; in others, they are present mainly on the basal parts, before fertile fronds develop (Womersley 1954). Superimposed on these cycles of vesicle numbers are vesicle features (see Tseng and Chang 1954; Yoshida 1978, 1983; Critchley 1983a). In *S. polyceratium*, winged pedicels (bladed stalks) are numerous during stationary periods (about 90%) and rare (less than 10%) at other times (Kilar and Hanisak 1988).

Intraindividual. Primary-branched laterals are produced sequentially from the main axis. As a lateral develops, a series of blades, vesicles, and, eventually, receptacles are produced. Variation occurs within and between primary laterals, reflecting different stages in development (Umezaki 1974, 1984). Blades of young laterals differ from those of adult laterals in their margins, shape, spacing, and size and number of cryptostomata (Terawaki and Goto 1986; Kilar and Hanisak 1988, 1989; Magruder 1988). Also, blades at the base of young *Sargassum* plants are larger than those in more distal parts of the plant (Soe-Htun and Yoshida 1986) (Fig. 5). Serrations on the leaf margin and the arrangement of cryptostomata are even less reliable criteria, varying within the same plant, and sometimes within the same blade (Ang and Trono 1987).

Interindividual. Individual plants have different traits or frequencies of traits. Mixed

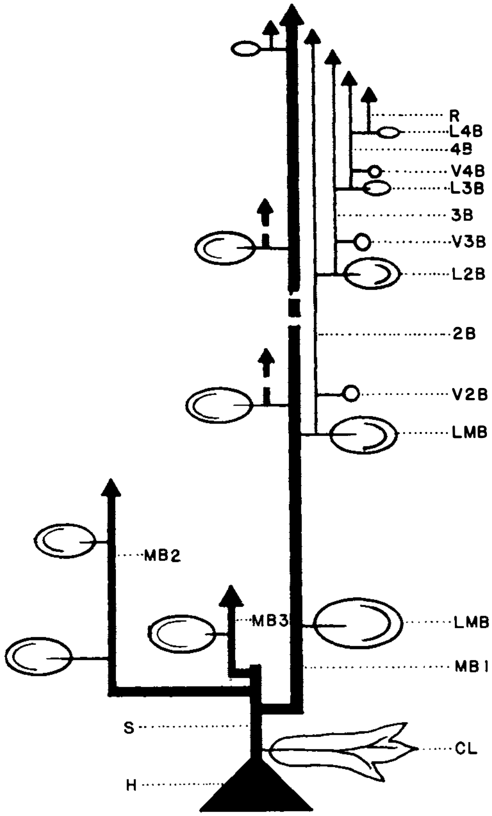

Fig. 5. Developmental process in *Sargassum*. H = holdfast; CL = cauline leaf; S = main axis; MB1 = first main branch; MB2 = second main branch; MB3 = third main branch; LMB = leaf of main branch; V2B = vesicle of secondary branch; 2B = secondary branch; L2B = leaf of secondary branch; V3B = vesicle of tertiary branch; 3B = tertiary branch; L3B = leaf of tertiary branch; V4B = vesicle of fourth order branch; 4B = fourth order branch; L4B = leaf of fourth order branch; R = receptacle.

stands of phenotypes are common among higher-plant populations but have been ascribed to *Sargassum* only recently. Divergent morphologies of *Sargassum* occur intermixed at distances of a few centimeters (Fig. 6). Forty-seven phenotypes of *S. polyceratium* were isolated on the basis of blade features, and many more could be distinguished if other characters were included (Kilar and Hanisak 1989). Some traits form a continuum; for example, blade shape ranges between linear and ovate. Plants with extreme length-to-width ratios appear different from the norm but are recognized as part of the same population by the numerous intermediates (Fig. 7).

Dimorphism between sexes is another example of interindividual variation. Receptacles on male plants are longer than those on female plants in *S. pteropleuron* Grunow (Prince, personal communication). Similarly, receptacles on male plants are longer than those on androgynous plants in *S. stenophyllum* (Kilar, unpublished data).

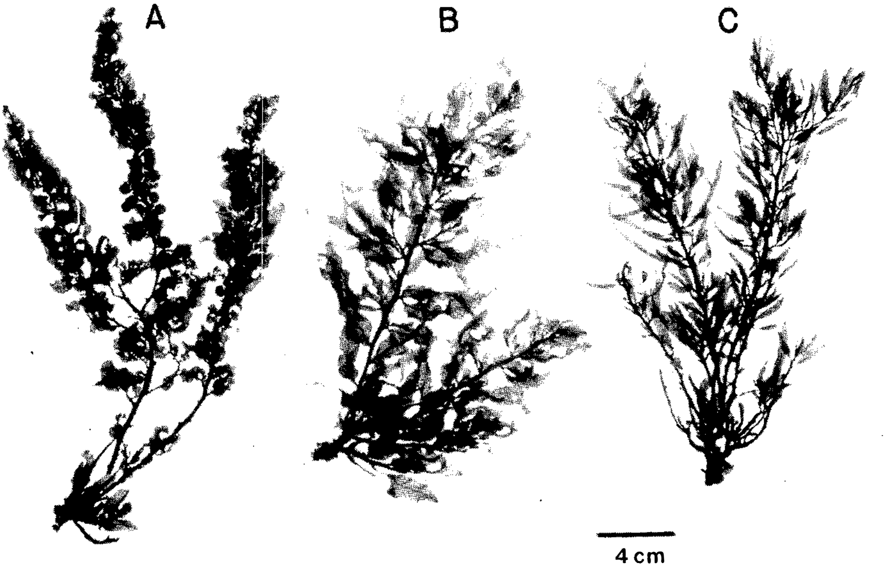

Fig. 6. Three phenotypes of *Sargassum polyceratium*. A, Curly-bladed plant. B, Bifurcated-bladed plant. C, Thin-bladed plant.

Sexual dimorphism has also been reported for *S. hystrix*; serrations on receptacles are distributed according to sex (Reinbold 1913, Collins and Hervey 1917).

Other between-plant differences are tied to development and have annual patterns. In *S. polyceratium*, bifurcate-bladed phenotypes are abundant late in the season (Fig. 8); about 30% of the plants of this species are anatomically different from other individuals and similar to *S. furcatum* Kützing (Kilar and Hanisak 1988, 1989). Because bifurcated blades are prevalent in some individuals and totally absent in others, these changes are not solely developmental. Genetic divergences on the spatial scale described here customarily have gone unreported but are thought to be widespread in the algae (e.g., Chapman 1972).

Environmental. Environmental variates act on phenotypic and genotypic levels: Genetically identical organisms reared under different conditions may express distinctive features, and divergent environmental conditions confer selective advantages to certain genotypes. Environmental conditions affect the morphology of established plants (phenotypic) and the survivorship of progeny (genotypic).

Transplant studies relate environmental variates to phenotypic expression. The placement of *S. cymosum* C. Agardh, *S. filipendula* C. Agardh, and *S. pteropleuron* into contrasting habitats typically has supported a genetic "canalization" (Stearns 1989) rather than environmental control of morphology (Paula and Oliveira 1980, 1982). Similar conclusions were reached for other fucoid algae (McLachlan et al. 1971, Sideman and

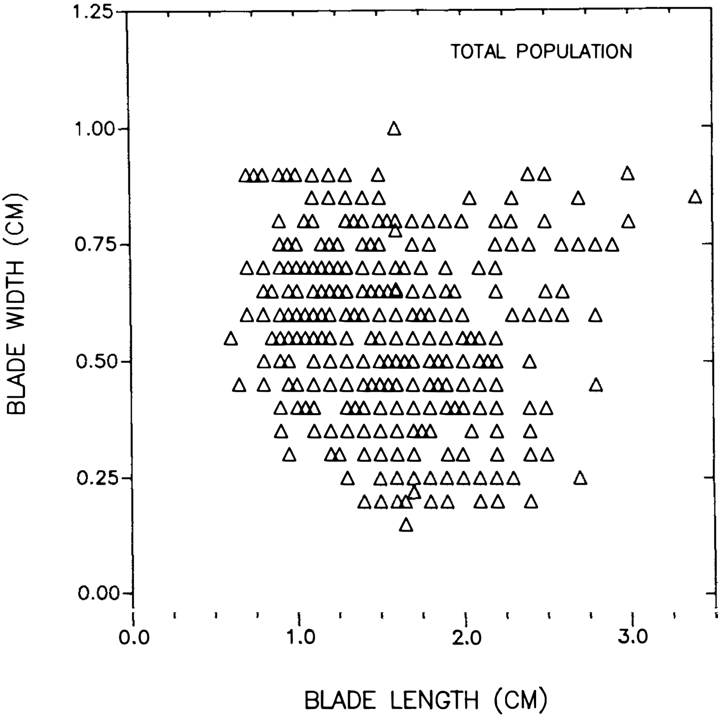

Fig. 7. Scatter diagram of blade length and blade width for the population of *Sargassum polyceratium* from the Content Keys, Florida. The diagram shows a continuum in blade shape, ranging from linear- to ovate-bladed individuals. Each point represents a single plant (n = 15 blades). (From Kilar and Hanisak, 1989.)

Mathieson 1985) and in several investigations on kelps (reviewed by Mathieson et al. 1981). Despite the recurrent theme of "environmental plasticity" in the *Sargassum* literature (e.g., Taylor 1960), the evidence of vegetative morphology tracking environmental conditions on a phenotypic level is not convincing. Currently, only Critchley (1983a) has shown that low (i.e., 10°C) and high (i.e., 25°C) temperatures and increased light intensities at 20°C increased the expression of mucronate vesicles in *S. muticum*; however, this work has not been verified in the field. (Light and temperature are triggers for reproduction in many brown algae [Bird and McLachlan 1976, Terry and Moss 1980, Hoopen et al. 1983, Maggs and Guiry 1987, Henry 1988]; for example, Deysher [1984] has noted that the relationship between temperature and reproduction in *S. muticum* appears to fit the "heat unit approach" [Wang 1960], in which populations experiencing higher average temperatures during their growing seasons have earlier reproduction than populations in colder environments.)

As each environment has an array of selective forces that drive natural selection or establish barriers to gene flow, habitat-linked variations in morphology should be a common occurrence. Different physiological responses are recognized in North Carolina nearshore (depth, 3 m) and offshore (depth, 30 m) populations (Peckol and Ramus 1985).

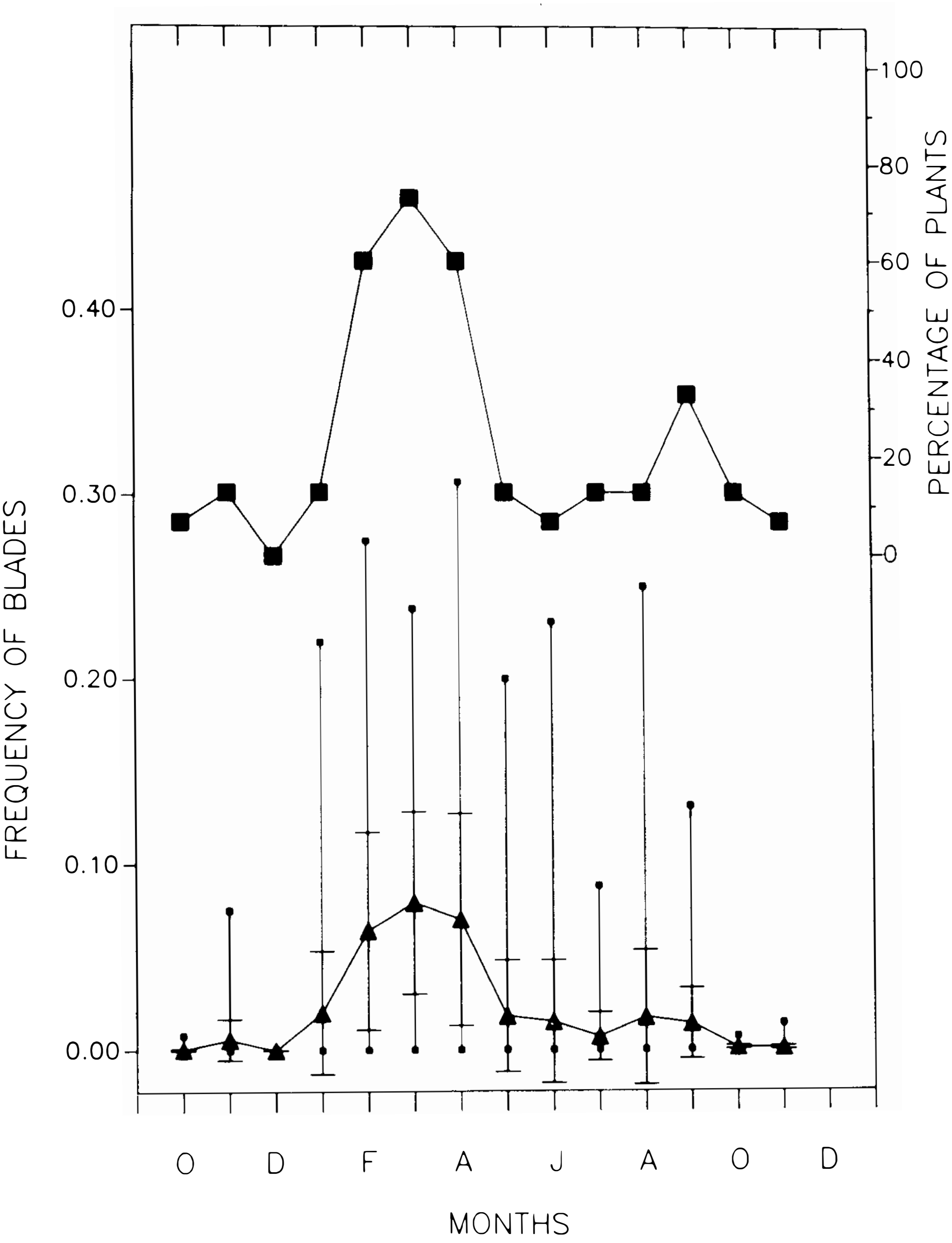

Fig. 8. Frequencies of blades (▲) and percentages of plants (■) with bifurcations (October 1984–November 1985). Data are means ± 95% confidence intervals and ranges (from Kilar and Hanisak 1988).

Shallow-water populations of *Sargassum* have a more compact growth form than deep-water populations, which generally have broader blades (Soe-Htun and Yoshida 1986, De Ruyter van Steveninck and Breeman 1987). Plants with many primary laterals show a similar pattern, with broader blades located near the base of the lateral, presumably because of the reduced light caused by self-shading (Kilar et al. 1989). Deep-water plants of *S. cristaefolium* are more variable in axis, blade, and vesicle characters (Soe-Htun and Yoshida 1986). Questions as to why some populations are more variable than others remain unanswered (Santelices, personal communications). However, after reviewing the higher-plant literature, Hawkes (personal communications) recognized that a knowledge of breeding systems (e.g., obligate outcrossing, mixed mating) is important. For example, mixed-mating breeding systems often lead to a large number of morphological forms (Briggs and Walters 1984).

Wave action affects the size of the plant, the occurrence of vesicles, the distribution of sex organs, and the morphology of receptacles. In high-energy environments, some species, such as *S. stenophyllum*, do not form vesicles. Plants of *S. cymosum* are monoecious with dense branching of receptacles in wave-exposed habitats and dioecious with lax branching in sheltered habitats (Paula and Oliveira 1982). Changes in the distribution of sex organs and the appearance of receptacles, as described here, cast doubt on the taxonomic usefulness of these features. Further work is needed to determine if such variability in these traits is inherent in other congenerics.

Plant morphology can be altered by wounds inflicted by grazers, or damage caused by physical disturbances (Kito 1975, Jephson and Gray 1977, Norton 1977b, Critchley 1983b, Ang 1985, Critchley et al. 1987). *Sargassum* responds to injury by (1) apical-dominance release, (2) early fertility, and (3) regeneration. In *S. muticum*, primary branches inhibit the growth of secondary branches, and secondary apices control the development of tertiary branches (Chamberlain et al. 1979). Abnormally large secondary branches are observed in *S. polyceratium* and *S. stenophyllum* when the primary branch is damaged. Laterals nearest the point of damage are larger and dominate those lower on the axis (Kilar and Hanisak 1988); Jephson and Gray (1977), Chamberlain et al. (1979), Fletcher and Fletcher (1975b), and Critchley et al. (1987) have made similar observations. However, the effect of apical release may be restricted to a critical growth period beyond which such potential would be lost (Ang 1985). Undamaged primary-branched axes of *S. cristaefolium*, *S. muticum*, *S. polyceratium*, and *S. stenophyllum* have profiles that are typically pyriform to conical (Norton 1977a, Soe-Htun and Yoshida 1986, Kilar and Hanisak 1988). When damage to the primary branch occurs late in the growth cycle, primary and secondary branches tend to become fertile with little extra growth of the damaged branch. Conversely, when damage occurs early in the growth cycle, the subservient branches become dominant and carry on growth with an increased tendency to reach fertility earlier (Jephson and Gray 1977). These effects on morphology and fertility can be substantial, with nearly half of the primary branches in *S. polyceratium*, for example, typically sustaining damage (Kilar and Hanisak 1988).

Primary-branched axes and blades regenerate from injured tissues that are close to the main stem. Regenerative blades are usually dichotomously branched and flat in culture and can develop into laterals under field conditions (Fagerberg and Dawes 1976, 1977; Fagerberg et al. 1979). Regenerative branches contain blades that are narrower and longer than those typical of the plant. Blades not forming laterals often grow abnormally large; however, it is often difficult to distinguish between cauline and regenerative blades. In areas of herbivory, regenerative blades may be the only ones present.

Interlocality. Pronounced differences (genotypic) in trait expression can occur between local and broadly distributed populations (e.g., founder effects, genetic drift [Hartl 1980]). Studies of spatial variation in morphological traits are few in the algae (e.g., Rice and Chapman 1985, Zupan and West 1988). Systematists recognize differences between populations through the taxonomic rankings of subspecific entities: "Subspecies" is usually reserved for geographic facies of a species; "variety," for a local facies of a species; and "form" for sporadic variants without distinctive patterns of distribution (Du Rietz 1930, Davis and Heywood 1963). Jephson and Gray (1977) and Critchley (1983c) have shown some discrepancies with descriptions of *S. muticum* from the alga's indigenous Japanese and introduced British Columbian (Canada) and European habitats. They noted that *S. muticum* in Japan (ca. 75–120 cm [Yendo 1907]) does not attain such lengths exhibited by species in either North America or Europe (ca. 5–6 m [Nicholson et al. 1981, Gruet 1976]). Certain vesicle traits (i.e., apiculations) are common in European material and seem to provide a disparity with the originally described (Yendo 1907) and British Columbian (Scagel 1956) populations.

Anecdotal accounts of geographical variability are numerous when floristic surveys are compared. In *S. filipendula*, for example, blade shape and size are consistent among broadly distributed collections (Bertossi-Aurelia and Ganesan 1973), whereas distribution of sexual organs and development of receptacles are incongruous. Populations are monoecious along the eastern coast of the United States (Simons 1906), both monoecious and dioecious along the western coast of Florida (Kilar unpublished data), and dioecious in Brazil (Paula 1978). The alga is reported year round in the Florida Keys and southern Cape Cod (Croley and Dawes 1970, Sears and Wilce 1975); elsewhere more restricted seasonal patterns occur (Conover 1964, Earle 1969, Peckol 1982). Receptacles develop acropetally or basipetally on the laterals in Florida and acropetally in more northern areas. At this time, it is difficult to ascertain whether these observations are geographical, environmentally induced, or the result of misidentifications.

Problem Areas

Any inspection of the literature on *Sargassum* cannot fail to demonstrate the prevailing state of uncertainty in the classification of many of its species. The existence of considerable variability in species descriptions renders specific determination arduous. Causes of this confusion are attributed to the following:

1. Phenotypic plasticity. Different environmental conditions alter morphologies to such an extent that local populations of the same species are not easily recognized (Taylor 1960, Soe-Htun and Yoshida 1986).
2. Ontogenetic forms. A plant's appearance may be considerably different during different phases of its life history, and some forms may converge on other congenerics (Womersley 1954; Critchley 1983a, 1983c; Ang and Trono 1987; Kilar and Hanisak 1988).
3. Polymorphism. Growing in the same habitat, individual plants of a species may express quite different traits or frequencies of traits (Kilar and Hanisak 1989).
4. Low-frequency traits. Many features are often reduced or absent from individual plants and populations and, consequently, are of little taxonomic value (Kilar and Hanisak 1988).

5. Overemphasis on obvious features. Species identifications are often based on a few obvious characters (e.g., blades) that can be among the most variable traits or whose significance is not well understood (e.g., cryptostomata).

6. Hybridization. Intermediate morphologies may be due to the intermixing of genomes (Taylor 1960, Paula and Oliveira 1982).

7. Polyploidy. Divergent morphologies may be due to increases in the chromosome numbers within (autopolyploidy) or between (allopolyploidy) species.

8. Designation of varieties and forms. A myriad of subspecific entities (Grunow 1915, 1916a, 1916b, Setchell 1931, 1933, 1935, 1936) produces further confusion, especially when distinctions between congenerics are not adequately described (Womersley 1954, Yoshida 1983).

9. Type specimens. Variation in *Sargassum*'s morphology cannot be contained within a single specimen or collection, especially when specimens are less complete than descriptions and figures, only apical portions are present, or fruiting receptacles are generally absent (Womersley 1954, Yoshida 1983, Hanisak and Kilar 1990).

10. Uncertainty as to which traits are taxonomically important. Confusion results from researchers' focusing on different traits. For example, Taylor (1960) used blade and vesicle features to separate the pelagic species *S. natans* from *S. fluitans*, whereas Parr (1939) used stem features—the end results are different.

11. Incomplete information. Ecological, developmental, and reproductive measures are wanting for most species (Womersley 1954; Earle 1969; Soe-Htun and Yoshida 1986; Kilar and Hanisak 1988, 1989).

Approaches to Problems

Modern studies of variation have provided substantial insight into our understanding of systematics (Thorpe 1976). Investigations relating variability to abiotic and biotic variates have provided valuable information showing the control by selective pressures of phenotypic expression and other aspects of microevolution (e.g., allopatric, stasipatric, and sympatric models of speciation). A critical revision of *Sargassum* is warranted that is based on "a wide field knowledge of developmental stages and ecological variations, together with a study of the type specimens" (Womersley 1954). Such an approach with other species has stimulated debate on the taxonomic ranking of species and challenged recognized species concepts (e.g., Thuret 1854, Williams 1899, Burrows and Lodge 1952, Paula and Oliveira 1982, Soe-Htun and Yoshida 1983, Rice and Chapman 1985, Sideman and Mathieson 1985, Rice et al. 1985). We recommend the following:

Seasonal Study. Confusion surrounding *Sargassum*'s taxonomy can be greatly alleviated if populations are sampled adequately throughout the year. Considerable attention should be given to sampling methodologies that document developmental patterns, ecological variates, and trait stability. Numerical models and patterns of blade, vesicle, receptacle, and lateral formation are rarely included in species descriptions (e.g., acropetal vs basipetal formation of receptacles on primary branches). Considerable reduction in variability can be achieved in blade-related features if measurements are related to the location on the lateral where the blade was positioned (e.g., degree of branching). For most Atlantic and Indo-Pacific species, distribution of sex organs (e.g., androgynous, androdioecious) has not been properly assessed (Fig. 3). Ecological measures (habitats, depth distribution, annual growth strategy, peak biomass period, and maturation periodicity) contribute vital information (e.g., Yoshida 1961, Marui et al. 1981,

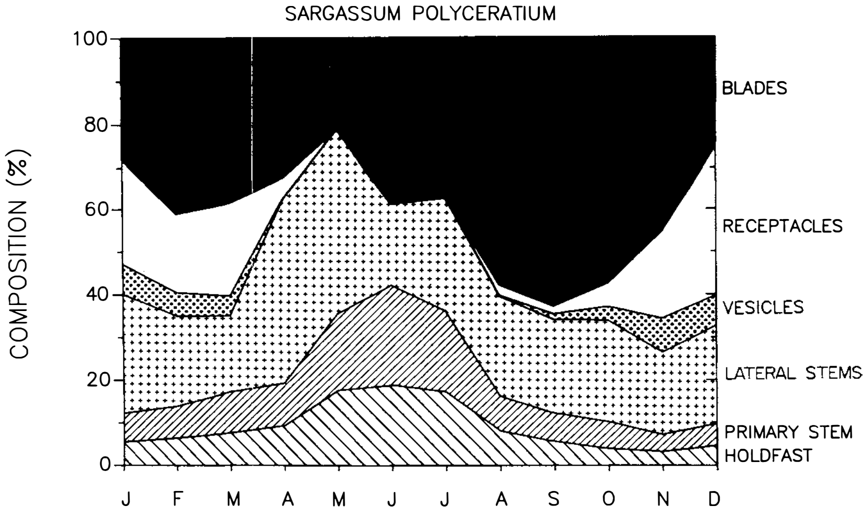

Fig. 9. Annual biomass allocation into blades, axes or stems, vesicles, receptacles, and holdfast for *Sargassum polyceratium*.

Yoshida 1983) and should not be discounted in species descriptions. We have found that measurements of biomass allocation into blades, axes, vesicles, etc. are useful in distinguishing developmental and ecological patterns (Fig. 9).

Stability in time and space is an essential characteristic of a good taxonomic trait. Variation among continuous traits can be compared with coefficients of variation (CV), a size-independent estimate of variation. As the relevant time scale is the plant's growth cycle, a time-series plot of CV estimates would distinguish temporally stable from temporally variable traits. Within- and between-plant levels of variation are the critical spatial estimators (Nested ANOVA; Sokal and Rohlf 1981; e.g., Table 1). High between-plant variance indicates polymorphisms or, possibly, a second species. Traits with high within-plant variance or low between-plant variance are best to distinguish species, as a single plant contains the necessary information. For screening traits for overall stability, bivariate plots of CV estimates and between-plant variation are advised (Fig. 10).

Reaction Norms. Are morphological features conservative, maintaining a consistent morphological form (environmental canalization, Stearns 1989), or highly variable, responding to "reaction norms" (Woltereck 1909)? As noted previously, environmental variates act at phenotypic and genotypic levels. When an organism produces phenotypes from a single genotype that varies as a continuous function of an environmental condition, the relationship is called a reaction norm (Fig. 11). The different phenotypic expressions of the same genotype are referred to as polyphenisms: "Polyphenism is the analog among phenotypes of the term polymorphism among genotypes" (Stearns 1989).

Transplant techniques are useful in establishing phenotypic responses of macroalgae to different habitats. Previous studies have examined morphological and physiological reactions. Paula and Oliveira (1982) conducted the only reported morphological study of transplants with *Sargassum*. Plants of *S. cymosum* from exposed habitats that were transplanted into sheltered habitats remained dwarf but formed broader blades of a paler

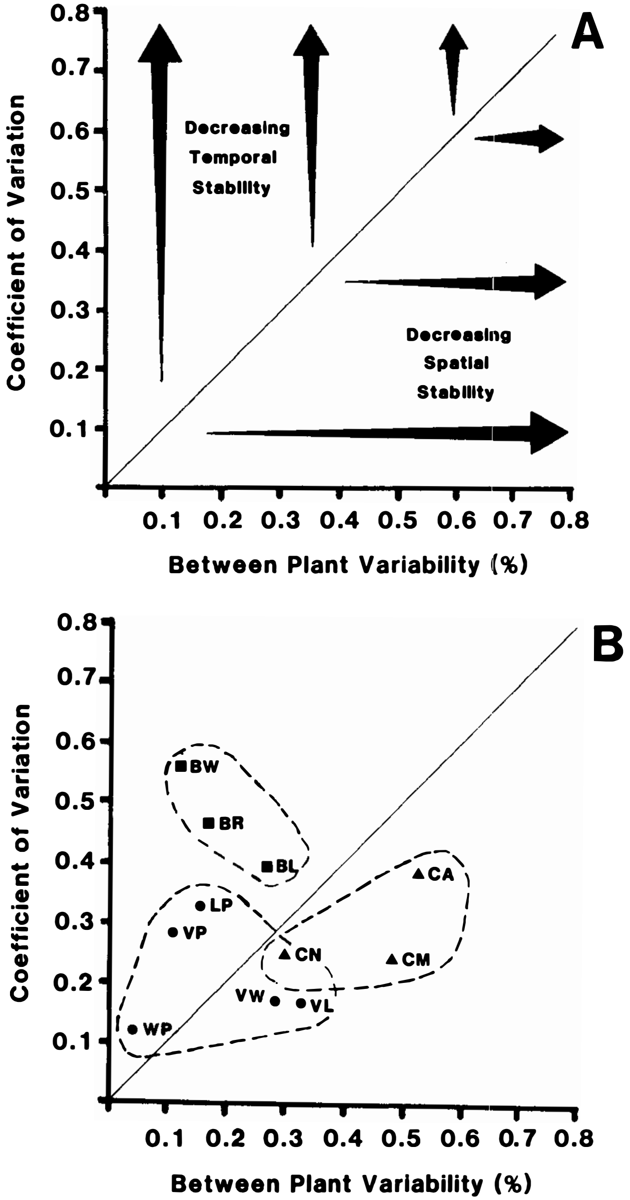

Fig. 10. Coefficient of variation plotted against between-plant variability. A, Temporal and spatial stability of traits decreases when values are plotted for each month of the growth cycle. B, Groupings of blade, vesicle, and cryptostomate traits of *Sargassum wolfii* Earle. Vesicle features are the most stable. BL = blade length; BW = blade width; BR = length/width ratio; CA = cryptostomate area; CM = cryptostomate major axis; CN = cryptostomate minor axis; LP = pedicel length; VL = vesicle length; VP = vesicle length/pedicel ratio; VW = vesicle width; WP = vesicle width/pedicel ratio.

Table 1. Partitioning of Variance Within and Between Plants for Selected Traits of *Sargassum wolfii* (December 18, 1984)

Trait	Variance (%)	
	Between	Within
Blade		
Length (L)	25.9	74.1
Width (W)	11.5	88.5
L/W	14.9	85.1
Cryptostomata		
Major Axis	46.9	53.1
Minor Axis	28.5	71.5
Area	51.0	49.0
Vesicles		
Length	32.2	67.8
Width	28.2	71.8
Pedicel (p)	9.7	90.3
L/P	14.6	85.6
W/P	3.9	96.1

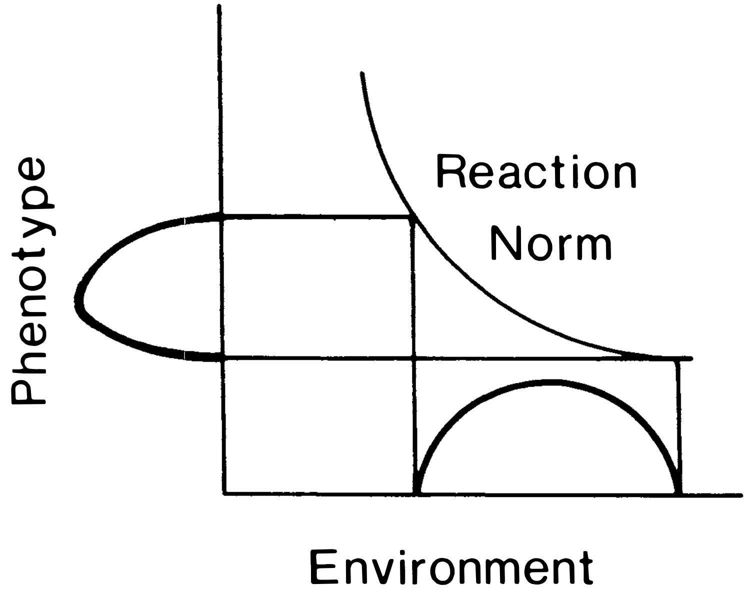

Fig. 11. Example of a reaction norm. Reaction norms are phenotypic expressions of a single genotype to environmental variation. Genotypes of the same species can have different reaction norms. From Suzuki et al. (1986).

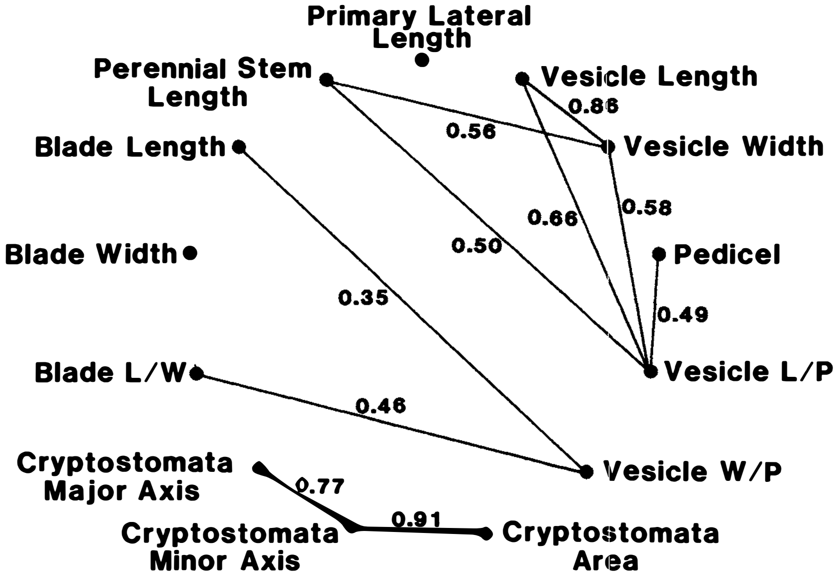

Fig. 12. Morphological trajectories of continuous traits of *Sargassum wolfii*. Values are coefficients of determination. (April 1985; Bay Port, Florida.)

color. Transplants of *S. filipendula* that form receptacles basipetally continued to produce them basipetally when placed into habitats in which *S. filipendula* formed them acropetally (Kilar and Hanisak unpublished data). Dawes et al. (1988) observed the physiological responses of three transplanted populations of *S. pteropleuron* and found that plants from each population were capable of acclimatizing to their new habitats (see chapter by Chiang et al., this volume). Because of the limited information, the effects of polyphenism (environmental plasticity) remain undetermined in *Sargassum.* We recommend that the following criteria be adopted for future studies: (1) a broad range of morphological features be analyzed, (2) the duration of the study allow for a complete renewal of primary branches, (3) numerous sites be selected along an environmental gradient, and (4) reciprocal transplants be made. If changes in morphology remain subtle, then the hypothesis that environmental plasticity accounts for the morphological variability in *Sargassum* can be rejected, a necessary first step in resolving the taxonomic dilemma.

Wave action, light, depth, temperature, and predation are linked to changes in *Sargassum*'s morphology (Paula and Oliveira 1982, Critchley 1983a, De Ruyter van Steveninck and Breeman 1987). *In situ* studies along gradients of environmental variates would show relationships between environment and morphology; trait frequencies and trajectories and reproductive periodicity would be particularly useful. As plant fitness is not determined by a single character, trajectories among characters should be examined for patterns (Fig. 12). If gradient and transplant studies are combined, genotypic and phenotypic responses to environmental signals could be established. We may find that an alga may be better understood by knowledge of its habitat rather than a general, often confused, species description (Price 1978).

Interlocality Studies. The general consensus is that studies are needed to compare local and widely distributed populations (this workshop; Critchley 1983a; Soe-Htun and Yoshida 1986; Kilar and Hanisak 1988, 1989). The understanding of variation between plants, among populations within a locality, and among geographical sites would increase our knowledge of the biological species and the evolutionary processes governing variation. Intraspecific mosaic patterns occur in the larger brown algae, as suggested by the morphological treatments of *Desmarestia* (Chapman 1972), *Fucus* (Rice and Chapman 1985), and *Alaria* (Widdowson 1971). Chapman (1972) has noted that "some of the samples (of *D. ligulata* [Lightfoot] Lamouroux) showed some discontinuity of variation, but between these a complete interconnecting series of samples was found." We suspect that similar studies of western Atlantic species of *Sargassum* would yield a number of new taxa and an improved species concept.

Numerical Taxonomy. *Sargassum* is a prime candidate for numerical taxonomic studies. Multivariate techniques are useful in distinguishing closely related taxa or in resolving subspecific entities. Many variates are evaluated simultaneously and quantitatively; the goals are to reduce the amount of data, search for patterns, or discriminate between populations that are not obvious at an univariate level. One such study was done by Rice and Chapman (1985) on *Fucus distichus* (Linnaeus) emend Powell. To be used properly, these techniques must account for genotypic and phenotypic responses of the organism (for further information, see Blackith and Reyment 1971, Sneath and Sokal 1973, Neff and Marcus 1980, Sokal and Rohlf 1981).

Culture Studies. The production of viable offspring, the identification of morphologically defined polymorphs or hybrids, and the determination of environmental barriers or triggers to growth can be accomplished by growing and crossing plants in culture. Previous studies have grown *in vitro* germlings, apical tips, subapical portions, intact plants, and laterals, usually for durations of about 30 days (Chauhan 1972, Fletcher and Fletcher 1975b, Norton 1977a, Kane and Chamberlain 1978, De Wreede 1978, Hanisak and Samuel 1987, Critchley 1983a). However, Terawaki et al. (1982, 1983a–d, 1984) successfully raised six species of *Sargassum* to maturity from embryos in tank and field cultures. Past studies examined (1) the liberation of oospores (Chauhan 1972); (2) substratum preference by germlings (Chauhan 1972); (3) the effects on growth of culture media, temperature, salinity, and light intensity (Chauhan 1972, Fletcher and Fletcher 1975b, De Wreede 1978, Thorhaug and Marcus 1981, Hanisak and Samuel 1987); and (4) morphogenesis (Fletcher and Fletcher 1975b, Norton 1977a, Kane and Chamberlain 1978, Critchley 1983a, Terawaki et al. 1982, 1983a–d, 1984). These studies have contributed much to our knowledge of *Sargassum*, and these techniques should be used to address more systematic questions: Can congenerics form hybrids? How morphologically and physiologically variable are the progeny of native populations? Are crosses between allopatric populations equally viable? Do breeding systems determine trait variability? Answers to such questions will promote an understanding of intra- and interspecific boundaries.

Genetic Studies. Researchers have turned to molecular biological techniques of gel electrophoresis (Cheney and Babbel 1978, Blair et al. 1982, Innes and Yarish 1984, Innes 1988), restriction fragment length polymorphism (RFLP) analysis (Bhattacharya and Druehl 1989), DNA sequencing (Markowicz et al. 1988, Bhattacharya and Druehl 1989) and karyotyping (Ogawa 1974, 1977, 1978) to resolve taxonomic inconsistencies. Such techniques are valuable in morphologically simple algae, for which morphology offers few clues. The presence of phenolic and arsenic compounds in *Sargassum* (L. Druehl, personal communications) makes techniques that involve electrophoresis or isolation of DNA difficult. However, recent techniques, such as those of Rice and Crowden (1987), are promising. Molecular techniques do provide another source of information. If the gene, DNA fragment, or isoenzyme can be related to developmental processes or morphology, then the ecological and systematic relevance of the marker can be more appropriately judged. In *Sargassum*, it is not at all clear where along a continuum of morphological features one species begins and another ends. Karyotyping may prove useful, as chromosome numbers are recorded for several species of *Sargassum* from Japan (Kunieda 1928; Okabe 1930; Abe 1933; Inoh 1947; Inoh and Hiroe 1954a, 1954b; Ogawa et al. 1969). Although the results of these studies are mixed, chromosome numbers may discriminate western Atlantic taxa.

Conclusions

Darwin (1859) was first to recognize that variation is inherent in all living things and that natural selection determines the fitness of individuals. Mendel (1948) established the vital framework that explained and placed limits on phenotypic expression. The question remains as to how selective pressures and genetic constraints affect phenotypic expression. Are frequencies of traits unrelated between populations (i.e., habitat specific)? Or, do underlying patterns exist that connect populations into a unified species? Russell (1978) noted that the number of different phenotypes may be limitless. When the complexity of *Sargassum*'s morphology is considered, the search for stable characters must account for developmental cycles, polymorphisms, environmental variates, and genetic differences among local and broadly distributed populations. The investigation of evolutionary processes operating on individuals will advance the understanding of systematics and adaptation most tellingly.

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A COMPARATIVE STUDY OF *SARGASSUM POLYPORUM* FROM THE RYUKYU ISLANDS (JAPAN) AND *SARGASSUM POLYCERATIUM* FROM THE FLORIDA KEYS (UNITED STATES)

John A. Kilar, Tetsuro Ajisaka, Tadao Yoshida,
and M. Dennis Hanisak

Abstract

Sargassum polyporum Montagne was collected from the Ryukyu Islands, Japan, and compared with *S. polyceratium* Montagne from the Content Keys, Florida (United States). Blades and vesicles, the most prominent features, were anatomically similar. Differences were observed in the size of cryptostomates; blade bifurcations; winged vesicles; and spines located on axes, vesicles, and blade pedicels. *S. polyceratium* was more variable morphologically than *S. polyporum*, with a greater proportion of variance concentrated among individuals. Multivariate statistical techniques (multigroup analyses of principal components and discriminant functions) distinguished *S. polyporum* from *S. polyceratium*. This study shows that (1) geographically separated populations can share important taxonomic characters, (2) the amount and distribution of variation in morphological characters differ between interspecific taxa, and (3) species descriptions must account for ontogeny and environmental conditions to eliminate taxonomic uncertainties when morphological traits cross perceived intraspecific boundaries.

Introduction

Sargassum is the largest genus in the brown algae, with more than 400 described species (Yoshida 1983), and is distributed throughout the tropical and temperate seas of the world (Nizamuddin 1970). Unlike most macroalgae, it is morphologically differentiated and relatively complex, exhibiting specialized anatomical features, such as leaf-like blades, stems (axes), vesicles, fruiting branches (receptacles), and a holdfast (attachment structure). The great variability in these features has long been recognized as a source of systematic confusion (Taylor 1960, Yoshida 1983, Soe-Htun and Yoshida 1986). Geographical isolation is often invoked to discriminate widely separated entities that are otherwise morphologically similar. Since the work of C. Agardh (1820), J. Agardh (1848, 1889, 1896), and Grunow (1915, 1916a, 1916b), few attempts have been made to contrast species of *Sargassum* from different geographical regions. As part of our involvement in the systematic workshop, representative specimens of the *Sargassum* (subgenus *Sargassum*) from the eastern shores of the Americas, Japan, China, Korea, and the Philippines were compared.

Several morphologically similar taxa were identified. However, of these specimens, *S. polyceratium* Montagne from the Caribbean Sea and *S. polyporum* Montagne from the East China Sea were the most analogous in form and warranted further investigation. Prince (1980) showed that *S. polyceratium* in Florida is a pseudoperennial (*sensu* Sears and Wilce 1975), with maximal growth from midfall to midwinter and minimal growth in midsummer. Also, Kilar and Hanisak (1988, 1989) described developmental patterns and intraspecific variation, and Kilar et al. (1989) related morphological form to algal productivity. Montagne (1842), Grunow (1916b), and Setchell (1936) provided descriptions of *S. polyporum*. Qualitative and quantitative data were collected to determine whether these entities should be synonymized. Plants were examined for between-plant variation and overall variability, and the data were analyzed by using univariate and multivariate statistics. Our study showed certain approaches that are useful for taxonomic studies of *Sargassum*.

Materials and Methods

Thirty plants of *S. polyporum* were collected randomly from the Ryukyu Islands (Irimote, Ishigaki, Miyako, and Okinawa Islands), Japan (25° N, 125° E) in June 1989 and compared with those of *S. polyceratium* from the Content Keys (24° 48′ N, 81° 30′ W) in the Florida Keys (United States). The description of *S. polyceratium* was based on monthly (14 months) collections of 30 random plants (from Kilar and Hanisak 1988). In addition, herbarium specimens from the U.S. National Museum, Mote Marine Laboratory, Harbor Branch Oceanographic Institution, Kyoto University, and Hokkaido University were examined.

Quantitative data consisted of taxonomically important, continuous characters. Blades on mature uprights were selected randomly from distal (n = 30) and proximal (n = 15) locations and measured for length (± 1 mm), width (± 1 mm), cryptostomatal area (μm^2), and number of branches. For each blade, the area of the largest cryptostomate was calculated (i.e., area of an ellipse) by using the length of the major and minor axes (± 20 µm). Vesicles were assessed for length (± 1 mm), diameter (± 1 mm), and pedicel length (± 1 mm). Plants were evaluated for overall size (± 1 cm; the distance from the base of the holdfast to its most distal point) and the number and size (± 1 mm) of perennial stems.

Statistical analyses included both univariate and multivariate techniques, following the recommendations of Sokal and Rohlf (1981) and Pimentel and Smith (1986). To account for site-specific temporal effects, we used blade length:width (l:w) ratios to standardize data. Trait measurements were tested for homogeneity of variances (Bartlett's test), transformed to satisfy the assumption of equality of population variance, and tested for collinearity (Pearson's Correlation Analysis). ANOVA models were one-way analyses with equal or unequal sample sizes. Nested ANOVA models partitioned variance within and between plants. Coefficients of variation provided a size-independent index of variation. Traits with a low between-plant variance (V_b) and low coefficient of variation (CV) were the most spatially stable and the least variable, respectively.

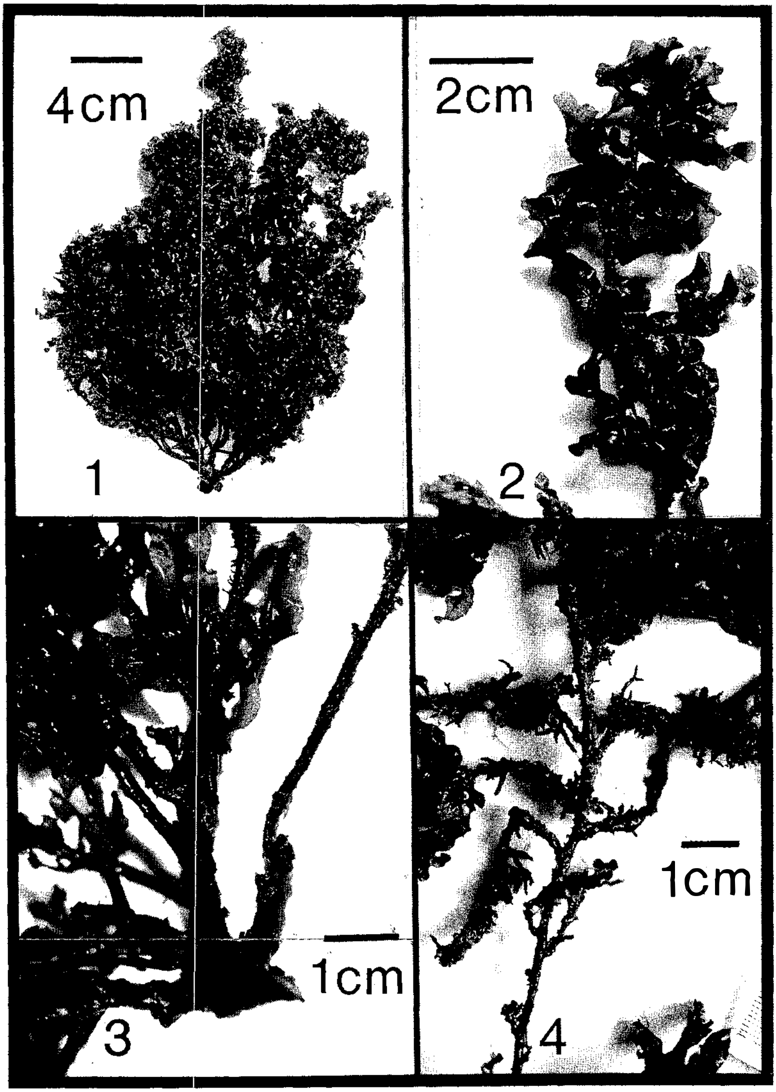
Multigroup discriminant function (MDA) and principal component (PCA) analyses were used. Initially, data were investigated for redundant variables, multivariate normality, and equality of population dispersions. Discriminate function analysis was used to test for differences among traits between the two taxa (MANOVA), classify plants into groups, and determine which traits were analogous or distinct between the taxa (ANOVA). Principal component analyses were performed on a matrix of nonredundant, transformed, and normalized (z-scores) variables. Bivariate scatter plots of the scores of the individual plants on selected pairs of components were made both without previous identification of individual points and with these points identified by their *a priori* group.

Results

Description of Species

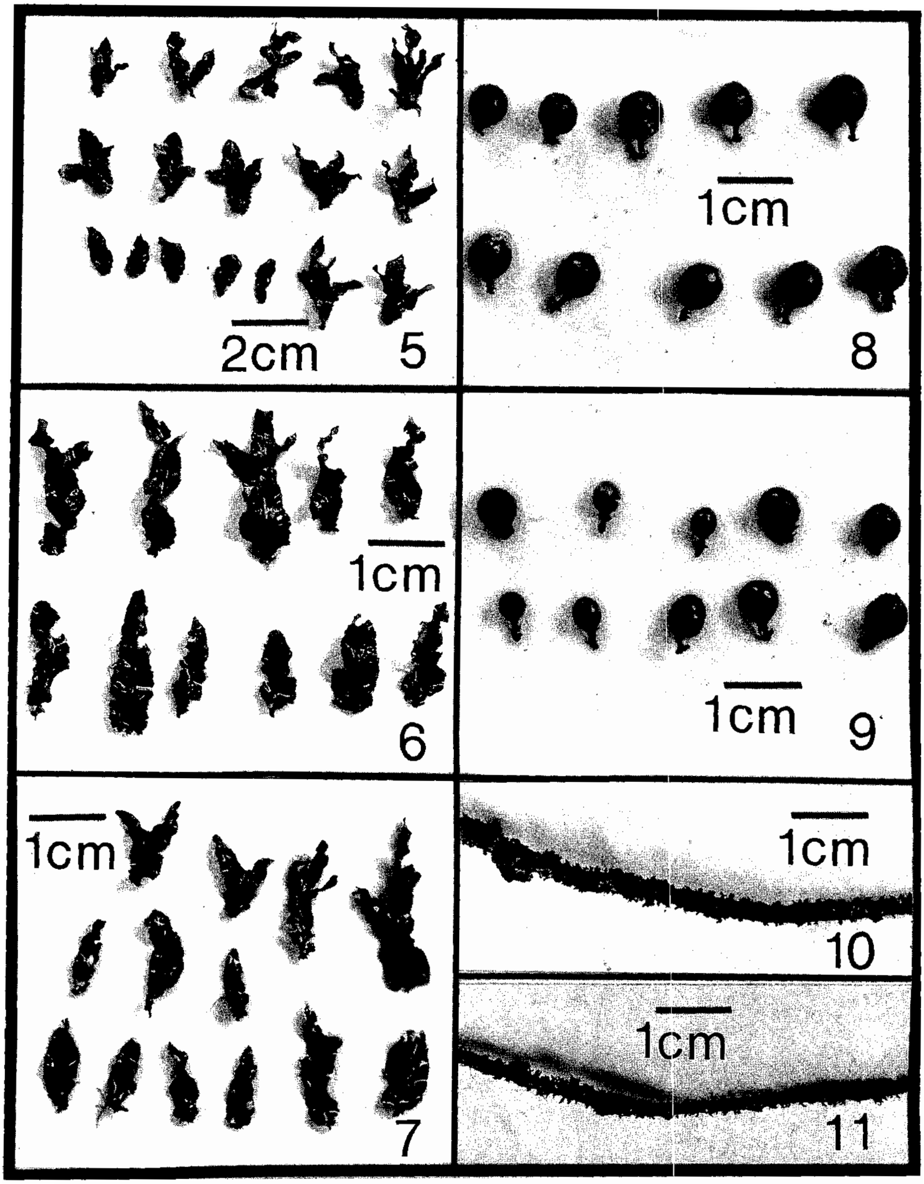
Sargassum polyporum Montagne (Figs. 1–11)

Holdfast conical-discoid, up to 2 cm in diameter. Main axis terete, to 3 cm high and 4 mm in diameter, with warty surface; primary branches reaching 42 cm long, terete, always with spines, usually with many highly branched spines; secondary branches issued at about 5-mm intervals, up to 17 cm long, always with spines, alternately or spirally branched, phyllotaxis one in two or one in three turns. Blades sessile or with short petiole,



Figs. 1–4. ***Sargassum polyporum.*** **Liquid-preserved specimen from Shiraho, Ishigaki Island (June 6, 1989). Fig. 2, Distal tip. Fig. 3, Perennial stem (main axis). Fig. 4, Secondary-branched axes with receptacles. Note hard spines along axes.**

petiole usually with spines, linear, narrowly spatulate, or narrowly elliptical, flat to spirally twisted and usually one to two times branched or alternately pinnately furcate (one to seven times) on the upper to middle part, 1–5 cm long and 3–10 mm wide, l:w ratio 1:1 to 7:1, symmetrical or asymmetrical base, obtuse at apices, margins usually dentate at base or nearly entire, undulate, or straight in lateral view. Midrib distinct, percurrent or



Figs. 5–11. ***Sargassum polyporum.*** **Liquid-preserved specimen from Ishigaki (Figs. 5–7, 9, 11) and Taketomi (Figs. 8, 10) Islands (June 5–6, 1989). Fig. 5, Distal blades of a primary branch. Figs. 6–7, Proximal blades of a primary branch. Figs. 8–9, Vesicles with and without spined pedicels. Figs. 10–11, Primary-branch stems (axes) with spines.**

vanishing near apex. Cryptostomata distinct, sometimes disposed in a single row on both sides of midrib or scattered over surface, opening circular to elliptical, 50–140 µm in diameter. Vesicles spherical to obovoid, up to 6.5 mm long, usually smooth at apices, rarely with hard spines; pedicels terete or compressed, shorter than vesicles or nearly the same length, sometimes with a few spines or dentate wings.

Receptacles terete, to 8 mm long and 1 mm wide, often forked, warty, racemosely arranged.

Habitat: From depths of 1–5 m, in tide pools or lagoons, often forming dense stands on dead coral.

Sargassum polyceratium Montagne (Figs. 12–22)

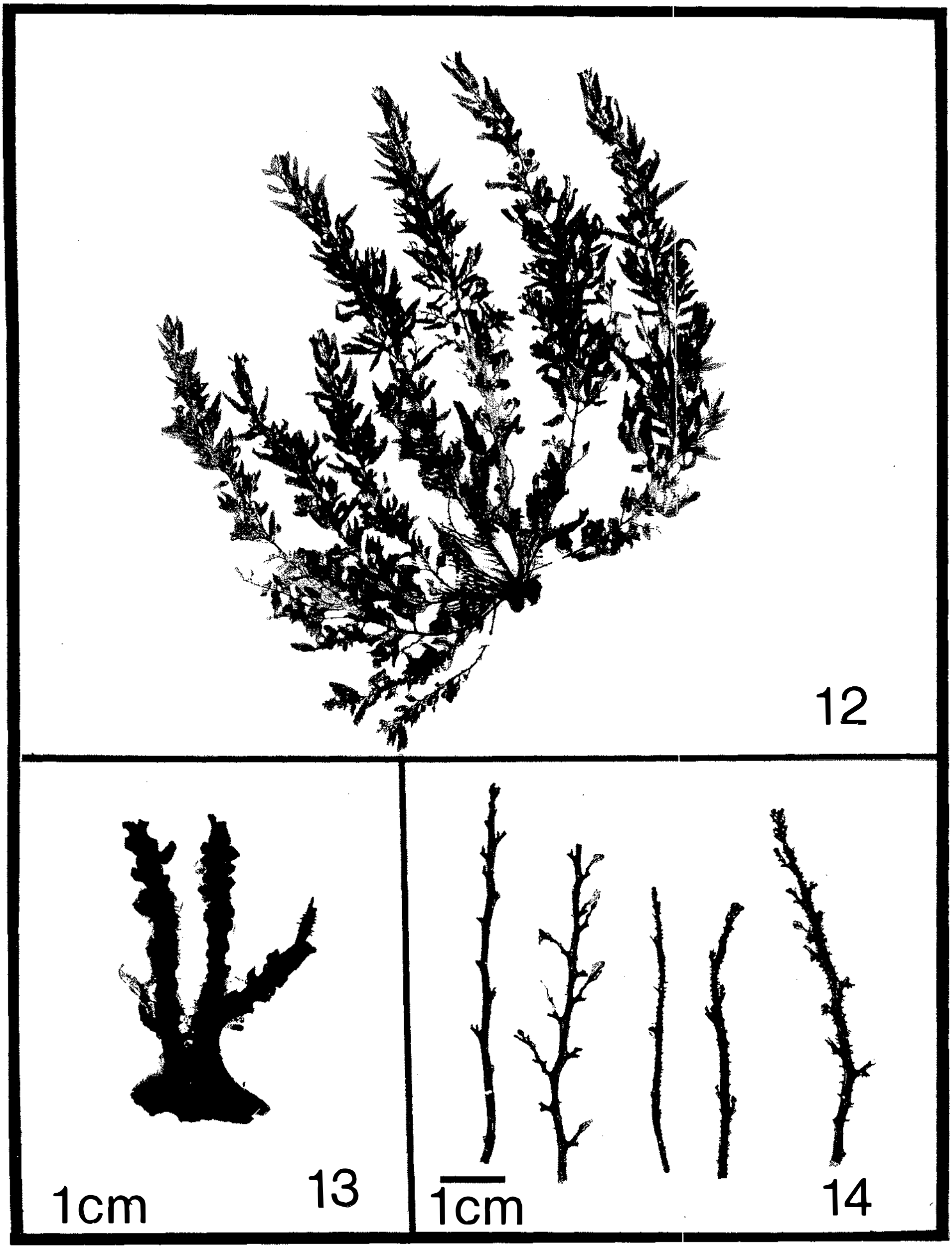
Holdfast conical-discoid, up to 3 cm in diameter. Main axis terete, usually one per holdfast, 2–6 cm high, 3–4 mm in diameter, with warty surface; primary branches 3–14 per plant, typically 9–15 cm in height, ranging to 40 cm, terete, spines early in season, falling off with onset of growth; secondary branches issued at about 5-mm intervals, generally without spines, ranging from short spur branches to well-developed lateral axillary branches, alternately or spirally branched, phyllotaxis one in two or one in three turns. Blades typically simple, sessile, flat or recurved, ovate or lanceolate with serrate margins, becoming linear toward end of growing season, 6–43 mm long, 1–12 mm wide, l:w typically 1.5:1 to 5:1, rarely up to 13:1, forked blades rare (typically 2–7% of blades, up to 30%), margins nearly entire on new branches, sometimes double serrated on older branches, twisted, or undulate, broadly rounded or even transverse symmetrical bases early in season, becoming more asymmetrical, apex broadly obtuse to acute. Midrib distinct and percurrent, now and then winged (typically 1–10% of blades, rarely up to 41%). Cryptostomata distinct, opening circular to elliptical, variable in number (ca. 50–225 per blade) and size, up to 216 µm in diameter on distally located blades, slightly larger on proximal blades, generally disposed randomly on blade, occasionally in two single rows on either side of midrib on more linear blades. Vesicles spherical to elliptical, numerous at distal end of a mature frond, sometimes apiculate (ca. 0.5–12% of bladders) or leafed (ca. 0–5.5% of bladders); bladders to 4.0–4.5 mm (longitudinal plane) by 3.5–4.0 mm (diameter); pedicels simple, ca. 2.0 mm long, rarely to 7 mm, shorter during stasis and with wings or spines. Receptacles occur throughout most of year, without spines, short, androgynous, forked, and not densely massed, racemosely arranged, formed acropetally on frond with short pedicels when fully developed.

Habitat: From depths of 1–5 m, occurring on coral rubble, and forming dense stands on shallow, fringing reefs of dead coral.

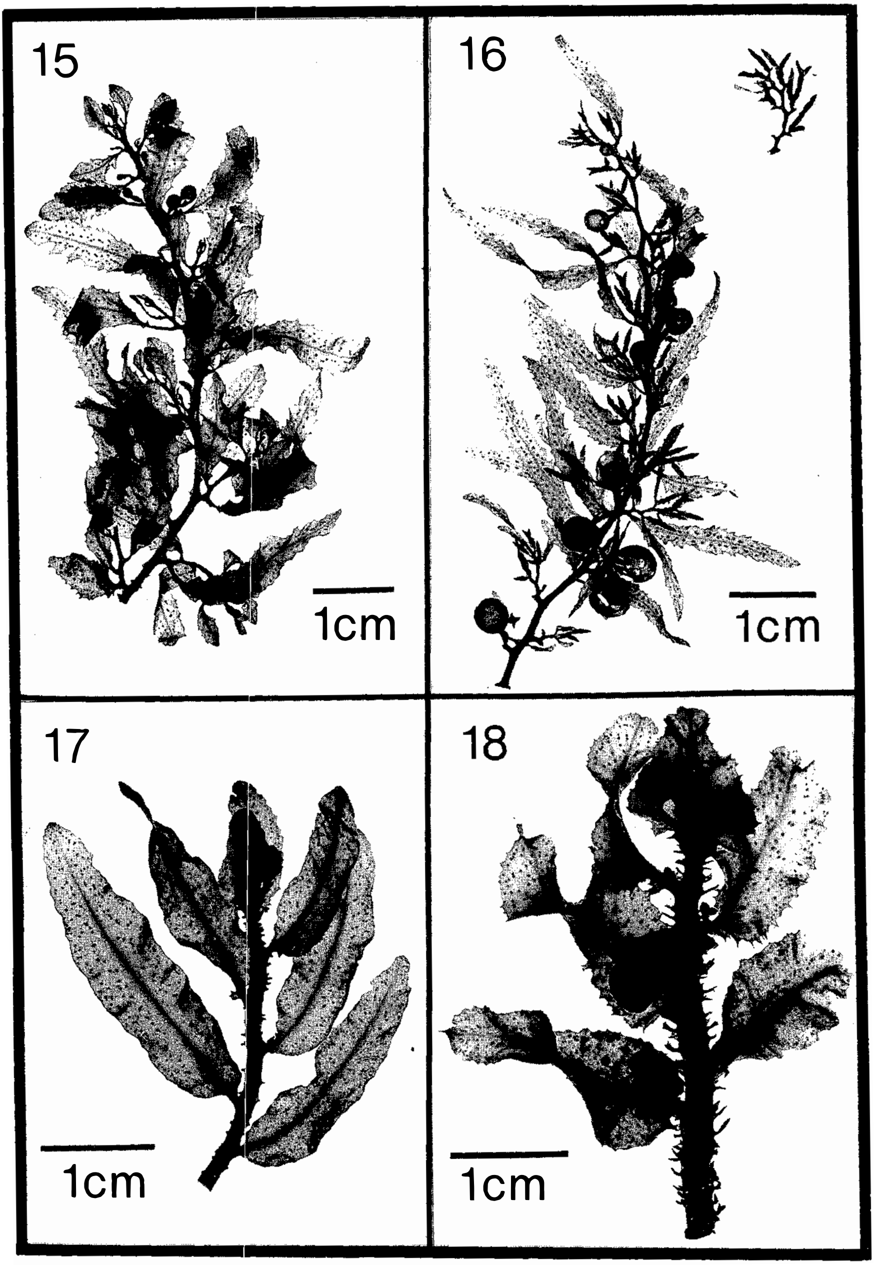
Remarks: Deciduous spines take the place of cryptostomata early in the season, forming papillated blades and hard spines (lumps) on axes. The plant is a pseudoperennial with maximal growth from midfall to midwinter. Maximal biomass occurs October-December; minimal biomass, June-July (stasis).

Statistical Analysis

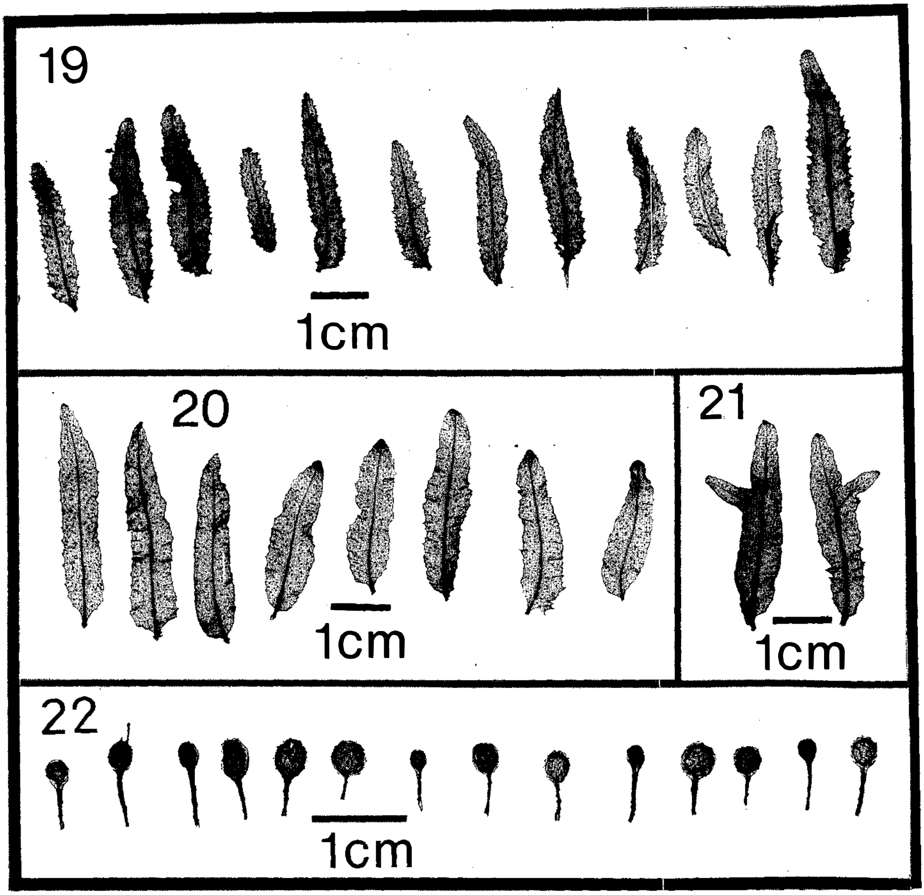
To correct data for site-specific temporal effects, we compared l:w ratios of *S. polyceratium* for the months May through December with the ratios of June plants of *S. polyporum*. The ratios of proximally and distally located blades for *S. polyporum* in June and for *S. polyceratium* in November were not statistically different (Table 1). Of the initial 25 continuous traits examined, 18 variables were suitable for multivariate analyses.



Figs. 12–14. *Sargassum polyceratium*. Dried (Fig. 12) and thawed, frozen (Figs. 13–14) specimens from the Content Keys, Florida (November 25, 1987). Fig. 13, Holdfast and perennial stems (main axis). Fig. 14, Smooth and hard-spined annual stems or primary-branch axes.



Figs. 15–18. ***Sargassum polyceratium.*** **Thawed, frozen specimens from the Content Keys, Florida. Figs. 15–17 collected on November 25, 1987, and Fig. 18 on June 9, 1987. Fig. 15, Distal tip, vegetative thallus. Fig. 16, Distal tip, with receptacles. Fig. 17, New annual stem or primary-branch axis. Fig. 18, Annual stem or primary-branch axis during stasis.**



Figs. 19–22. *Sargassum polyceratium*. Thawed, frozen specimens from the Content Keys, Florida (November 25, 1987). Fig. 19, Distal blades of primary-branched axis. Fig. 20, Proximal blades of primary-branched axis. Fig. 21, Bifurcated blades. Fig. 22, Vesicles (the pedicels of these specimens are slighly larger than typical).

Redundant traits were removed; for example, the area of the cryptostomate was highly correlated ($r^2 > 0.90$) with lengths of the major and minor axes. In this instance, the length of the major axis was retained. For similar reasons, vesicle length was included and vesicle diameter excluded.

Statistical differences in group centroids were observed between *S. polyceratium* and *S. polyporum* (MDA; MANOVA, $F_{18,11} = 28.4$, $p < .001$), with individual plants of each species sorting into their respective group ($p < .05$). Cryptostomatal size, proximal blades (width, length), blade bifurcations, main-axis length, spined vesicles, and winged vesicles distinguished these taxa. The morphology of distal blades and vesicles was otherwise identical (Table 1).

Bivariate plots of the first and second and the first and third principal components

Table 1. Means and Univariate F-ratios of Continuous Traits of *Sargassum polyporum* (June) and *S. polyceratium* (November)

	S. polyporum	*S. polyceratium*	F Ratio	*p*
Distal blades				
Length (mm)	16.2	17.9	1.14	>.05
Width (mm)	5.7	5.4	0.86	>.05
l:w	3.27	3.26	0.00	>.05
Cryptostomatum				
Area (μm^2)	6648	19382	33.2	<.001
Major axis(μm)	100.5	172.5	42.4	<.001
Minor axis (μm)	80.1	136.2	34.8	<.001
No. of branches	1.61	0.00	54.0	<.001
Proximal blades				
Length (mm)	15.9	18.8	4.59	.039
Width (mm)	7.0	5.9	5.22	.029
l:w	3.29	3.28	0.00	>.05
Cryptostomatum				
Area (μm^2)	4423	13268	139.9	<.001
Major axis (μm)	82.7	141.8	118.7	<.001
Minor axis (μm)	63.3	118.5	193.0	<.001
No. of branches	0.80	0.00	14.3	<.001
Vesicles				
Length (mm)	4.58	4.32	0.85	>.05
Diameter (mm)	4.07	3.99	0.10	>.05
Pedicel (mm)	1.85	2.03	1.86	>.05
l:p	2.74	2.34	1.87	>.05
l:d	1.13	1.10	0.85	>.05
% Spines	79.7	20.4	40.1	<.001
% Alate	2.7	11.4	6.30	<.001
% Apiculate	0.0	5.9	2.94	>.05
Perennial stalk				
No.	2.67	3.00	0.22	>.05
Length (cm)	1.53	2.18	2.11	>.05
Plant size (cm)	34.4	31.22	6.38	>.017

Note. DF1 = 1, DF2 = 2. l:w = length:width ratio; l:p = length:pedicel ratio; l:d - length: diameter ratio.

separated *S. polyporum* from *S. polyceratium* (Fig. 23). The first two components accounted for 43% of the total variance; the third principal component added 15%. The majority of the variance in the first principal component was accounted for by the length of the cryptostomate's major axis; the number of distally located, bifurcated blades; and the frequency of spined vesicles. The second principal component was determined by the length of proximal blades, the length:diameter (l:d) ratios of the vesicles, and the number and length of the main axis. The third principal component was formed by the widths of proximal and distal blades and plant size.

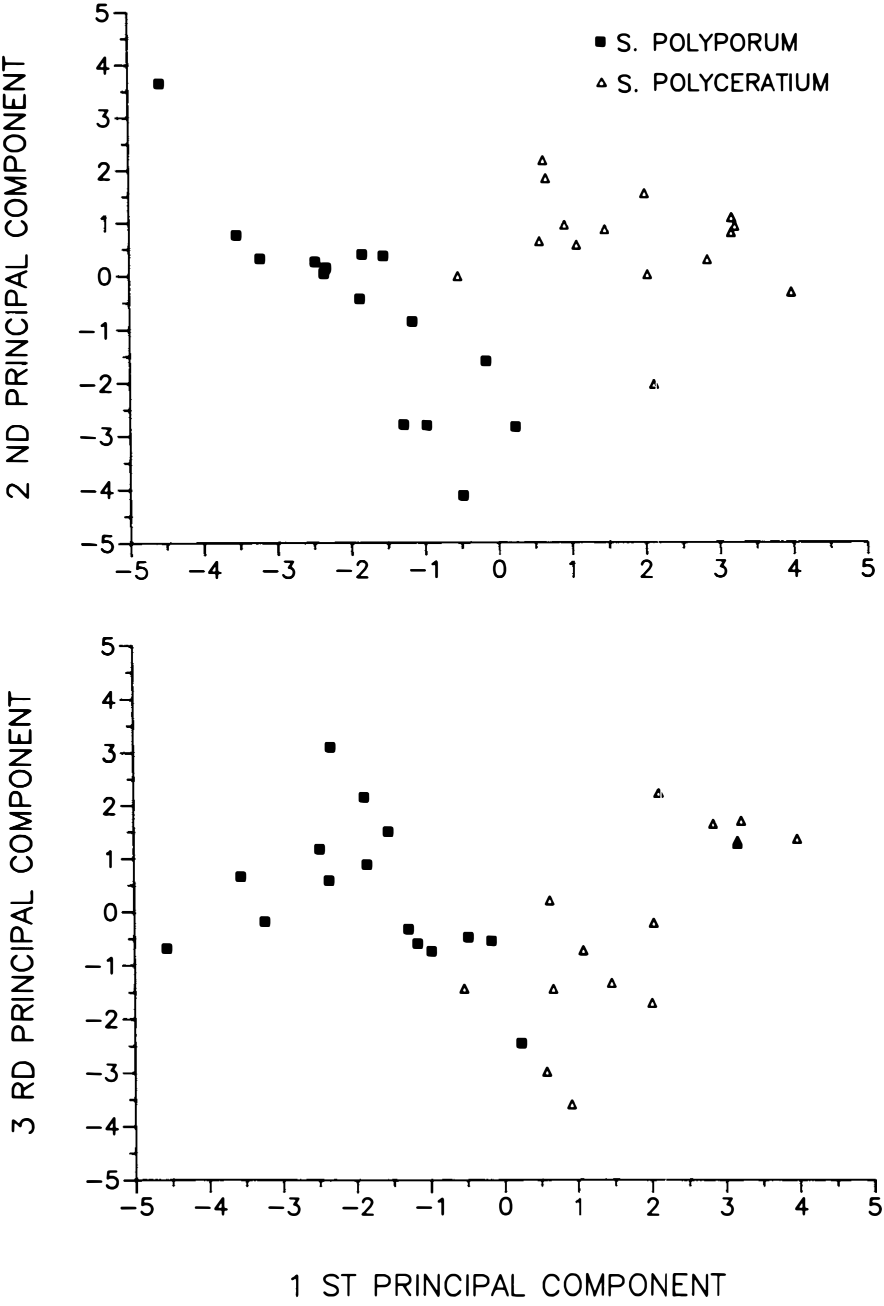


Fig. 23. Bivariate scatter plots of the component scores of the individual plants of *Sargassum polyceratium* and *S. polyporum* on first and second, and first and third principal components.

Table 2. Variance (%) Attributed Between Plants (V_b) and Coefficients of Variation (CV) of Selected Continuous Characters

	S. polyporum			*S. polyceratium*		
	n	V_b	CV	*n*	V_b	CV
Distal blades						
Length	450	0.045	0.393	125	0.833	0.537
Width	450	0.461	0.260	125	0.444	0.159
l:w	450	0.026	0.439	125	0.841	0.331
Cryptostomatum						
Area	450	0.244	0.449	450	0.841	0.461
Major axis	450	0.250	0.243	450	0.821	0.241
Minor axis	450	0.178	0.257	450	0.790	0.250
Proximal blades						
Length	224	0.078	0.370	125	0.546	0.239
Width	224	0.447	0.208	125	0.615	0.197
l:w	224	0.178	0.306	125	0.551	0.228
Cryptostomatum						
Area	224	0.253	0.619	255	0.836	0.450
Major axis	224	0.260	0.296	255	0.819	0.230
Minor axis	224	0.248	0.298	255	0.791	0.270
Vesicles						
Length	168	0.194	0.194	175	0.358	0.142
Diameter	168	0.157	0.191	175	0.565	0.145
Pedicel	168	0.167	0.371	175	0.300	0.321
l:p	168	0.116	0.405	175	0.503	0.321
l:d	168	0.251	0.085	175	0.197	0.138

Note. Traits with low V_b and CV are considered the most spatially stable and the least variable, respectively. *n* = sample size; l:w = length:width ratio; l:p = length:pedicel ratio; l:d = length:diameter.

Overall, measurements of V_b and CV were greater in *S. polyceratium* than in *S. polyporum* (Table 2). Characters with variance concentrated within individuals ($V_b < 0.15$) consisted of the length of distal and proximal blades and the l:w ratio of the distal blades for *S. polyporum* and the length of the vesicle and its pedicel and the l:p ratio for *S. polyceratium.* For both taxa, vesicle traits (i.e., length, diameter, and l:d ratio) were the least variable.

Discussion

Our reliance on the shape and size of blades and vesicles and on the few specimens of these *Sargassum* at the workshop had led us at first to conclude that *S. polyporum* and *S. polyceratium* were synonymous. After more quantitative procedures were adopted, blade and vesicle features were still found to be closely related, but many other traits diverged, such as the size of the cryptostomate and the number and degree of blade bifurcations. Statistical analyses and species descriptions support the recognition of two morphologically defined entities. However, geographical isolation and seasonal frequencies are the most reassuring (i.e., blade bifurcations in *S. polyceratium* do not approach those observed for *S. polyporum* [Kilar and Hanisak 1988, 1989]); other distinctions are not clear.

Temporal patterns in morphology are a major source of taxonomic uncertainty. Bifurcated blades occur in both species (Montagne 1842, Grunow 1916b, Setchell 1936, Taylor 1960) and vary temporally. At the workshop, the number of bifurcated blades on specimens of *S. polyporum* was comparable with the number on *S. polyceratium*, whereas the number on specimens of *S. polyporum* used for the description and statistical analyses had higher frequencies. Kilar and Hanisak (1988) have shown that the frequency of blade bifurcations changes seasonally in *S. polyceratium*, reaching a maximum late in the growing season (February to March). A similar pattern occurs in *S. stenophyllum* Martius (Kilar and Hanisak, unpublished data). Other traits of *S. polyceratium*, such as cryptostomatal area, deviate seasonally and with the age of the plant. Observed differences in the length and width of proximal blades could be related to plant development since blades are lost acropetally from the thallus (Norton 1977, Taniguchi and Yamada 1978, Terawaki et al. 1984, Kilar and Hanisak 1988). It is unknown whether such temporal patterns noted in *S. polyceratium* occur also in *S. polyporum.*

Patterns of variation are useful taxonomic indicators. The advantage of multivariate analysis over univariate is that no attempt to find the single best feature to describe a species is necessary (Pimentel and Smith 1986). The disadvantage is that key taxonomic characters are regularly not well defined or ranked as to spatial and temporal stability. Is trait variance concentrated within or between individuals? How variable is the character? The answers to these questions are critical for a workable taxonomy. For example, variation in blade length occurs within individuals in *S. polyporum* and among plants in *S. polyceratium.* Thus, several plants are necessary to perceive the variability in blades for *S. polyceratium.* Temporal variability is best examined over a seasonal cycle in *Sargassum.* Because we lack this information for *S. polyporum*, the CVs presented in this study are indicators of variation for the sampling period. For both species, vesicle length and diameter are among the least variable features. Based on these features, the taxa are identical.

S. polyceratium is morphologically more variable than *S. polyporum* and expresses more of its variability among plants. *S. polyporum* always has muricate axes (axes with hard spines). On the other hand, *S. polyceratium* has muricate axes early in its growth cycle, with some individuals retaining the spines throughout the year. Questions as to why some species vary little in morphology and are considered "good species," whereas others have a myriad of forms and varieties, remain unresolved. Answers to these questions are, in part, related to environmental conditions and plant breeding systems. As selective pressures acting on natural communities are necessarily more complex in more heterogenous environments, habitat complexity could have a profound influence on morphological and physiological variability. For example, deep-water plants of *S. cristaefolium* C. Agardh show more variation than shallow-water plants (Soe-Htun and Yoshida 1986). Russell (1986) reviewed the effects of stabilizing, disruptive, and directional selection acting on marine algae. Recently, Hawkes (personal communications) recognized that mixed-mating systems theoretically could lead to a large number of morphological forms. Russell (1986) noted that field observations generally provide insubstantial indications of genetic variation. Observations on *Sargassum* are to the contrary (Kilar and Hanisak 1988, 1989; Kilar et al. 1989; this study) and similar to those made on blue-green algae (Forest 1968, Stulp and Stam 1984), for which almost every collection of these organisms differed slightly from the others. The "great variability in form, size, and texture of leaves" of *S. polyceratium* has long been noted (Howe 1920) and recently has been attributed to ontogenetic forms (Kilar and Hanisak 1988) and polymorphism (Kilar and Hanisak 1989).

This study shows that geographically separated populations of *Sargassum* can share a number of taxonomically important characters. The similarities in the most pronounced traits, in blades and vesicles, suggests a close affinity or convergence in traits between *S. polyporum* and *S. polyceratium*, whereas the divergence in other traits, like blade bifurcations or cryptostomatal area, supports Montagne's (1842a, 1842b) conclusion that these taxa are separate entities. Geographical isolation alone may be sufficient to distinguish these taxa, as it is improbable that these populations share a common genetic pool. Discrepancies with descriptions of *S. muticum* from its indigenous Japanese and introduced British Columbian (Canada) and European habitats provide an example of intraspecific trait divergence; *S. muticum* (Yendo) Fensholt in Japan did not have the size or frequency in certain vesicle traits exhibited by the species in either North America or Europe (Jephson and Gray 1977, Critchley 1983). Studies over a complete growth cycle and in a variety of habitats are vital when morphological features cross recognized intraspecific boundaries. *S. polyceratium* and *S. polyporum* are also anatomically similar to *S. polyphyllum* J. Agardh from Hawaii (Magruder 1988) and *S. furcatum* Kützing and *S. vulgare* C. Agardh from the Caribbean (Taylor 1960). Similarly, Setchell (1936) noted that *S. polyporum*, *S. obtusifolium* J. Agardh (Hawaii), *S. torvum* J. Agardh (Australia), *S. polyphyllum J. Agardh, S. incisum* Dickie (Hawaii), and *S. pachycarpum* J. Agardh (Tasmania) belong to a similar "life-form" group. Investigations documenting phenotypic and genotypic responses (i.e., spatial and temporal patterns of variation) to divergent environmental conditions or reproductive strategies (i.e., mixed-mating systems) would advance the understanding of this morphologically complex genus.

Acknowledgments

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NOTES ON TWO "LOOK-ALIKE" SPECIES BETWEEN EAST AND WEST: *SARGASSUM POLYPORUM* MONTAGNE FROM RYUKYU ISLANDS IN JAPAN AND *SARGASSUM POLYCERATIUM* MONTAGNE FROM THE CARIBBEAN SEA

Tetsuro Ajisaka

Abstract

A collection of *Sargassum* subgenus *Sargassum* collected from Ryukyu Islands in Japan was compared with other species of *Sargassum* in which leaves are pinnately furcated. The Japanese specimens were identified as *S. polyporum* Montagne, and on gross morphological features, this species seems to resemble closely *S. polyceratium* Montagne from the Caribbean Sea.

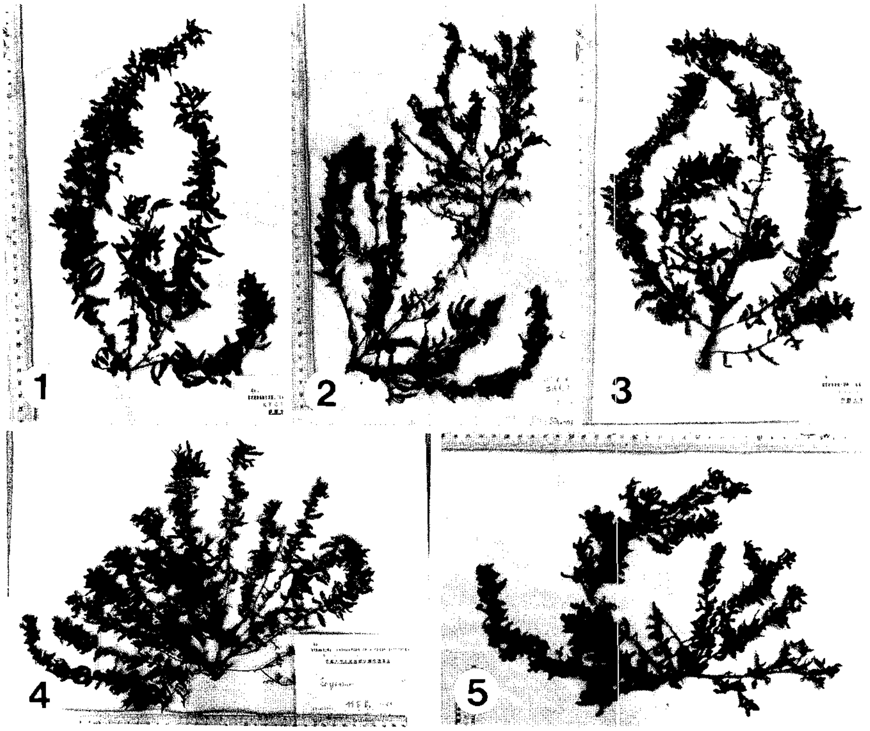
Introduction

Yoshida (1988) reported 20 species in the subgenus *Sargassum* from the shores of Japan. However, we cannot identify many specimens collected from the southern parts of Japan, especially the coasts of Iriomote, Ishigaki, Miyako, and Okinawa Islands (Ryukyu Islands), where a great many species of *Sargassum* subgenus *Sargassum* are growing. This chapter deals with one species of *Sargassum* (Figs. 1–20) that was collected from Iriomote, Taketomi, and Ishigaki Islands (Yaeyama Islands). Its morphological characters agree well with those of *S. polyporum* Montagne, which has been reported from Macao (Montagne 1842) and Hong Kong (Setchell 1936) and in this volume by Tseng and Lu. However, Japanese specimens show many characters that are also observed in *S. polyphyllum* J. Agardh from Hawaii and *S. polyceratium* Montagne from the Caribbean Sea.

Morphological characters of leaves and vesicles of *S. polyporum* from Japan and *S. polyceratium* from the Caribbean Sea were measured and compared with each other. Morphological characters reported in the literature on *S. polyporum* from China (Setchell 1936) and *S. polyphyllum* from Hawaii (Magruder 1988) were also compared.

Description of the Species from Japan

Holdfast conical or discoid, up to 2 cm in diameter; stem terete, to 3 cm high and 4 mm in diameter, with warty surface. Main axes up to 42 cm long, terete, always with spines, usually with many highly branched spines; secondary branches also spinous, issued at about 5-mm intervals, alternately or spirally inserted with phyllotaxis of one-half or one-third, up to 17 cm long. Leaves sessile or with short petiole, petiole usually with spines; leaves linear, narrowly spatulate, or narrowly elliptical, flat to spirally twisted and usually one to two times branched or alternately pinnately furcate (one to seven times) on the upper to middle part, 1–5 cm long and 3–10 mm wide, length to width ratio 1:1 to 7:1, symmetrical or asymmetrical at base, obtuse at apices, margins usually dentate at the base or nearly entire, wavy or straight in lateral view. Midrib distinct, percurrent or vanishing near apex. Cryptostomata sometimes disposed completely in one row on both sides of midrib, or scattered over surface; opening circular to elliptical, 0.05–0.14 mm in diameter. Vesicles spherical to obovoid, up to 6.5 mm long, usually smooth at apices, rarely with a sharp tip, with small cryptostomata; stalks terete or compressed, shorter than vesicle or nearly same dimensions as vesicle, sometimes with few spines or margins dentate.



Figs. 1–5. *Sargassum polyporum*. Dried specimens. Figs. 1–2, Plants collected from Shiraho, Ishigaki Island, June 6, 1989. Figs. 3–4, Plants collected from Taketomi Island, June 5, 1989. Fig. 5, A plant collected from Funauki, Iriomote Island, June 3, 1989.

Receptacles terete, to 8 mm long and 1 mm wide, often forked, warty, racemosely arranged.

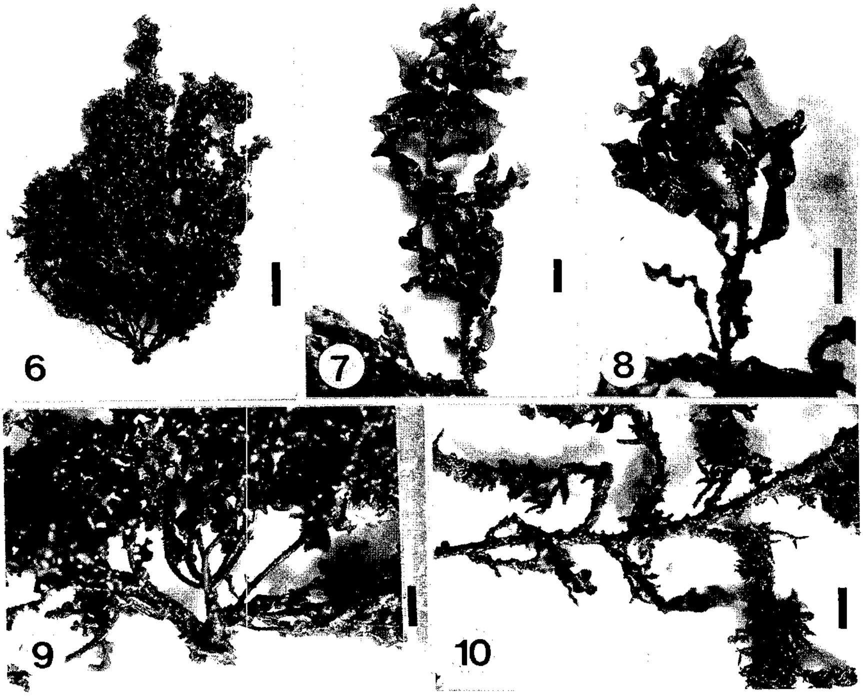
Habitat: From depths of 1–5 m in intertidal pools of lagoons, often forming dense stands on dead corals in the lagoon.

Japanese Distribution: Ryukyu Islands. Collected from Taketomi Island, Shiraho in Ishigaki Island, and Funauki Bay in Iriomote Island.

Comparison of Morphological Characters

From morphological characters described by Montagne (1848) and Setchell (1936), Japanese specimens were identified as *S. polyporum* Montagne. Although the original description was incomplete, the main features agreed well with those of Japanese specimens. Some minor differences were seen in the type specimen; for example, leaves and vesicles were smaller, and the stalk of the vesicle was longer than the vesicle. All the specimens were considered to be the same species because these characters had a wide range of variation. The specimens were collected in the same area, the western Pacific.

The many morphological characters were compared with those of *S. polyphyllum* J. Agardh from Hawaii, central Pacific. Magruder (1988) described the primary branches as

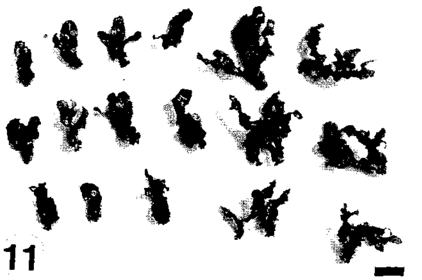


Figs. 6–10. *Sargassum polyporum*. Liquid-preserved specimens. Plants collected from Shiraho, Ishigaki Island, June 6, 1989. Fig. 6, Whole plant. Fig. 7, Upper part of a primary branch. Fig. 8, Upper part of a young secondary branch. Fig. 9, Holdfast, main axes, and lower part of primary branches. Fig. 10, Receptacle clusters on the middle part of primary branch. Scale for Fig. 6 = 5 cm; for Figs. 7–10 = 1 cm.

having many highly branched or peltate spines and the vesicle petiole as usually flattened or compressed with spines or wings and dentate, aculeate or incised. Japanese species also showed branched and/or peltate spines on the primary branches, and the vesicle petiole rarely had spines and/or wings. The stalk of the vesicle in the Hawaiian specimens was longer than the vesicle, but the stalk in Japanese specimens was shorter than the vesicle. Because the variations in these morphological characters were of wide ranges, the possibility that these two species should be merged was considered. In this case, *S. polyphyllum* J. Agardh (Agardh 1848) should be a synonym of *S. polyporum* Montagne (1842) according to nomenclatural priority. However, variations on the type specimens and other materials of each species should be examined.

On the basis of Taylor's (1960) description, the Japanese species was similar to a variety of the Caribbean specimens of *S. polyceratium* var. *ovatum* (Collins) Taylor. A study of *S. polyceratium* (De Ruyter van Steveninck and Breeman 1987) showed that two populations exist, depending on the depth of habitat. The numerical characters of these two populations were different and also had a seasonal variation. This species seems to have a wide range of variation in morphological characters.

Additional material of these taxa should be examined and compared.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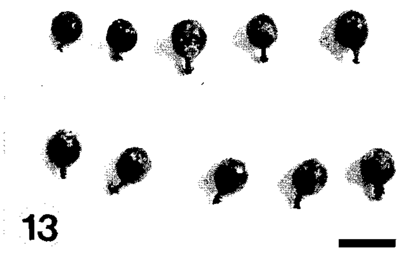
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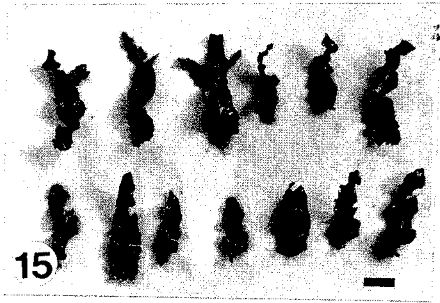
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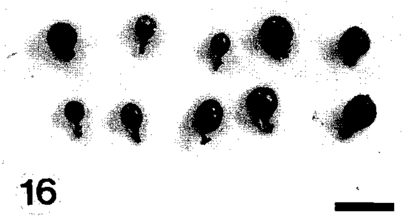
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Figs. 11–20. *Sargassum polyporum*. Liquid-preserved specimens. Figs. 11–13 and 19, From a plant collected from Taketomi Island (plant no. 13). Figs. 14–16 and 20, From a plant collected from Shiraho, Ishigaki Island (plant no. 1). Figs. 17 and 18, From a plant collected from Shiraho, Ishigaki Island (plant no. 8). Fig. 11, Leaves on the upper part of primary branch. Fig. 12, Leaves on the lower part of primary branch. Fig. 13, Vesicles on the primary branch. Fig. 14, Leaves on the upper part of primary branch. Fig. 15, Leaves on the lower part of primary branch. Fig. 16, Vesicles on the primary branch. Fig. 17, Leaves on the upper part of primary branch. Fig. 18, Leaves on the lower part of primary branch. Figs. 19 and 20, Primary branch axes with spines. Leaves and secondary branches have been cut away for viewing. Scale = 1 cm.

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Part II. *Sargassum* Subgenus *Bactrophycus*

KOREAN SPECIES OF *SARGASSUM* SUBGENUS *BACTROPHYCUS* J. AGARDH (SARGASSACEAE, FUCALES)

In Kyu Lee and Soon-Ae Yoo

Abstract

Twenty-one species of Korean *Sargassum* subgenus *Bactrophycus* are listed, and their distribution within Korea is given. Taxonomic notes are added. Half of the species have had their names changed as a result of re-evaluation after publication of studies from the first (Guam) workshop. Two species, *S. microceratium* and *S. muticum*, are confirmed for Korea. Three species previously reported from Korea, *S. giganteifolium*, *S. nigrifolium*, and *S. ringgoldianum*, are not recognized at this time.

Introduction

Early studies on Korean *Sargassum* subspecies *Bactrophycus* were done by Kützing (1843, 1849), J. Agardh (1889), Cotton (1906), Yendo (1907), and Okamura (1913, 1914, 1915, 1917). Kang (1966) reported 15 species and four subspecies of *Sargassum* subgenus *Bactrophycus* and their distribution on the Korean coasts, a foundation stone of Korean phycology. In fact, all the Korean coasts and subtidal zones are inhabited by *Sargassum* plants. They account for most of the primary production and are dominant species of benthic algal vegetation.

In 1974, one of us, I. K. Lee, began to study *Sargassum* as seaweed resources in Korea. The Koreans eat some species of *Sargassum* (including *Hizikia fusiformis*) or use them as fertilizer on the farms near the coast. Of the reported 17 species of Korean Fucales, 12 belong to *Bactrophycus*. Yoo (1976) dealt with the descriptions, figures, and a key of 24 species of Korean Fucales plants in her master's thesis. Of the 24 she described, 16 species belonged to *Bactrophycus.* Both of these studies (Lee 1974, Yoo 1976) used herbarium materials kept in the Pusan Fisheries University Herbarium and other nationwide collections. Because of the great morphological variations found in these taxa, we hesitated to publish the results. Instead, we did chemotaxonomic studies on the geographical variations of Korean Fucales plants (Yoo and Lee 1988a, 1988b; Yoo et al. 1988) to help solve the problem. Meanwhile, foreign papers, especially studies on *Bactrophycus* by Tseng et al. (1985) and Yoshida (1983), and authentic specimens that foreign scholars sent to Korean phycologists made us realize that several species of *Sargassum* had been called different scientific names from the beginning.

We introduce here Korean *Sargassum* subgenus *Bactrophycus* according to Tseng et al. (1985), including briefly the characteristics of the species, a key, and distribution on the Korean coasts.

Key to the Korean Species of *Sargassum* subgenus *Bactrophycus*

Kang (1968) and Yoo (1976) started their keys to species of *Sargassum* in Korea with the characteristics of the holdfast. We, however, have rearranged the key according to Tseng et al. (1985). Some sterile specimens of *Sargassum* species are excluded from the key.

1. Main axis (= "stem") elongated 2
1. Main axis (= "stem") abbreviated 3

  2. Vesicles cylindrical; plants dioecious . . . . *S. horneri* (Turner) C. Agardh
  2. Vesicles spherical to elliptical; plants monoecious . . . . *S. filicinum* Harvey

3. Main axis prostrate, rhizome-like, branched and entangled, forming attaching discs on ventral surface 4
3. Main axis erect above holdfast 5

  4. Main axis and attaching discs fused to form a solid basal system . . . . *S. yamadae* Yoshida et Konno
  4. Main axis and attaching discs never fused together . . . . *S. yezoense* (Yamada) Yoshida et Konno

5. Receptacles terete 6
5. Receptacles flat, compressed or triquetrous 14

  6. Main axis unbranched, growing annually, eventually becoming very elongated, to 10 cm or more, with two rows of prominent scars of fallen branches 7
  6. Main axis branched or unbranched, abbreviated, usually less than 3–4 cm; branches spirally arranged 9

7. Leaves all filiform . . . . *S. microceratium* (Turner) J. Agardh
7. Leaves, at least the lower ones, broad, elliptical to lanceolate 8

  8. Main axis and branches usually spinose; leaf coriaceous . . . . *S. confusum* C. Agardh
  8. Main axis and branches smooth, leaf papyraceous . . . . *S. pallidum* C. Agardh

9. Holdfast discoid 10
9. Holdfast platter-shaped or with rhizoidal outgrowth 11

  10. Vesicles spherical . . . . *S. muticum* (Yendo) Fensholt
  10. Vesicles fusiform . . . . *S. thunbergii* (Mertens ex Roth) Kuntze

11. Lower leaves hemiphyllous (not symmetrically developed) without midrib . . . . *S. hemiphyllum* (Turner) C. Agardh var. *hemiphyllum*
11. Lower leaves without symmetrical development, with midrib 12

  12. Holdfast platter-shaped . . . . *S. fulvellum* (Turner) C. Agardh
  12. Holdfast with rhizoidal outgrowth 13

13. Creeping rhizoidal filaments well developed . . . . *S. nipponicum* Yendo
13. Creeping rhizoidal filaments fused together . . . . *S. miyabei* Yendo

  14. Leaves linear to lanceolate, with entire margin . . . . *S. coreanum* J. Agardh
  14. Leaves in the middle part of branches having more or less serrate margins 15

15. Receptacles (at least female ones) often triquetrous . . . . *S. sagamianum* Yendo
15. Receptacles spatulate to oblanceolate 16

  16. Receptacles arranged in short, irregularly branched cluster . . . . *S. micracanthum* (Kützing) Endlicher
  16. Receptacles arranged in more or less elongated unbranched cluster 17

17. Main branches with obtuse protruberances . . . . *S. macrocarpum* C. Agardh
17. Main branches usually with smooth margins, sometimes with acute protruberances 18

  18. Upper leaves filiform; lower leaves lanceolate with serrate margins . . . . *S. autumnale* Yoshida
  18. Upper leaves not filiform; lower leaves ovate to lanceolate with entire margins 19

19. Holdfast conical; leaves coriaceous; upper leaves deeply serrate to midrib . . . . *S. siliquastrum* (Mertens ex Turner) C. Agardh
19. Holdfast dicoid; leaves membranaceous; upper leaves not deeply serrate to midrib . . . . *S. serratifolium* (C. Agardh) C. Agardh

Description of the Species

Sargassum **subgenus** ***Bactrophycus*** **section** ***Spongocarpus***

Sargassum horneri (Turner) J. Agardh (Fig. 1)

Yoo 1976, p. 94; Lee and Kang 1986, p. 318; SAP 034606, SAP 043896 in Yoshida 1983, p. 121.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This plant grows abundantly in the subtidal zone, forming an underwater forest whose canopy reaches to 20 m.

Sargassum filicinum Harvey

Yoo 1976, p. 100; Lee and Kang 1986, p. 318.

Distribution: Pusan, Cheju Island (southern part of Korea).

Remarks: This plant is not common on the Korean coasts. We collected only some fragments. Previously known only from Japan.

Sargassum **subgenus** ***Bactrophycus*** **section** ***Teretia***

Sargassum microceratium (Turner) J. Agardh

SAP 043904 in Yoshida 1983, p. 127.

Distribution: Wonsan (Genzan, in Japanese, the east coast).

Remarks: We did not collect this plant from South Korea. However, its growth in North Korea has been confirmed by Yoshida (1983).

Sargassum confusum C. Agardh (Fig. 2)

Yoo 1976, p. 85; Lee and Kang 1986, p. 318; SAP 034613, SAP 043902 in Yoshida 1983, p. 133.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This plant grows abundantly in Korea. All the plants whose upright stem forms main branches alternately in one plane have been identified as *S. confusum*, but their morphological diversity was great. Following Yoshida (1983), we have divided this confusing taxon into two species, *S. confusum* and *S. pallidum*, but many recognizable intermediates exist.

Sargassum pallidum (Turner) C. Agardh (Figs. 3, 4)

SAP 043898 in Yoshida 1983, p. 183; as *S. confusum* C. Agardh f. *validum* Yendo in Lee and Kang 1986, p. 318.

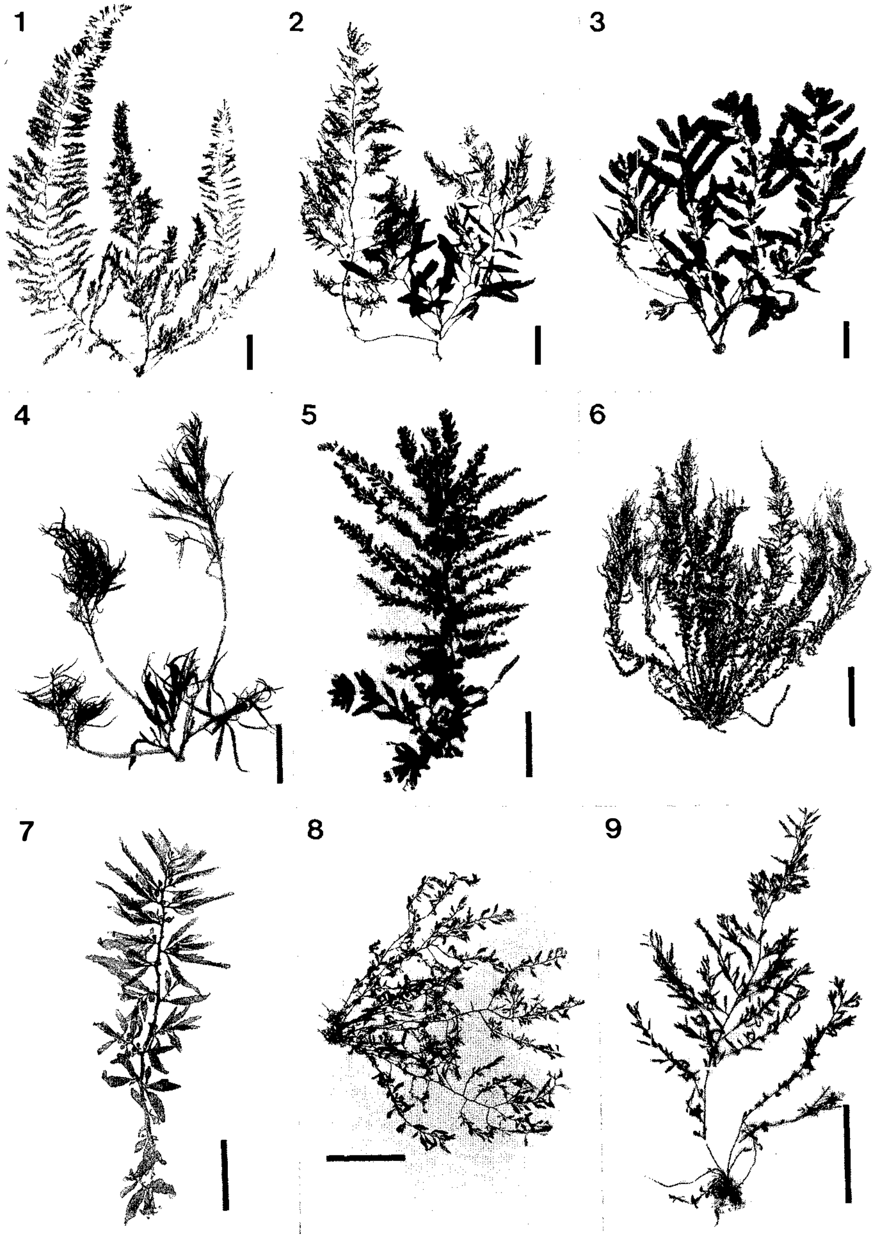
Distribution: Sunyoo Island, Daechon, Yonpo (the west coast); Kangneung (the east coast); Yongdu-Dong (Cheju Island).

Remarks: Our materials have somewhat thicker leaves than those of Yoshida's plants. The material collected from Sunyoo Island (Fig. 4) was the most similar to Yoshida's specimens.

Sargassum muticum (Yendo) Fensholt (Fig. 5)

SAP 034609, SAP 034608 in Yoshida 1983, p. 140.

Distribution: Gijang (the east coast), Kumoon Island (the south coast), Sunyoo Island (the west coast).



Figs. 1–9. Korean species of *Sargassum* subgenus *Bactrophycus*. Scale bar = 5 cm. Fig. 1, *S. horneri* (Editor's note: Not a typical specimen in the opinion of T. Yoshida). Fig. 2, *S. confusum*. Fig. 3, *S. pallidum* from Kangneung. Fig. 4, *S. pallidum* from Sunyoo Island. Fig. 5, *S. muticum*. Fig. 6, *S. thunbergii*. Fig. 7, *S. fulvellum*. Fig. 8, *S. hemiphyllum* var. *hemiphyllum*. Fig. 9, *S. nipponicum*.

Remarks: We think that this plant has been identified under the name of *S. kjellmanianum* in Korea. Yoshida (1983) confirmed the presence of this plant in Korea, and we presume that reexamining all the Korean herbarium specimens will clarify the wide distribution of this plant.

Sargassum thunbergii (Mertens ex Roth) Kuntze (Fig. 6)

Yoo 1976, p. 125; Lee and Kang 1986, p. 318; SAP 034605, SAP 043901 in Yoshida 1983, p. 147.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This plant is the dominant species and the most common along all the Korean coasts.

Sargassum fulvellum (Turner) C. Agardh (Fig. 7)

Yoo 1976, p. 74; Lee and Kang 1986, p. 318; SAP 034615 in Yoshida 1983, p. 151.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This species is well liked as food and is one of the edible *Sargassum*s. The Korean name of this plant, "mozaban," is used as the general name of the seaweed in Korea.

Sargassum hemiphyllum (Turner) C. Agardh var. *S. hemiphyllum* (Fig. 8)

S. hemiphyllum (Turner) C. Agardh in Yoo 1976, p. 103, and in Lee and Kang 1986, p. 318; SAP 034600 in Yoshida 1983, p. 157.

Distribution: Plentiful on Cheju Island, rare on the east and south coasts of the Korean peninsula.

Remarks: We have not found *S. hemiphyllum* var. *chinense* on the Korean coast. The Korean *S. hemiphyllum* plant is a striking contrast to the Chinese plant and resembles the Japanese var. *hemiphyllum* (Tseng et al. 1985).

Sargassum nipponicum Yendo (Fig. 9)

Yoo 1976, p. 108; Lee and Kang 1986, p. 318.

Distribution: Rare on the east, south, and west coasts of the Korean peninsula.

Remarks: Korean *S. nipponicum* has creeping rhizoidal filaments somewhat weaker than those of the Japanese plant, and the leaves have a few dentations, different from leaves of the Japanese one.

Sargassum miyabei Yendo (Fig. 10)

S. kjellmanianum Yendo in Yoo 1976, p. 120, and in Lee and Kang, 1986, p. 138.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This plant has been known under the name of *S. kjellmanianum* Yendo in Korea.

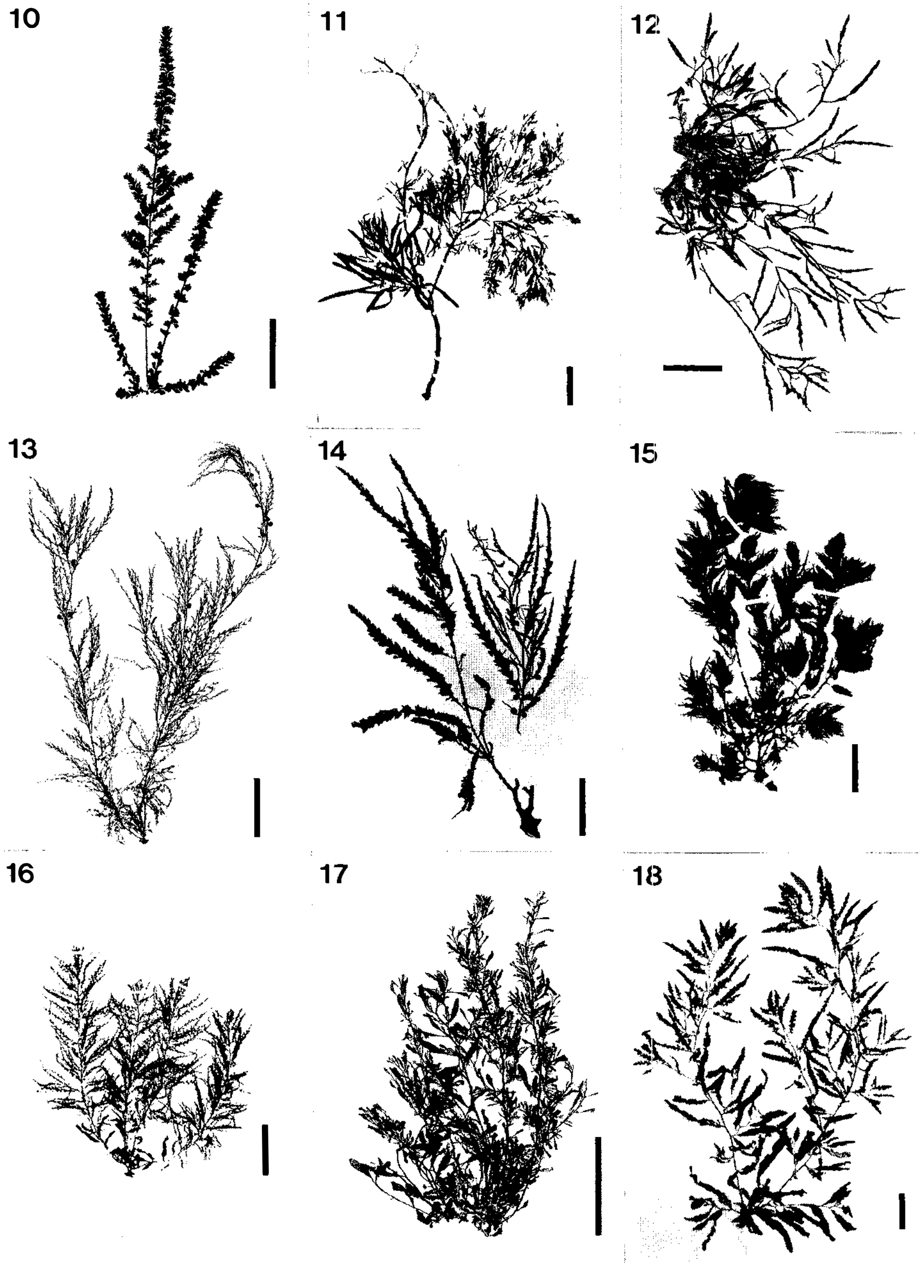
Sargassum* subgenus *Bactrophycus* section *Halochloa

Sargassum coreanum J. Agardh (Fig. 11)

Tseng et al. 1985, p. 6; as *S. ringgoldianum* Harvey in Yoo 1976, p. 45, and in Lee and Kang 1986, p. 318; *S. ringgoldianum* subspecies *coreanum* (J. Agardh) Yoshida in Yoshida 1983, p. 181, SAP 043898.

Distribution: All the coasts of the Korean peninsula and Cheju Island, but rare on the west coast.

Remarks: This plant is a very stable taxon that does not exhibit any geographical



Figs. 10–18. Korean species of *Sargassum* subgenus *Bactrophycus*. Scale bar = 5 cm. Fig. 10, *S. miyabei*. Fig. 11, *S. coreanum*. Fig. 12, *S. sagamianum*. Fig. 13, *S. micracanthum*. Fig. 14, *S. macrocarpum*. Fig. 15, *S. autumnale*. Fig. 16, *S. siliquastrum*. Fig. 17, *S. yezoense*. Fig. 18, *Sargassum* species.

variation. All the plants that have been identified under the name of *S. ringgoldianum* Harvey in Korea belong to this species according to Tseng et al. (1985).

Sargassum sagamianum Yendo (Fig. 12)

As *S. nigrifolium* Yendo in Yoo 1976, p. 111, and in Lee and Kang 1986, p. 318.

Distribution: Uljin, Kangneung (the east coast).

Remarks: According to Yoshida (1983), distribution of this plant is limited to the Kii peninsula, central Japan. However, our material, from eastern Korea, accords well with the original description and the type specimen. The plants known under the name of *S. nigrifolium* Yendo in Korea are *S. sagamianum* Yendo according to Yoshida's (1983) description and figures.

Sargassum micracanthum (Kützing) Endlicher (Fig. 13)

Yoo 1976, p. 68; Lee and Kang 1986, p. 318; SAP 034618 in Yoshida 1983, p. 192.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: This is a very stable taxon. We think there is no taxonomic problem in recognizing this species.

Sargassum macrocarpum C. Agardh (Fig. 14)

SAP 043895 in Yoshida 1983, p. 200; as *S. serratifolium* C. Agardh in Yoo 1976, p. 51, and in Lee and Kang 1986, p. 318.

Distribution: All the coasts of the Korean peninsula and Cheju Island, but rare on the west coast of Korea.

Remarks: All the Korean plants that we have identified under the name of *S. serratifolium* C. Agardh are found to be this species according to Yoshida (1983).

Sargassum autumnale Yoshida (Fig. 15)

Distribution: Yeosu (the south coast) and Gapado (Cheju Island).

Remarks: We have had no chance to confirm the reproductive season of this plant, but our material accords well with the original description. We have previously identified this plant under the name of *S. tortile* C. Agardh.

Sargassum siliquastrum (Mertens ex Turner) C. Agardh (Fig. 16)

SAP 043894 in Yoshida 1983, p. 215; Lee and Kang 1986, p. 318; as *S. tortile* C. Agardh in Yoo 1976, p. 57.

Distribution: All the coasts of the Korean peninsula and Cheju Island.

Remarks: Almost all of the plants known previously as *S. tortile* C. Agardh in Korea belong to this taxon.

Sargassum serratifolium (C. Agardh) C. Agardh

S. giganteifolium Yamada in Song and Kang 1985, p. 4.

Distribution: Marado, Mun-sum (Cheju Island).

Remarks: This plant was reported only once as *S. giganteifolium* Yamada by Song and Kang (1985). However, the description of the morphology and ecology of this plant accords quite well with that of *S. serratifolium* of Yoshida (1983).

Sargassum* subgenus *Bactrophycus* section *Repentia

Sargassum yezoense (Yamada) Yoshida et Konno (Fig. 17)

SAP 034598 in Yoshida 1983, p. 233; as *S. sagamianum* Yendo var. *yezoense* Yamada in Lee and Kang 1986, p. 318.

Distribution: Uljin, Ulreungdo Island (the east coast).

Remarks: Most of the plants that have been known as *S. sagamianum* Yendo or *S. sagamianum* var. *yezoense* in Korea belong to this species. We should reexamine the distribution of *S. yamadae* and *S. yezoense.*

Sargassum yamadae Yoshida et Konno

As *S. sagamianum* Yendo in Yoo 1976, p. 115; Lee and Kang 1986, p. 318.

Distribution: Kangneung (the east coast).

Remarks: This plant has a narrow range of distribution. Only a few plants that have been identified under the name of *S. sagamianum* Yendo might belong to *S. yamadae*. The Korean distribution should be reexamined.

Sargassum species (Fig. 18)

As *S. kushimotense* Yendo in Yoo 1976, p. 80; as *Sargassum* species in Lee and Kim 1977, p. 144.

Thallus up to 80–90 cm in height, greenish brown when living, dark green when dried. Holdfast conical, discoid, 3 cm in diameter. Stem terete, shorter than 5 cm, forking pseudodichotomously several times. Main branch terete below, soon triquetrous to flat upward, with wavy dentation at margin, twisting loosely. Leaves in lower part of main branch retroflexed, spreading horizontally, lanceolate to linear-lanceolate, papyraceous, 12–20 cm long and 2–2.5 cm wide; leaves on upper part smaller, 10–13 cm long and 1.5–2 cm wide. Cryptostomata present. Midrib elevated. Phyllotaxis of the leaves one-half. Vesicles ornamented with leaf-shaped coronae, elliptical, 1–1.5 cm long. Receptacles not observed.

Distribution: Kwangyang Bay (the south coast).

Remarks: This plant has characteristic large, lubricous, papyraceous leaves. We have observed Yoshida's authentic specimen of *S. kushimotense* Yendo and all the specimens preserved in the British Museum of Natural History and consider that this plant is a new species. Unlike *S. kushimotense* (Yendo 1907, p. 73), which has a flattened stem, our material has a terete stem, so that it might belong to section *Teretia* or *Halochloa*. Because we have not observed the receptacles, we reserve naming and classifying this plant.

Acknowledgments

We express our heartiest thanks to Dr. I. A. Abbott for the invitation to participate in this workshop and for advice on preparation of the manuscript. We also thank Dr. T. Yoshida for his valuable authentic specimens and reprints and his critical reading. We are pleased to acknowledge the financial support of the Calfornia Sea Grant College and Dr. J. Sullivan in participation at this workshop.

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Section II. Gelidiales

INTRODUCTION

Isabella A. Abbott

Many systematists always seem to be "stirring the pot." The more conservative among us avoid the occupation because the result is often unexpected problems. The more adventurous like it because stirring (i.e., constant reconsideration) forces examination of old issues from new points of view.

Gelidium and *Pterocladia* have been subjects of study since our first workshop. Our earlier studies enumerated taxa from various, often widely distributed, geographical regions. But we tended to become conservative; that is, we redrew the lines of old species that were not well known, but we included few new species.

Now it's time to stir things up. This volume includes three papers that make very different contributions. First, Richard Norris looks at Gelidiales from the point of view of its vegetative patterns and finds that the species examined show an indeterminate prostrate system with a determinate erect system—a pattern opposite from the classical picture of *Gelidium* and *Pterocladia*. Because of the numerous exceptions that must be dealt with in order to identify a species as belonging to *Pterocladia*, he recommends that the genus *Pterocladia* be abandoned and the species merged with *Gelidium*. Second, Ricardo Melo, a graduate student from Portugal who has been studying with Professor Neushul at the University of California, Santa Barbara, contributes a paper on the structure of *Gelidiella acerosa*, the type species of its genus. His work will help clarify what may be expected when examining a cross section of *Gelidiella*. Third, Joan Stewart tests several features proposed as diagnostic of one or the other of the genera *Gelidium* and *Pterocladia* and finds that some of them are acceptable, whereas others are not. Hers is a useful kind of evaluation and reconsideration. A fourth paper, by Dr. Santelices, was published in Pacific Science (vol. 45, no. 1, pp. 1–11, 1991). In that paper he demonstrated that *Pterocladia lucida*, the type species of the genus *Pterocladia*, shows a very different cystocarpic development from *P. capillacea*, the most widely distributed species. While *Pterocladia lucida* shows only one chamber (locule) for the cystocarps, *P. capillacea* has two, a feature of the genus *Gelidium*. But because of lack of extensive studies on the development of the cystocarp in most species of both genera, "pot stirring" is not evident at this time.

Call it stirring the pot if you will, but this constant retesting and reconsideration of basic assumptions is one of the most important features of taxonomy.

A PROPOSED PHYLOGENETIC SCHEME FOR THE GELIDIALES

Richard E. Norris

Abstract

A review of the anatomy of *Gelidiella* presents data suggesting that it is more primitive than other Gelidiales, and a phylogenetic system for Gelidiales is proposed that is based mostly on vegetative characters. Studies on cultures and field-collected specimens of several small species of *Gelidium* and *Pterocladia* showed that all of them have an indeterminate prostrate branching system and a determinate upright system. This branching pattern is in contrast to the classical types of *Gelidium* and *Pterocladia*, which have an indeterminate, upright, more or less extensively branched thallus with branches usually distichously arranged, and a determinate prostrate system forming a holdfast. Upright determinate branches in small species were of two types: (1) those with a single apical cell, with lateral branches developing adventitiously or in production of fertile branchlets, and (2) determinate bladelike upright branches having several marginal apical cells, often producing lobes on the blade, and sometimes ramisympodial development of upright branches. The latter species were placed in the genus *Onikusa*, and this genus was accordingly revised. The tendency toward ramisympodial branching in the revised *Onikusa* suggested that it may be related to *Acanthopeltis*. Other genera of Gelidiaceae were related to the proposed phylogenetic system. Retaining *Pterocladia* at the generic rank was not supported.

Introduction

The two families and 10 genera currently recognized in the Gelidiales are not well understood systematically, despite their common occurrence in widespread marine localities throughout most of the world and the considerable attention given to them as agarophytes. This problem has been reviewed recently by Santelices (1991) with a view toward developing new perspectives on this economically important group of red algae. In my analysis of Gelidiales from Natal, the great variation of vegetative thalli in different species of *Gelidium* and *Pterocladia* has been particularly impressive. This is especially true in the very small species of these genera, species that are not merely growth forms of larger species as has sometimes been suggested for other species (i.e., *Gelidium pusillum* [Dixon and Irvine 1977]). Fertile specimens, particularly gametophytes, are often rare in species of these genera. Therefore, I have concentrated particularly on an attempt to relate and separate genera and species on the basis of characters of the vegetative thalli, and I have had some success in estimating what appear to be phylogenetically significant relationships among species and genera of Gelidiales.

Review of the Vegetative Structure of Gelidiales

Apical growth of Gelidiaceae was reviewed by Fan (1961), who found the structure remarkably constant in all the genera studied even though mature thalli of these taxa have a considerably different form. The basic pattern of growth involves transverse divisions of a single apical cell in each branch; the width of the apical cell often is greater than its length. The proximal products of the apical cell division divide twice longitudinally, forming initials of two branches of the second order. In the species described by Fan (1961), all divisions forming second-order branches occur perpendicularly to the narrow axis of the elliptical (in face view) apical cell, and second-order cell rows expand in more or less a single plane that parallels compression or flattening of the thallus. Third-order branch initials, as well as those of subsequent orders, are cut off by periaxial and other cells of the second order in a plane perpendicular to the plane of the second-order branches, and cortication is thereby produced that covers the basic branching pattern. The uniaxial structure of the thalli is also obscured because medullary cells, including the primary axis, all become much the same size and shape, and these cells become interconnected with one another by many secondary pit connections established early in development of the tissue.

Divisions of apical cell derivatives in *Gelidiella* were studied by Fan (1961) for *Gelidiella tenuissima* Feldmann et Hamel and were shown to have an arrangement similar to that of *Gelidium*. Sreenivasa Rao (1972) found that the type species of *Gelidiella, Gelidiella acerosa* (Forsskål) Feldmann et Hamel, has divisions of apical cell derivatives similar to those described by Fan, but sometimes in *G. acerosa*, the arrangement of cells is decussate rather than distichous. Maggs and Guiry (1987) described development in a new species of *Gelidiella*. They found it was essentially similar to development in species of Gelidiaceae in which two periaxial cells are produced distichously on each axial cell. The row of cells designated by Maggs and Guiry (1987) as "pericentral cells" are cells of the second order, and, in my estimation, this term should not be used for their derivatives as was done by these authors. Maggs and Guiry (1987) described the central (axial) cell as being narrower than surrounding medullary cells and as having unpigmented cell contents that stain deeply with aniline blue.

Rhizines (also known as hyphae and internal rhizoids) develop in all species of Gelidiaceae and are formed by internal cortical cells and sometimes by outer medullary cells. They grow mostly in a basipetal direction, and, according to Felicini and Perrone (1986), who studied them in *Pterocladia capillacea*, they are developed only in upright branches. The prostrate branching system may be invaded by rhizines that originated in upright branches. The absence of rhizines in thalli of Gelidiales has been used to define the genus *Gelidiella* and to separate the family Gelidiellaceae (Fan 1961) from the Gelidiaceae. This characterization was questioned by Maggs and Guiry (1987) in describing a new species of *Gelidiella, Gelidiella calcicola*, in which a few rhizines are present.

Thallus branches in the *Gelidium* group, according to Fan (1961), probably originate from terminal cells of the second-order cell rows. The distichous branching resulting in very flat thalli in many species is explained by the branch origin from the second-order cell rows. It is also recognized that adventitious branches in the Gelidiales often are formed and may account for the irregular branching pattern in some species.

Review of Reproductive Characters in Gelidiales

Reproduction in the Gelidiales was reviewed for most genera by Fan (1961) and studied more recently in *Gelidium* by Hommersand and Fredericq (1988). Reproductive areas are borne either on terminal parts of main branches or on lateral branchlets that are more or less specially modified. Fan (1961) found few differences in female reproductive systems in different genera. Distinctive features of reproductive cells in the Gelidiales are as follows: (1) Male cells are cut off from the spermatangial bearing cell by a transverse rather than oblique division as in most other red algae. (2) The female reproductive system has a one- or two-celled carpogonial branch borne on a suprabasal cell of the third order. In female reproduction, the basal cells of the third order in fertile regions form short nutritive filaments. After fertilization, the carpogonium fuses with surrounding cortical cells, and gonimoblast filaments develop. These filaments grow into the clusters of nutritive filaments where fusions take place, and it seems to be through the stimulation of these fusions that formation of carposporangia is initiated and development of cystocarps begins. Gelidiales cystocarps usually are bilocular; the locule is partitioned by the gonimoblast tissue and some associated vegetative cells. Each locule usually has a single ostiole. It is well known that *Pterocladia* has single-loculate cystocarps, but species are known in which biloculate cystocarps occur (*Pterocladia lindaueri* and *Pterocladia nana* [Fan 1961]).

Tetrasporangia are produced in most Gelidiales species, and monosporangia and bisporangia are known for a few (*Suhria, Gelidium pristoides*). They are developed in sori in distal regions of main branches or, more usually, on specially produced lateral branchlets. Sporangia replace outer cortical cells and, in some species, are arranged in pinnate rows along the axis of the branch. This arrangement is easily observed in simple species such as *G. calcicola* Maggs et Guiry (1987), in which tetrasporangia terminate cell rows of the third order and become arranged to form chevrons within the sorus.

Combining all the characters presently known to occur in the Gelidiales, Hommersand and Fredericq (1988) presented a revised and modernized description of this order. My reappraisal of previously published information on structure and reproduction of Gelidiales, along with new information obtained from my recent investigation of small *Gelidium* and *Pterocladia* species from Natal, has resulted in a hypothesis for phylogeny within the Gelidiales, and it is hoped that we may obtain a better understanding of Gelidiales systematics through this phylogenetic scheme.

Materials and Methods

Specimens were preserved in 5% formalin and returned to the laboratory where they were sorted. When adequate specimens of a species were available, small pieces were maintained in formalin preservative for future preparation of slides, and the remainder was dried on a herbarium sheet. A broad view of Gelidiales specimens has been obtained by examining the specimens in various herbaria. Some of these specimens have been cited in my previous publications on Gelidiaceae, but others will be provided in a manuscript on small Gelidiales species currently being prepared for publication. Dried specimens are filed in the South African Museum Herbarium (SAM), housed at the Compton Herbarium, Kirstenbosch, and the Herbarium of the University of Natal (NU). Some specimens from the International Indian Ocean Expedition were examined in this study; these are housed at the University of California Herbarium, Berkeley (UC) and at the Herbarium of the University of British Columbia (UBC). Citations of exact specimens used in this study are identified with their illustrations, in which NAT reference numbers refer to collections of the Natal benthic algal research program that are contained in SAM.

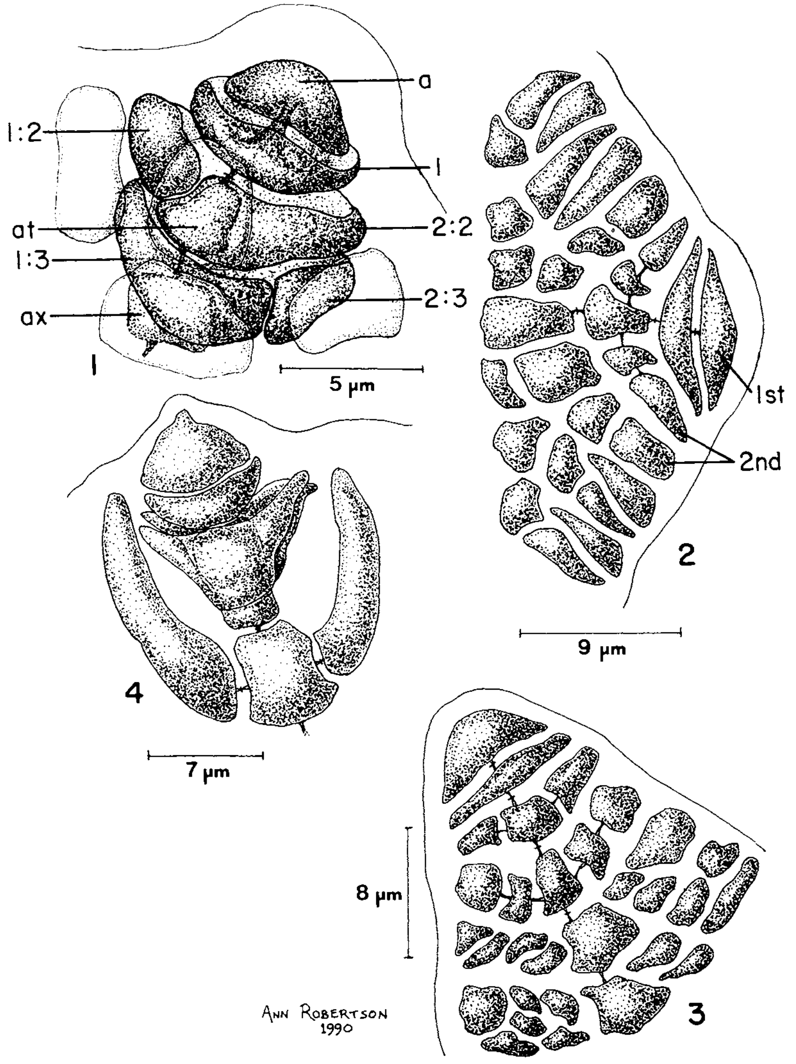
Slides of specimens were prepared by mounting whole branches or sections of branches in 50% corn syrup to which acidified aniline blue was added. Some slides were prepared by using unstained mounting medium. Branch apices, axial filaments, and rhizines were sometimes examined in squash preparations that were prepared by heating the material in the mounting medium and stain under a cover glass. After the preparation reached the boiling point, pressure was applied to the cover glass and the material was squashed so that internal cells could be viewed in a position close to their natural arrangement. Nuclei in cells were observed in aceto-carmine or aceto-orcein squash preparations of branch tips.

Results and Discussion

Apical Development. In reviewing details of thallus development for upright branches in many species in different Gelidiaceae genera, Fan (1961) noted little variation in this process. Development of upright branchs in the Natalian species does not seem to vary much within the Gelidiaceae, and Fan's observations can be confirmed. So far as I can determine, however, the arrangement of second-order filaments has not been reported for indeterminate axes of the prostrate branching system, and I have found that decussate or spiral arrangement of second-order branches in thallus apices often occurs in these branches in small species of *Gelidium*. As might be expected, branches that are mostly cylindrical, such as the prostrate system of *Gelidium arenarium* (Fig. 1), have second-order filaments spirally arranged. Upright axes of this species usually become flattened near their apices and convert to a distichous arrangement of second-order filaments (Fig. 2). Species such as *Pterocladia caloglossoides*, however, in which both prostrate and upright branches are compressed to flattened, always have a distichous arrangement of the second-order filaments in either prostrate (Fig. 3) or upright branches. This character should be carefully reexamined in species of Gelidiales that have indeterminate prostrate axes. Distichous, spiral, or decussate (Fig. 4) arrangement of second-order cell rows probably is directly related to cylindrical or flattened shapes of axes, and variations of this pattern could be significant in the taxonomy of this order. An influence of environmental factors on this character is possible, however, and should be carefully investigated.

The thallus axis has not been emphasized previously, and I consider the characteristics of the cells in this central row of filaments to be important. These cells often are recognized more easily in some of the small species of *Gelidium* and *Pterocladia* because of the common occurrence of narrow or thin branches in these species. Various authors have inferred that axial cells become indistinguishable from other medullary cells in older tissue because secondary pit connections are established with adjacent cells of that tissue. In following axial filaments of branches in different species, including *G. acerosa*, I have noted that these cells never seem to have any secondary connections and, therefore, their only lateral pit connections are the original pit connections to the two periaxial cells (Fig. 5). I have followed an axial filament to 23 cells behind the apical cell and observed no secondary pit connection on any of these cells. Furthermore, axial cells remain uninucleate, whereas adjacent medullary cells, cells that had established several secondary pit connections in addition to their primary connections, usually contain several nuclei. The ultimate loss of identity of the axial filament in thalli, therefore, is due not to loss of axial cell original character but to extreme stretching of axial cells by growth of adjacent tissues, making the cells very narrow and sometimes eventually causing them to be broken apart and difficult to find.

Cell division of the main-axis apical cell in *G. acerosa* and in species in the Gelidiaceae having broadened branch tips initiates not only the axial cell row but also the many cell rows that emanate from the cells of the second-order branches. In active meristematic regions, many species have meristematically active elongate surface cortical cells that divide proximally, forming a series of cuboidal cells that may also have one or two subsequent divisions. In actively growing branch tips, new branches also develop from internal filaments developing on second- or third-order filaments adjacent to the axial cells near the apical cells. These new filaments push through to the branch surface. The new filaments have cuboidal cells at first; the terminal cell elongates as it emerges



Figs. 1–4. Branch apices in various Gelidiales. Fig. 1, *Gelidium arenarium*, prostrate branch tip having spiral arrangement of divisions of periaxial cells. Numbers refer to order of divisions. From cultured plant collected at Mvoti, Natal, 16-III-1984 (NAT 2449). Fig. 2, *G. arenarium*, upright branch tip showing central axial apical cell (1st) and distichous arrangement of second-order (2nd) filaments. A field-collected plant from the same collection as Fig. 1. Fig. 3, *Gelidium (Pterocladia) calaglossoides*, prostrate branch tip with distichous arrangement of second-order filaments, the same as in upright branchlets. From cultured plant collected at Rocky Bay, Park Rynie, Natal, 28–VIII–1984 (NAT 2426). Fig. 4, *Gelidiella acerosa*, upright branch tip showing decussate arrangement of periaxial cells. Intertidal, Sordwana Bay, Natal, 14-X-1989 (NAT 6265).

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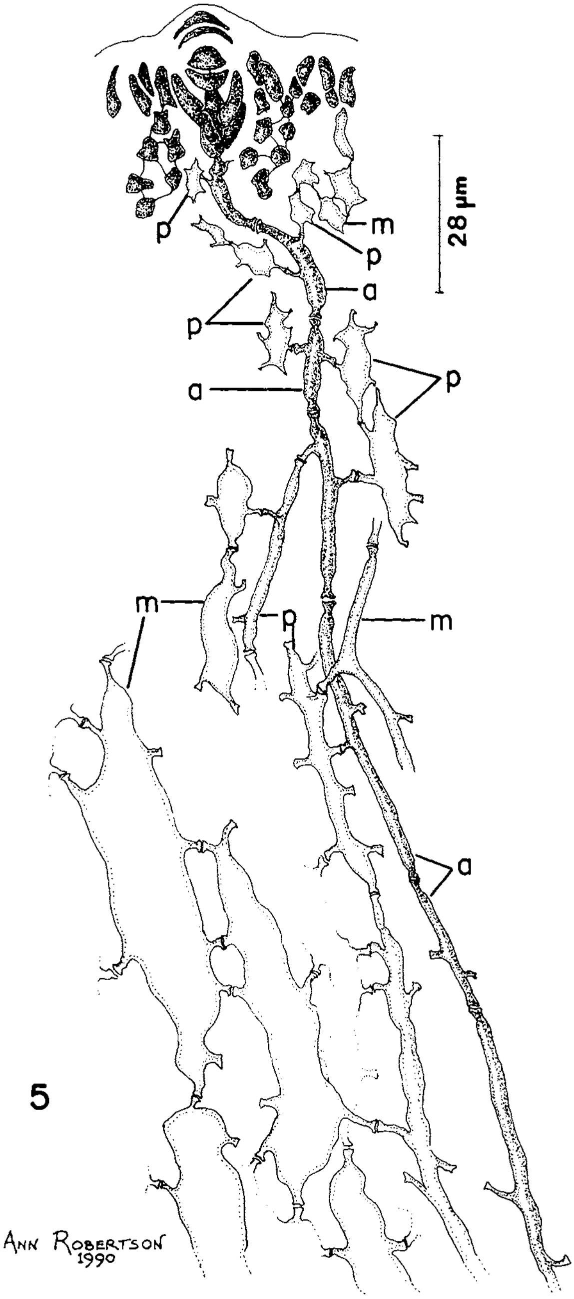


Fig. 5. *Gelidiella acerosa*, upright branch tip showing axial cell (a) and the axial filament. Note distal cell derivatives of apical cell that seem to be degenerating and only two lateral pit connections on each cell in the axial filament (which is more heavily stippled). Periaxial cells (P) and some medullary cells (m) are shown. Same collection as in Fig. 4.

between other cortical filaments. The filaments surrounding axial filaments in such branch tips also contribute to lengthening of the branch. This growth, along with intrusion of new filaments, causes lateral expansion of branch apices and adds to the total growth in length of the branch apex, growth that is a combination of uni- and multiaxial systems; the multiaxial growth is a secondary development that is responsible for growth both distally and laterally. The difference between this growth system and that of a true multiaxial system is not only the presence of an axial filament but also the limited time that adjacent meristems are active; new ones are produced continuously by the activities of products of the primary axial cell.

Growth of *G. acerosa*, the type species of the genus, was described by Sreenivasa Rao (1972) who found little difference from the description of Fan (1961) for *G. tenuissima.* The apical cell activity in *G. acerosa* that occurs in my specimens produces no distichously arranged branches of the second order. Instead, they are arranged decussately (Fig. 4), a condition said to occur occasionally in the Indian plants described by Sreenivasa Rao (1972). In my specimens, sometimes the proximal cell in a pair of cells produced by division of the apical cell is the active one in subsequent divisions, leaving an inactive caplike cell distal to it. Several of these cells may accumulate in branch apices (Fig. 5). The apical filament in *G. acerosa* often projects beyond the cortical surface for one or two cell diameters. The two periaxial cells developed on each axial cell in this species always seem to be arranged decussately on adjacent axial cells. Each periaxial cell forms a cell row of the second order, and subsequent cell rows develop from each of these cells and their derivatives. The tendency is for some branch tips to be compressed, and this lateral growth may be attributed to continuous, more vigorous development of one pair of decussate second-order rows of cells and associated branches over the other.

Emergent branches on axes often are in a single plane in *G. acerosa*, the same plane as the axis compression, if it exists. Many specimens of *G. acerosa*, however, have emergent branches in other planes as well; their derivation is from initials formed by the opposite pair of second-order cell rows or by adventitious development. Emergent branches in Natalian thalli of *G. acerosa* usually are not compressed in the specimens I have observed.

Some Gelidiaceae species, particularly those with broad apices, have actively dividing apical cells of the second-order cell rows. These apical cells divide obliquely rather than transversely as the apical cell of the branch does. In some species, apical cells of the second-order cell rows sometimes broaden and divide transversely, resulting in secondary branching of the erect thalli. Because the cell rows of the second order originate in a distichous arrangement on erect axes in most species, the thallus branching pattern is also distichous. Adventitious branching commonly occurs in most Gelidiales, and, in some species, this is the only way in which lobes or secondary emergent branches originate.

The genus *Onikusa* is particularly interesting because its type species *Onikusa pristoides*, has several active apical cells in the broad branch tips (Rodríguez and Santelices 1988), but only one of them is reported to divide transversely. In my survey of this species, however, I have found several apices in which two transversely dividing apical cells occur in addition to the obliquely dividing apical cells. Another species assigned to *Onikusa* (see following) has many more transversely dividing apical cells in several meristematic regions on a single broad and deeply lobed blade.

Thallus Attachment. Thalli of *G. acerosa* are attached by a prostrate stoloniferous system of branches that penetrates between porous materials (worm tubes and so forth) on the substratum. The rhizomatous branches sometimes produce short lateral branchlets that may have coralloid branching at the tip, and such branchlets, when embedded in the substratum, provide a firm anchor for the plant. Groups of multicellular filaments emanating from the stoloniferous branches, common attachment organs in species of *Gelidium* and *Pterocladia*, are also present in *G. acerosa* (Sreenivasa Rao 1972), but elongate unicellular rhizoidal cells do not seem to be present. Species that have attaching branchlets composed of multicellular filaments may be advanced phylogenetically or, possibly, may be a separate line of evolution through the type of multicellular system present in *G. acerosa*.

Small species of *Gelidium* and *Pterocladia* have unicellular rhizomatous attaching cells that occur on the ventral side of prostrate axes in no special groups or, more commonly, in small peglike branchlets consisting mostly of rhizomatous attaching cells. In some species, the base of the rhizomatous cluster of cells may have a short multicellular "root" where it emerges from the prostrate branch. The rhizomatous attaching branchlets often occur in no special relationship to formation of upright branchlets, or they may be part of a nodal arrangement in which one or more upright branchlets are associated with the attaching branchlet.

Secondary Pit Connections. Most internal nonreproductive cells in thalli of Gelidiales have secondary pit connections with adjacent cells, thereby creating a strong tissue with many interconnections. The only internal cells that do not form secondary pit connections are cells in the axial filament. Cells in the apical region adjacent to the axial filament, just proximal to the meristem, are very active in the establishment of secondary pit connections. In *G. acerosa*, these cells form small connecting cells on their proximal outer lateral side, and a section through the axial filament region clearly shows these cells forming in opposite directions on either side of the axis.

Rhizines. Rhizines (sometimes known as hyphae or rhizoidal filaments), are present in all Gelidiales except, by definition, the Gelidiellaceae, and apparently function in strengthening thalli. Although some authors consider rhizines part of the primary development of the thallus, it seems more accurate to consider rhizines as a secondary tissue that develops early in the thallus. Those near branch tips are formed mostly from inner cortical cells, but rhizines also are present in the medullary tissue in later stages of development in many species (Felicini and Perrone 1986). Rhizines are formed in a manner similar to cells establishing secondary pit connections (Fan 1961); they grow mostly in a basipetal direction but sometimes traverse the thalli (Felicini and Perrone 1986). Rhizines often contribute a major tissue in formation of midribs in some Gelidiaceae. According to Felicini and Perrone (1986), rhizines do not develop in apices of the prostrate system of *P. capillacea* but may be present in this part of the thallus by invasion from erect branches. In contrast to the absence of rhizines near prostrate branch tips of *P. capillacea*, I have found rhizines very close to tips of prostrate branches in several species of *Gelidium* (*Gelidium abbottiorum, Gelidium elegans, Gelidium pteridifolium, Gelidium reptans, G. arenarium*). Even in very small species of *Gelidium* such as *G. arenarium*, rhizines are often present near tips of prostrate branches, both in field-collected specimens and in cultured plants.

Although it will be necessary eventually to check their structure with electron microscopy, rhizines appear to be unicellular and unbranched in all the thalli of Gelidiaceae that I have examined. Consequently, I think that they deserve a term that does not denote a structure having rows of cells, such as rhizoidal filaments. The term hyphae is intimately associated with the structure of fungi, in which it also defines a uniseriate row of cells. Rhizines become extremely long, probably reaching lengths of well over a millimeter. They can be defined further as having extremely thick walls, narrow lumina, and a swollen tip in which a nucleus is present in actively growing cells.

In my estimation, rhizine development in thalli was an important phylogenetic step. The cell type may have evolved first as an attachment cell, being produced by most proximal (ventral) cells on prostrate thalli as is found in *Gelidiella antipai* Celan (1938). On the other hand, rhizines, originating mostly in branch apices and having extremely thick walls, may have evolved in an unrelated manner from the rhizoidal attachment cell. They share a similar method of production, however, forming proximally on bearing cells and growing basipetally, and both are usually unicellular and unbranched and have relatively thick walls.

Cystocarps. Bilocular cystocarps having ostioles into each locule are the usual type for most Gelidiaceae. It has been speculated that *Gelidium* cystocarps develop as a result of several fertilizations (Hommersand and Fredericq 1988), and development of uniloculate cystocarps, present in most species assigned to *Pterocladia*, may be the result of fertilizations occurring on only one side of the thallus. Unilocular cystocarps could also be caused by unilateral production of carpogonia. A third possibility, however, is that among the several to many carpogonia produced on both sides of a fertile branch, only one carpogonium is receptive at any given time. Fertilization of this receptive carpogonium may prevent the development of all other carpogonia in that fertile branch. In such a process, either unilocular or bilocular cystocarps may develop, according to the regions of the branch in which nutritive filaments are produced or into which gonimoblast filaments grow. Further definitive studies on this subject are needed in a variety of species before the loculate condition of cystocarps in the Gelidiaceae is the basis for phylogenetic speculation. Currently, because of the common occurrence of biloculate cystocarps, and until developmental details can be determined for additional species, I think that the biloculate condition probably is the more primitive one in the Gelidiaceae. In addition, cystocarps in other groups of red algae usually are uniloculate, and the biloculate condition in the Gelidiaceae is unusual.

Redefinition of Gelidiellaceae. Fan (1961), in establishing the Gelidiellaceae, considered that absence of rhizines, production of tetrasporangia in "stichidia," and absence of gametophytes were the most basic characters of the new family. Sreenivasa Rao and Trivedi (1980) have discovered the female gametophyte of an undefined species of *Gelidiella*, which, if this is truly a species of that genus, alters the family definition to include the gametophyte stage in its life history.

As a result of my analysis of the type species of *Gelidiella, G. acerosa*, I support Fan in the conclusion that family status should be recognized for these taxa, and I offer the following characters as important in the family definition: (1) absence of rhizines; (2) absence of rhizoidal attachment cells or groups of these cells on the prostrate branches, with production of multicellular attachment filaments (unicellular rhizoidal attachment cells are present on some species assigned to *Gelidiella*, species that should be reexamined and carefully compared with the type species of the genus); and (3) the presence of a decussate arrangement of second-order cell rows in erect branches (this is in contrast to a distichous arrangement of these cell rows in similar branches of the Gelidiaceae; however, cylindrical species in this family should be examined from this point of view). Currently, I think that the Gelidiellaceae are more primitive in the phylogeny of Gelidiales (Fig. 11), mainly because the total absence of a structure such as rhizines probably would not occur in a derived pattern of phylogeny. Also, it seems to me that decussate arrangement of second-order cell rows is a more primitive condition than are thalli formed in a basic distichous branch pattern.

Gelidiellaceae and Gelidiaceae share three unique characters that relate them in a single order, the Gelidiales. They both have uniaxial thalli having only two periaxial cells, they both have a single cap layer in the pit plugs (Pueschel 1989), and *Gelidiella* and Gelidiaceae species are all agarophytes.

The Hypothetical Most Primitive Gelidiaceae. Thalli having rhizines fall into two general types within the Gelidiaceae: those that are mainly upright and have a determinate rhizomatous basal attachment system of limited growth and those in which indeterminate branches are mainly prostrate and with upright branches of limited growth. The former type of thalli may have evolved through a *G. acerosa* type of ancestor, and the evolution of rhizines may have occurred in such an extensive upright branching system more readily than in a prostrate system in which the strengthening function would not be an environmentally stimulated factor.

If thalli having an indeterminate prostrate system of branches is ancestral (Fig. 11), prostrate branches may not have rhizines, but, in the Gelidiaceae, they always produce creeping, multicellular attachment filaments. Upright branches may be produced in this type of thallus in which at least a few rhizines are present. Emergent branches usually do not occur in the upright branches of these thalli except in formation of reproductive sori in some species or, if they are stimulated to develop adventitiously, often after an injury.

The possible two hypothetical most primitive Gelidiaceae in the system proposed can be defined as follows:

1. Thalli have a monopodial indeterminate prostrate branching system and produce determinate upright branches with a single apical cell; upright branches may remain unbranched, and adventitious branching may occur. Rhizines are present in at least the upright branches; apical cell derivatives form two periaxial cells, and the arrangement of second-order filaments is in a spiral or decussate pattern in both prostrate and upright branches. Attaching filaments develop on the ventral side of prostrate branches, emerging from most cells in contact with the substratum, and no particular accumulation of attaching cells into peglike attaching branchlets occurs. Fertile regions are restricted to upright branches, mostly covering the branch on all sides. Cystocarps are bilocular, with carposporangia borne in short chains (a combination of characters not occurring in known species of Gelidiaceae; carposporangia in chains usually are considered to be more primitive in other groups of red algae). Tetrasporangia are irregularly divided but tend to be cruciate, borne on cells of the second-order filament, and radiate in all directions from the axial filament.
2. Thalli are similar to those of *G. acerosa* but contain rhizines in the upright branch system; the tendency is toward distichous arrangement of second-order filaments and, in consequence, compression of the thallus. Both erect and prostrate branching systems are indeterminate.

Thallus Forms and Phylogeny in the Gelidiaceae. It can be speculated (Figs. 11 and 12) that the following more highly advanced thalli have developed from the primitive type of thallus.

Type 1: Many of the extant most primitive small species of *Gelidium* and *Pterocladia* have a form in which the main indeterminate growth system is prostrate on the substratum. These species often are important in forming intertidal turf communities. The upright branches that are produced seem to be intimately connected with the development of reproductive cells, and in some species, almost the entire upright branch is ultimately consumed in the formation of reproductive tissue. Only distal regions of upright branches in other species produce reproductive tissue. Other species may have a more extensively developed upright branch system that may branch to continue development, for a comparatively short time, of additional upright vegetative tissue. The pattern of growth, however, is distinctive; the upright branch is determinate, and its development is complete on maturity of the reproductive tissues. Development of most lateral branches terminates in small reproductive branchlets, or branches may be formed adventitiously after injury of the distal region. No distinct separation exists between this type of thallus and the type in which the prostrate system is determinate and the upright growth of branches is indeterminate. The difficulty is in the analyses of determinate or indeterminate growth in prostrate and erect branch systems, analyses that have not been carefully made for many species. Also, a more precise definition of indeterminate growth must be analyzed more thoroughly and agreed on by red algal specialists. Although it is tempting to suggest that a new genus be described to accept these species, at this time, it is only recommended that more attention be given to the prostrate species, with a view toward trying to determine if other characters may also be important in delimiting taxa within these categories. A new genus may emerge from such detailed analyses.

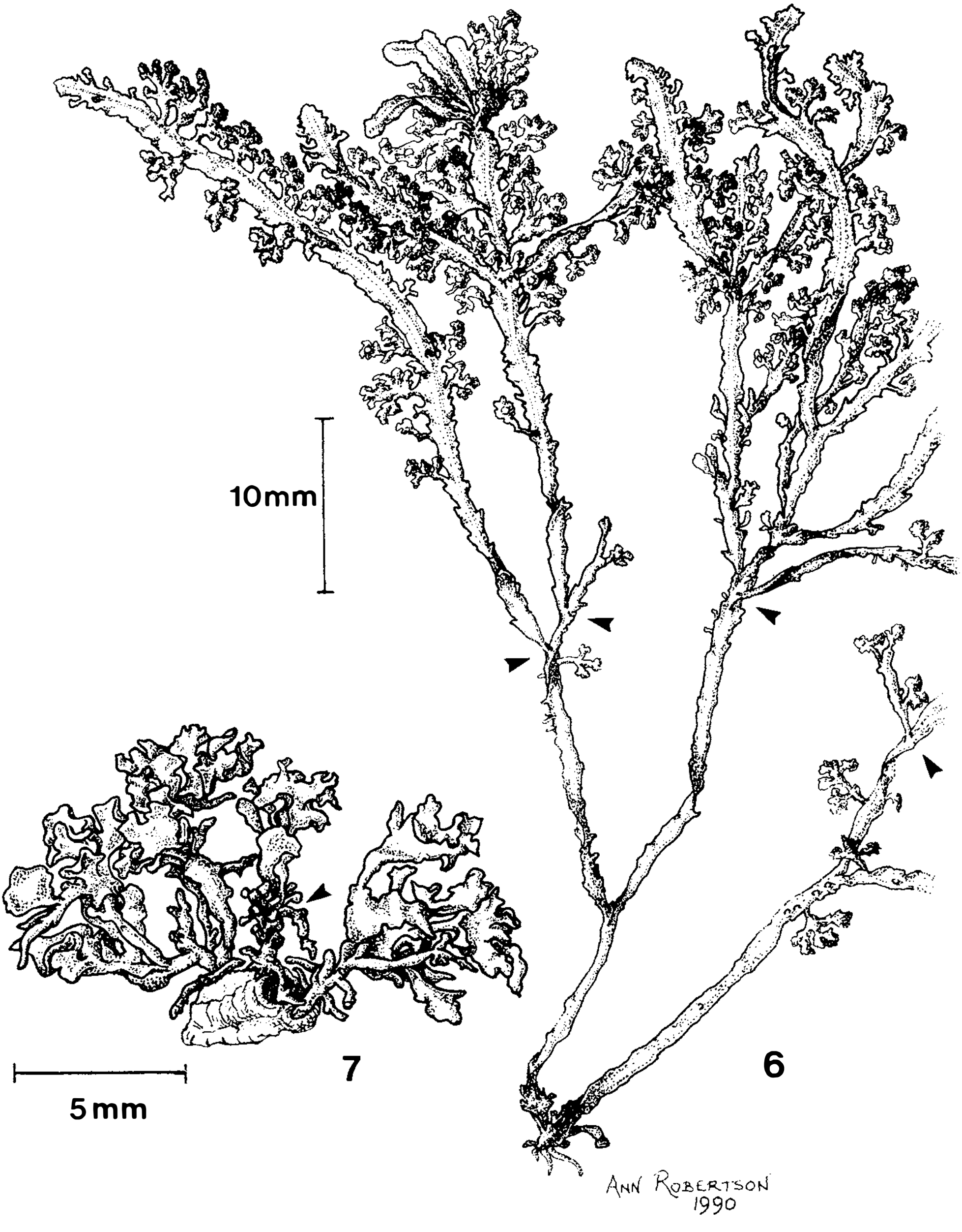
Type 2: The most advanced thalli in type 2 have upright indeterminate branches that are attached by a determinate rhizomatous holdfast. The upright branches usually are compressed to flat and pinnately branched, while the lateral branch apical cells are formed in a more or less regular distichous sequence. Fertile parts of thalli are restricted to distal ends of branches or are developed on specially produced lateral branchlets. Most well-known larger species of *Gelidium* and *Pterocladia* have this structure.

Other species that I have placed in this category provisionally have a pinnately branched upright system of branches that is more or less indeterminate in growth and an indeterminate prostrate system of branches. The species that produce small to extensive patches of larger upright thalli, such as *G. abbottiorum* R. E. Norris (from Natal), *Gelidium coulteri* Harvey (from California), and the European *Gelidium latifolium* (Greville) Bornet et Thuret and *Gelidium sesquipedale* (Clemente) Thuret, therefore, should be classified as type 2 thalli in which indeterminate growth develops in both prostrate and erect thalli.

Type 3: The closely imbricated branches on the axis that typify *Yatabella*, the only genus with type 3 thalli, are probably of the type formed in pinnately branched species of *Gelidium.* I do not have material of *Yatabella* for study, and I cannot do more now than speculate on the relationship of this genus to the others.

Type 4: Type 4 is a thallus type found in *O. pristoides*. Prostrate branches are cylindrical and indeterminate in growth. Upright branches have a midrib formed by accumulation of rhizines in addition to a thickened cortex and winged margins. One or two transversely dividing apical cells are present in a broad branch axis, and other obliquely dividing initials are present at the tips of second-order cell rows. Thalli develop in a manner approaching a ramisympodial scheme (Fig. 6). The first branch often grows to a considerable length, and secondary branches are initiated adventitiously on the midrib in a proximal position on the first branch. Upright branches often have pinnate lobes; fertile areas usually are produced on marginal proliferous lobes or branchlets.

Type 5: Type 5 thalli have a determinate rhizomatous holdfast and indeterminate upright branches on which winged margins become well developed by extensive growth of the second-order cell rows. Rhizines accumulate in the axis, which often also becomes



Figs. 6 and 7. Habits of two species of *Onikusa*. Fig. 6, *Onikusa pristoides*, the type species. Note sympodial branches, adventitiously produced from the midrib (arrowheads). Chalumna, Cape Prov., near East London (29-X-1989). Fig. 7. *Onikusa foliacea*, older upright blades produced from prosrate branches attached to a shell. Note upright axis being formed by ramisympodial branching (arrowhead). Intertidal, Palm Beach, Natal, 15-V-1983 (NAT 1482).

thickly corticated, forming a midrib, and inner cortical tissue in these thalli becomes enlarged, perhaps functioning as storage cells. More primitive species have branching mainly from the midrib, but marginal branching occurs in what are probably more advanced types. Some species of *Ptilophora* belong in this category (Fig. 12).

Type 6: Thalli of type 6 have a determinate prostrate system and form a holdfast. Pinnately branched upright branches have winged margins and a midrib; lateral lobes of the thalli develop into extensive pinnate lobes, sometimes a pinnately branching system (Fig. 12). Some species of *Ptilophora*, (i.e., *Ptilophora pinnatifida* [J. Agardh] Kylin) are quite large and have regularly pinnately lobed or branched thalli. *Suhria vittata* has a less regularly pinnately branched thallus beset with marginal proliferations and is attached by a small, non-rhizomatous holdfast. It is usually epiphytic on large laminarialean hosts.

Type 7: Type 7 thalli are similar to the basic type 1 *Gelidium* thalli, but they have a determinate prostrate branching system forming a discrete holdfast, and the blade surface produces small proliferous branchlets that may be fertile. Similar surface bladelets are caused by environmental influences in *Ptilophora* Norris (1987a), but details of their formation are unknown in *Porphyroglossum*. In many ways, these thalli are identical to those of some species of *Ptilophora*, but the absence of enlarged internal cortical cells is given important status as a differentiating character. I have not been able to examine *Porphyroglossum* in detail.

Type 8: Type 8 thalli consist of prostrate indeterminate branches from which emerge foliose upright branches (Figs. 7–9), often lobed, that have several marginal transversely dividing apical cells that usually lie relatively close to one another (Fig. 10). Upright foliose branches have determinate growth, but a new meristem often develops near the base of this branch that continues growth of the plant (Figs. 7–9). Most development of the plant is by monopodial growth of the prostrate branching system (Fig. 7), but additional secondary development occurs by a more or less ramisympodial initiation of new branches on proximal parts of upright determinate foliose branches, which may be rhizomatous, continuing the prostrate system, or foliose and determinate. *Acanthopeltis*, a genus in which an extensive upright branching system develops through ramisympodial branching, was probably derived from this type of thallus.

Type 9: Ramisympodial branching has been confirmed as the primary axis-forming method of growth in type 9 thalli. The branch is a broad but small blade, and the new axis is initiated proximally on the blade. The prostrate branches are determinate and form a discrete holdfast. Mature thalli of *Acanthopeltis* resemble the growth of type 8 thalli (Fig. 12), but the ramisympodial system is much better organized in *Acanthopeltis* than it is in *Onikusa foliacea*, in which secondary branches are formed in more irregular positions and may become prostrate rather than always forming a new erect blade as in *Acanthopeltis*. The determinate blades in *Acanthopeltis* also terminate their growth at a much earlier stage than those of *O. foliacea* do, resulting in smaller bladelets that have a much more uniform size and shape.

Taxonomic Adjustments

Revision of *Onikusa* Akatsuka (1986): This genus was typified by *O. pristoides* (Turner) Akatsuka (*Gelidium pristoides* [Turner] Kützing) and established to separate species of *Gelidium* that have winged margins and midribs; obtuse branch apices; tetrads of outer cortical cells, as seen in surface view; and reproductive structures borne on marginal or surface proliferations of the thalli. Rodríguiz and Santelices (1988)

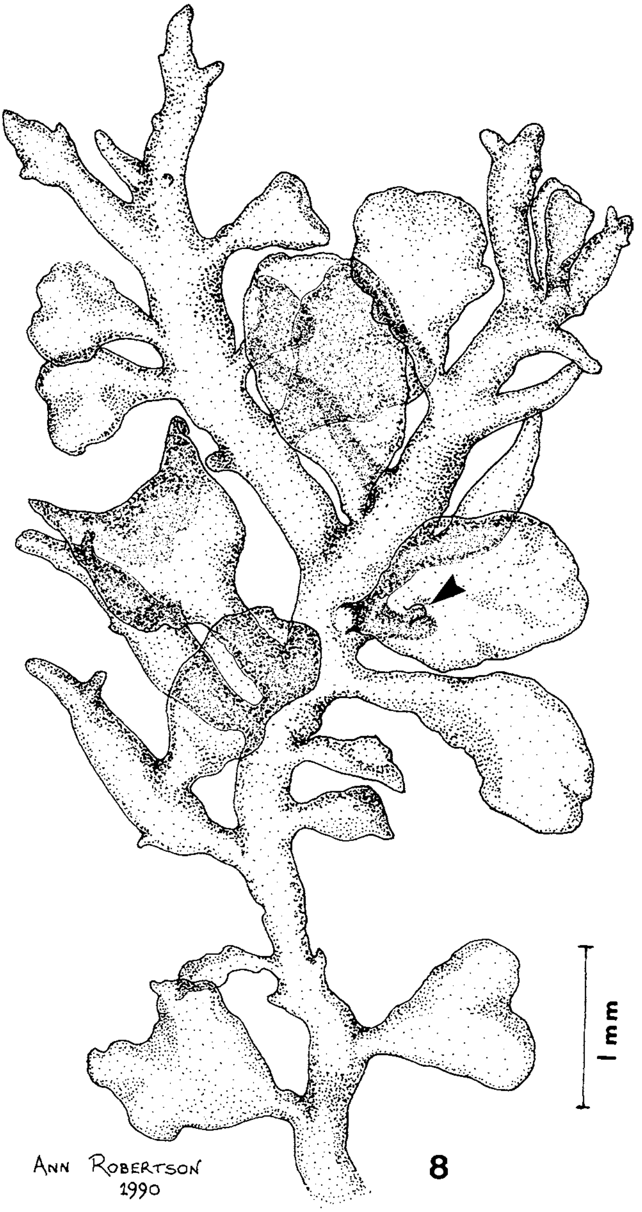


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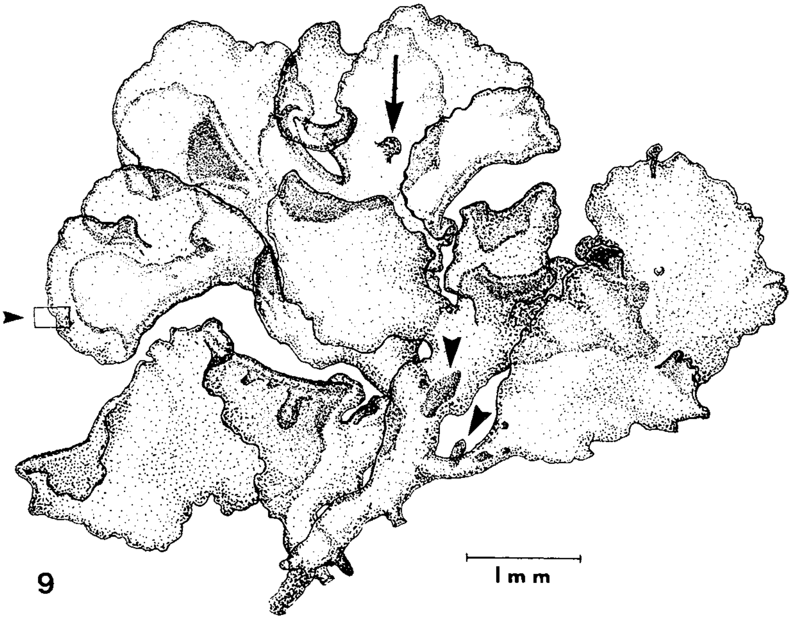
Fig. 8. ***Onikusa foliacea*, prostrate branch showing primary growth. Upright blades are mostly immature, but one blade (arrowhead) is forming a meristem in proximal region. Intertidal, Mvoti, Natal, 16-III-1984 (NAT 1626b).**



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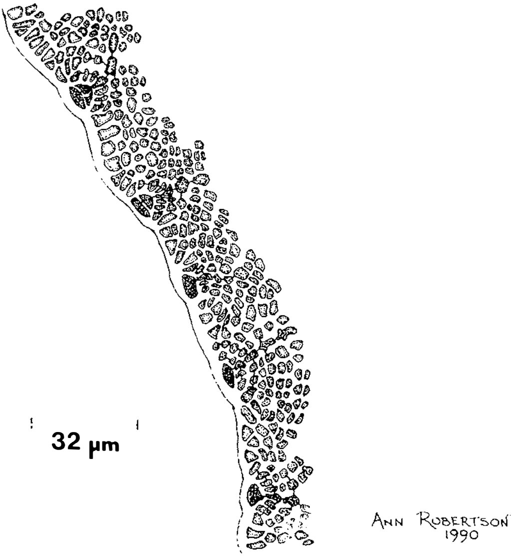

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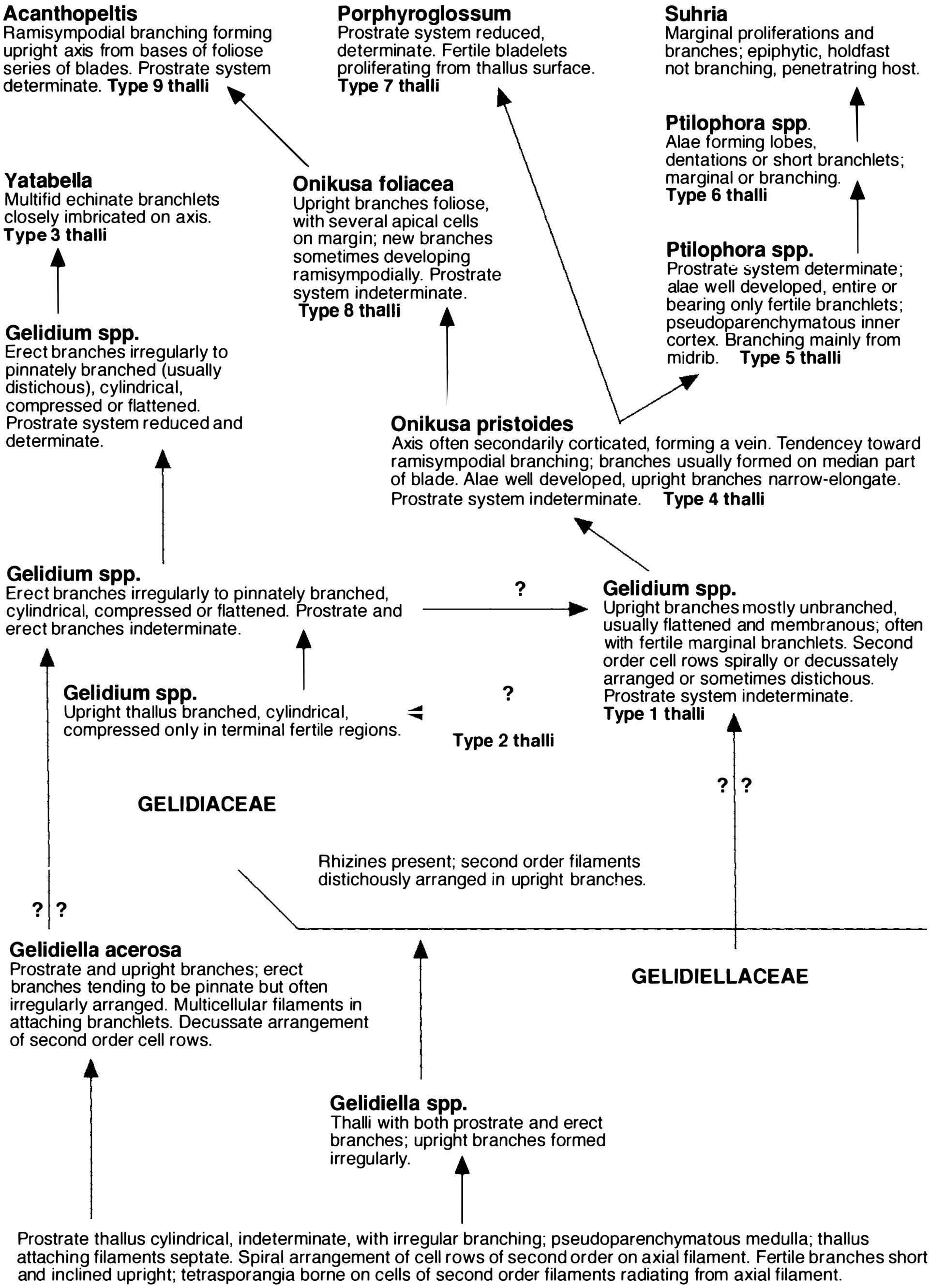
Figs. 9 and 10. *Onikusa foliacea*. Fig. 9, Almost mature upright blade, deeply lobed and having several marginal meristematic regions. Note initiation of new meristems in proximal part of blade (large arrowheads) and one new meristem in a more distal position (arrow). Fig. 10, Enlarged view of blade margin in region of blade in Fig. 9 identified by small arrowhead. Note the five apical cells (a and ma) active in this area, an axial filament (af) and cortex (c). Intertidal, Palm Beach, Natal, 29-V-1986 (NAT 3983).



Acanthopeltis
Ramisympodial branching forming upright axis from bases of foliose series of blades. Prostrate system determinate. **Type 9 thalli**

Porphyroglossum
Prostrate system reduced, determinate. Fertile bladelets proliferating from thallus surface. **Type 7 thalli**

Suhria
Marginal proliferations and branches; epiphytic, holdfast not branching, penetratring host.

Ptilophora spp.
Alae forming lobes, dentations or short branchlets; marginal or branching. **Type 6 thalli**

Yatabella
Multifid echinate branchlets closely imbricated on axis. **Type 3 thalli**

Onikusa foliacea
Upright branches foliose, with several apical cells on margin; new branches sometimes developing ramisympodially. Prostrate system indeterminate. **Type 8 thalli**

Ptilophora spp.
Prostrate system determinate; alae well developed, entire or bearing only fertile branchlets; pseudoparenchymatous inner cortex. Branching mainly from midrib. **Type 5 thalli**

Gelidium spp.
Erect branches irregularly to pinnately branched (usually distichous), cylindrical, compressed or flattened. Prostrate system reduced and determinate.

Onikusa pristoides
Axis often secondarily corticated, forming a vein. Tendencey toward ramisympodial branching; branches usually formed on median part of blade. Alae well developed, upright branches narrow-elongate. Prostrate system indeterminate. **Type 4 thalli**

Gelidium spp.
Erect branches irregularly to pinnately branched, cylindrical, compressed or flattened. Prostrate and erect branches indeterminate.

Gelidium spp.
Upright branches mostly unbranched, usually flattened and membranous; often with fertile marginal branchlets. Second order cell rows spirally or decussately arranged or sometimes distichous. Prostrate system indeterminate. **Type 1 thalli**

Gelidium spp.
Upright thallus branched, cylindrical, compressed only in terminal fertile regions.

Type 2 thalli

GELIDIACEAE

Rhizines present; second order filaments distichously arranged in upright branches.

Gelidiella acerosa
Prostrate and upright branches; erect branches tending to be pinnate but often irregularly arranged. Multicellular filaments in attaching branchlets. Decussate arrangement of second order cell rows.

GELIDIELLACEAE

Gelidiella spp.
Thalli with both prostrate and erect branches; upright branches formed irregularly.

Prostrate thallus cylindrical, indeterminate, with irregular branching; pseudoparenchymatous medulla; thallus attaching filaments septate. Spiral arrangement of cell rows of second order on axial filament. Fertile branches short and inclined upright; tetrasporangia borne on cells of second order filaments radiating from axial filament.

Fig. 11. A phylogenetic chart to show proposed relationships between genera and species in the Gelidiales.

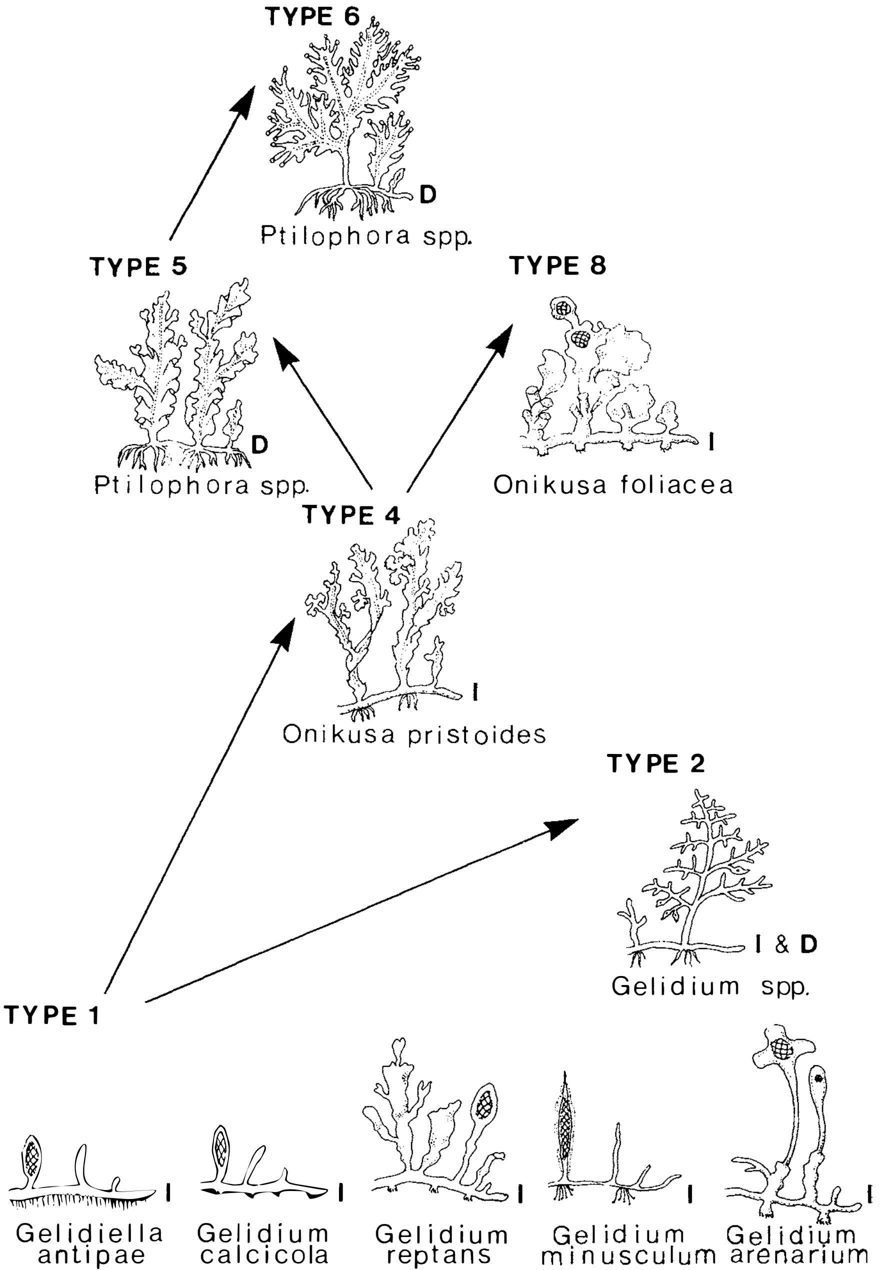


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Fig. 12. Diagrams of some thallus types in the Gelidiaceae to show possible relationships. Refer to Fig. 11 for descriptive details. I = indeterminate growth, D = determinate growth of prostrate branching system.

established that this species also has several active apical initials in positions relatively close together at branch apices, an important character in defining this genus. In their analysis, however, only one of the apical cells divides transversely in *O. pristoides*; the other in the same branch apex divides obliquely. As mentioned before, my observations on this species reveal that at least two transversely dividing apical cells occur on the distal margin of some upright blades. Conversion of obliquely dividing apical cells to those dividing transversely occurs by broadening of the obliquely dividing apical cells, with coordinated change in the division plane.

Additional characters are the same as in most other species of *Gelidium.* Rodríguiz and Santelices (1988) convincingly provided evidence that the occurrence of cortical cells in tetrads is a temporary condition of cell arrangement due to growth and not a permanent condition of the thalli that can be relied on for generic distinction.

Thalli of *G. pristoides* branch in a pattern different from that of the pinnately branching thalli that are customarily assigned to this genus. Narrow wings on branches of this species usually produce small fertile marginal branches, but the major branching of these thalli usually is produced adventitiously and emerges from the midrib (Fig. 6). The original axis may grow for only a short distance beyond the point of emergence of a new branch, or it may continue and produce a branch of almost indefinite length. This branching system is probably a primitive type of ramisympodial branching in which regular dominance is not achieved by newly initiated branches, or is achieved only by the secondary axis after considerable growth of the primary axis. Akatsuka (1986) did not mention the different branching pattern of this species in his characterization of *O. pristoides*, a character of major importance in defining this species and genus, and one that also occurs in some species of *Ptilophora.* Another character of the type species, *O. pristoides*, that was not mentioned in the genus description of *Onikusa* is the extensive indeterminate system of prostrate branches. Were it not for this character, I would be tempted to include *O. pristoides* as a species of *Ptilophora*. This combination of characters, however, seems to be unique. Thus, when it is considered along with the ramisympodial tendency of branching in *O. pristoides*—even though the growth of each branch is extensive—it seems best to emphasize the unique combination of characters of this taxon by recognizing it as a distinct, but emended, genus. The other species included by Akatsuka in *Onikusa japonica* (Harvey) Akatsuka, may remain in this genus, but it does not seem to have a tendency for branching on the midrib. Not having adequate specimens to make a study of these important characters, I leave a more complete investigation of this species and a decision on its position in *Onikusa* to future investigators.

The type 8 thallus in which upright blades with several apical cells are formed on an indeterminate prostrate branching system, and in which a type of ramisympodial branching occurs, is characteristic of a species that is commonly found along the central and south coasts of Natal, South Africa. The species grows in the intertidal area, forming a mostly monospecific turf that covers shellfish such as mussels and barnacles. This species is similar to *O. pristoides* in producing only bispores and monospores in the presumed sporophytes. It differs from the type species in having several marginal, actively dividing, dome-shaped apical cells (Fig. 10) in addition to obliquely dividing lateral initials. Older upright blades become deeply lobed, with the lobes sometimes pinnately arranged; and sori develop distally in lobes or in distal parts of more entire thalli. Mature blades develop new meristems proximally on the blade or in more distal positions, especially if these parts of the blade touch the substratum. The meristems produce a new blade or a short or more elongate cylindrical axis with a single apical cell and rhizoidal branchlets. In some of these Natalian thalli, proximal parts of a short series of broad blades form a short axis (Fig. 7), a condition resembling that of *Acanthopeltis*, and a phylogenetic link between *Onikusa* and *Acanthopeltis* is strongly suggested.

This Natalian plant resembles several described taxa of *Gelidium*: (1) *G. pusillum* forma *foliaceum* Okamura (1934) has a strong superficial resemblance to the Natalian species, but the Japanese plants were sterile and incompletely described, leaving doubt as to many critical characters. (2) *Gelidium foliosum* P. Dangeard (1951) is a species from Dakar and Port-Etienne, West Africa. (3) *Gelidium isabelae* W. R. Taylor (1945) originally was described from the Galapagos Islands, but it is also said to occur in the western Pacific (Silva et al. 1987). (4) *Gelidium pulvinatum* (C. Agardh) Thuret in Bornet (1892) occurs on the Atlantic coast of southern France and in West Africa (Lawson and John 1987) and has also been reported from the Pacific Ocean (Santelices 1977). Descriptions of these species do not mention the number of apical cells on the blade margins nor ramisympodial development of new growth. Until these important criteria can be clarified, I can only speculate on the possibility that the Natalian species is the same as one of these taxa. Because the general aspect of the Japanese *G. pusillum* forma *foliaceum* plants closely resembles that of the Natalian specimens in having a very broad blade, and because Okamura's illustration (pl. 17, fig. 4) shows signs of ramisympodial development of new thalli, I will elevate this varietal epithet to species level and apply it, for the time being, to the Natalian plants.

Onikusa foliacea (Okamura) R. E. Norris, new combination [*G. pusillum* forma *foliaceum* Okamura 1934, J. Imp. Fish. Inst. (Tokyo Fish. Inst.) 29, p. 51, pl. 17, figs. 1, 2; pl. 31, figs. 1, 2].

An additional taxonomic adjustment is necessary because of the conclusions made in the preceding discussion. As mentioned, development of rhizines seems to be an important evolutionary step in evolution of the Gelidiaceae, and the type species of *Gelidiella, G. acerosa*, has no sign of this cell type (see paper by R. Melo in this volume). The new species of *Gelidiella* described by Maggs and Guiry (1987), *G. calcicola*, should be transferred to *Gelidium* because (1) rhizines are present in its thalli, (2) it has rhizoidal attachment cells, and (3) products of the apical cell of upright branches divide in a distichous rather than a decussate manner as in *G. acerosa*. Several other small species of *Gelidium* and *Pterocladia* have very few rhizines in their thalli, and I predict that enlarging taxonomic problems will arise if this criterion does not remain a decisive factor in generic delimitations. I recommend, therefore, that a new combination be made: *Gelidium calcicola* (Maggs et Guiry) R. E. Norris comb. nov. (Maggs and Guiry, 1987, Br. Phycol. J. 22, p. 425, figs. 2–20).

Other species currently recognized as *Gelidiella* because of the absence of rhizines should be reexamined critically for rhizines, and the division of the immediate derivatives of the apical cell in these species should be analyzed more carefully. From present published accounts, it can be seen that distichous arrangement of second-order cell rows occurs in some species of *Gelidiella* (i.e., *G. antipai* Celan 1938), and it may develop that this is not an important character on which to separate *Gelidiella* from other Gelidiales. Currently, however, these two characters seem to be distinctive, along with the apparent absence of unicellular rhizoidal attachment cells, in redefining *G. acerosa*, the type species of the genus.

Comments on the Generic Status of *Pterocladia.* As reviewed by Rodríguiz and Santelices (1988), three main criteria can be used to separate *Pterocladia* from *Gelidium*: (1) a single loculate cystocarp having ostioles only on one surface, (2) outer cortical cells in surface view in basal-most parts of erect axes having an elongate shape (pyriform or elliptical) and an orientation with the longer cell axis parallel to the thallus long axis, and (3) apical initial of erect branches located at the base of a depression in the branch tip.

Fan (1961) thought that another character, the production of carposporangia in short chains in species of *Pterocladia*, was also important in separating that genus from *Gelidium* in which single carposporangia terminate gonimoblast filaments. He recognized that species of *Pterocladia* are known that have biloculate cystocarps (*P. nana* and *P. lindaueri*), but ostioles of these species are produced on one side rather than on both sides of the cystocarp as in other genera of Gelidiaceae. Rodríguiz and Santelices (1988) expanded the description of *Pterocladia* by noting that vegetative branches have characters 2 and 3, but they also noted that exceptions can be found in the known species of *Pterocladia*. Species of *Pterocladia* that I have examined on the Natalian coast (Norris 1987b) do not conform with the two vegetative characters of the genus noted by Rodríguiz and Santelices (1988), but cystocarps of *P. caloglossoides* have not been seen in the Natalian collections.

Although separation of the genus *Pterocladia* from *Gelidium* has been defended for many years, in my opinion, the only characters worthy of note in recognizing this taxon are the presence of ostioles on one side of the cystocarp and the production of short chains of carposporangia. All of the other characters that are used to separate some species into *Pterocladia* have several well-documented exceptions and may even be variable within the same species. The production of a single chain (or chains) of carposporangia terminating gonimoblast filaments has not been critically examined for all species of *Pterocladia* nor, in fact, for many species of *Gelidium* and should be investigated.

I recommend that separation of species into *Pterocladia* be abandoned because of the considerable number of exceptions known for each of the characters used to separate *Gelidium* and *Pterocladia*, and that species of *Pterocladia* be returned to *Gelidium*. Genera based on phylogenetically important characters are undoubtedly more meaningful in estimating systematics, but, in my estimation, *Pterocladia* has not been defined by using these character types.

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A NOTE ON THE ABSENCE OF HYPHAE (RHIZINES) IN THE THALLUS OF *GELIDIELLA ACEROSA* FORSSKÅL FELDMANN ET HAMEL (RHODOPHYTA)

Ricardo A. Melo

Abstract

Specimens of *Gelidiella acerosa* (Forsskål) Feldmann et Hamel, the type species of *Gelidiella* Feldmann et Hamel (Gelidiellaceae, Rhodophyta), from a wide geographical range were surveyed for the absence or presence of hyphae (also called rhizines) in the thallus and for the distribution and arrangement of tetrasporangia. No cellular structures resembling hyphae were found in the upright axes nor in the holdfasts. Tetrasporangia were always borne in swollen lateral branchlets, disposed irregularly in acropetal sequence. The results confirm that absence of hyphae, which is diagnostic at the generic and familial levels, is an invariable and therefore useful taxonomic character.

Introduction

The genus *Echinocaulon* Kützing *non* Spach was emended by Feldmann (1931, p. 158) and placed in the family Gelidiaceae, close to the anatomically similar genus *Gelidium* Lamouroux, even though cystocarps were lacking, making the systematic position of *Echinocaulon* uncertain. *Echinocaulon* differed from *Gelidium* in not having "rhizines intercellulaires" (also called hyphae) (Feldmann 1931, p. 161). Later, Feldmann and Hamel proposed a new name, *Gelidiella*, for this taxon, and again the diagnostic character between *Gelidiella* and *Gelidium* was mainly the absence of hyphae in *Gelidiella* (Feldmann and Hamel 1934, p. 529). In his revision of the Gelidiales, Fan (1961) proposed a new family, Gelidiellaceae, to receive *Gelidiella* Feldmann et Hamel, on the basis of two important differences between this genus and the other members of the Gelidiales: lack of hyphae and lack of a sexual generation.

Hyphae, also called rhizoidal filaments or rhizines, are specialized cells, 2–3 µm in diameter and up to 200 µm long (Dixon 1958), that have a very thickened wall and a very narrow and sometimes indistinct cell lumen. Hyphae originate from the basal pole of outer medullary or inner cortical cells and elongate basipetally between the cells of the thallus (Dixon 1958; Felicini and Perrone 1986). A nucleus is visible at the enlarged tip of the hypha (Dixon 1958; Melo unpublished results). Felicini and Perrone (1986) used a polarized light microscope to study *Pterocladia capillacea* (Gmelin) Bornet et Thuret and concluded that hyphae are a feature of the erect thalli only; the prostrate axes do not seem to produce their own hyphae. The pattern of hyphal distribution in the thallus of the Gelidiales has been suggested as a segregation character, but it has been shown that changes can occur during the life of the frond (Dixon 1958) or among conspecific thalli (Stewart 1968). Notwithstanding, the presence or absence of hyphae within a group generally has been accepted as a constant character (Santelices 1989).

In their original description of *Gelidiella*, Feldmann and Hamel (1934) stated that the tetrasporangia usually form in well-differentiated stichidia, which differ from the tetrasporangial ramuli of *Gelidium* in having regular growth (i.e., all tetrasporangia at one level are at the same developmental stage). A gradient exists between the undeveloped (undivided) sporangia near the apex and the well-developed ones closer to the base of the stichidium (acropetal development). Two types of stichidia were distinguished in *Gelidiella*: (1) the acerosa type, which is conical with closely packed and almost contiguous tetrasporangia, and (2) the pannosa type, which is compressed, with distinct tetrasporangia, disposed in regular transverse rows (Feldmann and Hamel 1934; Fan 1961).

Recently, Maggs and Guiry (1987) described a new species, *Gelidiella calcicola*, from the British Isles and northern France, and raised doubts about the validity of both the Gelidiellaceae and its single genus, *Gelidiella*, on the basis of the presence of rhizines (hyphae) in the holdfasts and on the arrangement of tetrasporangia in chevronlike rows in lateral stichidia in *G. calcicola*. These arguments were extensively reviewed and discussed by Santelices (1989), who suggested that the presence or absence of hyphae in populations of the various species of *Gelidiella* needed careful study and that the type species *Gelidiella acerosa* (Forsskål) Feldmann et Hamel should be examined before these already very complex taxa are reclassified.

Resolution of the taxonomic uncertainty of the Gelidiellaceae is important because *G. acerosa* is cultivated and harvested in many areas of the Pacific and Indian oceans for agar extraction (Chennubhotla et al. 1988; Santelices 1974; Tseng 1983; Umamaheswara Rao 1969; Uusitalo 1987). Abbott (1988) has pointed out that taxonomic stability is of foremost importance for the correct evaluation of any seaweed resource. The objectives of my study were (1) to determine the presence or absence of hyphae in different portions of the erect thallus and holdfast and (2) to examine the characteristics of the tetrasporangial branches in specimens of *G. acerosa* collected over a wide geographical range.

Materials and Methods

This report is based on specimens brought to La Jolla by Drs. J. N. Norris, U.S. National Herbarium (US) and by J. G. Stewart, A. Hancock Foundation Herbarium (AHFH); B. Santelices, Universidad Catolica Chile (SS/UC), brought specimens from China. Table 1 gives the information contained in the original labels of each herbarium sheet and the number of individual plants examined. Cross sections were made by using a freezing microtome or by hand at fixed points: (1) 5 mm below the tips of main erect axes, (2) at the branching of lateral branches of erect axes, (3) at the branching of erect axes from the holdfast, and (4) through the holdfast. Sections were hydrated, stained with 1% aqueous aniline blue or 10% aqueous alizarine-viridine, and mounted in dilute corn syrup. Thallus fragments were softened for several days in a chloral hydrate solution and squashed under a cover glass. Whole mounts of squashed mature tetrasporangial branchlets were used to examine the arrangement of tetrasporangia. Drawings were made with a camera lucida. More than 100 sections from the apex and base of erect axes and from the prostrate axes (holdfasts) were examined in specimens from all sources.

Observations and Discussion

The general morphology of the specimens examined closely resembles the descriptions given in the literature (Dawson 1944, 1953; Santelices 1977, 1988): thalli are caespitose, up to 5 cm tall in the Pacific specimens and as large as 15 cm in Caribbean Panamanian specimens. Erect, cylindrical, arcuate axes (up to 650 µm) arise from a creeping holdfast (up to 750 µm) attached to the substrate by rhizoids. Erect axes bear one to three orders of slightly compressed, opposite, subopposite, or secund pinnae that are shorter toward the apex. The internal anatomy also agrees with published accounts (Dawson 1953; Sreenivasa Rao 1973; Santelices 1977). A lenticular apical cell is very evident at the apex of branches (Fig. 1). It cuts off a segment cell below, which divides longitudinally to form two pericentral cells and a central cell. The central axial filament is

Table 1. List of specimens of *G. acerosa* studied

Source	No. of Specimens
Hainan Island, China (Guangdong Province)	
April 10, 1980: tetrasporangial (No. 80-2009)	4
April 19, 1980: not fertile (No. 80-2145)	4
Pacific Mexico (Gulf of California)	
Cabeza Ballena (east of Cabo San Lucas), March 3, 1937; lower littoral; coll. Remple, det. E. Y. Dawson (Hancock Exped. Sta. 621-37, AHFH 43222)	5
Isla Espíritu Santo, Bahia San Gabriel, February 14, 1940; abundant among coral clumps in shallow lagoon; temp. 21°C plus; tetrasporangial; coll. and det. E. Y. Dawson (Dawson 594, AHFH 2162)	10
Same date; in coral heads in shallow lagoon; temp. 21°C plus; coll. and det. E. Y. Dawson (Dawson 610, AHFH 2161)	11
San Jose del Cabo, Baja California, February 15, 1940; middle littoral on rocky reefs; tetrasporangial; coll. and det. E. Y. Dawson (Dawson 633, AHFH 2163)	7
Cabeza Ballena (near Cabo San Lucas, B.C.), November 9, 1946; granite reef with many tide pools and surf rocks; most species luxuriantly developed; temp. 26.6°C; coll and det. E. Y. Dawson (Dawson 3322, AHFH 54694, also duplicate Dawson 3322)	9
Cabeza Ballena (Baja California), March 11, 1949; intertidal rocky reef with abundant, large tidepools. Dominant *Sargassum, Ulva, Centroceras, Gelidiella, Cladophora*; coll. and det. E. Y. Dawson (Dawson 6780, AHFH 54683)	3
Caribbean Mexico	
Xel-ha, Quintana Roo, April 12, 1983; intertidal to 1 ft; coll. and det. D. L. Ballantine (US 14416)	2
Caribbean Panama	
Naranjo Arriba, Orange Keys, June 3, 1977; south point of Island; intertidal to subtidal; depth 0–25 ft on reef slope; tetrasporangial; leg. J. A. Kilar No. JAK-2061; as *Gelidiella* sp. (US 29019)	4
Galeta Point, Galeta Island, December 27, 1978; reef platform, shallow water, growing on hard substrate; depth ca. 1 ft; tetrasporangial; leg. J. A. Kilar No. JAK-101; as *Gelidiella* sp. (US 28994)	3
Cove of Shimmey Beach, Provincia de Colon, July 15, 1979; on Ft. Sherman side; reef platform, intertidal; depth 1–3 ft; tetrasporangial; leg. J. A. Kilar No. JAK-2000.1 (US 28018)	5
U.S. Virgin Islands	
Boiler Bay (St. Croix), January 18, 1977; tetrasporangial; coll. E. Gladfelter, det. I. A. Abbott; No. 14208 (US 89253)	2

discernible only a short distance below the branch apex. It becomes indistinct as the medullary cells enlarge (up to around 30–40 µm in diameter by 140 µm long) and form many secondary pit connections (Figs. 2, 3). The external cortical cells are small (4–6 by 6–10 µm) and anticlinally elongated; the internal cortical cells are more rounded and grade into the medulla (Figs. 2, 3).

Hyphae.* No hyphae were found in any of the sections made at the predefined positions (Figs. 2–4). Observation of squashed thallus fragments also did not show any cellular structures reminiscent of the morphology of hyphae. In squashes of thallus fragments softened with chloral hydrate, it was possible to observe the shape of the cells, which separated readily after squashing (Fig. 5). Some medullary cells had processes narrower than the rest of the cell body; others had a narrow diameter overall. In both these types of cells, pit-plugs were visible in the cell walls. In cross section, medullary cells were closely packed (Figs. 2, 3), and these small elements might be confused with hyphae. However, they differ from hyphae in several aspects: Hyphae in other Gelidiales (1) have a much more reduced cell lumen, (2) are much longer relative to the other cells, and (3) do not form secondary pit connections with other cells.

These negative results confirm previous work on *G. acerosa* (Feldmann 1931; Sreenivasa Rao 1973), *Gelidiella antipai* Celan (Boudouresque 1972), and *Gelidiella tenuissima* Feldmann et Hamel (Fan 1961), in which the absence of hyphae was an invariable character. As mentioned earlier, this was the basis for the distinction between *Gelidiella* (*Echinocaulon*) and other genera in the Gelidiales (Feldmann 1931) and has remained as an absolute-opposite character thereafter (Santelices 1989).

Tetrasporangia. In my study, the tetrasporangial stichidia observed in specimens from the different localities were all of the acerosa type (Feldmann et Hamel 1934; Fan 1961), with the tetrasporangia very compacted and irregularly disposed, never forming transverse rows (Figs. 6, 7). In almost all cases, a clear acropetal development was observed: Tetrasporangia in more advanced developmental stages (i.e., with cleaved tetraspores) were closest to the base of the tetrasporangial branchlet; undivided tetrasporangia were at the apex. Sometimes, only the cavities resulting from shed tetraspores remained throughout most of a stichidium, except apically where still undivided sporangia could be seen (Fig. 6). In general, the dimensions and other characteristics of the tetrasporangia were in agreement with the values reported previously (Table 2). Tetrasporangial dimensions (Fig. 9) varied between specimens from the Pacific (larger, 25 µm mean diameter x 54 µm mean length in Mexico and 25 x 58 µm in China) and those from the Atlantic (smaller, 23 x 36 µm), with the exception of specimens from the U.S. Virgin Islands, which were also large (27 x 58 µm). In specimens from Mexico, Gulf of California, and from the U.S. Virgin Islands, smaller undivided sporangia (15–20 µm) were present among mature tetrasporangia in branches where tetraspore shedding had occurred (Fig. 8). Egerod (1971) suggested that in fertile branches of *G. acerosa* from Thailand, division of tetrasporangia might be suppressed at times, resulting in the formation of monospores. Santelices (1977) also found undivided spores in Hawaiian specimens of the species. Dawson (1944, 1953) mentioned monospores (20–50 µm in diameter) being shed in a different species, *Gelidiella refugiensis* Dawson, from the Gulf of California.

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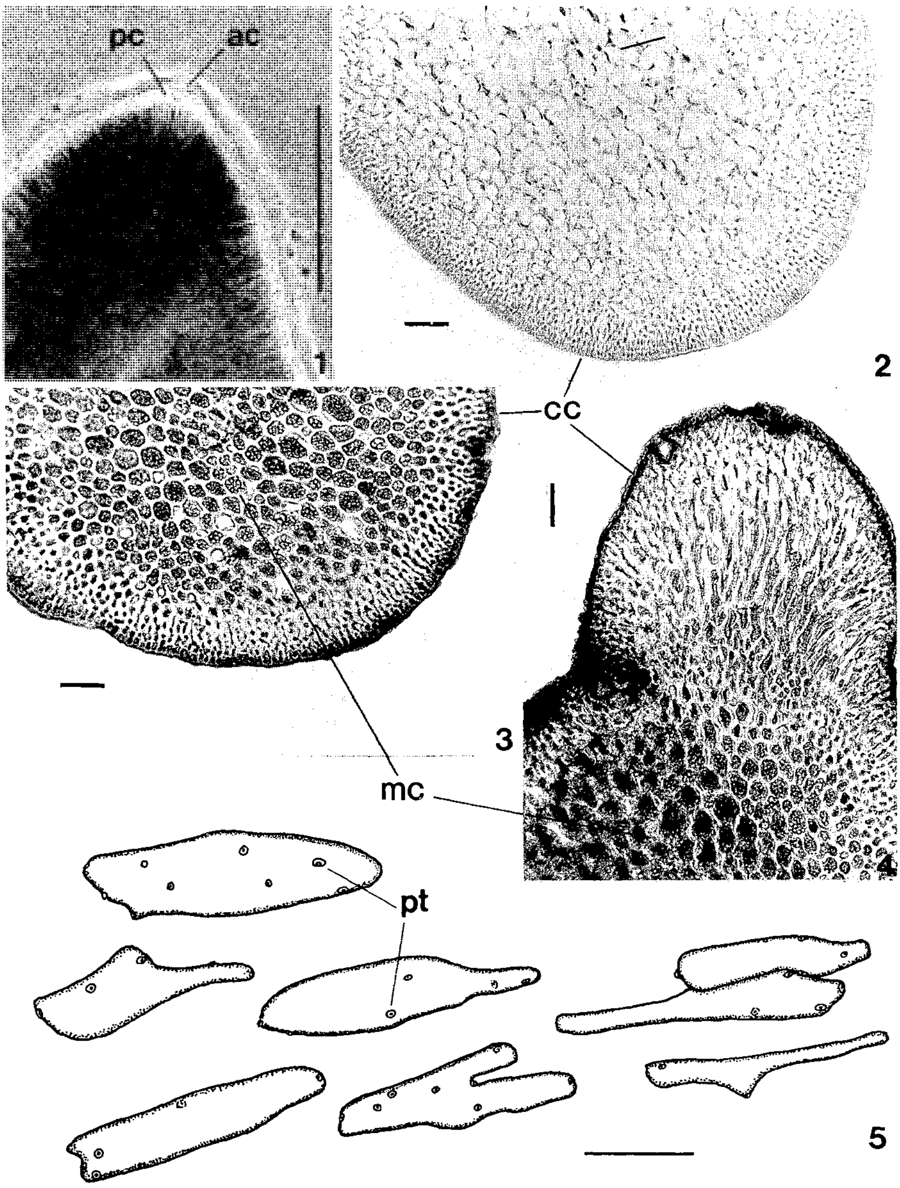
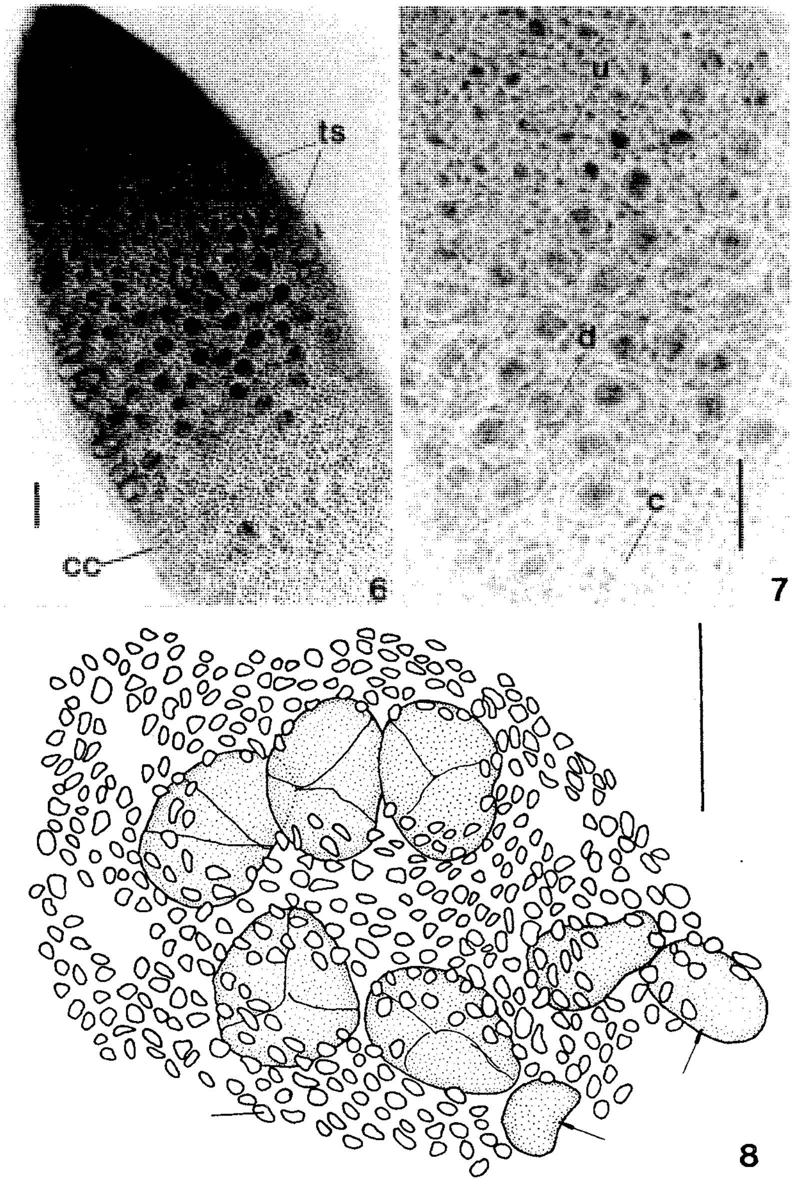
* Hyphae are called *rhizines* by R. E. Norris (this volume), whose well-reasoned arguments should be referred to.



Figs. 1–5. ***Gelidiella acerosa.*** **Fig. 1, Surface view of branch apex with lenticular apical cell (ac), two pericentral cells (pc) and a central cell (cc), phase contrast (US 89253). Fig. 2, Cross section of holdfast axis (China 80-2009). Fig. 3, Cross section of upright thallus close to apex below tip of erect main axis (China 80-2009). Fig. 4, Cross section of upright thallus through base of lateral branch (China 80-2009). Fig. 5, Squashed medullary cells showing irregular shape with narrower cell processes. Secondary pit connections are visible (pt) (China 80-2009). Scale bars = 50 μm. Figs. 2–4, cc = cortical cells, mc = medullary cells.**



Figs. 6–8. ***Gelidiella acerosa*.** **Figs. 6 and 7, Surface view of tetrasporangial branchlet (US 89253): Fig. 6, Tetrasporangia (ts) develop acropetally and are irregularly distributed. Fig. 7, Close-up of same branch (in Fig. 6) showing emptied cavities (c) left by shed spores, divided tetrasporangia (d), and undivided tetrasporangia (u) in acropetal sequence. Fig. 8, Surface view of tetrasporangial branchlets showing smaller undivided sporangia (monosporangia?) (arrows) among mature tetrasporangia (US 29018). Scale bars = 50 μm. Figs. 6, 8, cc = cortical cells.**

Table 2. Tetrasporangial characters of *Gelidiella acerosa*.

Tetrasporangia

- Size and shape:
  - Egerod (1971): cruciate, up to 52 µm long
  - Santelices (1977): oblong, cruciate, 20–30 µm wide, 40–50 µm long
  - Sreenivasa Rao (1971c): oblong, cruciate, 17–24 µm in diameter, 34–52 µm in length
  - Sreenivasa Rao (1973): tetrasporangial mother cells 10–16 µm in diameter, 24–35 µm long
  - Present study: oblong, irregularly cruciate, tetrahedral, mean length = 49 µm (28–75 µm), mean diameter = 25 µm (18–35 µm)
- Disposition
  - Feldmann et Hamel (1934): in stichidia; all tetrasporangia at the same level are equally developed: smaller, younger, undivided ones near the apex, larger, older ones toward the base, empty spaces at the very bottom, closely packed, almost contiguous
  - Santelices (1977, 1988): in swollen vegetative pinnae; sparsely and irregularly disposed, the lower usually in a more advanced stage of development than those near the apex
  - Sreenivasa Rao (1971c): borne in ultimate swollen, conical branches, swollen not seriately arranged
  - Present study: in swollen, conical lateral branches; irregular, compact, acropetal development
- Seasonality
  - Ramo Rao et al. (1976): number of stichidia/plant maximal in January (±40), down to ±10 in March-August
  - Umamaheswara Rao (1974): minima in August-September and February-March, maxima in April-June and October-December for number of stichidia/plant

Tetraspores

- Size and shape (released)
  - Chihara and Kamura (1963): globular, 24–27 µm in diameter
  - Sreenivasa Rao (1971b): initially ovoid then spherical, 21.4–24.9 µm in diameter
  - Umamaheswara Rao (1974): globular, 22–26 µm in diameter
- Shedding
  - Umamaheswara Rao (1974): maximum output in May–June and November–December; ±5–10 x 10^3 spores/g fresh weight/day; one diurnal shedding peak in the afternoon
  - Sreenivasa Rao (1971a): maxima in April–May and October–November for 25–30 days in each; two shedding diurnal periods: early morning and mostly in the afternoon; 2 x 10^4 spores/plant/season were shed
- Germination
  - Chihara and Kamura (1963): "*Gelidium*-type," apical cell differentiates early (6 days)
  - Sreenivasa Rao (1971B): "*Gelidium*-type," apical cell differentiated very late; spore nucleus divides 2 to 3 times before formation of the germ tube, only one nucleus migrates with cytoplasm into germ tube; this nucleus divides several times accompanied by wall formation
  - Umamaheswara Rao (1974): "*Gelidium*-type," apical cell differentiates late, three modes of germination differing in site of initial divisions

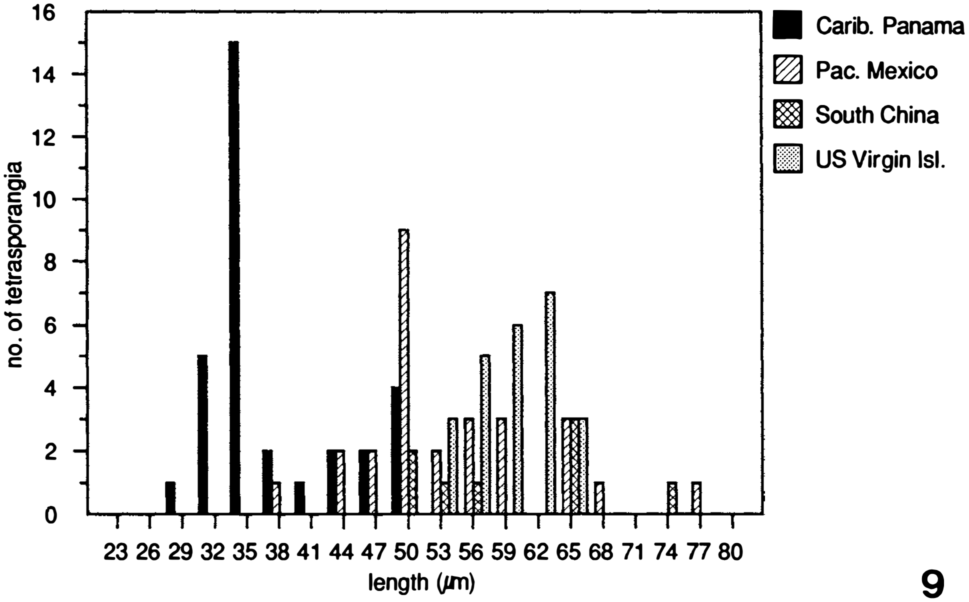


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Fig. 9. Length of mature (divided) tetrasporangia in specimens of *Gelidiella acerosa* from different geographical locations (see Table 1).

As pointed out by Santelices (1989), tetrasporangial stichidia were not used by Feldmann (1931) to segregate *Gelidiella* from *Gelidium*, nor by Fan (1961) to segregate the Gelidiellaceae. Tetrasporangial stichidia also occur in species of *Gelidium* and *Pterocladia* and so are not useful as diagnostic characters at the generic level. However, Maggs and Guiry (1987) assigned their new species to *Gelidiella* partly on the basis of its tetrasporangial stichidia.

In conclusion, it stands that in a diverse geographical sampling of specimens of *G. acerosa*, the type species of *Gelidiella* Feldmann et Hamel, absence of hyphae throughout the thallus and tetrasporangial sori produced acropetally in swollen branches, but not in regular transverse rows, were invariable characters.

Acknowledgments

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SEPARATION OF CALIFORNIA SPECIES OF *GELIDIUM* AND *PTEROCLADIA*: AN EVALUATION OF VEGETATIVE CHARACTERS

Joan G. Stewart

Abstract

Despite efforts by numerous workers to discover vegetative characters useful for separating species of the two major genera in Gelidiaceae, it is still difficult to distinguish nonreproductive specimens of *Gelidium* from *Pterocladia* thalli in parts of the world where species of both genera can be of similar size and share similar branching patterns. Rodríguez and Santelices (1988) evaluated several criteria that had been proposed earlier. They reported that the occurrence of apical cells in notches or depressions appeared to be diagnostic for purposes of recognizing species of *Pterocladia*. My experience with California material suggested that apical notches, although conspicuous in some specimens of *P. capillacea*, were associated with development of cystocarps rather than being a regular feature of vegetative growth. For the study reported here, I used the procedures described in the earlier study of Rodríguez and Santelices to test the usefulness of the same characters. Comparisons were extended to two species of *Gelidium* and two additional *Pterocladia* species that occur along the Pacific coast of California and Baja California. My data support the conclusions of Rodríguez and Santelices that the arrangement of cortical cells as seen in surface view cannot be used to separate species of the two genera. Other criteria suggested in this previous study were not useful when applied to the taxa included in the present study.

Introduction

A major unresolved question about how to identify taxa allied with the genera *Gelidium* and *Pterocladia*, many of which are economically valuable sources of high-quality agar, is how to separate species of one genus from those of the other. Various supplemental criteria have been proposed since *Pterocladia* was first recognized as distinct because of the unilocular structure of its cystocarps. Because cystocarps are not common, and indeed are lacking from parts of the ranges of some of the most abundant species, it would be useful if criteria based on vegetative morphology could be used to separate species of the two genera. In 1985, Santelices and Stewart reported that the only reliable feature for distinguishing *Gelidium* from *Pterocladia* was the female reproductive morphology. Vegetative features (branching pattern and axis dimensions) and habitat often can be used to identify species within a genus in a limited geographical area, but pairs of species in each genus may have parallel morphology, and generic affiliation is often dubious for numerous specimens even in a single locality. In the second workshop on taxonomy of economic seaweeds, Rodríguez and Santelices (1988) tested three vegetative characters for applicability to generic separation; the position of the apical cell in relation to cortical cells was considered useful. Their data indicated that shape and disposition of cortical cells (as proposed by Akatsuka 1981, 1986) were of limited value to segregate species of the two genera.

Of the 25 species studied by Rodríguez and Santelices (1988), 17 were represented by single specimens, seven by two, and one by five. Material included thalli from Japan, Chile, Hawaii, California, New Zealand, Taiwan, Peru, and South Africa. I used their procedures to study large samples of five species from California and adjacent northwestern Baja California, Mexico. California thalli were selected to represent plants collected throughout the year and from different habitats. Fertile specimens were included for assessment of possible effects of reproductive development on apical anatomy. Additionally, several thalli of *P. lucida* J. G. Agardh, the type species for that genus, and of

P. capillacea (Gmelin) Bornet et Thuret, the most common and widespread species of the genus, from Hawaii were evaluated.

Materials and Methods

Table 1 lists the collections that were sectioned for data on cortical cells. All specimens, including others referred to in the text but not listed in Table 1, are in my herbarium, deposited at the Los Angeles County Museum (LAM), and, unless otherwise noted, were collected and identified by me.

As described by Rodríguez and Santelices (1988), patterns of size and arrangement of cortical cells, as seen in surface view, were examined by using a compound microscope. For *P. capillacea*, *G. coulteri* Harvey and *G. nudifrons* Gardner, 30 axes from each species were assessed. For these three taxa, each of the 10 collections listed in Table 1 included several thalli, and the axes were selected from different thalli. For *P. media* Dawson (Stewart 1974) and *P. caloglossoides* (Howe) Dawson (Stewart and Norris 1981), 13 and 20 axes, respectively, were studied. Sections were cut from near the base and from midway between apex and base of main axes; entire apices were viewed to determine the patterns near the apical cell and in the region 500 µm to 1000 µm farther back from the apex (subapical). Data were recorded to correspond with the categories (cortical cells aggregated or not aggregated, and regularly or irregularly arranged) shown in Figure 3 of the study of Rodríguez and Santelices (1988).

Positions of apical cells, relative both to adjacent cortical cells and to the cell-wall material that extended beyond the cells of the apex, were recorded by using a camera lucida. Thalli of *P. caloglossoides* and *P. media* are small with narrow axes. Before the representative apices (Figs. 4 and 5) for these species were selected, numerous thalli were examined to verify the position of apical cells. Variant morphological forms of *P. capillacea* were examined to confirm the consistency of the contrast illustrated in Figures 2 and 3.

Results

Table 2 summarizes the observations on aggregation and arrangement of cortical cells. Relative sizes of cells are also given, because this character was generally consistent within single sections except for *P. capillacea*. Cortical cells in all parts of all axes of *G. coulteri* and *G. nudifrons* were consistently small, irregularly rounded, and nonaggregated. For *G. coulteri*, in one each (of 30) of the midthallus sections and of the basal sections, cells were somewhat more elongate, and occasionally paired cells could be found, but nowhere were cells consistently arranged in any pattern.

For *G. nudifrons*, slightly elongated cells occurred in one basal section, and occasionally cells were in packets of 2 to 4 (+). Such aggregations or arrangements were scattered and in no case were characteristic of the appearance of cortical cells. For both of these species of *Gelidium*, surface-viewed cortical cells were strikingly uniform in all parts of all thalli, suggesting that cell division was regularly indeterminate throughout the year and in both proximal and distal portions of the plants.

Cortical cells in *P. capillacea* tended to be larger than cortical cells in the two *Gelidium* species and often were elongated (longer in the dimension parallel to the axis than in width); this was noted more often in middle and basal sections than in sections

Table 1. Pacific Coast Collections Studied for Data of Table 2

Taxon JS No.	Repro.	Month	Ht (cm)	Habitat
Gelidium coulteri				
50	–	June	6	Intertidal, exposed, central California
795	♀	July	4	Intertidal, exposed, central California
1492b	♀	February	2	Intertidal, exposed, southern California
583b	♀, ⊕	May	2	Intertidal, exposed, southern California
1038b	–	June	3	Intertidal, exposed, southern California
1059	⊕	July	4.5	Intertidal, exposed, southern California
1363	–	August	7	3 m, quiet water, southern California
3082	⊕	October	3.5	Intertidal, exposed, southern California
1423	⊕	November	6	Intertidal, exposed, southern California
4647	–	April	4.5	Intertidal, exposed, Baja California
Gelidium nudifrons				
1481b	⊕	January	23	17 m, southern California
442a	⊕	April	25	20 m, Coronados Islands, Baja California
1548	⊕	May	21	17 m, southern California
3031	⊕	June	16.5	12 m, southern California
4570	♀	July	19	12 m, San Clemente Island, southern California
1716	–	August	22	5 m, Coronados Islands, Baja California
4646	–	September	16	Subtidal, Santa Barbara Island, southern California
2090c	♀	October	10	13 m, southern California
1443a	⊕	November	13	17 m, southern California
2128b	♀	December	12	10 m, southern California
Pterocladia caloglossoides				
1822	⊕	January	<1	13 m, southern California
1085	⊕	January	<1	15 m, southern California
1887	♂	February	<1	19 m, southern California
2139	⊕	February	<1	13 m, southern California
2356	–	March	<1	Low intertidal, Gulf of California, Mexico
2165	⊕	March	<1	18 m, Catalina Island, southern California
V-176	–	July	<1	3 m, central California
2644	♂	July	<1	19 m, southern California
3340	⊕	August	<1	Intertidal, Pacific Mexico
2669	–	December	<1	17 m, southern California

Table 1 (continued)

Taxon				
JS No.	Repro.	Month	Ht (cm)	Habitat
Pterocladia capillacea				
2293	–	January	13	Intertidal, southern California
909	–	February	6	High intertidal, southern California
1511	–	March	12	Intertidal, southern California
4642	–	April	8	Mid-intertidal, Baja California
1241	–	May	15	Subtidal, Catalina Island, southern California
629	–	May	8	High intertidal, southern California
4644	–	June	9	Shallow subtidal, Baja California
2496	♀	June	10	Low intertidal, southern California
1362	–	August	12	Shallow subtidal, southern California
4645	⊕	September	23	Subtidal, Santa Barbara Island, southern California
1472	♂	December	13	Low intertidal, southern California
Pterocladia media				
10383[a]	–	December	5.5	Intertidal, central California
42[b]	⊕	November	4	Intertidal, central California
2163	⊕	April	1.5	Intertidal, central California
P.B.-A.1138	–	?	?	(Presumed intertidal, southern California)
1424	–	November	4	Intertidal, southern California
1702	⊕	July	3	Intertidal, southern California

[a] R. Setzer number.
[b] S. Bentley number.
– = none found.
⊕ = tetrasporangial.
Note. "Exposed" indicates an open coastal site with moderate to strong water movement.

closer to the apex. Within a section, elongate and rounded polygonal cells frequently were mixed in various proportions, but generally no pattern of aggregation was seen.

Cortical cells in *P. caloglossoides* and *P. media* thalli were consistently rounded and nonaggregated. Close to the apical cell, in both primary and lateral axes, cells were characteristically arranged in short symmetrical rows, with little or no differentiation into cortical and medullary anatomy. When few cells were present on either side of the central cell, cortical cells close to the apex tended to be aligned both vertically and horizontally. This suggests that cell division is regulated and determinate in these small sized taxa. Cells in *P. caloglossoides* were variable in size within a single thallus and when several thalli were compared. Figures 1–7 show the positions of apical cells on main axes. Figure 1a illustrates the alignment of apical cells in virtually all axes examined of *G. nudifrons* and *G. coulteri*. These cells varied in size, shape, and extent of protuberance but confirmed

Table 2. Aggregation, Size, and Arrangement of Cortical Cells as Seen in Surface View*

	Not aggregated	Not aggregated	Not aggregated
	Arrangement irregular; cells polygonal/round, small	Arrangement regular; cells elongate with long axis parallel to branch	Arrangement irregular; cells variable in size and shape
Species	%	%	%
Gelidium coulteri n = 120	98	2	0
Gelidium nudifrons n = 120	99	1	0
Pterocladia caloglossoides n = 80	96	4	0
Pterocladia capillacea n = 120	41	32	27[a]
Pterocladia media n = 52 (apical and subapical) n = 36 (basal and median)	100[b]	0	0

* Note. Data summarize the percentage of sections examined in which cells appeared primarily in one of three categories. Data were pooled for basal, median, subapical, and apical regions (n = number of axes x four regions). Compare first two columns of data with data shown in right- and left-hand columns in Figure 3 of Rodriguez and Santelices (1988).

[a] Cells in one basal section large, irregularly shaped (not elongate).

[b] Cells variable in size in some sections.

the pattern found by Rodríguez and Santelices (1988) for these same species. Apical notches were observed under low magnification on JS 2128b, a cystocarpic specimen of *G. nudifrons*. With higher magnification, two positions for apical cells were recognized. Figure 1b illustrates cases that perhaps represent early stages in the development of gametangial structures, analogous to observations for *P. capillacea* (see following). The apex shown in Figure 1c, when examined closely, had lateral branching that appeared dichotomous at first (see description of branching pattern).

Apical cells in spermatangial, tetrasporangial, or nonreproductive *P. capillacea* thalli were flush with, slightly extended from, or slightly behind the apex margin in all axes (Figs. 2a, 2b). On cystocarpic thalli, they often lay in a depression or notch as shown in Figure 3. Numerous thalli (in addition to plants listed in Table 1) bearing cystocarps on older, proximal branches were examined to reconstruct a developmental sequence. If it is assumed that successively proximal branchlets are older and that development of reproductive cells and associated structures is acropetal, observations suggest that divisions of apical cells slow or halt in the early stages of development of the

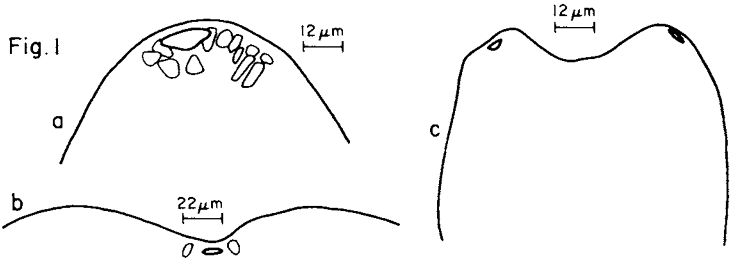
Fig. 1


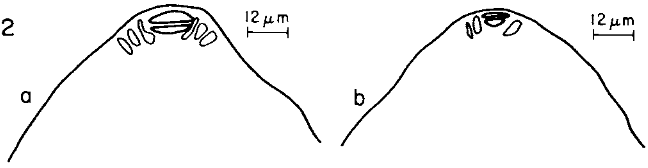
Fig. 2


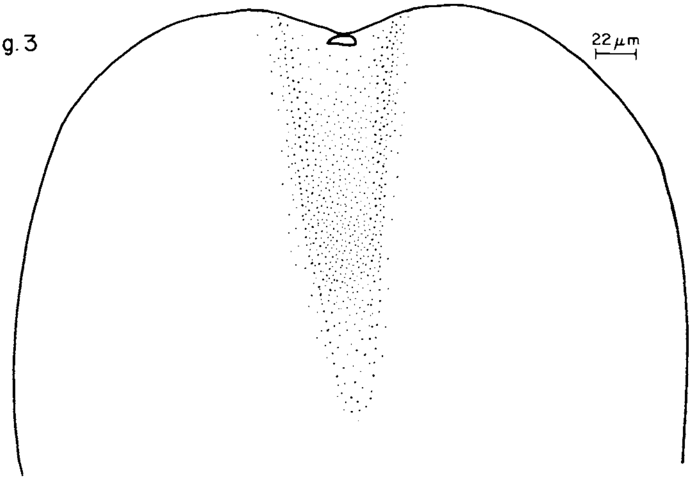
Fig. 3


Fig. 1. Apices of *Gelidium nudifrons* showing positions of apical cells. a, JS 1481b. b and c, JS 2128b.

Fig. 2. Apices of *Pterocladia capillacea*. a and b, JS 1511.

Fig. 3. Apex on cystocarpic *Pterocladia capillacea* thallus; JS 1473.

carposporophyte while surrounding cortical filaments continue to divide and extend the margin to either side of the apical cell. Apical depressions or notches on older branches are deeper and are subtended by an elongate, wedge-shaped, less-pigmented region (stippling on Fig. 3) bounded by ridges parallel to the axis. For this report, these sequences are described from surface morphology as seen with low magnification; the purpose is to correlate the presence of apical notches or depressions with the

Fig.4

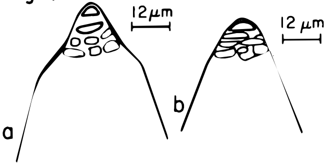


Fig.5

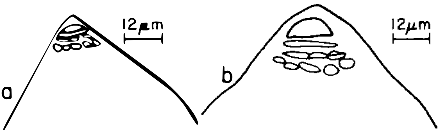


Fig. 6

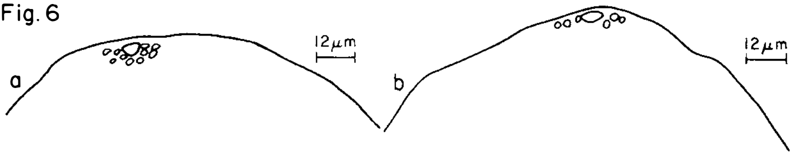


Fig. 7

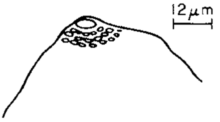


Fig. 4. Apices of *Pterocladia caloglossoides*. a, from HAHF 54708, cystocarpic. b, JS 1085, tetrasporangial.

Fig. 5. Apices of *Pterocladia media*. a, leg. M. Snyder "*Gelidium crinale* var. *luxurians*," UC 262565, cystocarpic. b, from JS 2163, tetrasporangial.

Fig. 6. Apices of *Pterocladia lucida*. a and b, leg. D. Rudie, Bay of Plenty, near Auckland, New Zealand in May.

Fig. 7. Apex of *Pterocladia capillacea*, JS 4214, Oahu, Hawaiian Islands.

development of cystocarps rather than to describe reproductive anatomy. Apical notches and a less-pigmented, yellowish or pale central region just behind the apex (as shown in Fig. 3) are useful for recognition of female gametangial thalli. Apical cells were somewhat depressed on several axes on thalli bearing early stages of developing tetraporangial sori; deeper notches, typical of cystocarpic apices, were not observed on either tetrasporangial or spermatangial thalli. On the basis of this character, collections can be quickly sorted to obtain reproductive stages for more detailed studies.

On thalli of *P. caloglossoides*, all apical cells (145 in addition to apices observed for data of Table 2) protruded as shown in Figures 4a and 4b. Apical cells on 47 apices of *P. media*, as well as on apices examined for the data in Table 2, similarly extended ahead of the axis tip (Figs. 5a and 5b).

Apices on a single specimen of *P. lucida* were mostly as in *P. capillacea*, with apical cells flush with, slightly protuberant, or slightly below rows of marginal cortical cells (Figs. 6a, 6b). When slightly depressed, the depression was shallow-sided and broad, not as shown in Figure 5b of the 1988 study of Rodríguez and Santelices. Figure 7 shows an apical cell on a specimen of *P. capillacea* (JS 4214) collected in Hawaii (Oahu Island) in October.

The shapes of cells that initiated lateral branches were similarly variable on axes of all species. Thalli of *G. coulteri* and *G. nudifrons* from California are usually easily identified on the basis of their branching pattern. In addition, *G. coulteri* occurs in the mid- to low intertidal zone, whereas *G. nudifrons* is always subtidal. *G. coulteri* develops closely and regularly spaced lateral branchlets that remain mostly unbranched and short, giving a distinctive appearance to specimens of this species. *G. nudifrons*, by contrast, is sparsely branched; lateral branching follows no predictable pattern and is often initiated near apices in an apparent dichotomy. *P. caloglossoides* and *P. media* are sparsely and irregularly branched, but because the axes are thin and narrow, with relatively fewer cells in either dimension, the initials of branches were easily recognized and always resembled apical cells on primary axes. Thalli of the two *Gelidium* species and of *P. capillacea* are thicker, with cells near the apices congested and overlapping. Farther back, lateral apical cells were identified by their position in branch initials. Figure 8 shows frequently observed shapes of apical cells of secondary branches close to primary apices in *G. coulteri.* The inverted cone-shaped cells described as representing lateral initials (Rodríguez and Santelices 1988) were seen distinctly along margins in *P. lucida* and less frequently in *G. nudifrons*. For *P. capillacea*, cells tending to this shape were found in numerous collections for all seasons, for all sizes of thalli, and from various habitats.

Discussion

If the position of the apical cell on primary axes could be relied on to distinguish species of *Gelidium* from species of *Pterocladia* (otherwise separated on the basis of bilocular or unilocular cystocarps, respectively), this easily determined characteristic would be a useful criterion for many purposes. My results, however, do not support the distinction proposed by Rodríguez and Santelices (1988). Their observations of apical cells in depressions in *P. capillacea* were based on two collections (see their Table 1), with reproductive state not described. Among the extensive California collections of this same species that I evaluated, the only thalli in which apical cells occurred in distinct depressions were cystocarpic. The sunken position of the apical cells on these reproductive apices could be interpreted as the consequence of cessation of divisions of the apical cell, with continuing divisions of cortical cell filaments. In all the other species, distinctive, easily recognized apical notches were found only on a cystocarpic specimen of *G. nudifrons*.

On specimens of the larger, coarser species, marginal cells that represent potential apical cells of secondary branches cannot be recognized close to primary apices except when a protrusion from the margin indicates a branch initial. Shapes of these lateral branch apical cells varied similarly among species; I found no pattern that separated species or genera. Cells in Figure 8 are arranged to suggest how the several shapes could be related by developmental sequences. Marginal, inverted, cone-shaped cells (as described and illustrated by Rodríguez and Santelices 1988) were seldom recognized near apices and did not characterize any single species.

My results support the conclusion of Rodríguez and Santelices that arrangements of surface-viewed cortical cells in apical, subapical, and middle portions of thalli of all species (*Gelidium* and *Pterocladia*) are generally variable, probably because of different rates of growth and division. In the study by Rodríguez and Santelices, cortical cells close to the base of axes in *P. capillacea* (including *P. tenuis*), *P. lucida*, and *P. caerulescens* differed from the basal-most cortical cells of *Gelidium* species. They were elongated, pyriform, or elliptical, with their longer dimensions nearly parallel to the axis of the thallus. This observation suggested that size and disposition of cortical cells in "basal-most parts of erect thalli where cell division and cell elongation have ceased" possibly could be useful to

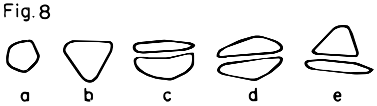


Fig. 8. Apical and subapical cells of secondary axes of *Gelidium coulteri*.

compare thalli. Some thalli of *P. bulbosa* in their study showed this characteristic; others resembled *Gelidium* thalli, having rounded, irregularly disposed cortical cells close to the base of axes. In my study, 30 axes of *P. capillacea*, representing a range of seasonal, habitat, and reproductive forms, were evaluated for this distinction. Cortical cells in 12 (40%) of the basal sections clearly resembled the elongate regularly aligned cells drawn to illustrate the arrangement of *Pterocladia* species in Figure 3 of the study of Rodríguez and Santelices. Ten basal sections (33%) showed intermingled elongate cells and rounded cells in approximately equal numbers. In seven basal sections, cells were predominantly more rounded than elongate. Cells were large and quite irregularly shaped in one section. These analyses of the data summarized in Table 2 tend to corroborate the suggestion that cortical cells near the bases of axes of many *P. capillacea* thalli differ from corresponding cells of several *Gelidium* species. Cortical cells in all parts of thalli of *P. media* and *P. caloglossoides*, however, were mostly rounded and irregularly arranged. One specimen had elongated cells near the base, but the elongation was perpendicular to the long axis of the thallus. The shape of cortical cells therefore could not be used to separate species of *Pterocladia* from species of *Gelidium.*

The earlier study (Rodríguez and Santelices 1988) tested the suggestion that a bending, or geniculum, at the base of branches might be found consistently in species of *Gelidium*, whereas branches of *Pterocladia* are often basally constricted but are unbent. This distinction, as pointed out in a study of *Pterocladia capillacea* (Stewart 1968), was intended only to contrast that particular species with the two common similarly sized species of *Gelidium* (*G. robustum* and *G. purpurascens*) that co-occur with *P. capillacea* along the California coast. It was not then, or subsequently in any comparison of gelidiaceous taxa, considered a useful means of separating genera, as recent data (Rogriguez and Santelices 1988) have shown.

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Section III. *Gracilaria*

INTRODUCTION

Isabella A. Abbott

In the six years that have elapsed since the first workshop in Guam, many changes have been made in the taxonomy of the groups that were studied, but none was more dramatic than in the red algal genus *Gracilaria* and the taxa closely allied with it, *Hydropuntia* (=*Polycavernosa*) and *Gracilariopsis*. From the position of knowing virtually nothing about taxa in the Pacific, where sometimes only the type specimen was known (this condition is still true in the Indian Ocean), we progressed to a stronger position by virtue of sharing specimens and knowledge. At present, we are going back and reconsidering some of the "old" names. Perhaps the biggest change resulted from work by Zhang and Xia of China, who discovered a new species that shares the main features of two recognized genera, *Gracilaria* and *Polycavernosa*. With my involvement, they restudied previously named species and found that many of them (but not all) shared these features as well. As a result of this work, only *Gracilaria* is now recognized.[1]

In this volume, Zhang and Xia present a new species, and a new variety, of *Gracilaria* and are able to distinguish 21 species of *Gracilaria* for the coast of China.

In his first scientific paper in English, our newly found Vietnamese colleague, Nguyen H. Dinh, presents a list of 13 species of *Gracilaria* and two of *Gracilariopsis* for Vietnam, surely numbers that can be increased with more collecting. We are happy to be able to bridge the geographical gap between South China and Thailand.

In the final paper of the *Gracilaria* group, Suzanne Fredericq (who was the first graduate student to be included in the workshop meetings) and James Norris report a study of two cylindrical Atlantic/Caribbean species of *Gracilaria*. They found that *G. cylindrica* should be included within the circumscription of *G. blodgettii*. In the previous workshop (vol. 2), Abbott had removed *G. cylindrica* of Weber-van Bosse from inclusion in the Caribbean material.

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[1] Abbott, I. A., Zhang Junfu, and Xia Bangmei, 1991, Pac. Sci. 45(1):12–27.

STUDIES ON TWO NEW *GRACILARIA* FROM SOUTH CHINA AND A SUMMARY OF *GRACILARIA* SPECIES IN CHINA

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

Abstract

A new variety of *Gracilaria asiatica*, var. *zhengii* Zhang et Xia, and a new species, *G. chouae*, are described from South China. The new variety is characterized by simple to spare branching, the branches divaricate, with rounded axils. This is in contrast to abundant branching and more angular axils of *G. asiatica* var. *asiatica*. *G. chouae* is characterized by its small cystocarp, thin pericarp with cell contents arranged mostly anticlinally, showing very few periclinal connections. A summary of the number of species of *Gracilaria* now recognized in China is given.

Introduction

For many years, a simple to sparingly branched species of *Gracilaria*, distributed near Xiamen (Amoy), Fujian Province, in southeast China, has remained unnamed. Because of the branching differences and the coarseness of the thalli, we think that this material can be assigned to *G. asiatica* Zhang et Xia (1985) as a new variety. A second taxon shows close morphological similarity to *G. bursa-pastoris* (Gmelin) Silva from England and *G. parvispora* Abbott from Hawaii. Both of these names have been applied to the Chinese plants, but after reexamination of the Chinese material, we think that these two represent a new species, *G. chouae*, which differs in features of the cystocarp from the British and Hawaiian plants.

Description of the Species

Gracilaria asiatica var. *zhengii* var. nov. (Figs. 1–8)

Differt a var. asiatica plantis simplicibus aut sparsissime ramosis; ramificibus ad angulum rotundatas.

Differs from variety *asiatica* by the simple to spare branching, generally of only one to two orders (Figs. 1–3). Branches elongate, up to 30 cm (or more), divergent, with rounded angles at divisions from the main axes; tapered gradually toward apices and not constricted where attached to next lower order. Vegetative anatomy (Fig. 4) resembles that of variety *asiatica* as do cystocarpic structure (Figs. 5–6), tetrasporangia (Fig. 7) and deep "*verrucosa*-type" spermatangia (Fig. 8).

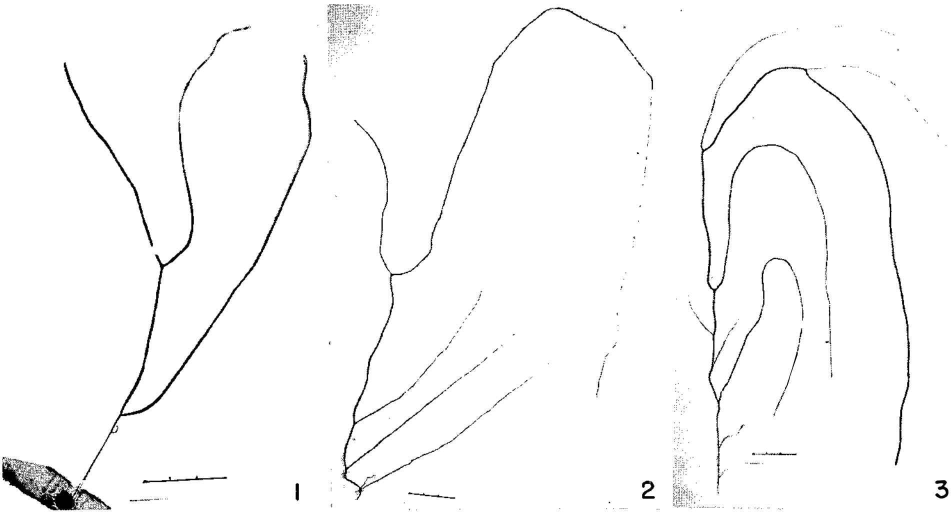
Etymology: This variety is named in honor of Zheng Shudong, engineer of the Institute of Oceanology, Academia Sinica, who has worked for many years along the coasts of China, and who has been very helpful to us in our collecting trips.

Holotype (Fig. 1): Growing on gravel and shells in lower littoral to upper subtidal zone in comparatively calm waters, Baozhuyu Xinglinwan, Xiamen, Fujian Province, China, April 8, 1982, leg. Zhang Junfu and Xia Bangmei AST 82-582 (AST).

Isotypes: AST 82-0528a, tetrasporangial (Fig. 2) from the same place and date as holotype; AST 82-586, spermatangial (Fig. 3) from Xiaodun Island, Tongan County, Fujian Province, China, April 12, 1982, leg. Zhang Junfu and Xia Bangmei.

Syntype: Nanshandao, Zhanjian, Guangdong Province, China, March 23, 1989, AST 89-0001, cystocarpic.

Remarks: The internal vegetative structure and reproductive organs (tetrasporangia, spermatangia, and cystocarps), including the nature of the pericarp—a useful feature for



Figures 1–3. *Gracilaria asiatica* var. *zhengii*. Fig. 1, Isotype (AST 82-586), spermatangial. Fig. 2, Holotype (AST 82-528), a cystocarpic plant. Fig. 3, Isotype (AST 82-528a), tetrasporangial.

distinguishing species—agree well with *G. asiatica* var. *asiatica*. We segregate as variety *zhengii* the material that is heavier and coarser than variety *asiatica* and more sparingly branched, with branches more divergent. Although these features may reflect only ecological differences, we are not aware of other types of plants, or intermediate ones, at this time. Furthermore, this new variety shows close similarity to the sparingly branched *G. rubra* Chang et Xia and *G. hainanensis* Chang et Xia from China. However, the last two species differ from *G. asiatica* in having branches abruptly constricted at their bases. *G. asiatica* further differs from them in having star-shaped contents in the cells of the pericarp (Fig. 6). Of the three species, *G. rubra* has more abundant and conspicuous upper absorbing filaments than do *G. asiatica* and *G. hainanensis.*

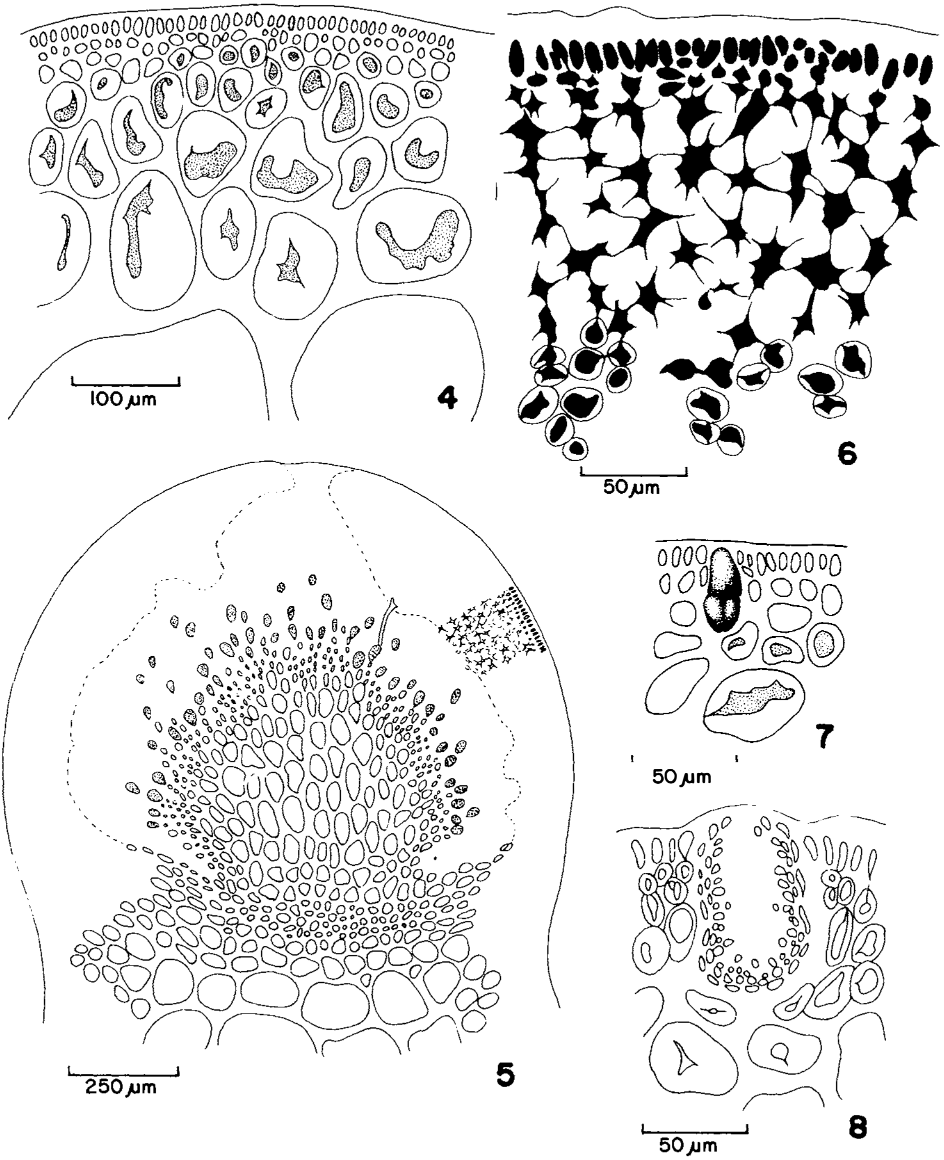
Gracilaria chouae sp. nov. (Figs. 9–31)

G. bursa-pastoris sensu Tseng et al. 1962; Chang and Xia 1962, 1976; Tseng 1983; Xia and Yamamoto 1985. *Non G. bursa-pastoris* (Gmelin) Silva.

G. parvispora sensu Xia 1985, *non G. parvispora* Abbott.

Plantae ad 15–20 (–40) cm altitudine, fragilium, succulentarum, alterne, subsecunde vel furcate ramosis; cortice ex 1–2 stratis cellularum constante, cellulis externis radiatum elongatis, ad 7–10 µm diam., 10–17 µm altitudine, tetrasporangiis dispersis, 31–43 µm diam.; spermatangia in conceptaculis corticalibus 30–53 µm profundo et 30–43 µm, diam.; cystocarpis minutis 664–913 µm long. ad 650–880 µm lat.

Thallus erect, solitary or caespitose, arising from a small disc, cylindrical throughout, usually 15–20, but up to 40 cm long, 2–3 mm in diameter, with two to four orders of branches. Texture succulent; easily broken, and brittle when dry; adheres well to paper on drying. Light red when fresh. Branches irregularly alternate (Fig. 9), occasionally



Figs. 4–8. ***Gracilaria asiatica*** **var.** ***zhengii*****. Fig. 4, Transection of part of main axis, showing relationship of cortical to medullary cells (AST 89001) from Guangdong Province. Fig. 5, Longitudinal section of cystocarp (AST 89-001). Fig. 6, Longitudinal section of pericarp (AST 89-001). Fig. 7, Transection of part of cortex with tetrasporangium (AST 82-782, from Fujian Province). Fig. 8, Transection of part of cortex with spermatangia (AST 82-586, an isotype).**

furcate (Fig. 12), but strongly mixed with unilateral or secund branching in whole (Figs. 10, 11) or in part (Figs. 9, 12, 13); gradually taper toward apices and not constricted where attached.

In transverse section, medulla consists of large pseudoparenchymatous cells, 232–598 µm in diameter (Fig. 14), with walls 6.6–8.3 µm in diameter. Medulla surrounded by one to two layers of cortical cells, which are small, roundish, and 23–33 µm in diameter; outermost layer pigmented and consisting of cells 10–17 µm by 7–10 µm in diameter. Transition from medulla to cortex abrupt.

Tetrasporangia scattered among cortical cells, ovoid or subspherical in surface view (Fig. 16), 31–432 µm in diameter, ovoid or oblong in transverse section (Fig. 17), 26–63 µm by 17–33 µm in diameter, surrounded by slightly modified cortical cells; cruciately divided.

Spermatangial conceptacles of "*textorii*-type" (Fig. 18), scattered over surface of frond in small, shallow, well-defined depressions, 30–53 µm deep and 30–43 µm in diameter; separated by modified, elongated cortical cells, characteristic of this type of conceptacle.

Cystocarps (Figs. 22, 23) protrude prominently, conical or hemispherical, 664–913 µm by 650–880 µm, slightly rostrate, not constricted at base. Gonimoblast composed of some large pseudoparenchymatous cells developing from a fusion cell, with many upper absorbing filaments connecting gonimoblast to pericarp (Fig. 24); carpospores round or ovoid, 20–36 µm by 10–20 µm in diameter. Pericarp 100–191 µm thick, consisting of 7–12 layers of cells (Figs. 26, 27); outermost layer pigmented, cells ovoid-oblong; remaining pericarp cells 7–10 rows of rounded or horizontally elliptical cells, arranged in somewhat irregular vertical rows, with secondary pit connections inconspicuous; three to five innermost layers of small irregularly shaped cells.

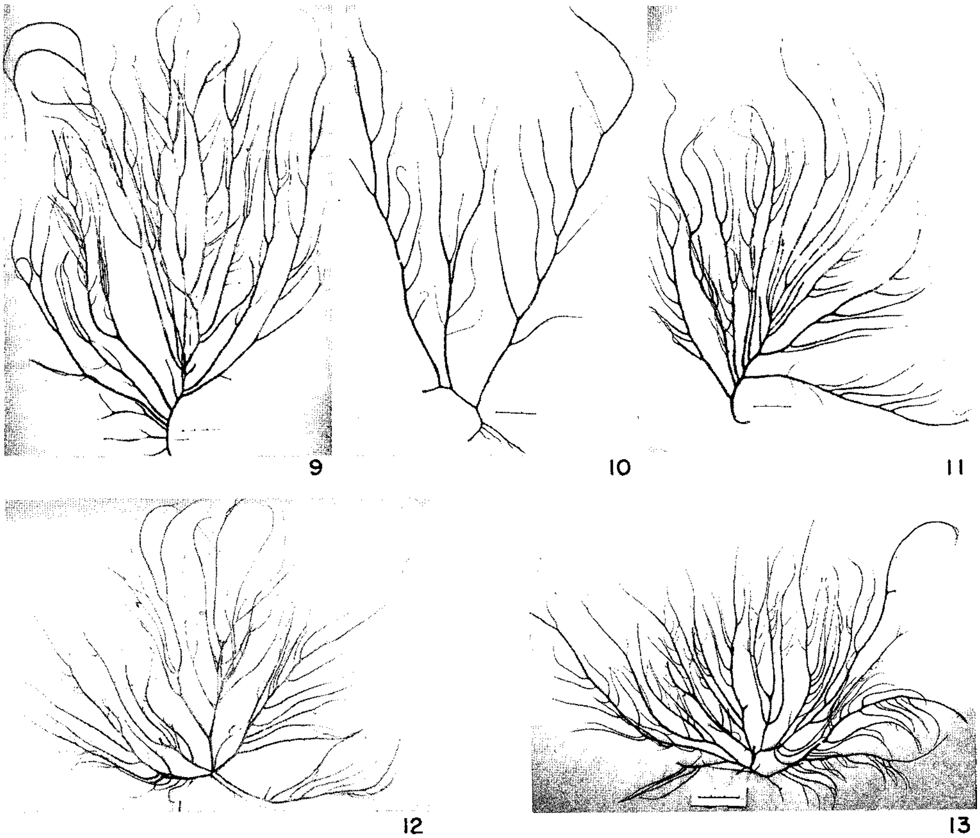
Etymology: Named in appreciation of the studies on marine algae, both Chinese and foreign, of Dr. Ruth C. Y. Chou.

Holotype: AST 82-686 (Fig. 9), cystocarpic, growing on gravel or shells in lower littoral tide pools or in the subtidal zone, Budaiao, Dongshan, Fujian Province, China, April 25, 1982, leg. Zhang Junfu.

Isotypes: From the same collection as holotype, AST 82-684 (Fig. 10), spermatangial; AST 82-685, tetrasporangial (Fig. 11).

Other Material: (All Fujian Province, China.) Xiaodun, Tongan County, April 12, 1982, AST 82-571, AST 82-573, tetrasporangial; AST 82-574, spermatangial. Xiaan, Guleibandao, April 19, 1982, AST 82-604; May 8, 1982, AST 82-765. Duimianyu, Dongshan County, April 22, 1982, AST-621, spermatangial; AST 82-622, cystocarpic; AST 82-623, tetrasporangial; AST 82-624. Chenshanao, Dongshan County, April 24, 1982, AST 82-669, spermatangial; AST 82-670, tetrasporangial; AST 82-671, cystocarpic. Baidian, Dongshan County, April 26, 1982, AST 82-725. Weiyou, Dongshan County, April 26, 1982, AST 82-732, cystocarpic; AST 82-733, spermatangial, tetrasporangial. Dongshan, in May (Tseng 1371), tetrasporangial, cystocarpic; in June, AST 54-2393, cystocarpic; in December, Tseng 2268. Pingtan Island, in April, AST 59-2307; AST 59-2336; in May, AST 53-844, tetrasporangial, and AST 59-4161, cystocarpic; in June, AST 53-1002, cystocarpic, and AST 53-1003, tetrasporangial. Xiamen, in March, Tseng A967, Tseng 1322; in April, Tseng 197, Tseng 197a, cystocarpic, Tseng A1050.

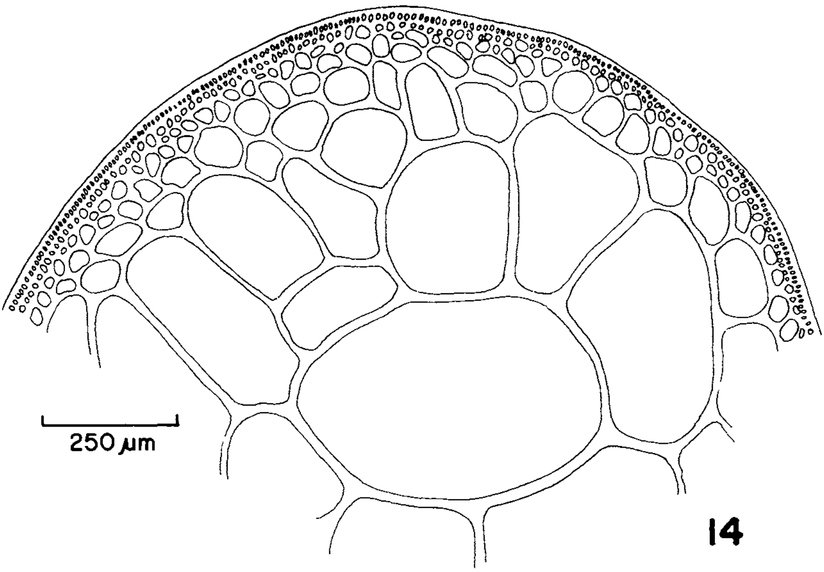
Remarks: *G. bursa-pastoris* was characterized by Harvey (1849), and later by Ohmi (1958), as having succulent, brittle, alternate or subsecund branches, with broad insertions of the nonconstricted branches that had patent and rounded axils, numerous absorbing filaments in the cystocarp, and shallow saucer-like spermatangial cavities.



Figs. 9–13. *Gracilaria chouae*. Figs. 9 and 10, Herbarium specimens showing branching patterns of plants. Note tendency in each specimen to unilateral (secund) branching, a characteristic of this species as well as of *G. parvispora* from Hawaii. Fig. 11, Holotype (AST 82-686), cystocarpic from Budaiao, Fujian Province. Figs. 12 and 13, Isotypes (AST 82-684, spermatangial, and AST 82-685, tetrasporangial; both from the same collection as the holotype).

Chang and Xia (1976) thought that this characterization matched Chinese material rather well. However, the structure of the pericarp that Ohmi (1958, fig. 7c) had depicted as having star-shaped cells with prominent secondary pit connections contrasted sharply with the Chinese material, which had pericarpic cells that were rounded to oval-obovate (Chang and Xia 1976, fig. 3, numbers 1 and 2).

Recently, Abbott (1985) named a new species of *Gracilaria* for the Hawaiian material previously identified as *G. bursa-pastoris*, using as distinguishing features the small cells of the pericarp and their star-shaped contents, together with the large cells of the gonimoblast (Fig. 25). This description of *G. parvispora* appears to include what has been called *G. bursa-pastoris* in Japan (Ohmi 1958; Yamamoto 1978), and although we have not examined Japanese material, we think that it is more like the Hawaiian than the Chinese material, particularly with respect to the structure of the pericarp.



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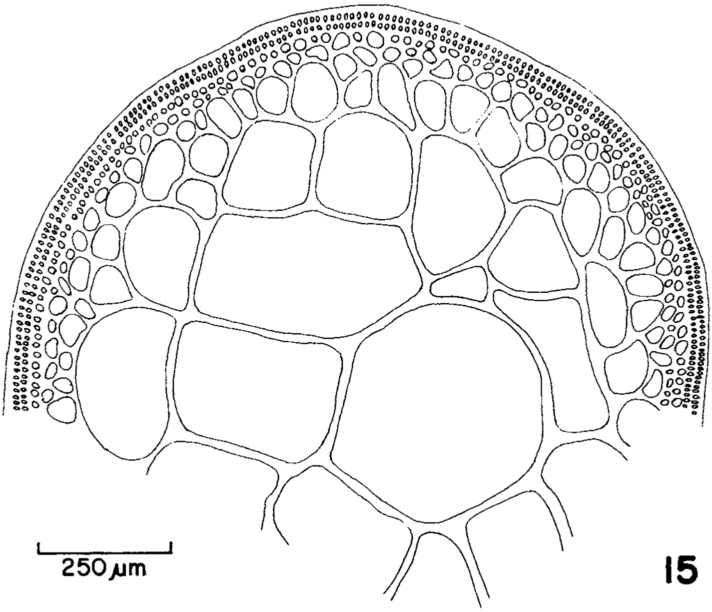

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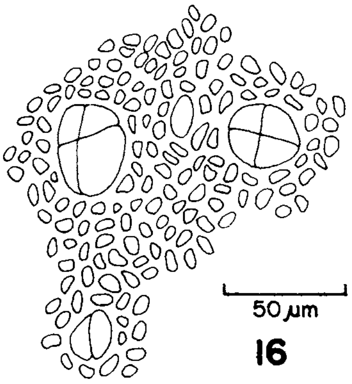
Fig. 14. ***Gracilaria chouae*****. Transection of part of main axis, showing relationship of cortical to medullary cells (AST 82-671), from Fujian Province.**

Fig. 15. ***Gracilaria parvispora*****. Transection of part of main axis, showing relationship of cortical to medullary cells (H84115, AST), collected from Coconut Island, Hawaii.**



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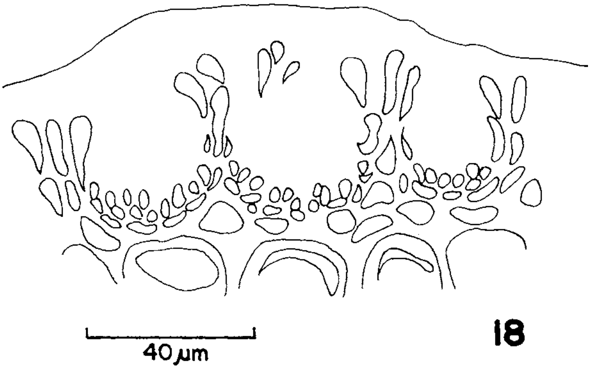

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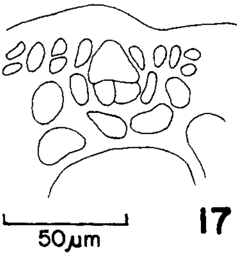

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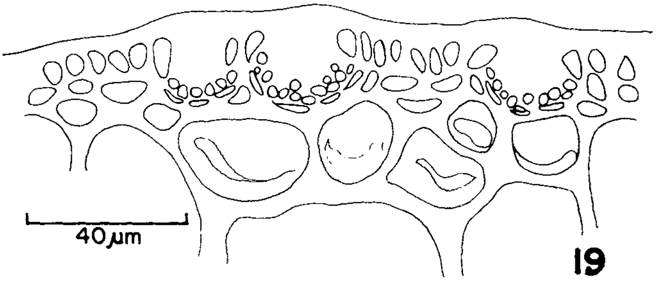

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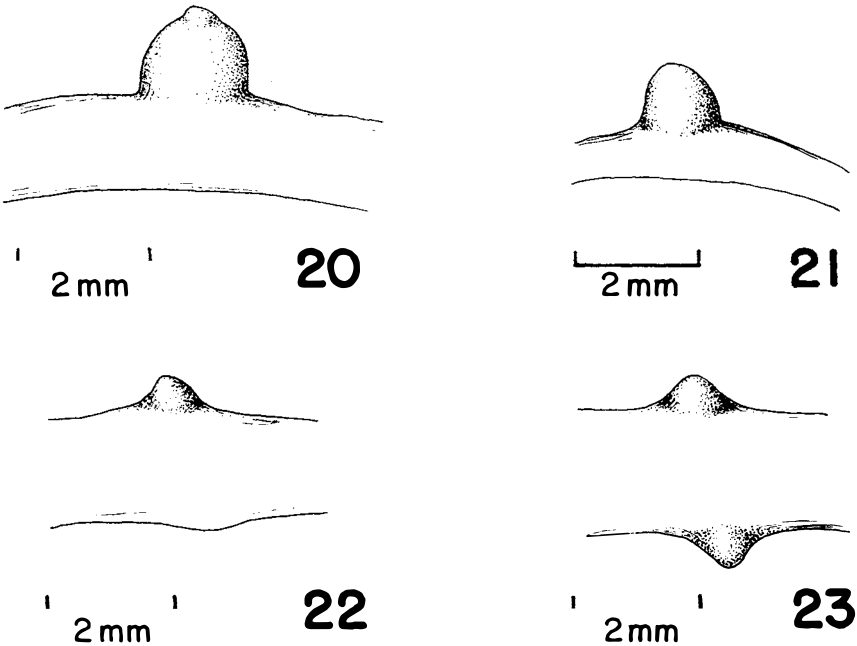
Figs. 16–18. *Gracilaria chouae*. Fig. 16, Part of cortex with tetrasporangia in surface view (AST 82-685), from Fujian Province. Fig. 17, Tetrasporangium in transectional view (same specimen as Fig. 16). Fig. 18, Shallow "*Textorii*"-type spermatangial arrangements in transection of AST 82-684 (isotype).

Fig. 19. *Gracilaria parvispora*. Transection of "*Textorii*"-type spermatangial arrangement (Doty 33102, Anuenue Fisheries Research Station, Honolulu, Hawaii).

In external appearance, particularly the unilateral branching pattern, *G. chouae* and *G. parvispora* look alike, although plants of *G. parvispora* tend to be more robust and shorter than the Chinese plants. The differences lie in some characteristics of the pericarp, such as thickness, shape, and arrangement of pericarpic cells and contents, and in the sizes of the cystocarps. The cystocarp of *G. chouae* is conspicuously smaller (664–913 µm by 650–880 µm; Figs. 22, 23) than that of *G. parvispora* (1080–1411 µm by 1245–1509 µm; Fig. 20). We judge the cystocarps shown in Figures 15–18 to be in similar stages of carposporangial and gonimoblast development and think that their external sizes and shapes are therefore valid features for comparison. In this comparison,

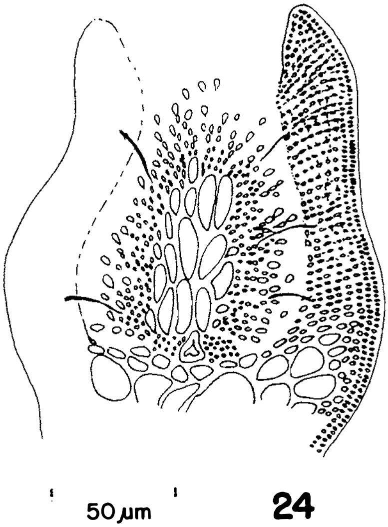


Figs. 20–23. *Gracilaria* species. External views of cystocarps judged to be the same age from examination of nearby gonimoblasts. Fig. 20, *Gracilaria parvispora* (H84115). Fig. 21, *Gracilaria bursa-pastoris* (British Isles, Swanage, c 1890, leg. E. George—BM). Figs. 22, 23, *Gracilaria chouae*, AST 82-671 and AST 82-686 (holotype), respectively.

G. parvispora has the largest (Fig. 20) cystocarp, *G. bursa-pastoris* (Fig. 21) has an intermediate sized one, and *G. chouae* (Figs. 22, 23) has the smallest of the three. Moreover, the pericarp of the Hawaiian plants (Fig. 28) is 200–300 µm thick, compared with 75–185 µm for Chinese specimens (Figs. 26, 27). In *G. parvispora*, the inner cells of the pericarp are connected anticlinally and periclinally, with distinct star-shaped cell contents (Fig. 28). In *G. chouae*, the inner cells are arranged mostly anticlinally in vertical rows, with fewer periclinal connections (Fig. 27) and no star-shaped contents. Other similarities between *G. parvispora* and *G. chouae* include the vegetative structure (compare Figs. 14 and 15), the gonimoblast and absorbing filaments (compare Figs. 24 and 25), and the spermatangial configuration (compare Figs. 18 and 19).

A comparative examination of two British specimens of *G. bursa-pastoris*, one from Swanage (Fig. 30) and the other from Sidmouth, Devon (Fig. 31), both previously examined by C. J. Bird of Halifax, showed that although the specimens differed from each other in branching pattern, their anatomy was similar. In particular, the structures of their pericarps were identical (Fig. 29). However, the features of the pericarp differ from those of *G. parvispora* (Fig. 28) and *G. chouae* (Fig. 27), as well as from British *G. verrucosa* (Hudson) Papenfuss (Zhang and Xia 1985, fig. 10).

When the International Seaweed Symposium met in Qingdao in 1983, and a mini-symposium on *Gracilaria* taxonomy was held, the international interchange on species



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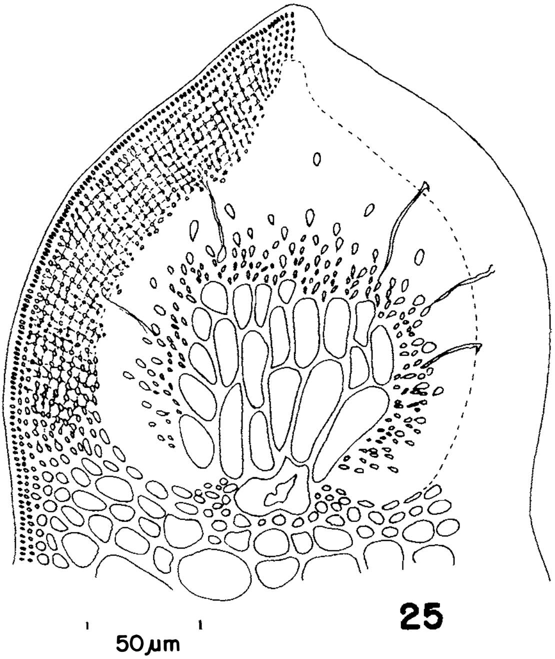

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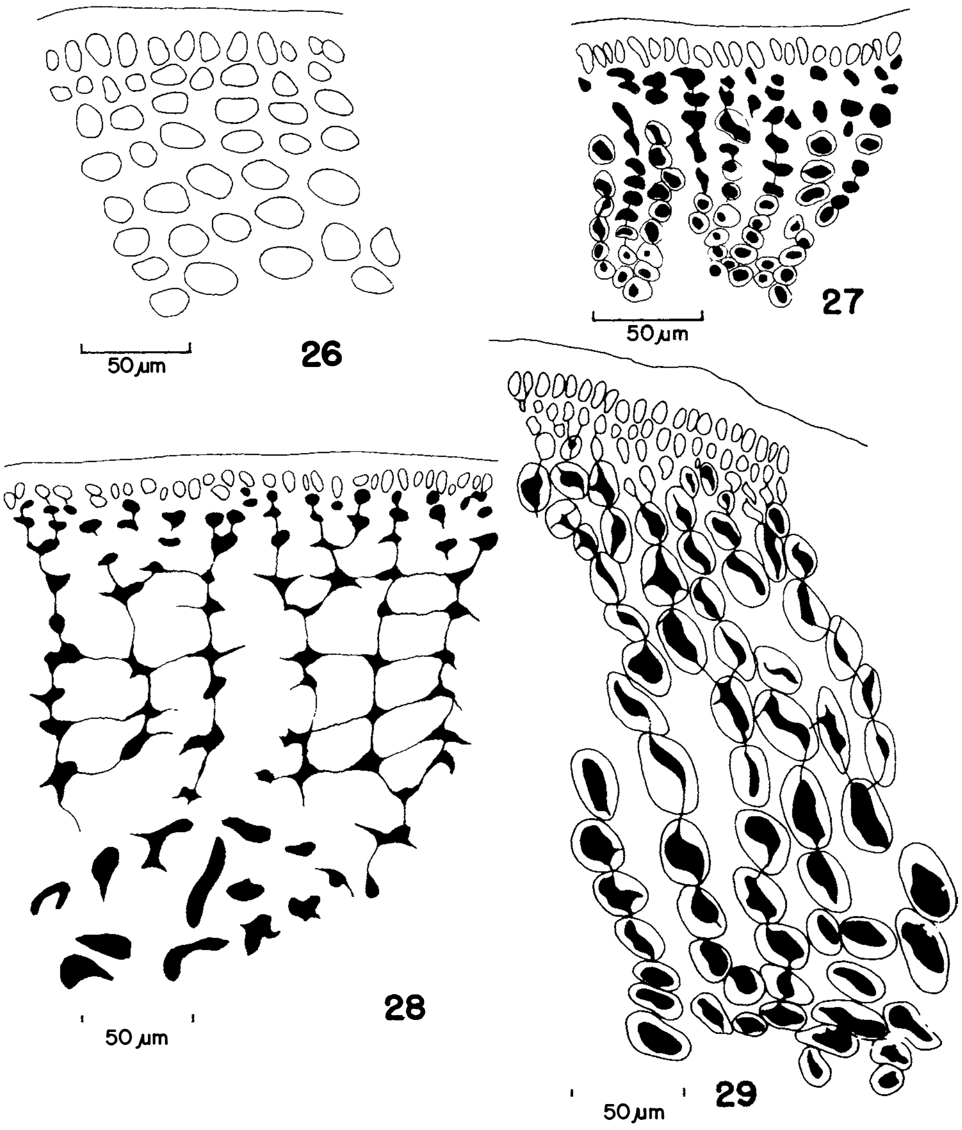
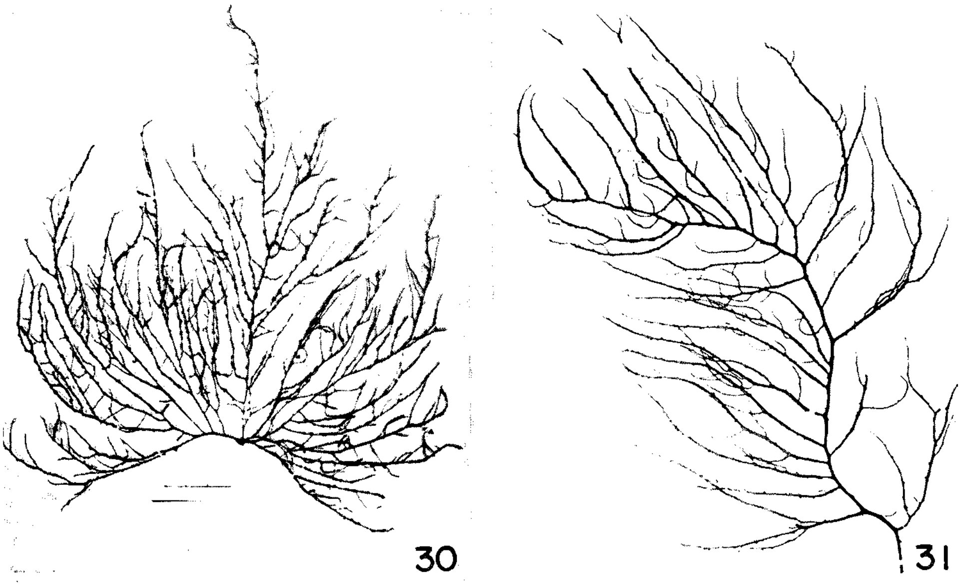
Fig. 24. *Gracilaria parvispora*. Longitudinal section through broad cystocarp showing upper absorbing filaments (H84115, AST).

Fig. 25. *Gracilaria chouae*. Longitudinal section through relatively narrow cystocarp showing upper absorbing filaments (AST 82-671).

limits, application of names, what constitutes adequate descriptions, and so forth started an intense examination and reexamination of specimens and concepts. We consider the structure of the pericarp a primary diagnostic character for distinguishing species (Zhang and Xia 1984). In our earlier and newly described species and varieties, *G. asiatica*—long known as *G. verrucosa* from China (Zhang and Xia 1985)—*G. tenuistipitata* var. *liui* (Zhang and Xia 1988), *G. chouae*, and *G. asiatica* var. *zhengii* (Zhang and Xia, in this paper) are all mainly based on pericarpic features. Because of a re-examination and critical study of Chinese specimens, the earlier reported (Chang and Xia 1976) 21 species of *Gracilaria* in China (excluding two species of *Polycavernosa*) have been reduced to 18 species. This was accomplished by Xia (1986), who placed *G. cacalia, G. crassa*, and *G. minor* into the synonymy of *G. salicornia*. In 1989, Fredericq and Hommersand restored the genus *Gracilariopsis* with its type species, *G. lemaneiformis*, thus excluding it from the genus *Gracilaria*. In 1988, we named a new species, *Gracilaria heteroclada*. It was transferred to *Gracilariopsis* in a recent paper by Abbott et al. (1991). New varieties were added to *G. tenuistipitata* (var. *liui*, Zhang and Xia 1988) and *G. asiatica* var. *zhengii* in this paper. Including the two species of *Polycavernosa* now placed in *Gracilaria*, and the new *G. mixta*, described by Abbott et al. (1991), we now recognize 21 species and two varieties from China.



Figs. 26–29. *Gracilaria* species. Longitudinal sections through pericarps. Figs. 26, 27, *Gracilaria chouae*; Fig. 26, AST 82-671; Fig. 27, AST 82-686 (holotype). Fig. 28, *Gracilaria parvispora* (H84115, AST). Fig. 29, *Gracilaria bursa-pastoris*, from Swanage, England (BM).



Figs. 30, 31. *Gracilaria bursa-pastoris*. Habits of two specimens from England. Fig. 30, from Swanage (BM). Fig. 31, from Sidmouth, Devon (BM).

Acknowledgments

We are especially grateful to Dr. I. A. Abbott for critically reading and correcting the manuscript. We also would like to thank the Keeper of Botany, British Museum (Natural History), for loaning specimens of *G. bursa-pastoris* and *G. verrucosa*. Thanks also are due to Lu Baoren, Leng Zengfu, and Zhou Xiantong for their help in the preparation of the manuscript. We acknowledge the wonderful opportunities we have had in being able to share our specimens and knowledge with so many taxonomists interested in economic algae, and for this good fortune, we will always be grateful to Dr. James Sullivan of the California Sea Grant College.

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VIETNAMESE SPECIES OF *GRACILARIA* AND *GRACILARIOPSIS*

Nguyen H. Dinh

Abstract

Reexamination of specimens of *Gracilaria* and *Gracilariopsis* from Vietnam shows that there are 13 species of *Gracilaria* and that all but two of the previously listed *Gracilariopsis* species belong in *Gracilaria*. This report combines and corrects the previously published lists of Dawson, Pham, and Nguyen.

Introduction

Gracilaria is well represented on the shores of Vietnam and has been reported on by Dawson (1954b), Pham (1969), and Nguyen (1969, 1972). Although realizing the potential economic value of the species of *Gracilaria* and its relatives, we in Vietnam were not able to study specimens with other scholars of these genera, and thus were not able to select useful species for collection or aquaculture. This report is intended to show that some of the species known in Vietnam are good candidates for commercial uses.

Table 1 shows the species of *Gracilaria, Gracilariopsis* and *Polycavernosa* (now placed in *Gracilaria* by Abbott et al. (1991) that have been reported from Vietnam. From the 21 names in this table, 15 species are treated in the following list, with three names of uncertain position because of unavailable specimens. These three are not counted in the final list. Two of them, *Gracilariopsis nganii* Pham and *Gracilariopsis phanthietensis* Pham are not known beyond their first collections; the specimens are thought to be in Saigon. However, *G. nganii* resembles in its pattern of branching (Pham 1969, fig. 2.110, left) *Polycavernosa fastigiata* (=*Gracilaria edulis*), according to Prof. Abbott (personal communication, 1989), who has had far more experience with these species than I. Details of the cystocarp and, more importantly, spermatangial plants are necessary in order to determine the status of these species. I have misplaced the specimen of the third entity, *Gracilaria chorda*, which I reported (Nguyen 1969) on earlier. It is unlikely to be this species that is known from northern Asiatic coasts.

List of Species from Vietnam

1. *Gracilaria tenuistipitata* Chang et Xia (Chang and Xia 1976, p. 102)
   Gracilaria verrucosa (Pham 1969) non *G. verrucosa* (Hudson) Papenfuss
   Gracilaria confervoides f. *ecorticata* (Pham 1969) non *G. confervoides* f. *ecorticata* May
   Gracilaria verrucosa (Nguyen 1972) non *G. verrucosa* (Hudson) Papenfuss
2. *Gracilaria firma* Chang et Xia (Chang and Xia 1976, p. 143)
   Gracilaria blodgettii (Nguyen 1969) non *G. blodgettii* Harvey
   Gracilariopsis rhodotricha (Dawson 1954b; Pham 1969) non *G. rhodotricha Dawson*
3. *Gracilaria salicornia* (C. Agardh) Dawson (Dawson 1954a)
   Gracilaria crassa (Dawson 1954a; Pham 1969; Nguyen 1969) non *G. crassa* Harvey ex J. Agardh
   Gracilaria cacalia (Nguyen 1972) non *G. cacalia* (J. Agardh) Dawson
4. *Gracilaria heteroclada* Zhang et Xia (Zhang and Xia 1988, p. 131)
   (=*Gracilariopsis heteroclada* (Zhang et Xia) Zhang et Xia in Abbott et al. 1991, p. 22)
   Gracilaria bursa-pastoris (Nguyen 1969, 1972) non *G. bursa-pastoris* (Gmelin) Silva
5. *Gracilaria asiatica* Chang et Xia (Zhang and Xia 1985, p. 175)
   Gracilaria verrucosa (Dawson 1954b; Nguyen 1969) non *G. verrucosa* (Hudson) Papenfuss
6. *Gracilaria arcuata* Zanardini (Zanardini 1857, p. 265). Previously reported by Nguyen (1969).

Table 1. *Gracilaria, Gracilariopsis*, and *Polycavernosa* Species Reported from Vietnam

Dawson (1954)

Gracilaria crassa Harvey
Gracilaria eucheumoides Harvey
Gracilaria verrucosa (Hudson) Papenfuss
Gracilariopsis rhodotricha Dawson

Pham (1969)

Gracilaria verrucosa
Gracilaria confervoides
  f. *ecorticata* May
Gracilariopsis nganii Pham
Gracilaria arcuata Zanardini
Gracilaria crassa J. Agardh
Gracilaria eucheumoides Harvey
Gracilaria coronopifolia J. Agardh

Gracilariopsis phanthietensis Pham
Gracilariopsis rhodotricha Dawson

Nguyen (1969)

Gracilaria crassa J. Agardh
Gracilaria chorda Holmes
Gracilaria verrucosa (Huds.) Papenfuss
Gracilaria blodgettii Harvey
Gracilaria hainanensis Zhang et Xia
Gracilaria arcuata Zanardini
Gracilaria gigas Harvey
Gracilaria salicornia (C. Agardh) Dawson
Gracilaria bursa-pastoris (Gmelin) Silva

Nguyen (1972)

Gracilaria cacalia (J. Agardh) Dawson
Gracilaria foliifera (Forsskal) Børgesen
Polycavernosa ramulosa Zhang et Xia
Polycavernosa fastigiata Zhang et Xia

7. *Gracilaria* articulata Chang et Xia (Chang and Xia 1976, p. 113). A new record for Vietnam.
8. *Gracilaria gigas* Harvey (Harvey 1859, p. 331). Previously reported by Nguyen (1969).
9. *Gracilaria hainanensis* Chang et Xia (Chang and Xia 1976, p. 105). Previously reported by Nguyen (1969).
10. *Gracilaria eucheumoides* Harvey (Harvey 1859, p. 331). Previously reported by Pham (1969).
11. *Gracilaria spinulosa* (Okamura) Chang et Xia (Chang and Xia 1976, p. 148). A new record for Vietnam. (Editor's note: This species was omitted from the key to species that follows, but it would be associated with the flattened, foliose species with modified margins.)
12. *Gracilaria punctata* (Okamura) Yamada (Yamada 1941, p. 203). A new record for Vietnam.
13. *Gracilaria textorii* (Suringar) De Toni (De Toni 1895, p. 27). (Editor's note: *Gracilaria foliifera*, reported by Nguyen [1972], is not listed in the text; perhaps the author meant to indicate that the specimen represented *G. textorii instead.)*
14. *Gracilaria edulis* (Gmelin) Silva
    = *Polycavernosa fastigiata* Zhang et Xia. For synonymy, see Abbott et al. 1991.
    Gracilaria coronopifolia (Pham 1969) non *G. coronopifolia* J. Agardh
    Gracilaria arcuata (Pham 1969) non *G. arcuata* Zanardini
    = *Gracilariopsis* sp. of Dawson (1954b)
15. *Gracilaria* bangmeiana Zhang et Abbott (in Abbott et al. 1991, p. 23)
    =*Polycavernosa ramulosa* Chang et Xia. Non *Gracilaria ramulosa* J. Agardh
    = *Hydropuntia ramulosa* (Chang et Xia) Wynne

Key to the Species of *Gracilaria* from Vietnam

1\. Thallus compressed or flattened throughout (except at base) 2
1\. Thallus terete throughout 5

  2\. Thallus very thick, prostrate throughout, marginal lobes extending into terete or compressed branches . . . . *G. eucheumoides*
  2\. Thallus not thick; erect, tending to be foliose 3

3\. Margins entire, branches dichotomous . . . . *G. textorii*
3\. Margins not entire, branches irregular 4

  4\. Thallus slightly thickened, commonly curved or twisted, with marginal lobes . . . . *G. punctata*
  4\. Thallus thin, margins dentate . . . . *G. denticulata*

5\. Thallus jointed throughout, or at least somewhere jointed 6
5\. Fronds not jointed 7

  6\. Segments lumpy because of constrictions along axes and nodes, or with no constrictions; branches short, of irregular pattern and length . . . . *G. salicornia*
  6\. Segments narrowed at points of branch attachments only; branches elongate . . . . *G. articulata*

7\. Fronds with percurrent axes 8
7\. Fronds with axes inconspicuous or not clearly different from branches 10

  8\. Branching tending to be secund, branches of nearly the same diameter as axis . . . . *G. hainanensis*
  8\. Branching irregular or alternate 9

9\. Branching irregular with three to four orders of branching; lower branches may become leading . . . . *G. firma*
9\. Branching alternate with one to two orders of branching; thallus delicate . . . . *G. tenuistipitata*

  10\. Thallus densely branched from a central stipitate area, forming finely divided bushes . . . . *G. asiatica*
  10\. Thallus not densely branched 11

11\. Branch pattern mixed in part or in whole; secund, alternate, or irregular . . . . *G. heteroclada*
11\. Branch pattern irregular but not mixed 12

  12\. Thallus coarse and thick 13
  12\. Thallus not coarse and thick 14

13\. Thallus with cylindrical, thick branches of few orders; ultimate branches short, delicate, or spinous . . . . *G. gigas*
13\. Thallus of flattened, broadened axes or segments, with the ends shortened, furcate, divaricate, blunt, or pointed . . . . *G. arcuata*

  14\. Thallus erect, bladelike, with tooth-like to fringed margins . . . . *G. denticulata*
  14\. Thallus not bladelike, segments frequently divided 15

15\. Plants less than 6 cm tall, branching congested near apex, width of segments nearly uniform throughout . . . . *G. ramosissima*
15\. Plants more than 6 cm tall (up to 11 cm tall), branching clustered and fastigiate distal of mid portions, axes and branches becoming thinner and delicate distally . . . . *G. edulis*

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I appreciate the great opportunity I had to attend the International Workshop on Taxonomy of Economic Algae of the Pacific in La Jolla. I thank the Chinese and American scholars, Professors I. A. Abbott, Zhang Junfu, and Xia Bangmei, who helped me in my studies. We could understand each other, using Chinese, French, and English languages—truly international. I want to give my great thanks to Dr. James Sullivan, California Sea Grant director, who went to much trouble to make it possible for me to attend the workshop and to gain much experience on seaweeds.

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STUDIES ON CYLINDRICAL SPECIES OF WESTERN ATLANTIC *GRACILARIA* (GRACILARIALES, RHODOPHYTA): *G. CYLINDRICA* BØRGESEN AND *G. BLODGETTII* HARVEY

Suzanne Fredericq and James N. Norris

Abstract

Studies of two western Atlantic species of *Gracilaria* have shown that *G. cylindrica* Børgesen, described from between St. Jan (St. John) and St. Thomas, Virgin Islands, is conspecific with *G. blodgettii* Harvey, a taxon originally described from Key West, Florida. On the basis of an analysis of topotype material and recent liquid-preserved spermatangial and cystocarpic collections from Puerto Rico, we found no inherent differences to support treating these two entities as distinct taxa. Special attention was focused on analyzing in detail the developmental sequence of spermatangial parent cells. Using recent collections of *G. blodgettii* from Puerto Rico, we photographed and diagrammed on a cell-by-cell basis the origin of spermatangial parent cells leading to the characteristic very shallow *textorii*-type male sori. The oldest validly published name for this species is *G. blodgettii* Harvey (1853) vs *G. cylindrica* Børgesen (1920).

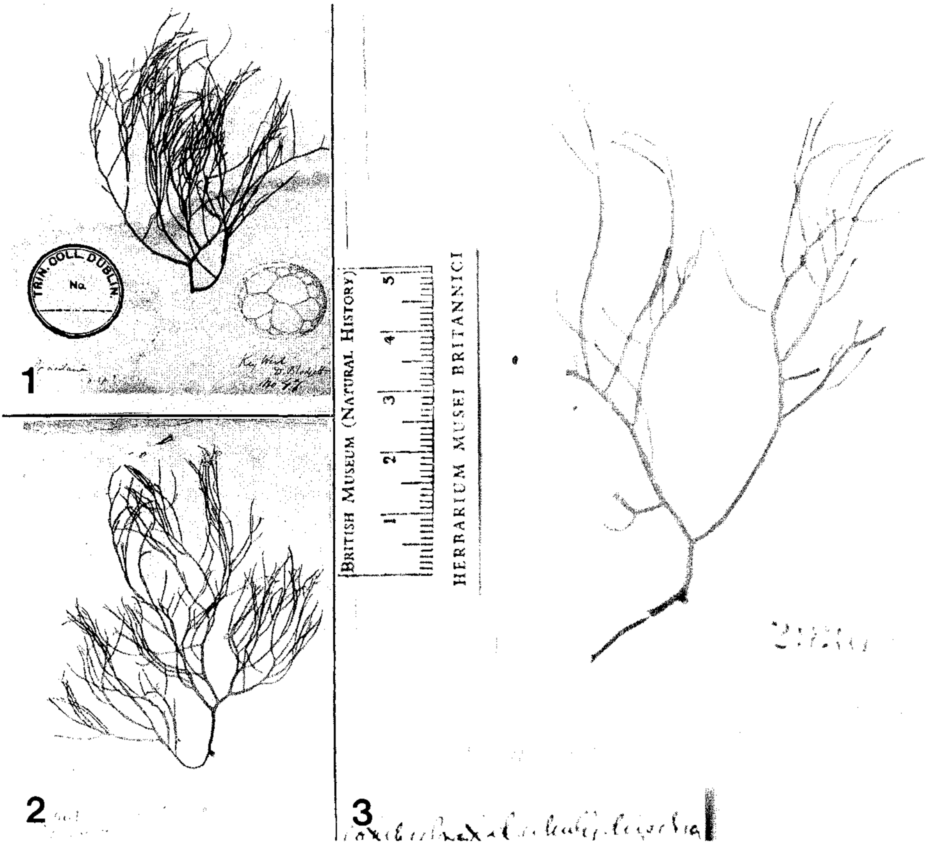
Introduction

In most floristic treatments and checklists, *G. blodgettii* Harvey (Harvey 1853, p. 111) and *G. cylindrica* Børgesen (Børgesen 1920, p. 375) are viewed as separate species (e.g., Taylor 1960, Ortiz Sotomayor 1976, Almodovar and Ballantine 1983, Wynne 1986). To some authors, however, the distinction between these two terete taxa is less evident. For example, Chapman (1963) noted that specimens of *G. blodgettii* from Jamaica graded into *G. cylindrica* and a species he referred to as *G. verrucosa*, and are difficult to assign. Yamamoto (1985) also thought that these Caribbean species appeared closely related. Earlier, Taylor (1960) pointed out that some specimens of *G. cylindrica* were perhaps intermediate with *G. blodgettii.* Because of these conflicting taxonomic interpretations in the literature, we investigated whether *G. blodgettii* and *G. cylindrica* as found in the Caribbean are distinct or possibly the same taxon.

Gracilaria (?) *blodgettii* was described by Harvey (1853), who was not sure of its generic placement; the description was based on specimens collected by Dr. Blodgett from Key West, Florida Keys, Florida. Diagnostic for this new species were branches and branchlets being constricted at their base of insertion and attenuated to an acute point; a medulla consisting of a few very large, thin-walled, irregularly polygonal cells; and a cortex of vertically subseriate, very small, pigmented cells. The lectotype specimen of *G. blodgettii* is housed in Trinity College, Dublin (TCD; Fig. 1); isolectotype specimens are in TCD (Fig. 2; tetrasporangial thallus, C. J. Bird annotation) and in the Agardh Herbarium, Lund (LD 29309) (Fig. 3).

Børgesen (1920) described *G. cylindrica* on the basis of cystocarpic and tetrasporangial deep-water specimens from "many places in the sound between St. Jan [St. John] and St. Thomas; and in the sea to the north of American Hill," Virgin Islands. Børgesen was of the opinion that *G. cylindrica* resembled *G. blodgettii* in having basally constricted branches and a terete habit but differed in being less densely ramified and having obtuse rather than acute branch apices. Lectotypic (Fig. 4) and isolectotypic specimens (e.g., Fig. 5) are located in Copenhagen (C), and a syntypic specimen is housed in Leiden (L-1841) (Fig. 6).

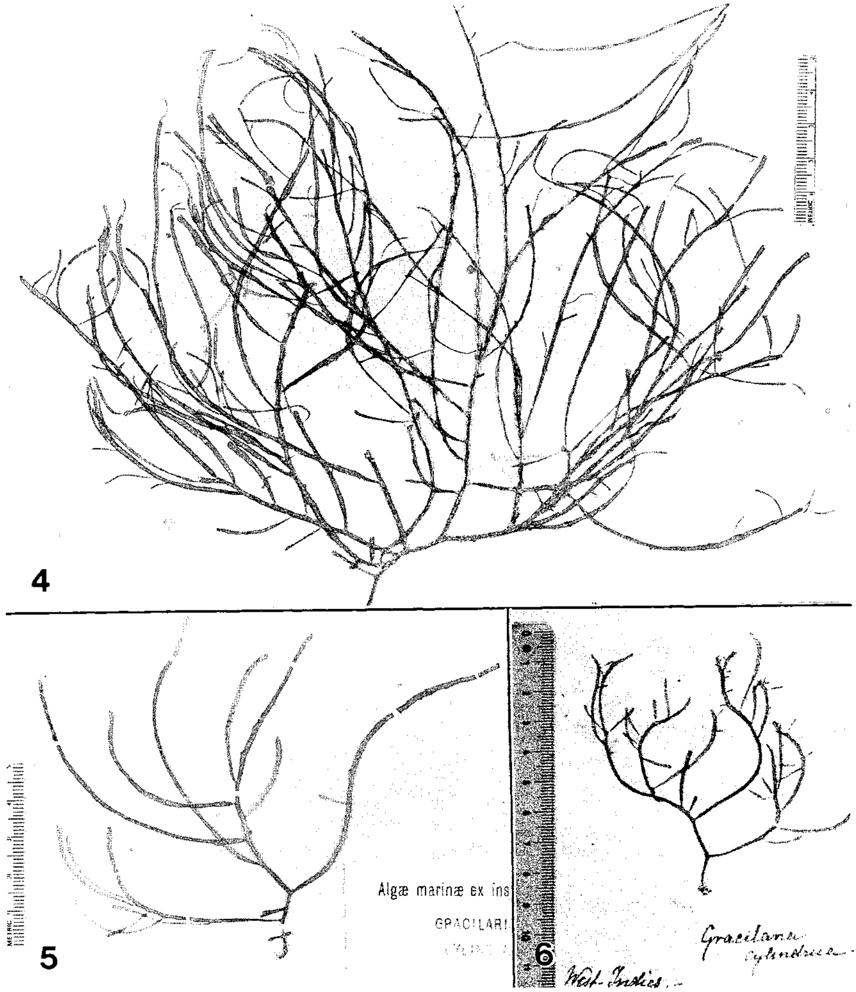
Both taxa are distributed throughout the Caribbean (Taylor 1960), reaching their northernmost distribution in the outer shelf of North Carolina (Schneider and Searles 1973,



Figs. 1–3. *Gracilaria blodgettii*. Fig. 1, Lectotype from Key West, Florida, Blodgett #47 (TCD). Fig. 2, Isotype (TCD). Fig. 3, Isotype (LD, 29309).

Schneider 1975) and southernmost in Guadeloupe (Taylor 1960), with *G. cylindrica* recorded even farther south in Brazil (Joly et al. 1968). Reportedly, they are deep-water species, with *G. blodgettii* dredged from depths of 11 to 36 m and *G. cylindrica* from 15 to 110 m (Taylor 1960). Cheney and Dyer (1974) reported *G. blodgettii* from a depth of 20–60 m in the Florida Middle Ground, off the west coast of Florida in the eastern Gulf of Mexico.

One character commonly used to discriminate species of *Gracilaria* is the type of spermatangial arrangement (Dawson 1949, Yamamoto 1978, Bird and McLachlan 1982). Schneider and Searles (1973) and Reading and Schneider (1986), who used material from the continental shelf off North Carolina, found that the male reproductive apparatus in *G. blodgettii* was organized in shallow pits. Abbott (1988) observed such *textorii*-type spermatangial conceptacles in specimens of *G. cylindrica* from the Virgin Islands.



Figs. 4–6. *Gracilaria cylindrica* Børgesen. Fig. 4, Lectotype from St. Jan, Virgin Islands (C, Børgesen #1973). Fig. 5, Lectoisotype (C, Børgesen #1973). Fig. 6, Syntype (L, Børgesen #1841).

Reports of *G. blodgettii* from outside the Caribbean have been disputed by Abbott et al. (1985). The assignment of this taxon to specimens from China (Zhang and Xia 1984, Xia 1985, Xia and Yamamoto 1985); Japan (Yamamoto 1985), including the Ruykyu Islands (Ohmi 1958, Yamamoto 1978); Taiwan (Chiang 1985); the Philippines (Yamamoto 1989); and Java (Abbott 1988) has been cautioned against and should be reexamined. Abbott (1988) concluded that specimens from Indonesia referred to by Weber van Bosse (1928) as *G. cylindrica*, but bearing *verrucosa*-type conceptacles, belonged instead to a new species and described them as *Polycavernosa vanbosseae* Abbott [=*Hydropuntia vanbosseae* (Abbott) Wynne 1989; *Gracilaria*]. Specimens from Caribbean Panama referred to as *G. cylindrica* by Hay and Norris (1984) possess distinct *verrucosa*-type conceptacles and represent an undescribed species (personal observations).

Some reports on the amount of tubular nutritive cells within a mature cystocarp have been published. Ortiz Sotomayor (1976) found numerous such cells ("absorbing filaments") linking gonimoblast tissue to pericarp in cystocarps of both *G. blodgettii* and *G. cylindrica* from Puerto Rico. Schneider and Searles (1973) only occasionally saw tubular nutritive cells ("radial trabeculae") in *G. blodgettii* from the North Carolina outer shelf.

Materials and Methods

Specimens fixed in 5% buffered formalin/seawater were stained with aceto-iron-hematoxylin-chloral hydrate (Wittmann 1965) and mounted in 1:1 Hoyer's: water mounting medium according to the procedure of Hommersand and Fredericq (1988). Material not liquid-preserved in formalin was stained and mounted in a mixture of 50% aniline blue/corn syrup (Tsuda and Abbott 1985). Herbarium abbreviations follow Holmgren et al. (1981).

Specimens Examined

Florida: Key West, A. H. Curtiss, *s.n.*, iv.1896, ● (NY), and ● (US 93064); Dry Tortugas: Southwest Channel, depth 6 fa., 20.vi.26, W. R. Taylor-1383 (NY); off Southwest Channel, dredged 18 fa., 11.vi.25, W. R. Taylor-918 ♂, ♀, and W. R. Taylor-600 ● (NY); east of Southwest Channel, dredged 18 fa., 18.vi.26, W. R. Taylor-1429 ●, ♀ (NY); 1 mile NNW of Loggerhead Key, dredged 45 fa., 4.vi.25, W. R. Taylor-927 ♀, ● (NY); 2.5 mi. NNE of Loggerhead Key, dredged 40 ft., 25.vi.25, W. R. Taylor-991 ● (NY).

Virgin Islands: St. Jan: ♀ vic. Annaberg, depth 30 m, 14.iii.06, Børgesen-1973 (C); Cruz Bay, depth 30 m, 29.iii.06, Børgesen-2205 ♀, 24.iii.06, Børgesen-2129 ♂, 8.iii.06, Børgesen-1841 ●, ♀, and 5.iii.06, Børgesen-1743 (all C); vic. Cruz Bay, depth 30 m, 23.iii.06, Børgesen-2096 ♀, and 17.iii.06, leg. Dr. Mortensen, Børgesen-2028 ♀ (both C). St. Thomas: M. Hay, January and June 1982, algal plain, 18–36 m, MH-1960 ●, MH-1985 ♂, MH-3141, MH-3146 ●, MH-3174 ●, MH-3163 ♂, MH-3184 ♀, MH-3185 ♀, and MH-3191 ♀ (all US).

Puerto Rico: Off Media Luna Reef, La Parguera, in sand, 28.ii.67, 13–18 m, Almodovar et al. (US 45026); Media Luna Reef, La Parguera, ii.89, Ballantine, *s.n.* ♂, ♀, ● (all US); 1.5 km seaward of Media Luna Reef, La Parguera, 17 m (US 95752, 95754, 156536, and 156537), and 2.x.85, Ballantine-2149 (US 95627).

Jamaica: Scots Cove, border St. Elizabeth and Westmoreland, W. R. Taylor (US 60744).

Cuba: Bahia Honda, 7.vi.14, Henderson and Bartsch (US 73583).

Results

Vegetative Growth. Type material of *G. blodgettii* Harvey from Key West, Florida (Figs. 1–3) and of *G. cylindrica* Børgesen from the Virgin Islands (Figs. 4–6) shows that mature thalli of *G. blodgettii* reach an average height of about 10 cm and that those of *G. cylindrica* range from 10 cm to 20 cm. The thalli of both species are single, erect, and attached to the substrate by a discoid holdfast, with branches reaching a width of up to 2 mm. The small type specimens of *G. cylindrica* (Fig. 6) are similar in shape and branching pattern to those of *G. blodgettii* (Fig. 3). The branching pattern in type and type-locality material of these two species is variable, ranging from frequently dense (Figs. 1, 2, 4) to spare (Figs. 3, 5, 6), and from irregularly alternate (Figs. 1, 2, 4) to a tendency of becoming secund (Figs. 3, 5, 6). Third- and higher-order branches are often beset with short branchlets, 1 mm wide to 3 mm long (Figs. 4, 7, 8). The branchlets of *G. blodgettii* are spindle-shaped or obtuse (Fig. 3), whereas, when present, those of *G. cylindrica* are primarily obtuse (Figs. 5, 6). Although most branches of the second order may not be constricted at their bases, the majority of third- and higher-order branches and branchlets are basally constricted.

Recently collected liquid-preserved material from Puerto Rico shows that the thalli are terete throughout. Branchlets terminate either in spindle-shaped (Figs. 7, 8) or obtuse tips (Fig. 9), and both conditions may exist on a single thallus (Fig. 10). Color is variable, ranging from light pink to crimson-brown. Thalli are relatively coarse (Figs. 7, 9) to slender (Fig. 8). Not cartilaginous in nature, the thalli collapse on drying on herbarium sheets, often disguising their terete nature.

Whereas the transition between cortex and medulla is gradual in young branchlets, it typically becomes abrupt in mature branches, as Harvey depicted in his drawing of a cross section on the herbarium sheet of *G. blodgettii* (Fig. 1). In young branchlets, the medullary cells are multinulcleate and rich in cytoplasm, and the terminal cortical cells are anticlinally obovoid. On the other hand, in first- and second-order branches, the pigmented cortex typically consists of one to two layers of cortical cells that become periclinally compressed and a medulla whose cells become hyaline. A cortical cell is generally subtended by a flattened subcortical cell (Figs. 13, 14), and the medulla typically consists of only a few large and irregular roundish cells.

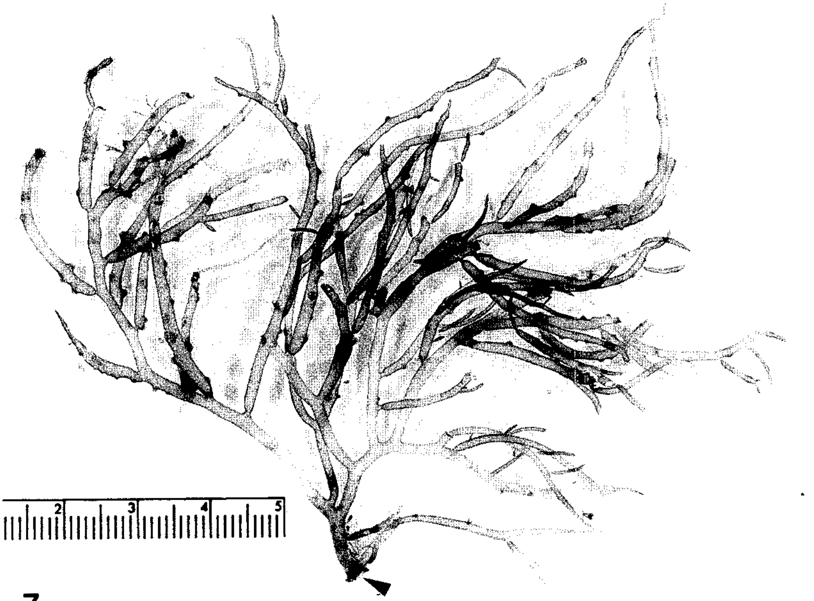
Cortical cells are typically periclinally compressed, uninucleate or multinucleate, reaching a width of 9–15 µm and up to 18 µm long. The average spacing between terminal cortical cells is 5 µm.

Male Reproductive Apparatus. A transection through a male branch from topotypic material of *G. blodgettii* and type material of *G. cylindrica* reveals that spermatangial parent cells and their spermatangia are organized into very shallow spermatangial sori, i.e., *textorii*-type sensu Yamamoto (1978). They are also seen in Figs. 15, 16.

In material of *G. blodgettii* from Puerto Rico (Figs 17, 18), two different focal views seen from the surface of a second-order male branch indicate that the spermatangia are organized into broadly ellipsoid patches or sori that reach an average length of 25 µm and a width of 20 µm (Figs. 11, 12). The spermatangia (Fig. 11) are at the level of the terminal undifferentiated cortical cells; the spermatangial parent cells, linked to one another by primary pit connections, are at the level of the subcortical/medullary cells (Fig. 12). In a transverse section, each male sorus that has reached full maturity has an average depth of 12–18 µm and consists of 12–20 spermatangial parent cells.

The sequential development begins with a generative outer cortical cell producing a series of spermatangial parent cells that lead to the establishment of a spermatangial sorus (Figs. 19–40 and accompanying diagrams 19–38). The last diagram for each figure number reflects the situation as seen in the photograph. For each number, the diagram or diagrams in front of the last diagram show the most likely hypothetical developmental pathway. Tracing back the pit connections on a cell-by-cell basis gives a reliable indication of how the spermatangial parent cells were previously cut off. The diagrams do not take into account size, shape, or plane of orientation of the spermatangial parent cells.

First, an outer cortical cell divides by an anticlinal concavo-convex division into a pair of spermatangial parent cells (Figs. 19, 20). This generative outer cortical cell is commonly the only cell subtended by a periclinally compressed larger subcortical cell (Fig.



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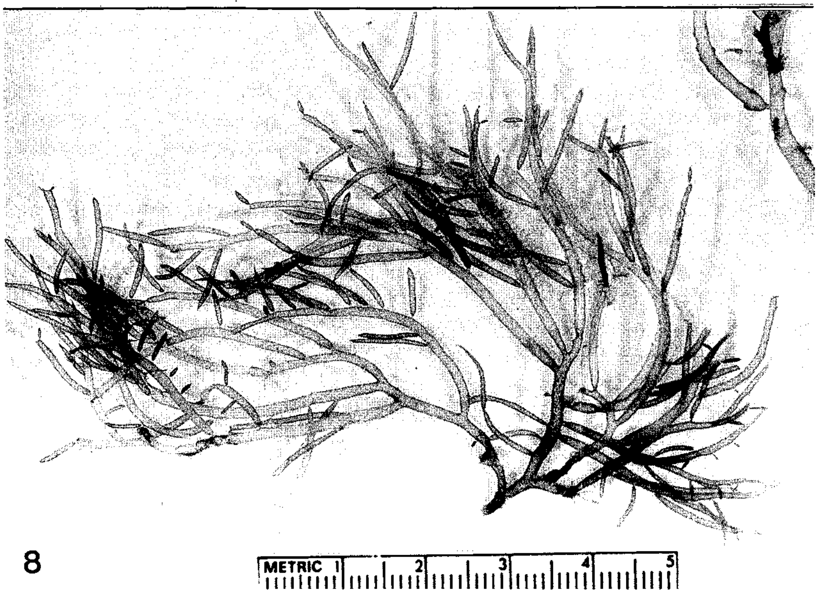

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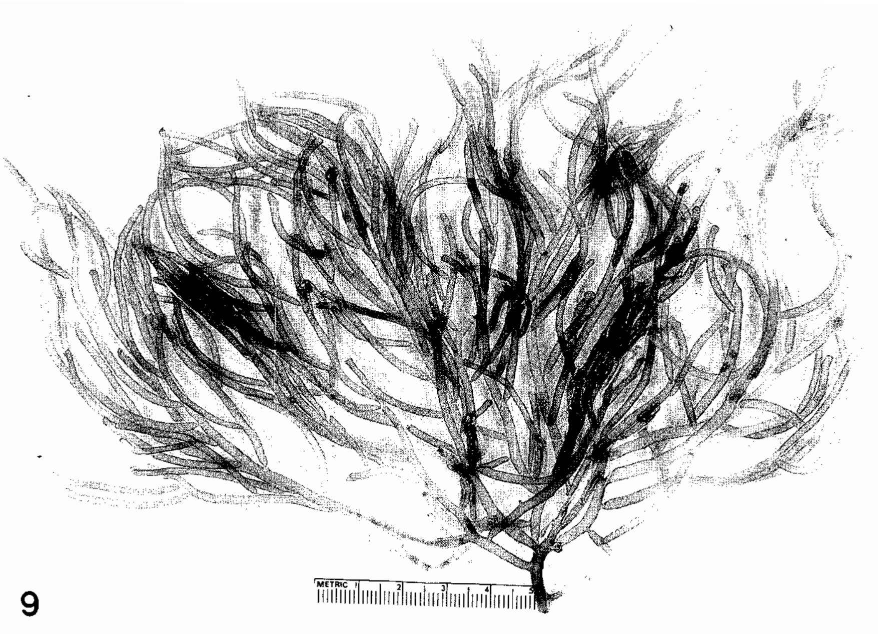
Figs. 7, 8. ***Gracilaria blodgettii*** **from Puerto Rico (liquid-preserved). Fig. 7, female specimen (US 156536) showing discoid holdfast (arrowhead), with majority of third- and higher-order branches and branchlets basally constricted. Fig. 8, Slender, small male specimen (US 156537) with majority of third- and higher-order branches and branchlets basally constricted.**



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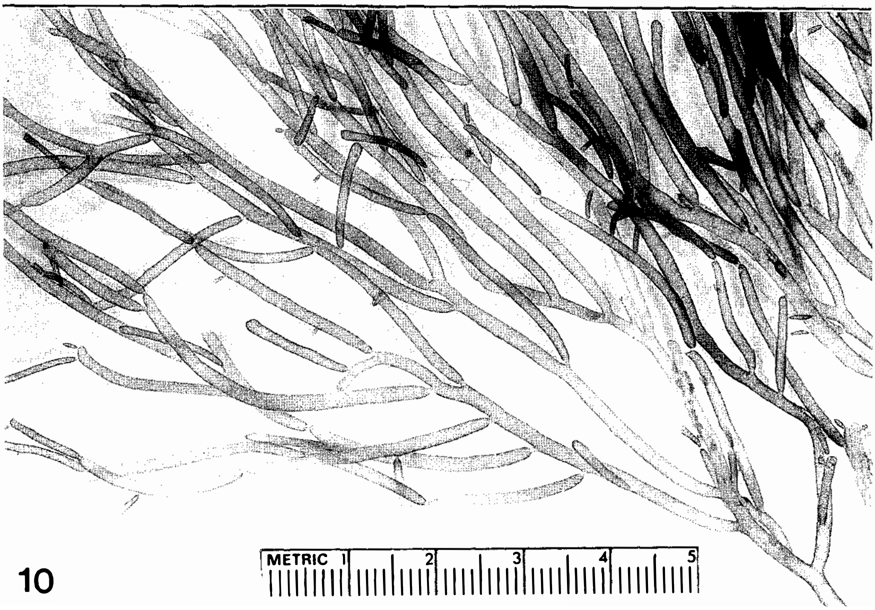

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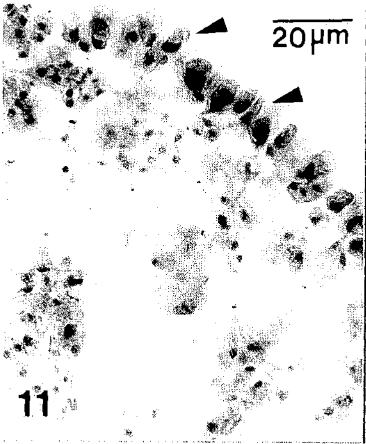
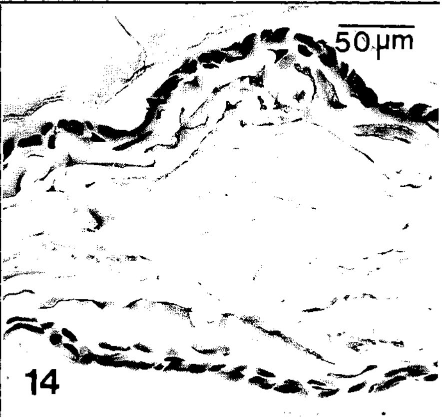
Figs. 9, 10. *Gracilaria "cylindrica"* from Puerto Rico (liquid-preserved). Fig. 9, specimen (US 95752) with majority of third-order branches and branchlets basally constricted. Fig. 10, Close-up of Fig. 9, showing obtuse or spindle-shaped branchlet tips.

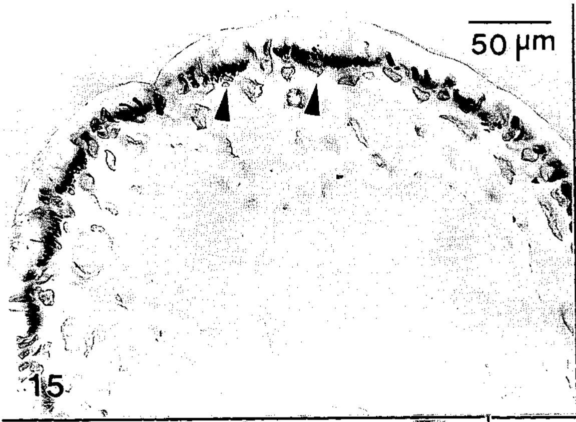


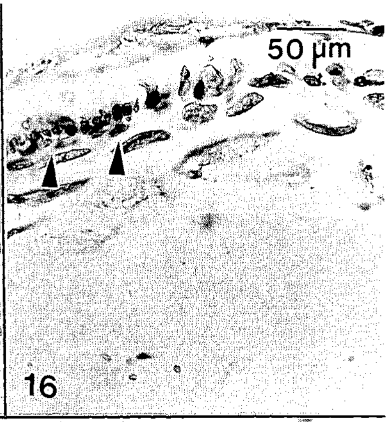


Figs. 11–13. Vegetative morphology of *Gracilaria blodgettii* from Puerto Rico (US 95754). Fig. 11, Transverse section through young branchlet showing multinucleate medullary cells and anticlinally obovoid terminal cortical cells (arrowheads). Fig. 12, Transverse section through a first-order branch showing vacuolate, large-celled medulla and one- to two-celled cortex (aniline blue). Fig. 13, Transverse section through a second-order branch (aniline blue).

Fig. 14. Transverse section through second-order branch in lectotype specimen of *Gracilaria cylindrica* (C, Børgesen #1973; aniline blue).

19). Occasionally, a subcortical cell subtends more than one outer cortical cell, which may (Fig. 27) or may not (Figs. 20, 26) become generative. The parent cell initial, connected by a primary pit connection to its subcortical cell, then divides in a plane different from the first one, leading to three spermatangial parent cells (Fig. 21). As soon as three spermatangial parent cells are established, each may cut off a single, colorless, uninucleate spermatangium by a concavo-convex septum (Fig. 22). One of the parent cells then divides further at either oblique or straight angles, leading to four (Figs. 23–25, 27) spermatangial parent cells. It is common that at the four-cell stage no spermatangia have yet been initiated (Figs. 23–25, 27). A subcortical cell occasionally bears two sets of





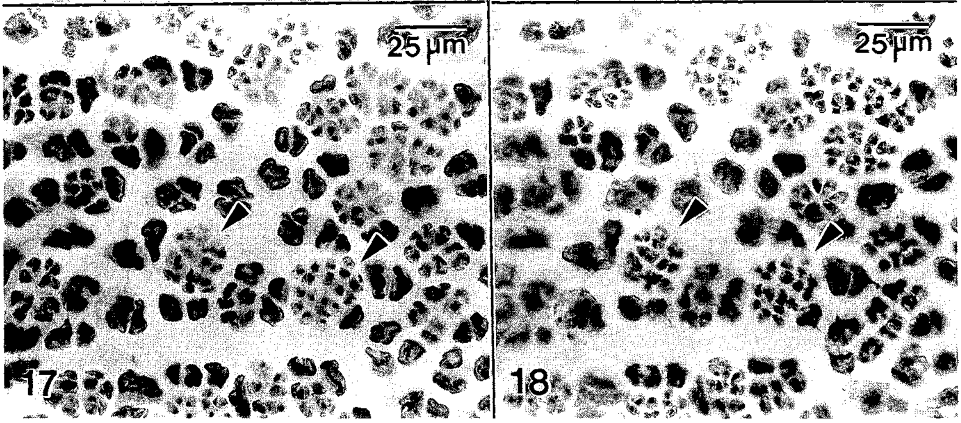


Fig. 15. Transverse section of male specimen of *Gracilaria blodgettii* from Dry Tortugas, Florida (NY, W. R. Taylor #918), showing shallow spermatangial sori (arrowheads; aniline blue).

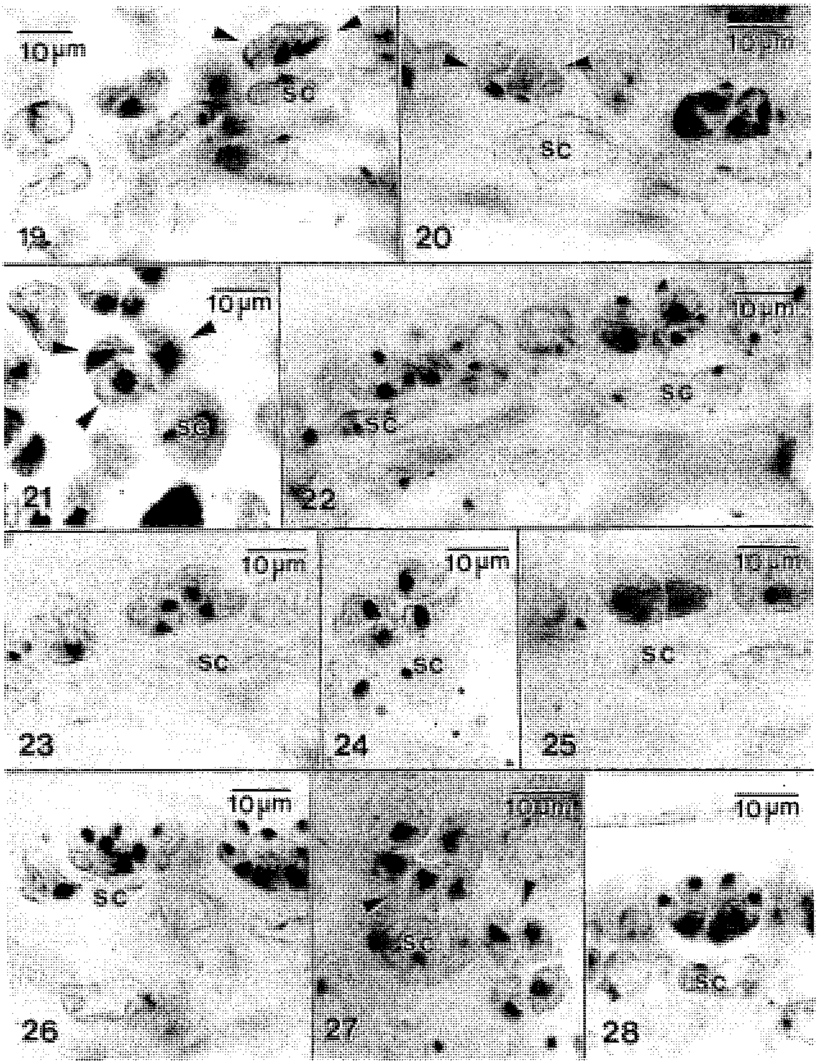
Fig. 16. Transverse section of a male syntype specimen of *Gracilaria cylindrica* (C, Børgesen #2129) showing spermatangial sori (arrowheads; aniline blue).

Figs. 17, 18. Two different focal planes showing surface view of spermatangial sori of *G. blodgettii* from Puerto Rico (US 156537). Fig. 17, at level of spermatangia (arrowheads); Fig. 18, at level of spermatangial parent cells (arrowheads).

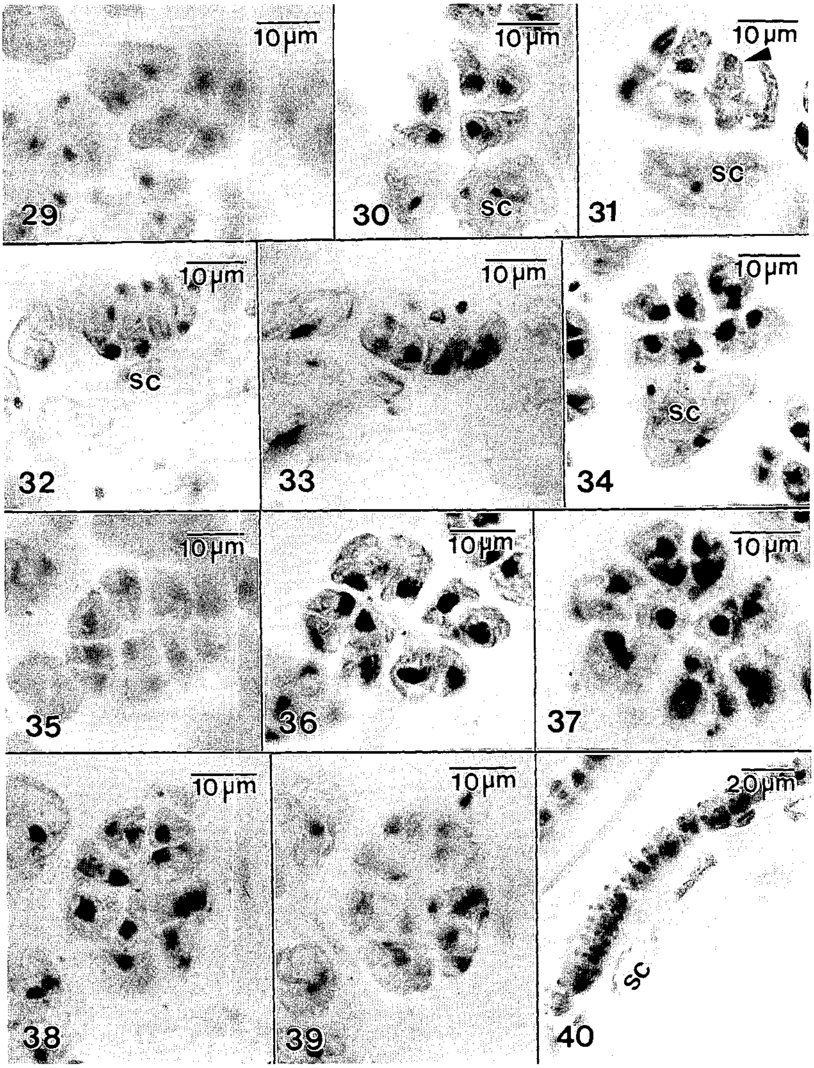
spermatangial parent cells (Fig. 27), indicating that both the outer cortical cells became generative.

At the five-cell stage, a small and shallow male sorus is recognizable, in which each spermatangial parent cell has cut off a spermatangium (Fig. 28). When a pit connection is seen between the central spermatangial parent cell (which is the spermatangial parent cell initial) in a transverse section, it indicates that the section cut straight through the center of the young male sorus. When such a pit connection is absent, the section went instead through the marginal spermatangial parent cells.

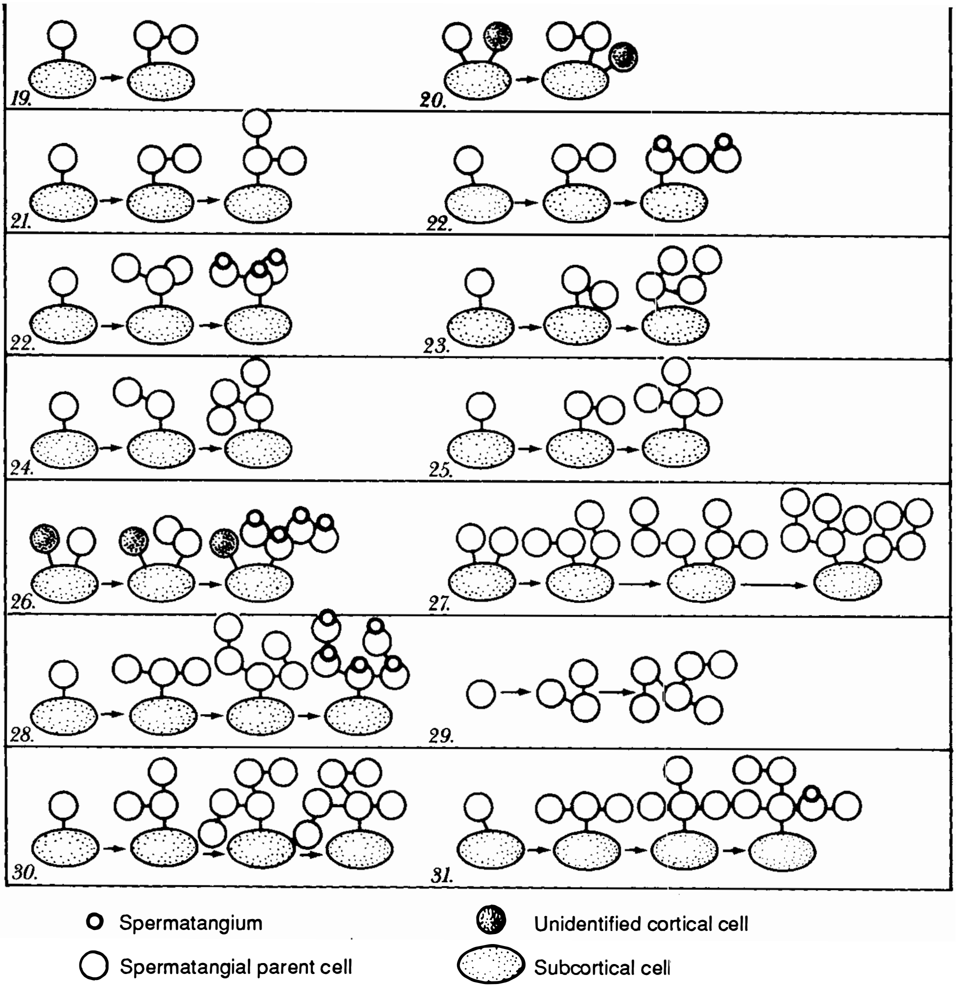
A surface view shows that a spermatangial sorus becomes ellipsoid when six to eight



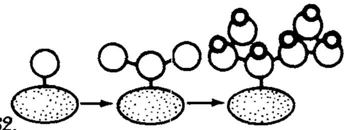
Figs. 19–28 and diagrams 19–28. See text for explanation of diagrams. Spermatangial *Gracilaria blodgettii* from Puerto Rico (US 156537). Development of spermatangial parent cells into spermatangial sori. sc = subcortical cell. Figs. 19, 20, Outer cortical cell divided into pair of spermatangial parent cells (arrowheads; transverse section). Fig. 21, Three spermatangial parent cells (arrowheads; surface squash). Fig. 22, At left and right: three spermatangial parent cells (arrowheads), with spermatangia in focus (transverse section). Figs. 23–25, Four spermatangial parent cells (transverse section). Fig. 26, Four spermatangial parent cells, each with a spermatangium (transverse section). Fig. 27, Subcortical cell bearing two sets of spermatangial parent cells (arrowheads), five at left and four at right (surface squash). Fig. 28, Five spermatangial parent cells, each with a spermatangium (transverse section).



Figs. 29–40 and diagrams 29–38. See text for explanation of diagrams. Spermatangial *Gracilaria blodgettii* from Puerto Rico (US 156537), showing development of spermatangial parent cells into sori. sc = subcortical cell. Figs. 29, 30, Six spermatangial parent cells (surface squash). Fig. 31, Six spermatangial parent cells with one spermatangium (arrowhead) in focus (surface squash). Figs. 32, 33, Six spermatangial parent cells, each with spermatangium (transverse section). Fig. 34, Eight spermatangial parent cells (surface squash). Fig. 35, Ten spermatangial parent cells (surface squash). Fig. 36, Eleven spermatangial parent cells (surface squash). Fig. 37, Fourteen spermatangial parent cells (surface squash). Figs. 38, 39, Two different focal planes showing a spermatangial sorus containing 12 spermatangial parent cells (surface squash): Fig. 38, at level of parent cells; Fig. 39, at level of spermatangia. Fig. 40, Transverse section through mature spermatangial cortex.



See text and caption for figures 19–38.



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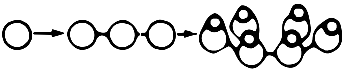

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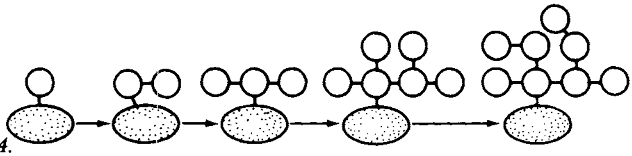

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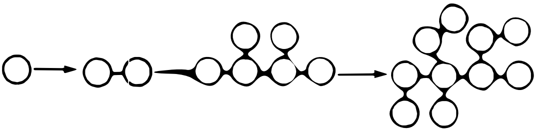

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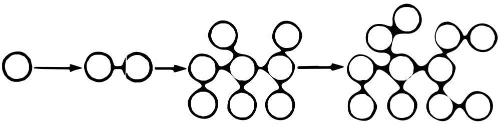

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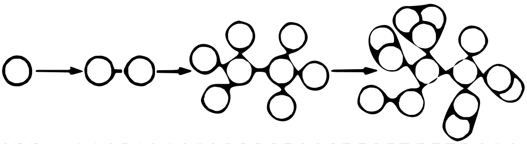

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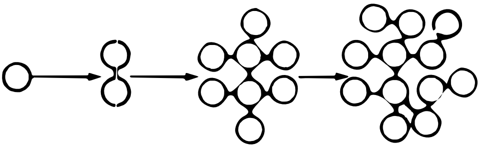


38.

spermatangial parent cells cut off sequentially become organized in two cell rows (Figs. 29–31, 34). Whereas surface views of young sori show exclusively on either the spermatangial parent cells or the spermatangia, a transverse section representing the equivalent developmental stage reveals both types of cells (Figs. 32, 33).

When 10 spermatangial parent cells have been cut off, the sorus becomes three cells wide or more (Figs. 35–39). A sorus of up to 14 spermatangial parent cells (Fig. 37) can be readily distinguished on a cell-by-cell basis, but a sorus may consist of up to 20 such parent cells. A view of a male sorus at the level of spermatangia (Fig. 39) shows that the spermatangia develop centripetally within a sorus. Occasionally in a mature spermatangial cortex (Fig. 40), neighboring sori are continuous instead of being interspersed among undifferentiated vegetative cells.

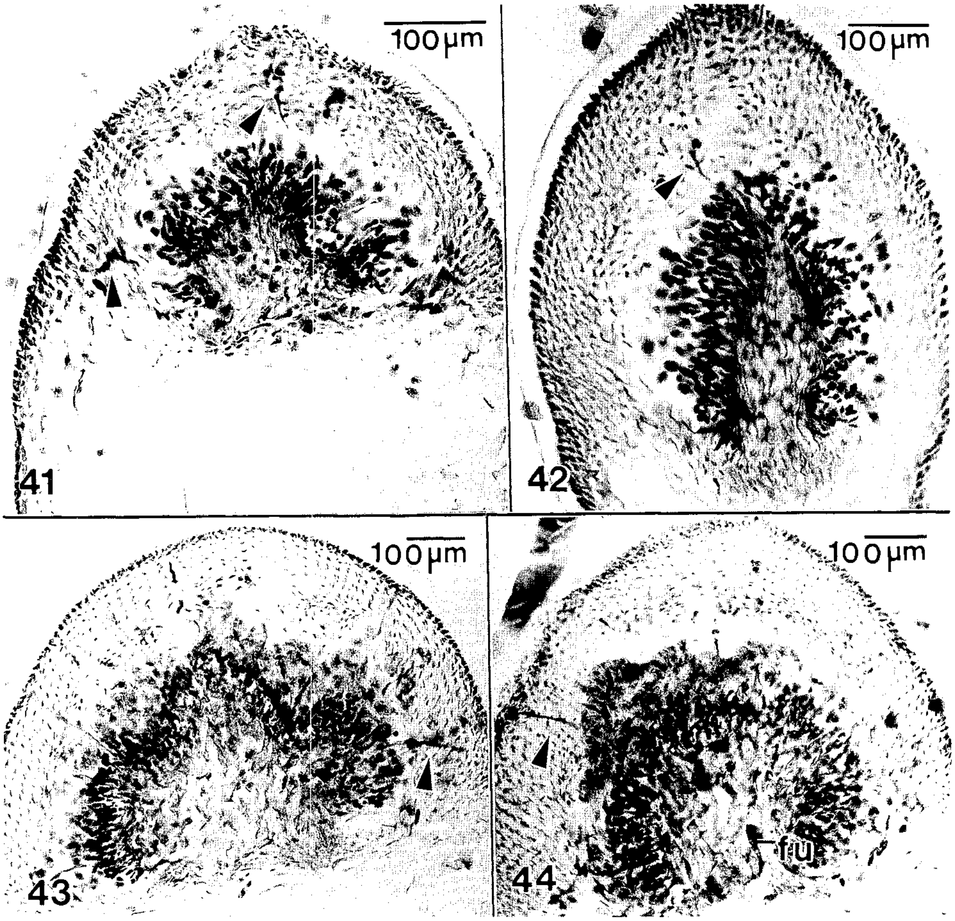
Cystocarp Development. Transverse sections through mature cystocarps in topotypic material of *G. blodgettii* (Figs. 41, 42) and type material of *G. cylindrica* (Figs. 43, 44) reveal that both possess a sterile gonimoblast that bears tubular nutritive cells that reach a well-developed pericarp of 10–15 cell layers. A globose fusion cell also persists (Fig. 44).

Unfertilized carpogonial branches were not available in the material examined. After fertilization, the multinucleate fusion cell cuts off small, roundish, uninucleate gonimoblast cells and typically becomes globose distally (Fig. 45). The lowermost part of the fusion cell incorporates, laterally around pit connections, multinucleate neighboring vegetative cells for a distance of up to three cortical cell files (Figs. 45, 46). On further division of the uninucleate gonimoblast cells, the gonimoblast cells form pit connections with the fusion cell (Fig. 47), and the lowermost gonimoblast cells (Fig. 49) expand in size and become multinucleate. These multinucleate gonimoblast cells bear distally small clusters of uninucleate gonimoblast cells while issuing, at their lower side, multinucleate, tubular nutritive cells (Figs. 47–49) toward the pericarp. At this stage, the multinucleate gonimoblast cells have not yet formed secondary pit connections with neighboring cells, and thus a sterile gonimoblast has not yet developed (Fig. 48).

While the divisions of gonimoblast cells continue laterally and upward in such young cystocarps, the tubular nutritive cells increase in length, with their tips fusing directly onto pericarp cells (Fig. 50). Distal uninucleate gonimoblast cells do not increase in size (Fig. 51) until they become transformed into carposporangial initials. The transition from gonimoblast cell into carposporangial initial comes about by their gradual enlargement (Fig. 52). Inner gonimoblast cells that are not transformed into carposporangial initials make up the sterile gonimoblast (Fig. 53). Further maturation of the cystocarp follows the same pattern as in young cystocarps; the only difference is a gradual incorporation of a greater number of inner gonimoblast cells into a vacuolate sterile gonimoblast and a large number of carposporangia (Figs. 54, 55) in the mature condition.

Carposporangial chains distal to the sterile gonimoblast can reach a length of up to six cells (Figs. 56, 57). The basal-most initials commonly are rectangular, reaching a width of up to 9 µm before expansion (Fig. 57). Carposporangia are usually obovate in side view and roundish in top view, and may be up to 45 µm long and 35 µm wide.

Mature cystocarps (Figs. 58–60) typically consist of a persisting fusion cell, even after the formation of carposporangia, sterile gonimoblast, tubular nutritive cells, and a pericarp with a central ostiole (Fig. 60). Tubular nutritive cells (Figs. 58–60) in the material examined were fusing abundantly with pericarp cells. The pericarp consists of 10–15 layers of squarish/roundish cells organized in anticlinal rows (Fig. 61).

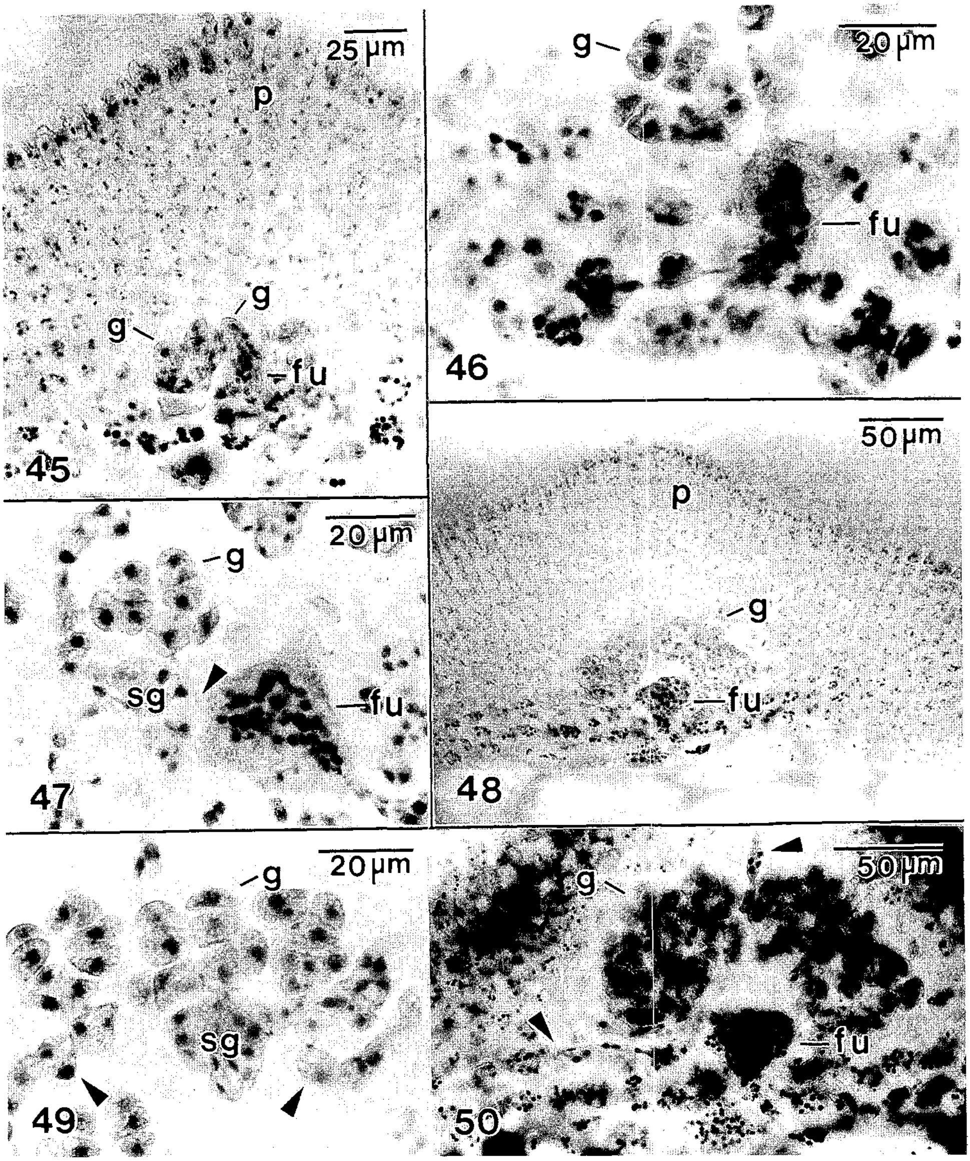


Figs. 41–44. Transverse sections through mature cystocarp showing tubular nutritive cells (arrowheads; aniline blue). Figs. 41, 42, *Gracilaria blodgettii* from Dry Tortugas, Florida (NY, Taylor #918). Fig. 43, Lectotype of *Gracilaria cylindrica* (C, Børgesen #1973). Fig. 44, Cystocarp from lectotype of *G. cylindrica* (C, Børgesen #1973) showing a globose fusion cell (fu).

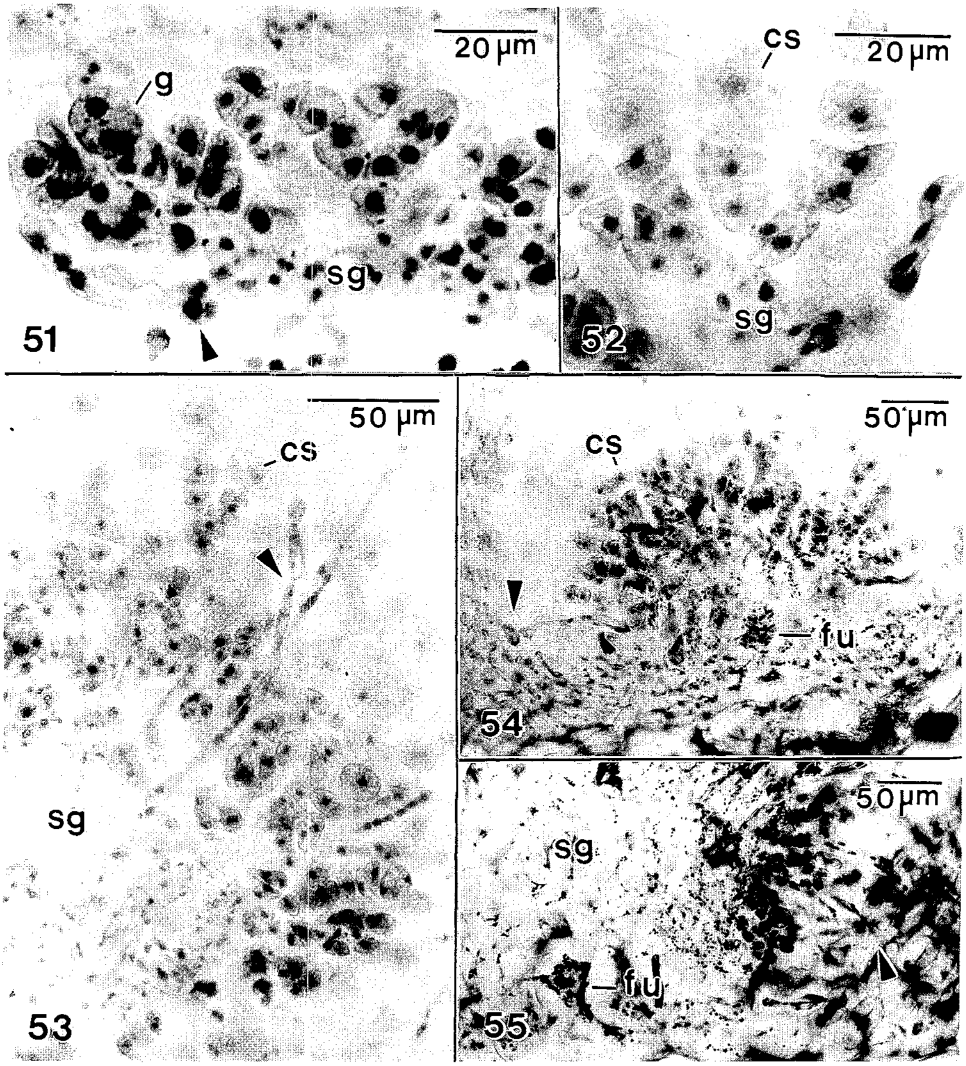
Cystocarps are generally abundant and scattered over the surfaces of second- and third-order branches of a female thallus. Hemispherical and urceolate to globose, cystocarps project considerably from the thallus, are up to 1.5 mm in diameter and 2.0 mm tall, and are not constricted at the base.

Discussion

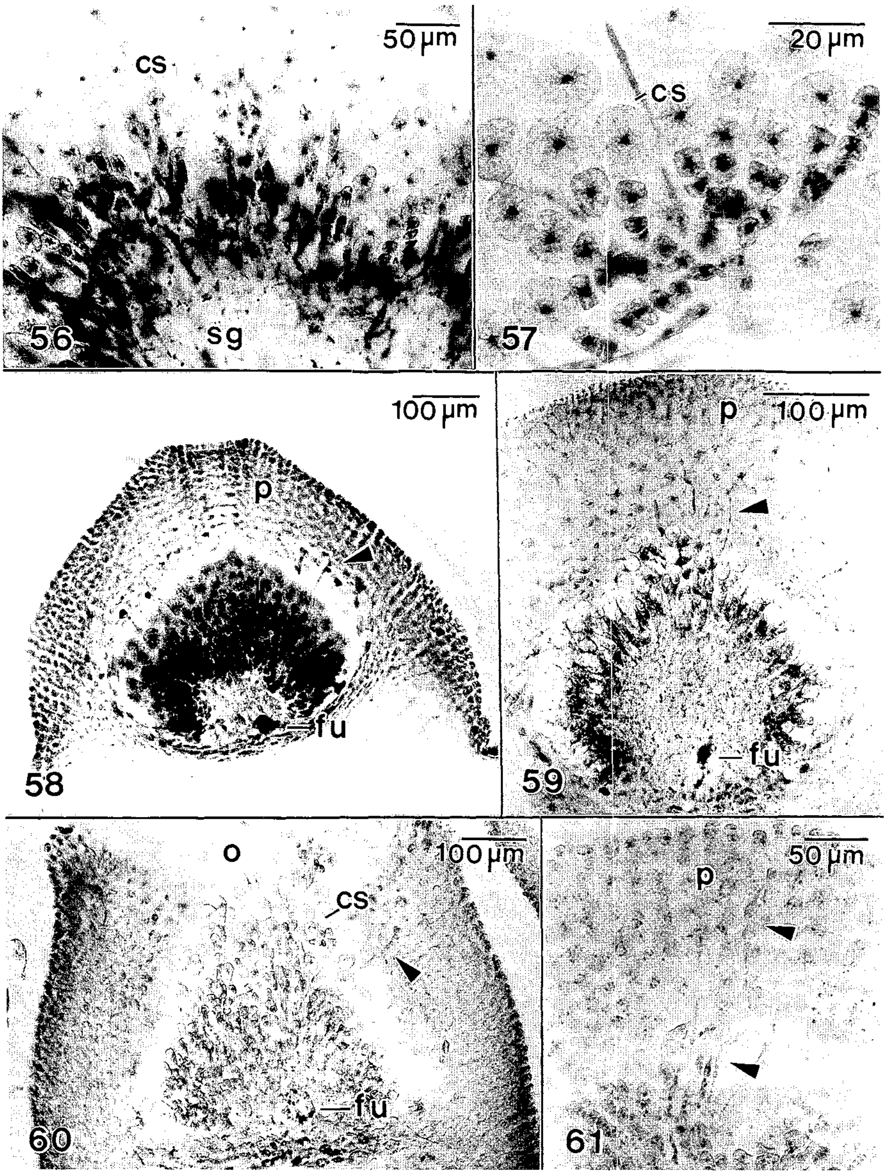
Of great interest are the new findings on the development of the male reproductive



Figs. 45–50. *Gracilaria blodgettii* from Puerto Rico (US 156536), showing stages of postfertilization development. fu = fusion cell, g = gonimoblasts, p = pericarp, sg = lower or sterile gonimoblast cell. Fig. 45, Young cystocarp with fusion cell, gonimoblasts (arrowheads), and pericarp. Fig. 46, Multinucleate fusion cell with small cluster of gonimoblast cells. Fig. 47, Uninucleate gonimoblast cells; lower gonimoblast cell with pit connection (arrowhead) to fusion cell has become multinucleate. Fig. 48, Young cystocarp before initiation of sterile gonimoblast. Fig. 49, Lower gonimoblast cells with young files of uninucleate gonimoblast cells distally, and multinucleate tubular nutritive cells proximally (arrowheads). Fig. 50, Cystocarp with tubular nutritive cells (arrowheads).



Figs. 51–55. ***Gracilaria blodgettii*** **from Puerto Rico (US 156536) showing stages of postfertilization development. cs = carposporangia, fu = fusion cell, p = pericarp, sg = lower or sterile gonimoblast cell. Fig. 51, Lower gonimoblast cell bearing cluster of uninucleate gonimoblast cells distally and tubular nutritive cells proximally (arrowheads). Fig. 52, Initiation of carposporangia. Fig. 53, Sterile gonimoblast, carposporangia, and elongate tubular nutritive cells (arrowheads). Figs. 54, 55, Cystocarp with fusion cell and tubular nutritive cell fusing (arrowhead) with pericarp cell.**



Figs. 56–61. *Gracilaria blodgettii* from Puerto Rico (US 156536) showing stages of postfertilization development. cs = carposporangia, fu = fusion cell, o = ostiole, p = pericarp, sg = sterile gonimoblast cell. Fig. 56, Sterile gonimoblast with rather straight clusters of carposporangia. Fig. 57, Chains of carposporangia. Fig. 58, Mature cystocarp with tubular nutritive cells (arrowheads; aniline blue). Fig. 59, Mature cystocarp with tubular nutritive cells (arrowheads). Fig. 60, Mature cystocarp with ostiole in pericarp. Fig. 61, Tubular nutritive cells (arrowheads) reaching the pericarp.

apparatus in *G. blodgettii.* Compared with other Caribbean species with *textorii*-type male configuration, such as *G. cervicornis* (Turner) J. Agardh (Oliveira et al. 1983), the sori of *G. blodgettii* Harvey (including *G. cylindrica* Bøgesen) that we examined are markedly uniformly shallow, a condition Reading and Schneider (1986) found in material they identified as this species from the outer continental shelf off North Carolina. This shallowness seemingly results because the marginal spermatangial parent cells within each sorus grow only slightly acropetally in relation to the central ones and do not cut off more derivative parent cells beyond the 20-cell stage. The compactness of terminal cortical cells also seems to be a limiting factor determining sorus width; the wide spacing between individual outer cortical cells in *G. blodgettii* could thus also allow the establishment of relatively wide sori. The number of spermatangial parent cells within a sorus may be fixed for each species, and potentially may be a character of taxonomic importance.

Because a subcortical cell commonly subtends only a single terminal cortical cell in *G. blodgettii*, the shallow sori in this species frequently appear to be continuous over entire patches on the male branches. This shallow *textorii*-type configuration may be mistaken for the superficial *chorda*-type configuration inherent to species belonging to *Gracilariopsis* Dawson (e.g., Dawson 1949, Fredericq and Hommersand 1989b). In *Gracilariopsis*, however, both spermatangial parent cells result from division of an outer cortical cell and are restricted to a pair or group of three by concavo-convex longitudinal divisions. Further, each spermatangial parent cell cuts off only a single spermatangium by a transverse division (Fredericq and Hommersand 1989b).

The *textorii*-type sorus of *G. blodgettii* clearly differs in size from *verrucosa*-type configuration of *G. verrucosa* (Hudson) Papenfuss, the type species of *Gracilaria* Greville (e.g., Yamamoto 1978, Fredericq and Hommersand 1989a). In *G. verrucosa*, the spermatangial parent cells are generated in extensive filaments from intercalary cortical cells that line an intercellular space forming a much deeper "conceptacle" (Fredericq and Hommersand 1989a). Because the spermatangial parent-cell primordia in *G. blodgettii* are ordinary terminal rather than intercalary cortical cells as in *G. verrucosa*, and because both taxa generate spermatangia by a concavo-convex septum, it seems that both types of cortical cell may function as spermatangial parent cell primordia and are thus found within the genus *Gracilaria*.

Conclusion

Whether there are two species has been in question almost since Bøgesen (1920) described *G. cylindrica*. For example, Taylor (1960) remarked that some shallow-water specimens were perhaps intermediate between *G. cylindrica* and *G. blodgettii* in the western Atlantic, "but usually the two species are easily distinguished," and Bird et al. (1987) , using data from analytical pyrolysis of herbarium material, suggested "a concrete difference between these two entities." However, in our studies of recent collections, whose identity was based on comparative studies of type specimens and topotypic material, we found no inherent differences to support treating *G. blodgettii* Harvey and *G. cylindrica* Bøgesen as two distinct taxa.

Therefore, in the western Atlantic, both coarse and slender terete specimens that possess basally constricted third- and higher-order branches and branchlets, spindle-shaped and obtuse branchlets on a single thallus, a medulla of a few large cells, a cortex of one to two cell layers, very shallow *textorii*-type male sori, and cystocarps with

numerous tubular nutritive cells linking gonimoblast with pericarp should be referred to as a single species as follows: *Gracilaria blodgettii* Harvey (Harvey 1853, p. 111) LT: TCD
=*Gracilaria cylindrica* Børgesen (Børgesen 1920, p. 375, figs. 364–365) LT: C.

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Section IV. *Eucheuma*

INTRODUCTION

Isabella A. Abbott

The two previous workshops (Abbott and Norris 1985, Abbott 1988) produced major papers on the systematics of *Eucheuma*, principally by Maxwell S. Doty, who dealt with the species used in commerce. Nonetheless, taxonomic problems remain in the genus, including those species that are not used for commercial purposes. No students of this group attended the third workshop, however.

Dr. Yoshida, in tidying up the nomenclatural problems that occur in the Japanese flora, has contributed the following paper on a Japanese species of *Eucheuma*.

TYPIFICATION OF *EUCHEUMA AMAKUSAENSE* OKAMURA

Tadao Yoshida

Eucheuma amakusaense Okamura [=*amakusaensis*] has a nomenclaturally complicated history. Okamura (1902) first published this name in his *Nippon Sorui Meii* (Enumeration of Japanese Algae), with a brief description of features in the form of a key that can be translated as follows: Frond terete or compressed, branched pinnately from the margins, or from the surface, often becoming verticillate; frond decumbent at first and later erect; projections from the surface trigonal in shape (p. 35).

In 1916, the second edition of *Nippon Sorui Meii* was published, and Okamura added other diagnostic characters, describing the frond as "radiating from a point, decumbent, 14–21 cm long, 4.5 mm wide, branched pinnately, cartilaginous and fleshy color. Locality: Ushibuka, Amakusa Island (Kumamoto Prefecture, Kyushu)." The next treatment of the species was his *Nippon Kaisoshi* (1936, p. 594), in which he gave a more detailed description and added as a locality Koshiki Island, Kagoshima Prefecture. Later Segawa gave an illustration in his *Colored Illustration of the Seaweeds of Japan* (1956, pl. 51, No. 400). Shinmura (1975) reported that the distribution was restricted to the west coast of Kyushu and described the mode of spore germination of this species. Ohmi and Shinmura (1976) noted its field culture.

Unfortunately, this name was treated only in Japanese, and no mention had been made in a western language until Doty (1988) referred to it in his "Prodromus" included in the results of the second workshop. According to Article 36.2 of the International Code of Botanical Nomenclature (ICBN), we must treat the name as validly published in 1902, although it was not accompanied by either a Latin description or an illustration.

Several specimens in the Okamura herbarium are now deposited in the herbarium of the Faculty of Science, Hokkaido University (SAP). Only one collection of several plants from Ushibuka, Amakusa Island, Kumamoto Prefecture, seems to have been examined by Okamura when the name was published. One of them (Fig. 1) must be chosen as the lectotype. Because the original materials are present, there is no need for neotypification.

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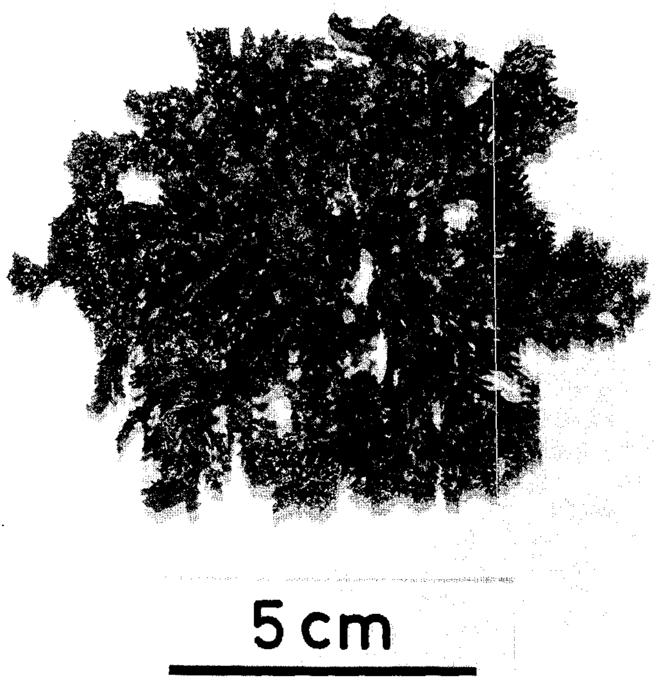

Fig. 1. Lectotype of *Eucheuma amakusaense* Okamura. Ushibuka, Amakusa Island, Kumamoto Prefecture, no date (SAP, herb. Okamura).

Section V. Taxonomic Index