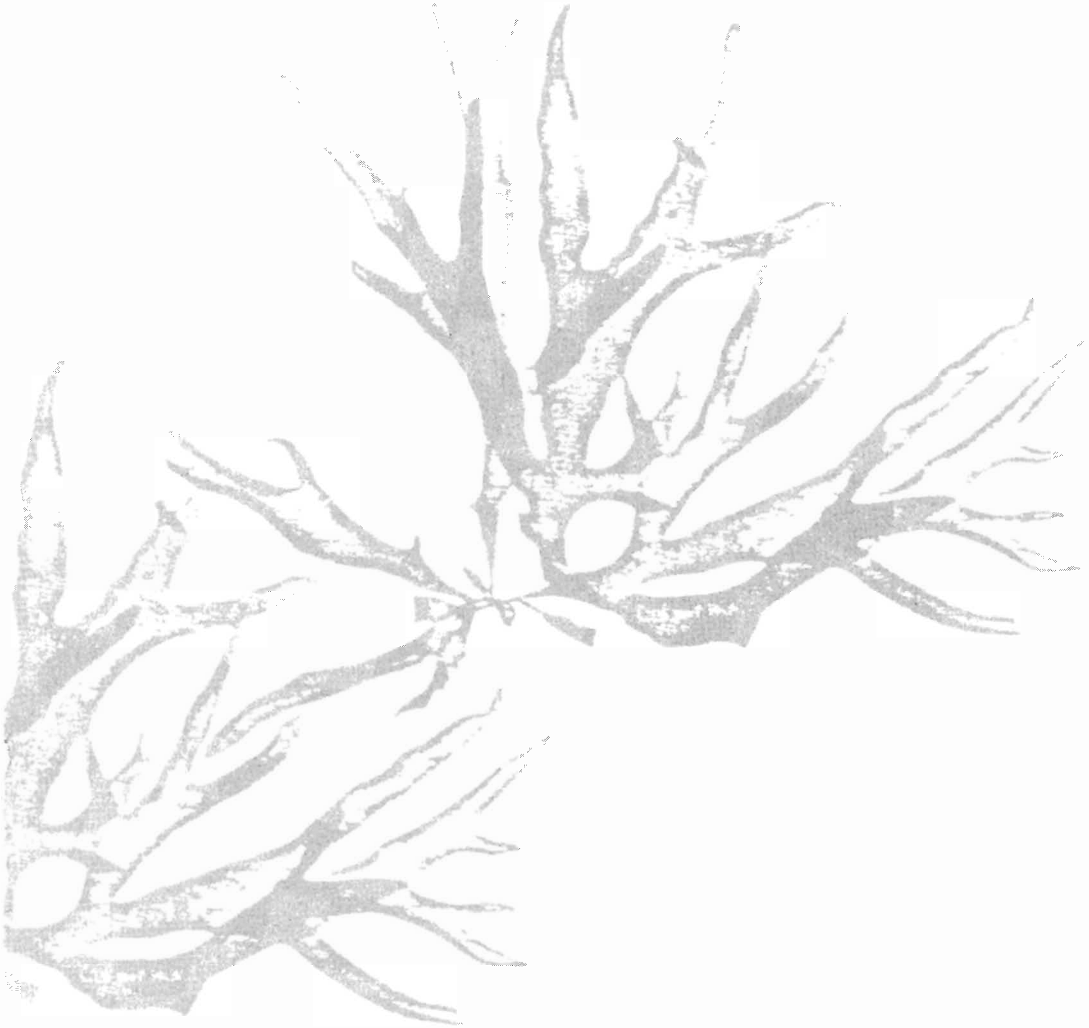
TAXONOMY OF ECONOMIC SEAWEEDS

With reference to some Pacific and Caribbean species

Isabella A. Abbott and
James N. Norris, Editors



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Preface

James J. Sullivan
Program Manager, California Sea Grant College Program

Eight years ago the best known commercial seaweed in California, and perhaps in the United States, was the giant kelp, *Macrocystis pyrifera*. I like to think that the National Sea Grant College Program, and especially the California program, has made many more species of economically important seaweeds well known.

However, the Sea Grant programs of the different coastal states have tended to specialize in species that abound in their territorial waters; few opportunities have arisen in which specialists could work together on common regional, let alone international, problems. When Roy Tsuda of the University of Guam suggested to me that the taxonomy of economically important tropical and subtropical algae was the single greatest obstacle in the progress of seaweed aquaculture and marine natural products chemistry in the Pacific, I asked Isabella Abbott of the University of Hawaii if she would convene a workshop on that subject. She and Roy strongly recommended that an international group of experts on a number of current commercial species meet in Guam.

Taxonomy is the hidden, but important, foundation of the superstructure of aquaculture and mariculture, whether of mollusks, crustaceans, fish, or seaweeds—all groups of organisms on which California Sea Grant has supported research. The taxonomy of those animal species that are important to aquaculture is, with few exceptions, well known. But the species of seaweeds that are of commercial interest are not as well known, and the names attached to many of them are frequently so uncertain that the algae cannot be sold readily. For example, when sole is offered for sale, everyone expects to get a flat, bottom-dwelling fish; but when *Gracilaria*, a seaweed with much potential as an agar source, is offered for sale, the buyer doesn't know the species name or the quality of the colloid he is buying. This can be important. For example, of two Hawaiian species of *Gracilaria*, one provides three to four times better gel strength in the agar than does the other species.

When I arrived in Guam to observe the workshop, I was amazed to find the participants working night and day in efforts to resolve specific problems in taxonomy. They were enthusiastic and voluble in their thanks for the opportunity to share their systematics problems and knowledge with others equally interested. They demonstrated that a workshop divided into four or five working groups of specialists had many pluses in its favor over a symposium or seminar format. In this particular meeting, it was heartwarming to see the concentration and intellectual exchanges among those whose first languages were English, Mandarin, Japanese, Spanish, and Belgian—and the results in this volume show the great headway they made. This kind of basic research can be easily shared with large numbers of persons who have had neither the training nor years of dedication that it takes to become a specialist. I feel certain that this volume will be one of the most heavily used of all of our publications.

As program manager of the California Sea Grant College Program, I join the directors of Sea Grant programs in Hawaii, Alaska, Washington, and Oregon in thanking the participants for their efforts, and especially Roy Tsuda for his hospitality and his attention to the needs of the invitees. We thank Isabella Abbott for the success of the workshop and, together with James Norris, for the production of the results of the workshop in this volume.

Introduction

Isabella A. Abbott, Workshop Convenor

The value of any seaweed crop is enhanced by the name under which the seaweed is sold, for the kind and quality of the seaweed product is announced with its name. Thus, though chemists may say that the agar from *Gelidium* species is the same as that from *Gracilaria* species, industry will pay more for *Gelidium* than for *Gracilaria.* (It might be so because the agarose fraction is higher in *Gelidium*, and agarose commands a higher price on its own.) In the case of the seaweeds that produce the colloid carrageenan, some species form only kappa-carrageenan (which produces a firm gel), others produce only iota-carrageenan (which forms a soft gel), and still others form only lambda-carrageenan (which does not gel).

In geographic areas or developing countries where the identity of seaweeds is not known or is uncertain, the economic potential for using this untapped seaweed resource is unrealized. For Japan and China, on the contrary, which have and use many named seaweed species, the financial gain in the world market can be more easily accomplished, since demand for certain colloids currently exceeds supply. One of Chile's major exports is seaweed, sold for extraction of colloids in other countries.

The suggestion for this workshop to deal with the taxonomy of economically important algae was made by Dr. Roy Tsuda of the University of Guam. It was hoped that a funding agency would recognize the importance of such a meeting to the seaweed industry. When Dr. Sullivan proposed the possibility of sponsoring the workshop, the response was immediate, emphatic, and galvanizing. This enthusiasm carried through to the actual workshop itself and persisted through nearly a week of meetings.

We chose to focus on the four economically important seaweeds that have warm-water representatives because the useful temperate algae are fairly well known and do not have taxonomic or nomenclatural problems that approach those in the tropics. The groups we chose are *Gelidium, Pterocladia, Gelidiella, Yatabella, Acanthopeltis* (treated as one group, the Gelidiales), *Gracilaria, Polycavernosa, Eucheuma*, and *Sargassum.*

The reasons for holding the workshop as soon as possible were that new information is presently forthcoming in nearly all of these taxa, both in terms of academic, formal descriptions and in terms of descriptions used in production management. The widespread use of the name *Gracilaria* "*verrucosa*," for example, for either academic or commercial publications, would no longer be acceptable to most scientists who have worked with the genus. To have postponed the workshop for a few years would have put it beyond the time of "substantial new contributions" and would also have allowed for incorrect names to be perpetuated.

Finally, the ages of the specialists had to be considered (it takes a long time to train a good systematist). Many who were trained in this field have adopted other interests and no longer contribute to systematics. The participants were chosen first for their expertise, then for their current involvement in research, and lastly to represent a spread of ages. That more than half of them were not from the United States attests to the emphasis given to taxonomy abroad. Participants were selected on the basis of their international reputations as experts in the genera they were asked to focus upon. Each participant brought specimens: some to show, some to give away. Some brought microscope slides and others brought literature as well.

A certain amount of leeway was allowed the contributors in ways of constructing keys and of expressing descriptions since each is a specialist in his or her own right. However, descriptive sequences and a uniform order of subject material were judged to be matters of editorial prerogative. These contributions were peer-reviewed very critically, for no one is more critical than another specialist in a particular genus. No specialist wants his specialty disturbed or confused!

In accord with the very recent decision of our "flowering plant" colleagues (e.g., the journal *Taxon*) in systematics, we have instituted the practice of using the names of our Chinese colleagues in Chinese fashion (in which the surname is first, followed without punctuation by the given name). Exceptions are made for C. K. Tseng and Young Meng Chiang, who asked that their names be listed as shown because they are not known otherwise in the West.

Specimens studied in this workshop are deposited in the following herbaria: Algal Herbarium, Academia Sinica, Institute of Oceanology, Qingdao, Shandong, China (AST); Department of Botany, Bernice P. Bishop Museum, Honolulu, Hawaii (BISH); Herbarium of Faculty of Science, Hokkaido University, Sapporo, Japan (SAP); Herbario, Sala de Sistematica, Departamento de Biología Ambiental y de Poblaciones, Instituto de Ciencias Biologicas, Pontificia Universidad Católica de Chile, Santiago, Chile (SSUC); Herbarium, Department of Botany, National Taiwan University, Taipei, Taiwan (TAI); Gilbert M. Smith Herbarium of Hopkins Marine Station of Stanford University (GMS); Algal Collection of the U.S. National Herbarium, Smithsonian Institution, Washington, D.C. (US); and the personal herbaria of H. Yamamoto, Japan (HYX) and Joan G. Stewart, San Diego, California (JSX). Herbarium abbreviations are from *Index Herbariorum* (Holmgren, P. K., Keuken, W., and Schofield, E. K. 1981. 7th Ed. vii + 452 pp. Utrecht: Bohn, Scheltema & Holkkema), except personal herbaria, which are cited with the person's initials and, in accordance with botanical convention, are followed by an "X."

We are grateful to Robert H. Sims, Alice R. Tangerini, and Katina E. Bucher for their assistance in preparing the photographs, and additionally for help with the countless details necessary for publication. We also acknowledge help from Jane E. Lewis and the departmental secretaries at the University of Hawaii, Manoa.

We acknowledge with deep gratitude the support, planning, and foresight of Dr. James Sullivan, Program Manager, California Sea Grant College Program. We also thank the directors of the Hawaii, Alaska, Washington, and Oregon Sea Grant programs for their contributions to this important workshop and the National Sea Grant College Program for the transportation costs of some of the

foreign participants. We further thank the director, Dr. Stephen Nelson, and the staff of the Marine Laboratory, University of Guam, for the interest, help, and hospitality extended to us during the workshop.

Finally, as workshop convenor, I want to express my appreciation to my colleagues for the wonderful fellowship, hard work, and sense of achievement that came out of the conference. It is my strongest hope that future working meetings of this kind may be held from time to time. There are many geographical areas that have species of *Gracilaria* that we have not seen; the species of *Iridaea* (an important commercial source of carrageenan) in North and South America are a taxonomic headache; and we have barely touched the species of *Gelidium* and their variations in the western Pacific. The remaining subgenera and sections of tropical *Sargassum* species are a kind of taxonomic nightmare.

We have found a successful tool to the solution of vexing systematic problems: small working groups of specialists and dedicated taxonomists. I believe that this volume attests to their success.

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Abstract of Contents

Keys are provided to all Pacific species of the widely distributed *Sargassum* subgenus *Bactrophycus* (Phaeophyta), to the common Pacific species within the Gelidiales (Rhodophyta), to the species of *Polycavernosa* (Rhodophyta), and to the economically important species of the red algae *Eucheuma* and *Gracilaria*. Descriptions, geographic distribution, keys, and references to the most important or abundant economic species in these genera from the floras of Chile, Gulf of California, Caribbean, California, Hawaii, Guam, Taiwan, Japan, and China are also given. A list of *Gracilaria* species from the Philippines is included. An explanation of taxonomic features for worldwide species of *Eucheuma* is given along with a key to the species. Four sections, including two new, are recognized for the commercial species. Tables containing important taxonomic features are provided for some of the genera.

New species are described in *Gracilaria, G. pacifica* from California and *G. parvispora* from Hawaii; also described are a new species of *Gelidium, G. rex*, from Chile, and a new species of *Eucheuma, E. alvarezii*, from the Philippines. New keys to the Japanese species of *Gracilaria* and a translation from the Chinese of a key to the species of *Gracilaria* are provided. A new section, *Phyllocystae*, is described for *Sargassum* subgenus *Bactrophycus*. Studies on the developmental sequences of reproductive structures in four taxa of *Gracilaria* from the Caribbean indicate two different groups which are suggested to form the basis for two distinct genera, resulting in the transfer of two species to *Polycavernosa*.

SECTION I. *Sargassum* subgenus *Bactrophycus*

EAST ASIATIC SPECIES OF *SARGASSUM* SUBGENUS *BACTROPHYCUS* J. AGARDH (SARGASSACEAE, FUCALES), WITH KEYS TO THE SECTIONS AND SPECIES

C. K. Tseng, Tadao Yoshida, and Young Meng Chiang

Sargassum C. Agardh (Sargassaceae, Fucales), a very large seaweed genus with nearly 400 species, is widely distributed in warm and temperate waters, especially in the Indo-west Pacific region and Australia. In 1889, J. Agardh instituted a system of classification based on his idea of the evolution within the genus from a leaf-like or much flattened branch to one which is cylindrical, having true horizontal "leaves." He divided *Sargassum* into five subgenera, a system recognized by Grunow (1915, 1916) and Setchell (1933, 1936). Agardh's system may overemphasize certain vegetative features, and the grouping and placing of some of the species has been questioned in the past (e.g., Womersley, 1954) and continues to be debated. For instance, *S. piluliferum* (Turner) C. Agardh from Japan is placed in the Australian *S.* subgen. *Phyllotrichia* J. Agardh, which does not seem to us to be entirely logical. Separation of the first two subgenera *Phyllotrichia* and *Schizophycus* J. Agardh may also be questioned; Womersley (1954, p. 339) placed the species of *S.* subgen. *Schizophycus* under *S.* subgen. *Phyllotrichia.* The placing of several species in certain other subgenera also does not seem to be appropriate.

Of the five subgenera, *S.* subgen. *Bactrophycus* J. Agardh is known only in the eastern Asiatic region where it is an ecologically important group. In this region, its taxa can be clearly recognized as recently shown by Yoshida (1983). In his monograph on Fucaceae, Yendo (1907) created the *S.* sect. *Micracanthae* [typified by *S. micracanthum* (Kützing) Endlicher], which is characterized by flat receptacles with dentate margins. Later Yendo (in Okamura, 1916) raised this section to a subgenus, a rank subsequently followed by Okamura (1936). Yoshida (1983) placed *S. micracanthum* in *S.* sect. *Halochloa* (Kützing) Yoshida of *S.* subgenus *Bactrophycus,* thus reducing *S.* sect. *Micracanthae* to this subgenus. He also subdivided the *S.* subgenus *Bactrophycus* into four sections: *S.* sect. *Spongocarpus* (Kützing) Yoshida, *S.* sect. *Teretia* Yoshida, *S.* sect. *Halochloa,* and *S.* sect. *Repentia* Yoshida.

Setchell (1933) placed *S. mcclurei* Setchell and *S. herklotsii* Setchell together in the group "Sargasso Asiatica" and included them in *S.* subgenus *Arthrophycus* J. Agardh, a predominantly Australian group. Tseng (this volume) raises Setchell's group "Sargasso Asiatica," including *S. phyllocystum* Tseng et Lu and *S. emarginatum* Tseng et Lu, with the above-mentioned species to a section, *S.* sect. *Phyllocystae*, on the basis of the presence of phyllocysts that replace normal vesicles. He placed the new section in *S.* subgen. *Bactrophycus* instead of *Arthrophycus*. We agree with Yoshida's and Tseng's treatments.

At present, we recognize five sections in *S.* subgen. *Bactrophycus* with 35 species distributed in China (including Taiwan), Japan, Korea, and Pacific USSR. The only exception is *S. muticum*, now widely distributed in the North Pacific and North Atlantic, and believed to be accidentally introduced from Japan. The more numerous species of *S.* subgen. *Sargassum*[1] characteristic of the tropics and subtropics, are omitted owing to their extremely involved taxonomic and nomenclatural problems as well as difficulty in locating type materials. The remaining three subgenera with some exceptions are restricted to the southern oceans. Because of the limited time available for this workshop, we confined ourselves to *S.* subgen. *Bactrophycus*, leaving the other subgenera to a possible later date.

Finally, J. Agardh's system of subgeneric and sectional classification must be reinvestigated, and other studies, for example on embryological and conceptacle development, must be conducted to help in clarifying taxonomic problems.

Japanese species of *S.* subgen. *Bactrophycus* were recently described by Yoshida (1983), who discussed in detail 28 species. In all but one case, we have followed his taxonomy; herein we restore the species status of *Sargassum coreanum* J. Agardh. Therefore, there are to date 29 taxa of *S.* subgen. *Bactrophycus* in Japan, of which 22 species and 1 variety are endemic.

Half a century ago, Chinese species of *S.* subgen. *Bactrophycus* from Hong Kong were reported in some detail by Setchell (1933) who described and illustrated eight species. Additionally, Setchell described two new species of *S.* subgen. *Arthrophycus* which were transferred to *S.* subgen. *Bactrophycus* by Tseng (this volume). Among these species the systematic position of *Sargassum fusiforme* (Harvey) Setchell is still debatable. Further, specimens reported as *S. miyabei* Yendo and *S. nipponicum* Yendo are based on questionable records of fragmentary materials. They apparently are not either of these species, and are therefore deleted from the Hong Kong marine flora. Thus, only seven species of *S.* subgen. *Bactrophycus* can be accepted for Hong Kong, five of which were later reported from mainland China. Four more species were later added to the marine flora of mainland China (Tseng and Chang 1954, 1954a; Tseng and Lu 1978, 1979). A new species of *S.* subgen. *Bactrophycus* (listed as *Sargassum* species #1 in this volume) will be published soon by Tseng and Lu. Three species of *S.* subgen. *Bactrophycus* were recorded from Taiwan, one of which, *S. rostratum* J. Agardh, has not yet been found on the mainland. There are a few other records of *S.* subgen. *Bactrophycus* reported from China, but they have to be verified before their presence can be accepted. There are, therefore, 13 species and 1 variety of *S.* subgen. *Bactrophycus* from the Chinese waters, 7 of which occur also in Japan. To date there are altogether 35 species (1 with 2 varieties) of *S.* subgen. *Bactrophycus* in East Asiatic waters. There are a few reports on *S.* subgen. *Bactrophycus* from Korea and the Asiatic coast of USSR, but because of lack of available material for our present study, we reluctantly have not included discussion on these records.

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[1] Following Art. 22.1 (Voss et al., 1983) *Sargassum* subgen. *Eusargassum* J. Agardh (1889, p. 78) is treated as a synonym of the autonym *Sargassum* subgenus *Sargassum* since it included the type of the generic name, *S. bacciferum* (Turner) C. Agardh.

Key to the Sections of *S.* subgenus *Bactrophycus*

The five sections now recognized in *S.* subgenus *Bactrophycus* can be easily distinguished from each other by the following key:

1. Main axis upright throughout life 2
1. Main axis decumbent or procumbent .... IV. *S.* section *Repentia* Yoshida

2. Stem elongated .... I. *S.* section *Spongocarpus* (Kützing) Yoshida
2. Stem more or less abbreviated 3

3. Receptacles terete .... II. *S.* section *Teretia* Yoshida
3. Receptacles, especially female receptacles, complanated, flat or triquetrous (3-sided) 4

4. Receptacles generally simple, smooth; phyllocysts absent .... III. *S.* section *Halochloa* (Kützing) Yoshida
4. Receptacles, especially female receptacles, generally compound; dentate; phyllocysts present .... V. *S.* section *Phyllocystae* Tseng

Key to the Eastern Asiatic Species of the *S.* subgen. *Bactrophycus*

[Species in the key are numbered in parentheses to match the species list that follows. Eds.]

1. Plants dioecious, phyllocysts present; receptacles compound, female receptacles dentate, flat or triquetrous 33
1. Plants monoecious or dioecious, phyllocysts absent; receptacles simple, rarely compound, generally smooth 2

2. Main axis (= "stem") elongated 3
2. Main axis (= "stem") abbreviated 4

3. Vesicles cylindrical; dioecious .... (1) *S. horneri* (Turner) C. Agardh
3. Vesicles spherical to elliptical; monoecious .... (2) *S. filicinum* Harvey

4. Main axis prostrate, rhizome-like, branched and entangled, forming attaching discs on ventral surface 5
4. Main axis erect above holdfast 8

5. Lower branchlets (= "leaves") linear or ovate, with entire margin 6
5. Lower leaf lanceolate, with serrate or dentate margin 7

6. Leaves linear, elliptical to lanceolate; receptacles flat, clavate, often forked .... (28) *S. okamurae* Yoshida et Konno
6. Leaves ovate, short stipitate; receptacles compressed, spatulate, often with dentate margins .... (29) *S. nigrifolium* Yendo

7. Lower leaf retroflexed, branches triquetrous with sharp edges .... (31) *S. yamadae* Yoshida et Konno
7. Lower leaf not retroflexed, branches triangular with rounded edges .... (30) *S. yezoense* (Yamada) Yoshida et Konno

8. Receptacles terete 9
8. Receptacles flat, compressed or triquetrous 19

9. Main axis unbranched, growing annually, eventually becoming very elongated, to 10 cm or more with two rows of prominent scars of fallen branches 10
9. Main axis branched or unbranched, abbreviated, usually less than 3–4 cm; branches spirally arranged 12

10. Leaves all filiform .... (3) *S. microceratium* (Turner) J. Agardh[2]
10. Leaves, at least the lower ones, broad, elliptical to lanceolate 11

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[2] Tseng is of the opinion that *S. microceratium*, *S. confusum*, and *S. pallidum* represent ecological variants of a single species. Decision on this matter must wait until more evidence is available.

11. Main axis and branches usually spinose; leaf coriaceous .... (4) *S. confusum* C. Agardh[3]
11. Main axis and branches smooth, leaf papyraceous .... (5) *S. pallidum* (Turner) C. Agardh[4]

12. Holdfast discoid 13
12. Holdfast platter-shaped or with rhizoidal outgrowth 14

13. Vesicles spherical .... (6) *S. muticum* (Yendo) Fensholt
13. Vesicles fusiform .... (7) *S. thunbergii* (Mertens ex Roth) Kuntze

14. Holdfast platter-shaped .... (8) *S. fulvellum* (Turner) C. Agardh
14. Holdfast with rhizoidal outgrowths 15

15. Creeping rhizoidal outgrowths thick, 2 mm diam., fused to form a flat disc .... (9) *S. ammophilum* Yoshida et Konno
15. Creeping rhizoidal outgrowths thin, less than 1 mm diam., free 16

16. Lower leaf hemiphyllous, without midrib 17
16. Lower leaf not hemiphyllous, with midrib 18

17. Leaves small, lower one 1.5 cm long, 0.5 cm broad; receptacles simple .... (10a) *S. hemiphyllum* (Turner) C. Agardh var. *hemiphyllum*
17. Leaves large, lower one 3.5 cm long, 2.5 cm broad; receptacles often compound .... (10b) *S. hemiphyllum* var. *chinense* J. Agardh

18. Creeping rhizoidal filaments long, well developed .... (11) *S. nipponicum* Yendo
18. Creeping filaments short, less than 1 cm .... (12) *S. miyabei* Yendo

19. Main axis simple, abbreviated, usually less than 1 cm 20
19. Main axis branched once to several times, usually attaining more than 10 cm 22

20. Leaves coriaceous, ovate to lanceolate with entire margin .... (13) *S. segii* Yoshida
20. Leaves papyraceous, linear to lanceolate with more or less dentate or incised margin 21

21. Plants dioecious; receptacles linear to oblanceolate with smooth margin .... (14) *S. yamamotoi* Yoshida
21. Plants monecious; receptacles spatulate with dentate margins .... (15) *S. tenuifolium* Yamada

22. Leaves linear to lanceolate, with entire margins 23
22. Leaves in the middle part of branches having more or less serrate margins 24

23. Receptacles foliose .... (16) *S. ringgoldianum* Harvey
23. Receptacles linear to lanceolate .... (17) *S. coreanum* J. Agardh[5]

24. Receptacles (at least the female ones) often triquetrous 25
24. Receptacles spatulate to oblanceolate 26

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[3] See note 2.

[4] See note 2.

[5] Yoshida (1983) treated this taxon at subspecific rank as *S. ringgoldianum* ssp. *coreanum* (J. Agardh) Yoshida because of its geographic isolation from *S. ringgoldianum* and the difficulty in discriminating the species when young and immature. In this paper, Tseng believes the two taxa differ sufficiently in morphology to be recognized as separate species. (Editors).

25. Receptacles dentate .... (18) *S. trichophyllum* (Kützing) Kuntze
25. Receptacles not dentate .... (19) *S. sagamianum* Yendo

26. Receptacles arranged in short, irregularly branched cluster 27
26. Receptacles arranged in more or less elongated unbranched cluster 29

27. Receptacles linear with smooth margins; leaves large, up to 20 cm long .... (22) *S. giganteifolium* Yamada
27. Receptacles spatulate, with margins or apices dentate, notched, or crenulate; leaves less than 6 cm long 28

28. Leaves pinnately dissected; bright brown .... (20) *S. micracanthum* (Kützing) Endlicher
28. Leaves crenulate or serrate; dark brown .... (21) *S.* species #1[6]

29. Main branches with obtuse protuberances .... (23) *S. macrocarpum* C. Agardh
29. Main branches usually with smooth margins, sometimes with acute protuberances 30

30. Leaves narrow, linear to lanceolate, with serrate margins .... (24) *S. autumnale* Yoshida
30. Lower leaves ovate to lanceolate, with entire margins; upper leaves sometimes serrate 31

31. Receptacles dentate .... (25) *S. rostratum* J. Agardh
31. Receptacles not dentate 32

32. Holdfast conical; leaves coriaceous; upper leaves deeply serrate to midrib .... (26) *S. siliquastrum* (Mertens ex Turner) C. Agardh
32. Holdfast discoid; leaves membranaceous; upper leaves not deeply serrate to midrib .... (27) *S. serratifolium* (C. Agardh) C. Agardh

33. Leaves folded lengthwise .... (34) *S. emarginatum* Tseng et Lu
33. Leaves not folded lengthwise 34

34. Both male and female receptacles with teeth .... (35) *S. phyllocystum* Tseng et Lu
34. Male receptacles smooth 35

35. Female receptacles flat .... (33) *S. herklotsii* Setchell
35. Female receptacles triquetrous .... (32) *S. mcclurei* Setchell

List of the Species of *Sargassum* subgenus *Bactrophycus*

In the following list the 35 accepted species of *S.* subgen. *Bactrophycus* for the East Asiatic region are grouped according to their taxonomic sections. Their occurrence in Japanese and Chinese waters is noted and important references are provided. They are numbered to correspond to the numbers appearing before the species name in the above Key to Species, and figure numbers are given in parentheses.

I. *Sargassum* sect. *Spongocarpus* (Kützing) Yoshida

1. *Sargassum horneri* (Turner) C. Agardh (Fig. 1)
   Japan (Yoshida 1983, p. 116); China, including Taiwan (Tseng et al. 1962, p. 79; Chou and Chiang 1981, p. 143); Hong Kong (Setchell 1933, p. 38).
2. *S. filicinum* Harvey (Fig. 2)
   Japan (Yoshida 1983, p. 122).

II. *S.* sect. *Teretia* Yoshida

3. *S. microceratium* (Turner) J. Agardh (Fig. 3)
   Japan (Yoshida 1983, p. 125).

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[6] To be described by Tseng and Lu in *Oceanologia et Limnologia Sinica*.

4. *S. confusum* C. Agardh (Fig. 4)
   Japan (Yoshida 1983, p. 128); China (Tseng and Chang 1954a, p. 248 under *S. pallidum*).
5. *S. pallidum* (Turner) C. Agardh (Fig. 5)
   Japan (Yoshida 1983, p. 134).
6. *S. muticum* (Yendo) Fensholt (Fig. 6)
   Japan (Yoshida 1983, p. 138); China (Tseng and Chang 1954a, p. 362, under *S. kjellmanianum*).
7. *S. thunbergii* (Mertens ex Roth) Kuntze (Fig. 7)
   Japan (Yoshida 1983, p. 142); China (Tseng et al. 1962, p. 82); Hong Kong (Setchell 1933, p. 43).
8. *S. fulvellum* (Turner) C. Agardh (Fig. 8)
   Japan (Yoshida 1983, p. 148); Hong Kong (Setchell 1933, p. 40 under *S. enerve*).
9. *S. ammophilum* Yoshida et Konno (Fig. 9)
   Japan (Yoshida 1983, p. 152).

10a. *S. hemiphyllum* (Turner) C. Agardh var. *hemiphyllum* (Fig. 10)
Japan (Yoshida 1983, p. 154).

10b. *S. hemiphyllum* var. *chinense* J. Agardh (Figs. 11-12)
China, including Taiwan (Tseng et al. 1962, p. 81; Chou and Chiang 1981, p. 134); Hong Kong (Setchell 1933, p. 41).

11. *S. nipponicum* Yendo (Fig. 13)
    Japan (Yoshida 1983, p. 159).
12. *S. miyabei* Yendo (Fig. 14)
    Japan (Yoshida 1983, p. 162).

III. *S.* sect. *Halochloa* (Kützing) Yoshida

13. *S. segii* Yoshida (Fig. 15)
    Japan (Yoshida 1983, p. 166).
14. *S. yamamotoi* Yoshida (Fig. 16)
    Japan (Yoshida 1983, p. 171).
15. *S. tenuifolim* Yamada (Fig. 17)
    Japan (Yoshida 1983, p. 176).
16. *S. ringgoldianum* Harvey (Figs. 18-19)
    Japan (Yoshida 1983, p. 178).
17. *S. coreanum* J. Agardh [= *S. ringgoldianum* ssp. *coreanum* (J. Agardh) Yoshida] (Fig. 20)
    Japan (Yoshida 1983, p. 184).
18. *S. trichophyllum* (Kützing) Kuntze (Figs. 21-22)
    Japan (Yoshida 1983, p. 184).
19. *S. sagamianum* Yendo (Fig. 23)
    Japan (Yoshida 1983, p. 187).
20. *S. micracanthum* (Kützing) Endlicher (Fig. 24)
    Japan (Yoshida 1983, p. 190).
21. *Sargassum* species #1 (Fig. 25)
    China (Tseng et Lu, unpublished manuscript[7]).
22. *S. giganteifolium* Yamada (Fig. 26)
    Japan (Yoshida 1983, p. 195).
23. *S. macrocarpum* C. Agardh (Fig. 27)
    Japan (Yoshida 1983, p. 198).
24. *S. autumnale* Yoshida (Fig. 28)
    Japan (Yoshida 1983, p. 203).
25. *S. rostratum* J. Agardh
    Taiwan, Hong Kong (Okamura 1936, p. 362; Chou and Chiang 1981, p. 146).
26. *S. siliquastrum* (Mertens ex Turner) C. Agardh (Fig. 29)
    Japan (Yoshida 1983, p. 207; China (Tseng et al. 1962, p. 80); Hong Kong (Setchell 1933, p. 38).
27. *S. serratifolium* (C. Agardh) C. Agardh (Fig. 30)
    Japan (Yoshida 1983, p. 217).

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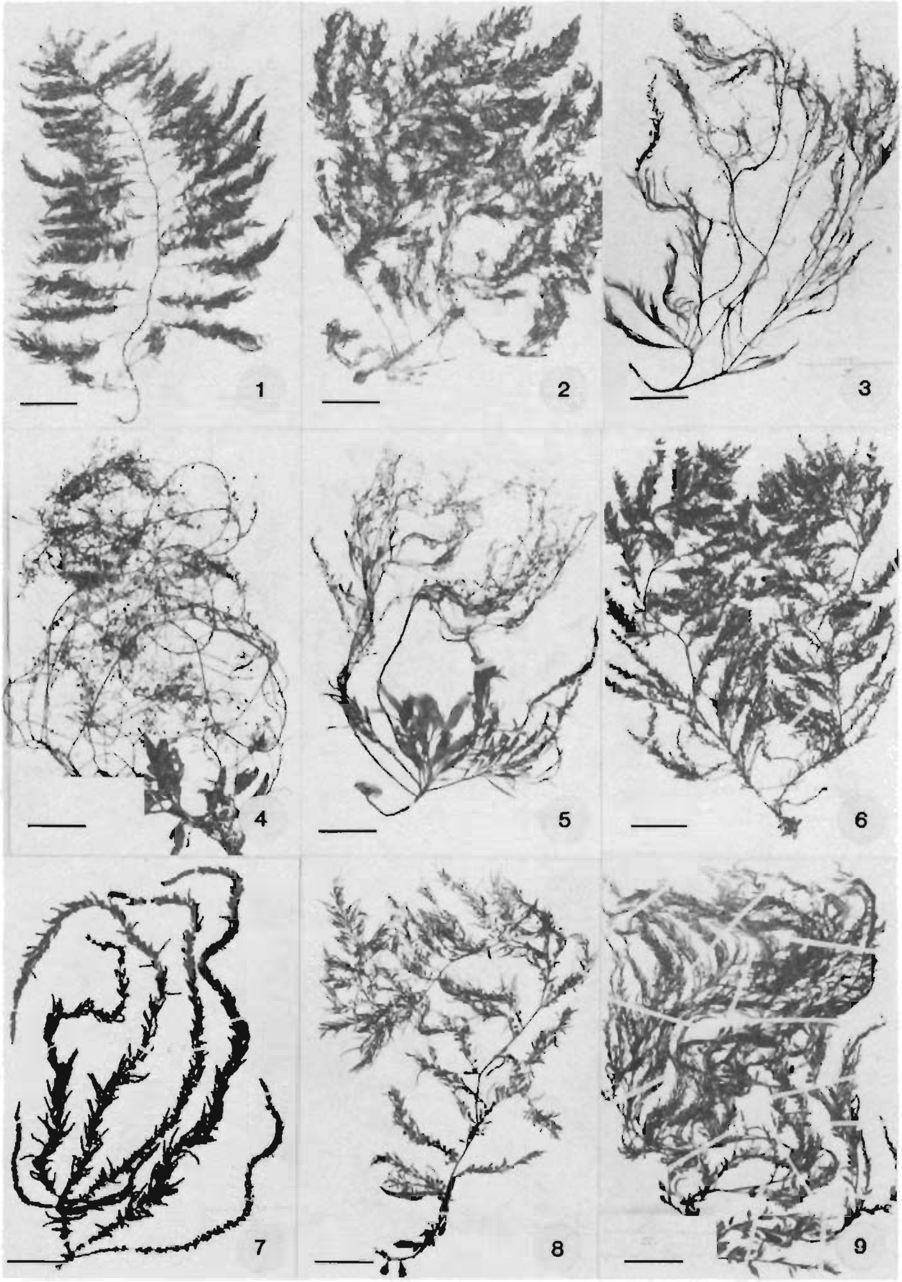
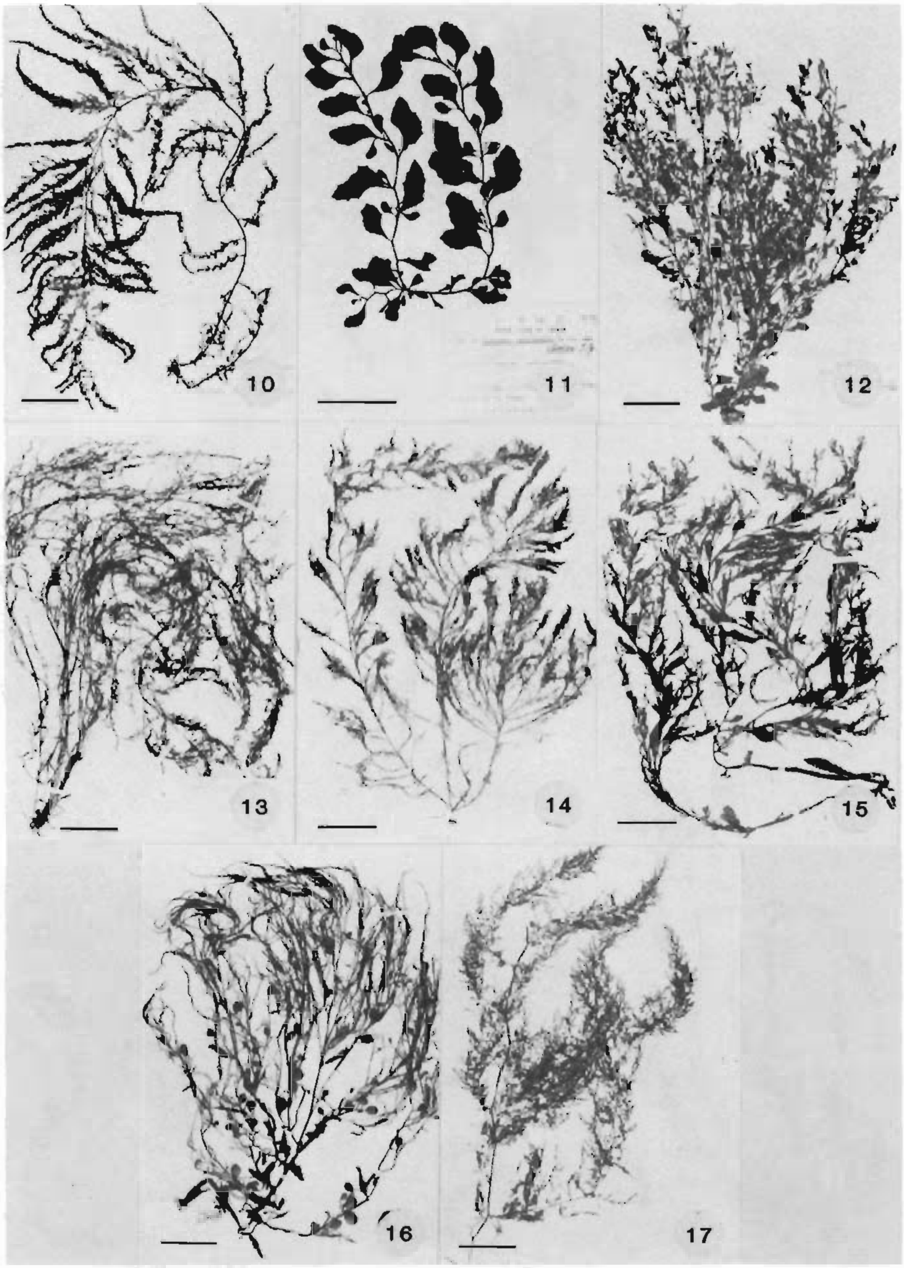
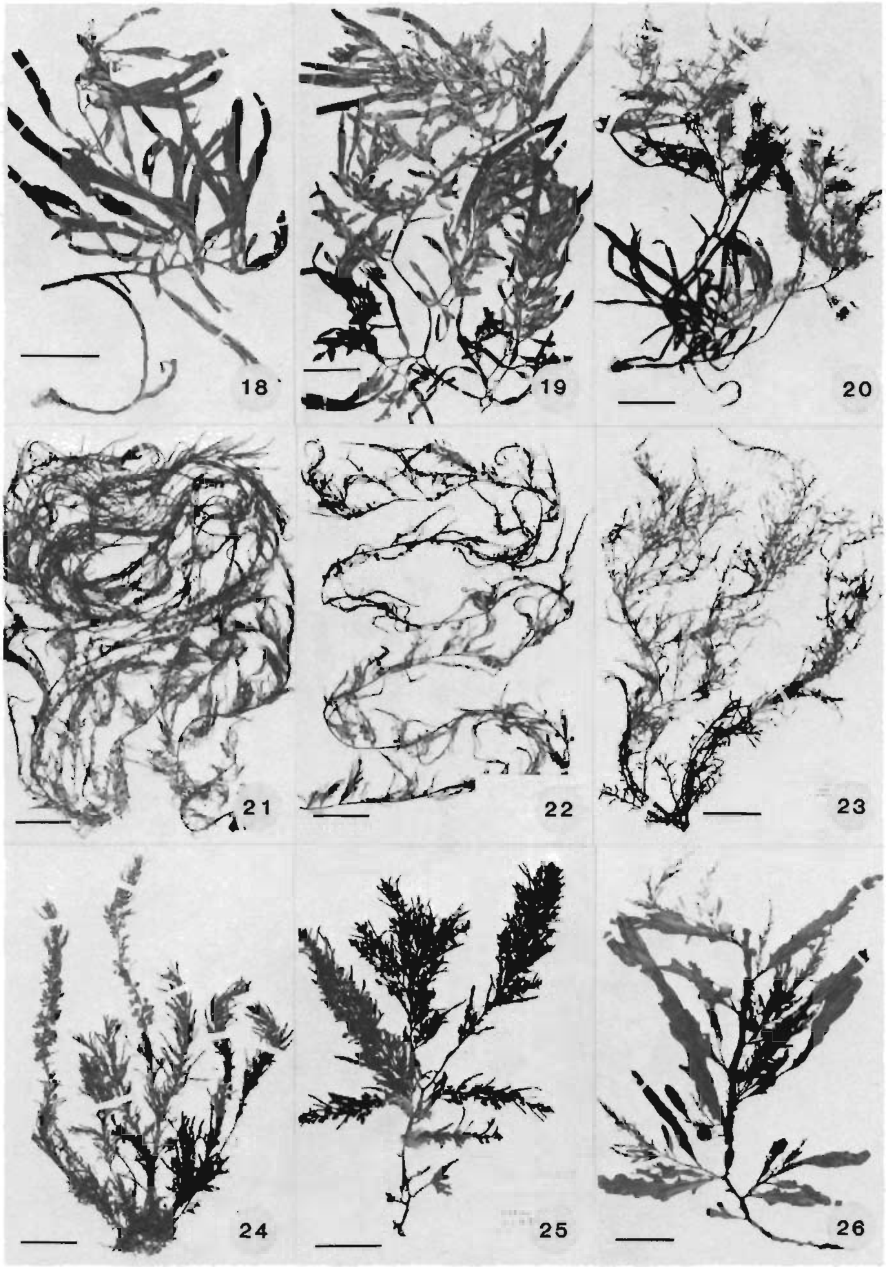
[7] See note 6.



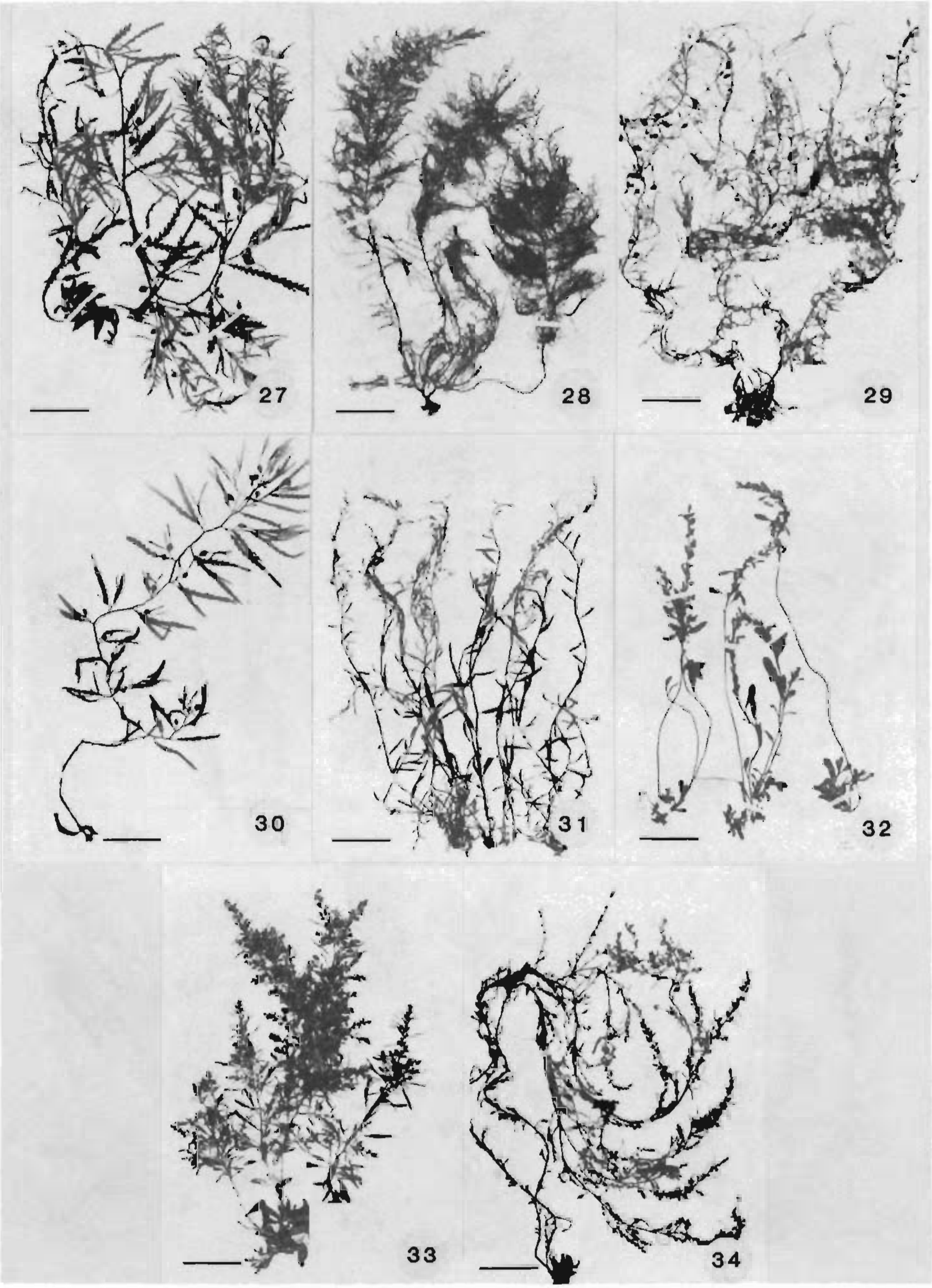
Figs. 1–9. East Asiatic species of *Sargassum* subgen. *Bactrophycus* (scale bar = 5 cm). Fig. 1. *S. horneri*, Japan (SAP). Fig. 2. *S. filicinum*, Japan (SAP). Fig. 3. *S. microceratium*, Japan (SAP). Fig. 4. *S. confusum*, Japan (SAP). Fig. 5. *S. pallidum*, Japan (SAP). Fig. 6. *S. muticum*, Japan (SAP). Fig. 7. *S. thunbergii*, Japan (SAP). Fig. 8. *S. fulvellum*, Japan (SAP). Fig. 9. *S. ammophilum*, Japan (SAP).



Figs. 10–17. East Asiatic species of *Sargassum* subgen. *Bactrophycus* (scale bar = 5 cm). Fig. 10. *Sargassum hemiphyllum* var. *hemiphyllum*, Japan (SAP). Fig. 11. *S. hemiphyllum* var. *chinense*, Taiwan (TAI). Fig. 12. *S. hemiphyllum* var. *chinense*, Taiwan (TAI). Fig. 13. *S. nipponicum*, Japan (SAP). Fig. 14. *S. miyabei*, Japan (SAP). Fig. 15. *S. segii*, Japan (SAP). Fig. 16. *S. yamamotoi*, Japan (SAP). Fig. 17. *S. tenuifolium*, Japan (SAP).



Figs. 18–26. East Asiatic species of *Sargassum* subgen. *Bactrophycus* (scale bar = 5 cm). Fig. 18. *S. ringgoldianum*, Japan (SAP). Fig. 19. *S. ringgoldianum*, Japan (SAP). Fig. 20. *S. coreanum*, Japan (SAP). Fig. 21. *S. trichophyllum*, Japan (SAP). Fig. 22. *S. trichophyllum*, Japan (SAP). Fig. 23. *S. sagamianum*, Japan (SAP). Fig. 24. *S. micracanthum*, Japan (SAP). Fig. 25. *S.* sp. 1, China (AST). Fig. 26. *S. giganteifolium*, Japan (SAP).



Figs. 27–34. East Asiatic species of *Sargassum* subgen. *Bactrophycus* (scale bar = 5 cm). Fig. 27. *S. macrocarpum*, Japan (SAP). Fig. 28. *S. autumnale*, Japan (SAP). Fig. 29. *S. siliquastrum*, Japan (SAP). Fig. 30. *S. serratifolium*, Japan (SAP). Fig. 31. *S. okamurae*, Japan (SAP). Fig. 32. *S. nigrifolium*, Japan (SAP). Fig. 33. *S. yezoense*, Japan (SAP). Fig. 34. *S. yamadae*, Japan (SAP).

IV. *S.* sect. *Repentia* Yoshida

28. *S. okamurae* Yoshida et Konno (Fig. 31)
Japan (Yoshida 1983, p. 223).
29. *S. nigrifolium* Yendo (Fig. 32)
Japan (Yoshida 1983, p. 226).
30. *S. yezoense* (Yamada) Yoshida et Konno (Fig. 33)
Japan (Yoshida 1983, p. 229).
31. *S. yamadae* Yoshida et Konno (Fig. 34)
Japan (Yoshida 1983, p. 233).

V. *S.* sect. Phyllocystae Tseng (described in this volume).

This section is based on the "Sargassa Asiatica" group of Setchell (1936).

32. *S. mcclurei* Setchell
Hong Kong (Setchell 1933, p. 44).
33. *S. herklotsii* Setchell
Hong Kong (Setchell 1933, p. 45).
34. *S. emarginatum* Tseng et Lu
China (Xisha Is.) (Tseng and Lu 1978, p. 3).
35. *S. phyllocystum* Tseng et Lu
China (Xisha Is.) (Tseng and Lu 1979, p. 1).

Descriptions of the Eastern Asiatic *Sargassum* Species not Included in Yoshida (1983)

Of the 35 species of *Sargassum* subgen. *Bactrophycus* listed above, 28 species (one species with two varieties, treated in the present paper as two independent species) have been fully described and well illustrated in the recent monograph by Yoshida (1983). We feel that it is unnecessary to repeat the descriptions of those species in this paper. For those that are not reported in Yoshida's monograph (including six species and one variety), we provide descriptions here.

(10b) *Sargassum hemiphyllum* (Turner) J. Agardh var. *chinense* J. Agardh.

Thallus up to 50 cm tall, pyramidal or paniculate above a holdfast of irregularly ramifying filaments; main branches 2 or 3, cylindrical to filiform, smooth and slightly compressed, 2–3 mm thick; lateral branches alternate, irregularly 1–3 cm apart. "Leaves" usually greenish-grown, becoming dark brown when dry; leaves of lower portion or of immature thalli cuneate, obovate, or oblong-elliptical, more or less attenuate below, often entire or minutely serrate on the upper margin, and frequently symmetrical; leaves of the upper portion of the thallus and on lateral branches usually borne at right angles, obliquely cuneate, veinless and with a short, filiform petiole; cryptostomata visible or sometimes absent. Vesicles obovate, oblong, or elliptical, obtuse or mucronate, 1–3 mm diam.; abundant, mostly on the lower portion of sublateral branches. Male receptacles simple and elongated; female receptacles robust, contorted, and usually compound. (After Chou and Chiang 1981.)

Distribution: China, including Hong Kong and Taiwan.

(21) *Sargassum* species #1 (to be described elsewhere by Tseng and Lu).

This species is here given a description, but no species name in order to avoid a "nomen nudum" (an invalid name because of lack of Latin description).

Thallus of medium size, to about 50 cm long, arising from subconical to conical holdfast; axis short, dichotomously branched once or twice. Main branches compressed; lower "leaves" retroflexed with margin entire; upper leaves with margin entire or somewhat undulate, crenulate, or even slightly serrulate; "leaves" lanceolate, costa percurrent, distinct or evanescent, dark brown, to 1–1.5 cm broad, 5–6 cm long. Vesicles without cryptostomata, ellipsoidal, about 4 x 6 mm, apiculate; stipitate. Receptacles complanate, spatulate, or obovate, usually solitary or in short racemes of two or three in axils of leaves, the whole inflorescence forming a panicle; male receptacles 3–5 mm broad, 10 mm long, notched at apices; female receptacles 4–5 mm broad, 5–6 mm long, broadly crenulate at apices. (After Tseng and Lu, in press, *Oceanologia et Limnologia Sinica*.)

Distribution: China (Zhejiang Province).

(25) *Sargassum rostratum* J. Agardh

Thallus pyramid-like, up to 35 cm tall; holdfast a single conical disc; branches cylindrical and slightly flattened, about 2 mm broad; secondary branches filiform, about 2–5 cm long and 2–3 mm broad, cuneate and stalked; margins undulate and entire or with indistinct, coarse teeth; midrib percurrent, dividing the "leaf" into two halves, each with one row of cryptostomata. Vesicles fusiform to elliptical, about 3–6 mm long and 1–3 mm broad, mucronate or crowned with tonguelike "leaflet" at apex, some slightly winged; pedicel cylindrical, or becoming flat at the top. Receptacles flattened and triquetrous at tips; both margins and apices serrate; pedicels short; usually solitary or arranged in pairs. (After Chou and Chiang 1981.)

Distribution: Taiwan; Hong Kong.

V. Sargassum sect. *Phyllocystae* Tseng (description follows, this volume).

Axis abbreviated, main branches with retroflexed basal "leaves"; normal (e.g., spherical, ellipsoidal, etc.) vesicles absent, replaced by more primitive phyllocysts, which are leaflike structures with inflated middle portions. Receptacles generally compound, in shortened racemes; female ones flat or triquetrous, commonly toothed. This proposed new section is taxonomically similar to "Group 'Sargassa asiatica'" of Setchell (1936, p. 17).

(32) *Sargassum mcclurei* Setchell

Thallus single or several arising from simple, expanded disc; primary axis short, terete, ca. 5 mm high; primary branches elongate, up to 1–1.5 m high, lower part complanate, upper part cylindrical, branched; "leaves" asymmetrical, cuneate below, broadly obovate above, becoming elliptical, with dentate-serrulate margin, without midrib or with short costa (rib) only near the petiole of lower "leaves"; middle part of upper "leaves" longitudinally inflated; ultimate "leaves" transformed into long-elliptical winged vesicles. Female receptacle elongate, obcuneate or triquetrous, angularly dentate; male receptacle elongate, obtuse and long elliptical, rarely dentate, borne in the axil of "leaves" and vesicles. (After Setchell 1933.)

Distribution: Hong Kong.

(33) *Sargassum herklotsii* Setchell

Thallus elongate, racemose, to about 50 cm long, arising from discoid holdfast; axis slightly compressed to cylindrical. Upper "leaves" linear-lanceolate, with acute or broadly obtuse, truncated apices costate, with sparsely punctate cryptostomata, generally inflated in median longitudinal line. Vesicles elongated silique-shape, upper (ultimate) ones without wings, shortly stipitate, attenuate to long mucronate. Receptacle simple, single to a few aggregated in the axil of upper part of branches; female receptacle flat, short obovate, rarely triquetrous (3-sided), with sparsely dentate margin; male receptacle elongate, slightly cylindrical, without dentation. (After Setchell 1933.)

Distribution: Hong Kong.

(34) *Sargassum emarginatum* Tseng et Lu

Thallus of medium size, arising from small conical holdfast 6 mm broad; stipe short, about 4 mm long, 2 mm broad; primary branches compressed, smooth, issuing in all directions, to 70 cm long, 3 mm broad; secondary branches compressed, smooth, up to 19 cm long, issuing alternately, with intervals 1.5–3 cm; branches with "leaves" to 8 cm long. "Leaves" broadly obovate, elliptical, or oblong, somewhat cuneate at base, to 1 cm broad, 2 cm long; margin irregularly dentate, apex obtuse, occasionally conduplicate (folded on itself); midrib inconspicuous to vanishing; with conspicuous cryptostomata. Vesicles phyllocystous, laterally unequal, inflated middle portion obovate or subspherical to 3 mm broad, 5 mm long, with cryptostomata; surrounding "leaves" broadly obovate or elliptical, usually with a shallow notch at the apex, sometimes folded lengthwise; upper "leaves" elliptical, winged, to 1 mm broad, 4 mm long. Receptacles racemose, to 7 mm long; male receptacles elongate, cylindrical, smooth or compressed, dentate, rarely single, generally in short racemes of two or more, often paniculate; female receptacles unknown. (After Tseng and Lu 1978.)

Distribution: Xisha Islands, China.

(35) *Sargassum phyllocystum* Tseng et Lu

Thallus of medium size, arising from a holdfast about 5 mm broad, composed of fused rhizoids; stipe terete, smooth, short, 3–4 mm long, to 2 mm diam.; primary branches subcylindrical to compressed, smooth, to 80 cm long, 2 mm wide; secondary branches similar, 15–20 cm long, alternately placed. "Leaves" lanceolate, midrib inconspicuous to vanishing, with cryptostomata, irregularly dentate, 1–2 cm long, 5–7 mm broad. Vesicles leaflike, laterally unequal, with inflated midportion elongately elliptical, generally 3 mm long, 1 mm wide. Male receptacles subcylindrical, dentate, rarely simple, generally in short raceme of two or three, each 5–6 mm long, 0.5–0.7 mm broad, sometimes leaflike; female receptacles triquetrous (3-sided), slightly compressed, conspicuously dentate, rarely simple, generally in short raceme of two or three, each 2–3 mm long, 1 mm broad. (After Tseng and Lu 1979.)

Distribution: Xisha Islands, China.

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SARGASSUM SECT. *PHYLLOCYSTAE* SECT. NOV., A NEW SECTION OF *SARGASSUM* SUBGENUS *BACTROPHYCUS*

C. K. Tseng

Instead of having the ordinary spherical, cylindrical, or similar kinds of vesicles of the other described sections of *Sargassum* (Yoshida 1983), the taxa assigned to this proposed section of the *S.* subgenus *Bactrophycus* have modified leaves (phyllocysts) that are characterized by inflated middle portions. Receptacles are generally compound, in shortened racemes. Female conceptacles are flat or triquetrous (3-sided) and commonly toothed.

Latin description:

Sargassum C. Agardh (1820) subgenus *Bactrophycus* J. Agardh (1889) sect. Phyllocystae Tseng, sectio nova

Caulis erectus, abbreviatus; rami principales retroflexis foliis basalibus. Vesiculae restitutae phyllocystis quae sunt foliiformes et inflatis partibus mediis. Receptacula plus minusve dentatis; receptaculis foeminibus comressis vel triquetris.

Type species: *Sargassum phyllocystum* Tseng et Lu (1979, p. 1, pl. 1, figs. 1.1–1.4).

Type locality: Zhongjiandao, Xisha Islands, China.

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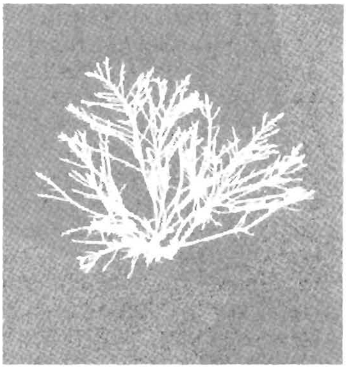
SECTION II. Pacific Gelidiales



PACIFIC SPECIES OF *GELIDIUM* LAMOUROUX AND OTHER GELIDIALES (RHODOPHYTA), WITH KEYS AND DESCRIPTIONS TO THE COMMON OR ECONOMICALLY IMPORTANT SPECIES

Bernabé Santelices and Joan G. Stewart

The order Gelidiales Kylin includes two families, Gelidiaceae and Gelidiellaceae, nine genera, and over 100 species. Five of the genera (*Acanthopeltis* Okamura in Yatabe, *Porphyroglossum* Kützing, *Ptilophora* Kützing, *Suhria* J. Agardh ex Endlicher, and *Yatabella* Okamura) are either monotypic or have few species with restricted geographic distributions. The genera *Beckerella* Kylin, *Gelidiella* Feldmann et Hamel, *Gelidium* Lamouroux, and *Pterocladia* J. Agardh are the most diverse in the order and include species with wide geographic distributions. Even though *Acanthopeltis japonica* Okamura, *Beckerella subcostata* (Okamura) Kylin, and *Gelidiella acerosa* (Forsskål) Feldmann et Hamel may be locally valuable, the important economic species are those of *Gelidium* and *Pterocladia*, which constitute the bulk of presently harvested algae for agar production.

At this time, the only reliable feature for distinguishing the genus *Gelidium* from the genus *Pterocladia* is based on female reproductive structures, there being only one in *Pterocladia* and two in *Gelidium*. Female plants therefore are crucial for identification. In *Gelidium* and *Pterocladia*, female plants are only occasionally found, and thus reliance on other features becomes a necessity. However, uniformity of other reproductive structures among most members of the Gelidiales makes generic and specific distinctions depend heavily on vegetative and habitat features. Moreover, species of these two economically important genera are everywhere vegetatively variable, and for taxonomic purposes large samples from a range of habitats must be compared in order to sort specimens into taxa. Even with this approach, the vegetative morphology exhibited within each taxonomic grouping will sometimes intergrade with specimens in other groups. The consequence is that often it is difficult or impossible to identify single specimens.

The separation and identification of species within both *Gelidium* and *Pterocladia* is of more than academic interest. It is becoming increasingly evident that species attributed to these genera produce different types of agar (G. A. Santos, pers. comm., 1984), which are suited for diverse industrial purposes. Clarification of the taxonomic status of these species is necessary for efficient management and utilization of the natural resource and must precede any effort to diversify their uses.

The present contribution includes three sections. First, we have developed a preliminary key to 26 species in six genera that are either abundant in single areas or common over large portions of the western or eastern Pacific coasts. This key is a first approximation to sorting out these species. Fourteen of these are species that are presently economically valuable and commercially used. Second, all species included in the key are tabulated according to the geographic areas represented by this workshop, with references to selected literature that is relevant to these areas. Third, we have compiled brief descriptions of the economically important species from published information. Because we have had a great deal more information available for some taxa than for others, the treatments are necessarily uneven. The eastern Pacific and Hawaiian taxa have been comparatively well characterized in recent studies (e.g., Dawson 1953; Santelices 1977, 1978; Santelices and Montalva 1983; Stewart 1968, 1974, 1976; Stewart and Norris 1981). By contrast, we examined only a limited number of specimens of what must be the most common species in Japan and Taiwan and saw no Chinese specimens. For descriptions of taxa from these regions we have relied on available literature (e.g., Akatsuka 1983; Akatsuka and Masaki 1983; Fan 1951; Okamura 1934; Segi 1955, 1957, 1959) and specimens kindly supplied by T. Yoshida from the Okamura herbarium (Hokkaido University, Faculty of Science, Sapporo) and Y. M. Chiang (National University, Taiwan) from his personal collections. The second author acknowledges with gratitude the Baja California specimens contributed by Luis Aguilar (Ensenada, Mexico).

For specific separation within the genera *Gelidium* and *Pterocladia* the vegetative features that have been found to be most useful are branching patterns and axis dimensions, together with the species' habitat. Tetrasporangial specimens are generally present in collections of most species; size and shape of sori vary similarly in most species of *Gelidium* and *Pterocladia*, but the shape of the branchlet bearing the sori can be used to distinguish a few species. At one time it was thought that the number and arrangement of internal rhizoids, or hyphae, observed in transections of axes, could distinguish genera or species. Comparisons of this feature within individual thalli and between thalli of the same population show it to be diagnostically unreliable.

Key to Common or Abundant Species of Gelidiaceae

(This key includes economically valuable species [*] from the Pacific coasts of the U.S.A. and Baja California, Mexico; the Gulf of California, Mexico; Chile; Hawaii; Taiwan; Japan; China [with one species from New Zealand], based on material available in 1984 at the Guam workshop. The numbers in parentheses correspond to the numbers in the descriptions that follow.)

1. Thallus lacking internal rhizoidal filaments (hyphae) .... (3) **Gelidiella acerosa* (Forsskål) Feldmann et Hamel
1. Thallus with internal rhizoidal filaments (hyphae) in medulla and/or inner cortex 2
    2. Thallus showing sympodial growth .... (1) **Acanthopeltis japonica* Okamura
    2. Thallus showing monopodial growth 3
3. Branches imbricate on terete axes; cortex thin with densely aggregated hyphae .... *Yatabella hirsuta* Okamura
3. Branches growing from margins of axes, not imbricate 4
    4. Thallus with conspicuous inner cortical zone of large cells .... (2) **Beckerella subcostata* (Okamura) Kylin
    4. Thallus without distinctive large cells in inner cortex 5

5. Cystocarps developing and protruding from one surface of the axis (unilocular); usually with one ostiole, rarely more; carposporangia borne in short chains .... 6 *Pterocladia* spp.
5. Cystocarps always developing and protruding from two surfaces of the axis (bilocular), with one or more ostioles on each surface of branch; carposporangia not in chains .... 9 *Gelidium* spp.
    6. Thallus with flat, broad (to 5 mm) axes with faint midrib (Australia, Tasmania, New Zealand) .... *Pterocladia lucida* (Turner) J. Agardh
    6. Thallus without centrally raised region, thus lacking midrib 7
7. Thallus pectinately branched; erect axes with short, cylindrical, or slightly clavate branches on margins; tetrasporangial sori terminal on swollen apices resembling bulbous stichidia .... *Pterocladia bulbosa* Loomis
7. Thallus pinnately branched 8
    8. Thallus light to dark green, sometimes almost blackish; to 7 cm high; regularly or irregularly branched; cystocarps to 2 mm long, bounded by sterile margins .... (13) **Pterocladia caerulescens* (Kützing) Santelices
    8. Thallus reddish to dark purple; to 37 cm high; branches often regularly arranged, with symmetrical outline to frond; cystocarps may have protruding peristome .... (14) **Pterocladia capillacea* (Gmelin) Bornet et Thuret
9. Thallus more than 15 cm high 10
9. Thallus less than 15 cm high 18
    10. Axes with few irregularly arranged branches 11
    10. Axes with many branches, various lengths, often regularly arranged 12
11. Ultimate axes mostly 0.3–0.6 mm broad; compressed proximally; to 25 cm high .... *Gelidium nudifrons* Gardner
11. Ultimate axes mostly 0.1–0.5 mm broad; flattened near base; to 30 cm high .... *Gelidium linoides* Kützing
    12. Few branches, except when fertile in which case branches may aggregate corymbosely; conspicuous spines of equal length evenly disposed along margins .... (11) **Gelidium rex* Santelices et Abbott (this volume)
    12. Many branches often regularly arranged at least on parts of axes; margins entire 13
13. Most axes less than 0.5 mm thick 14
13. Most axes more than 0.5 mm thick 16
    14. Flattened axes to 2 (–3) mm broad, distinctly tapered toward base and apically, from wider middle segments of axes 15
    14. Flattened axes to 2 mm broad, often narrow and slender in upper branches; variable, with 4 forms described .... (4) **Gelidium amansii* Lamouroux
15. Branches 0.7–2 mm broad; to 20 cm high; with mostly simple lateral branchlets .... *Gelidium tenue* Okamura
15. Branches to 3 mm broad; thalli mostly 7–12 cm high .... *Gelidium johnstonii* Setchell et Gardner
    16. All axes coarse, main axes usually 1–2 mm broad, subcylindrical near base, ultimate branches often more than 1 mm broad 17
    16. Ultimate and main branches 0.4–1 mm broad, rarely more than 1 mm broad; mostly 200–700 μm thick; .... (10) **Gelidium purpurascens* Gardner
17. Branching mostly tending to be regularly pinnate; some branchlets conspicuously geniculate; large plants (to 50 cm high) with coarse (0.4–1.7 mm thick) axes .... (12) **Gelidium robustum* (Gardner) Hollenberg et Abbott
17. Branching infrequently regular, long and short branches mixed; medium to tall (15–40 cm high); (single Okamura specimen examined: 250-650 μm thick, 1250–1950 μm broad from base to apex) .... (8) **Gelidium pacificum* Okamura
    18. Axes mostly less than 3 cm high .... *Gelidium pusillum* (Stackhouse) Le Jolis
    18. Axes more than 5 cm high 19

19. Axes mostly 5–10 cm high 20
19. Axes of some plants to 15 cm high 21
  20. Axes cylindrical or compressed, sparsely branched .... *Gelidium crinale* (Turner) Lamouroux
  20. Axes with numerous regularly arranged branches that are short, simple, and of similar length .... *Gelidium coulteri* Harvey
21. Erect axes compressed, to 4 mm broad, sparsely branched with a distinct midrib; tetrasporangial sori on branchlets growing on both the margins and surfaces of branches and axes .... (6) **Gelidium japonicum* (Harvey) Okamura
21. Erect axes compressed, mostly less than 2 mm broad; variously branched; without midrib 22
  22. Axes flattened, to 2 mm broad; irregularly branched; terminal tetrasporangial sori toward apices of axes, often on irregularly shaped or rounded proliferations .... (5) **Gelidium chilense* (Montagne) Santelices et Montalva
  22. Axes compressed or flattened; branching plumose above; or irregularly alternate and often proliferous, regular and distichous; or with lateral filiform branches or apices filiform on axes and branches 23
23. Axes strap-shaped, with distichous, irregular branching; tetrasporangial sori on apices with serrate or undulate margins 24
23. Axes linear, often with regular pinnate branching; tetrasporangial sori on simple, oblong, globular, or spatulate branchlets with smooth margins 25
  24. Axes to 12 cm tall, with flat (2 mm wide, 200 μm thick) branches in upper parts, irregularly alternate or almost digitate; margins of main axes and primary branches often with branch rudiments; tetrasporangial branchlets irregularly compound, crisped or contorted with serrate margins .... (7) **Gelidium lingulatum* Kützing
  24. Axes with subentire margins in basal parts, irregularly sinuous dentate or eroded dentate above; branching distichous and plumose along edges of upper axes; primary branches often deciduous, leaving scars on margins of lower axes; tetrasporangial sori in pinnately compound or densely congested branchlets; axes 0.7–1.2 mm broad above, to 1.5 mm broad below; 0.8–0.4 mm thick (base to apex) .... (9) **Gelidium pluma* Loomis
25. Primary branches broad and blunt, apices often filiform; usually with filiform branchlets; 1–1.5 mm broad above, 1.4–2.5 mm broad below; 0.1–0.5 mm thick (base to apex) .... *Gelidium planiusculum* Okamura
25. Primary branches broad, tapering to short, narrow ultimate segments; branches with rounded axil with respect to axis; some thalli with minute wart-like proliferations from branch surfaces, often with numerous short, simple branchlets on main axes; 2 mm broad above, 3 mm broad below; 0.2–0.35 mm thick (base to apex) .... *Gelidium vagum* Okamura

Descriptions of Common or Economically Important Pacific Species

(1) *Acanthopeltis japonica* Okamura (Fig. 3)

Thallus subcylindrical, sympodially branched, erect axes, attached to the substratum by several elongated haptera. Erect axes up to 15 cm high, 4 mm diam., completely invested with numerous spirally arranged leaflike structures at the terminal portions of the branches (sympodia). After the formation of the leaflet terminally on a branch, a new lateral branch is initiated as a protuberance at the base of the leaflet. This new branch gradually enlarges and elongates, forming a short cylindrical axis which terminally soon becomes broad and leaflike. A new branch is then initiated on the upper surface, at the base of the leaflet. Protuberances may be formed on the upper surfaces of the same leaflet, each developing into an axis, thus forming a dichotomy. The margins and surface of the leaflets also may have many bristle-like projections. (Modified from Fan 1961.)

Distribution: Japan.

(2) *Beckerella subcostata* (Okamura) Kylin (Fig. 4)

Thallus of several erect, flattened axes, with a midrib evident especially at the basalmost portion of axes, arising from a highly branched fibrous holdfast. Erect axes up to 50 cm high, 900 μm thick and 3 mm broad, branching up to 4 orders, opposite or irregularly alternate along both margins of the axes. Branches variable in length, uniform in width, slightly constricted at the base, and similar in shape and type of branching to the erect axes. Ultimate branchlets distichous, disposed at relatively uniform intervals of up to 9 mm.

Outer cortex, 4–5 layers of small-sized, deeply pigmented cortical cells up to 10 μm diam., followed by 2–3 layers of less-pigmented cortical cells. Inner cortex, 3–5 layers of large (up to 50 μm diam.) colorless cortical cells. Rhizoidal filaments abundant in the region between inner and outer cortex. Medulla broad, formed by longitudinally oriented filaments. Tetrasporangial sori scattered over the surface of terminal, elongated branchlets; tetrasporangia up to 25 μm diam. Cystocarps subterminal, at the tips of lateral and ultimate branchlets, bilocular, with prominent peristomes opening to both surfaces of the branchlets. (Modified from Fan 1961; Akatsuka and Masaki 1983.)

Distribution: Japan.

(3) *Gelidiella acerosa* (Forsskål) Feldmann et Hamel (Fig. 6)

Thallus up to 5 cm high, several tufted, entangled, cylindrical, and sometimes arcuate axes rising from a decumbent and arcuate axis, up to 500 μm diam., attached to the substratum by stoloniferous rhizoids. Erect axes cylindrical or very slightly compressed, to 600 μm diam., sometimes gradually tapering toward the apices and usually with sparse, filiform, distichously arranged opposite or subopposite branchlets, to 30 mm long, generally shorter apically and frequently incurved abaxially. External cortical cells anticlinally elongated in transection, to 4 μm diam. and 7 μm long. Internal cortical cells more rounded, grading into a medulla of larger, elongated cells of about 30 μm diam. Tetrasporangia in the apical portion of modified swollen branchlets of conical shape. Tetrasporangia oblong, 40 –50 μm long by 20 –30 μm broad, cruciately divided, sparsely and irregularly disposed on the branch, the lower usually in a more advanced stage of development than those near the apex. (After Santelices 1977.)

Pacific Distribution: Gulf of California, Mexico; Galápagos Islands; northern Peru; Hawaiian Islands; Guam; Phillipines; Japan.

(4) *Gelidium amansii* Lamouroux (Fig. 19)

Fronds linear, pinnately branched alternately or oppositely up to 4–5 orders, to 30 cm high and axes to 1.5 mm broad. Primary branches similar to erect axes, alternate or opposite, sometimes very regularly pinnate with equally long branches, but more frequently more or less irregular in branching. In early stages of growth the frond is more regularly pinnate with a pyramidal outline, becoming more irregular with age and size. All branches end in acute apices. Cortical cells up to 8 μm diam., deeply pigmented, of 2–3 layers increasing in diameter toward the inner cortex. Medullary cells rounded, up to 25 μm diam., with thick walls. Rhizoidal filaments dense and numerous in the inner cortex. Tetrasporangial sori on elongate-ovate or oblong-spatulate, claviform branchlets. Cystocarps swollen beneath the apex of branchlets, terminated by simple or branched apical segments. (Modified after Okamura 1934; Segi 1959.)

Distribution: Korea; China; Japan; Taiwan.

(5) *Gelidium chilense* (Montagne) Santelices et Montalva (Fig. 10)

Thalli up to 6 cm long, several erect, flat axes, lanceolate but with rounded and somewhat widened apices; attached by cylindrical creeping axes with stolons at irregular intervals. Branches throughout most of axis, but sparse in lower third, of 1–3 orders, the first order similar size and shape to the main axis,

Table 1. Comparison of Some Gelidiales.

Features	*Gelidium lingulatum*	*Gelidium chilense*	*Gelidium rex*	*Gelidium crinale*	*Gelidium pluma*	*Gelidium reediae*	*Gelidium pusillum*
Axes	cylindrical at the base, strap-shaped upwardly. With branch rudiments.	flat, similar to a sword blade.	cylindrical at the base, flattened above. Margins conspicuously dentate.	cylindrical	cylindrical at the base, flattened.	cylindrical at base, strongly flattened upwardly.	compressed
Branching	marginal branches in upper portions.	along most of the axis. Sparse in the basal third. Up to three orders.	devoid of branches in basalmost half, irregularly branched in apical portion.	sparse, appearing as dichotomous.	plumosely branched at apical half of axes.	pinnately branched up to 5 orders.	irregular, along margins.
Shape of branches	similar to main axes.	similar to main axes. Lineal, ending at the same level.	similar to main axis.	similar to main axes.	pinnae, simple or compound.	pinnae, simple or compound.	lanceolate or spatulate.
Fertile portions	pinnately or subpinnately arranged proliferations irregularly compound, crisped or contorted.	widened, portions of apex and branches, often folded longitudinally.	lobated or pinnately compound branchlets.	expanded parts at the end of axes and branches.	on pinnately compound twisted, densely congested branches.	on ultimate portion of enlarged, flat branches.	on ovoid to rounded branchlets.
Size of plants and main axes	up to 12 cm high, up to 2 mm broad.	6 cm high, up to 0.5 mm broad.	up to 30 cm high, up to 2 mm broad.	up to 7 mm high, up to 0.5 mm broad.	up to 20 cm high, up to 5 mm broad.	up to 5 cm high, up to 1.0 mm broad.	up to 3 cm high, up to 2 mm broad.
No. of layers of cortical cells	3–4	2–3	6	3–5	2–3	3–5	2–3
Size of external cortical cells	5–15 μm	6–8 x 8–10 μm	6–8 x 10–12 μm	4–6 x 6–8 μm	6–8 x 8–12 μm	4–6 μm	4–6 μm
Size of medullary cells	up to 35 μm	up to 20 μm diam.	up to 30 μm	6–15 μm diam.	up to 20 μm diam.	up to 20 μm diam.	up to 10 μm diam.
Rhizoidal filaments	not very abundant. Scattered in inner cortex and medulla.	very abundant in inner cortex and outer medulla.	numerous in inner cortex; scarce in inner medulla.	few, around the medullary cells.	abundant, in inner cortex, sparse in inner medulla.	abundant in inner cortex and external medullary cells.	abundant in inner medulla.
Tetraspores	ovoid 16–25 x 19–38 μm	globose-ovoid 10–30 x 20–50 μm	ovoid 20–40 μm	spherical 30 μm diam.	spherical about 30 μm diam.	ovoid 30 x 40 μm	ovoid 25–35 μm
Arrangement of tetrasporangia	irregular	irregular	irregular	without order	without order	without order	without order
Cystocarps	elongate up to 1 mm long, 0.8 mm thick.	ovoid, 0.6 x 0.8 mm, about 0.5 mm thick. With peristome.	ovoid, 0.5 mm surface view, 0.7 mm thick.	ovoid 0.5 x 0.6 mm, 0.5 mm thick	ovoid 0.5 x 0.7 mm, 0.5 mm thick	ovoid or spherical 0.3 x 0.5 mm, 0.5 mm thick	round or ovoid 0.6 mm, 0.5 mm thick

frequently irregular; producing second-order or terminal, ovate-lanceolate branchlets. Often first-order branches end in a truncate apex from which a group of branchlets originate.

Cortex 2–3 layers of globose-ovoid pigmented cells, decreasing in diam. towards the medulla. Medulla of colorless cells up to 20 μm diam. Rhizoidal filaments extremely abundant in the inner cortex and outer part of the medulla, decreasing in density toward the inner medulla. Tetrasporangia produced in short, cordate, rounded, or irregularly shaped proliferations usually having toothed or dentate margins, or on rounded and somewhat expanded apices of the main axes. Tetrasporangia globose-ovoid, 10–30 μm diam. and 20–50 μm long, cruciately divided. Cystocarps borne on small, rounded branchlets with dentate margins, ovoid in surface view, up to 600 μm thick and 800 μm long, with two locules, each with one or two ostioles. A peristome is evident in the mature cystocarp. (After Santelices and Montalva 1983.)

Distribution: Southern Peru; northern and central Chile.

(6) *Gelidium japonicum* (Harvey) Okamura (Fig. 20)

Fronds 4–20 cm high, single or caespitose, compressed, linear, to 2 mm broad, with midribs; proliferous on margins and surfaces, the proliferations sometimes growing into branches, making the branching more irregular. Branches narrow spatulate to oblong, becoming 2–3 times pinnately compound. Apices of all branches terminate in truncate or blunt ends. Margins of lower portions occasionally entire. Cystocarps oval or roundish, slightly flat, blunt or apiculate, consisting of two chambers. Tetrasporangia dense in unaltered or slightly dilated terminal branchlets. (Modified from Okamura 1901; Akatsuka 1983.)

Pacific Distribution: USSR; China; Japan; Taiwan.

(7) *Gelidium lingulatum* Kützing (Fig. 23)

Fronds up to 12 cm tall, attached by a short irregularly discoid holdfast. Erect axes cylindrical and simple or sparingly branched near the base. Upwardly strap-shaped (2 mm broad x 200 μm thick) with flat marginal branches in the upper parts; irregularly alternate or almost digitate. Larger branches similar to erect axes; smaller branches more irregular. Margins of both main axes and primary branches often have branch scars.

Cortex of the flat, erect axis with 3–4 layers of rounded, pigmented cells of 5–15 μm diam., inwardly increasing in size and decreasing in pigmentation. Medullary cells up to 35 μm diam., rounded and unpigmented. Rhizoidal filaments scarce, scattered in the inner cortex and medulla. Tetrasporangia and cystocarps occur on pinnately or subpinnately arranged proliferations that are irregularly compound, commonly crisped or contorted, with serrate margins. Tetrasporangia ovoid, cruciately divided, 16–25 μm diam. and 19–38 μm long. Cystocarps elongate, up to 800 μm thick and 1 mm long, with an ostiole on each side of the frond. (After Santelices and Montalva 1983.)

Distribution: Central and southern Chile.

(8) *Gelidium pacificum* Okamura (Fig. 14)

Fronds usually 15–20 (–30) cm high, the first and second orders of branching dominant, the third and fourth irregular; axis compressed, linear; branches flexuous, long and short mixed, often positioned at 90° to axis, to 2.5 mm broad. Cystocarps at apices of aggregated branchlets, the branchlets terminated by simple or branched, pointed or expanded tips. Tetrasporangia in rounded sori on more or less expanded branchlets. Rhizoidal filaments dense in inner cortex, scattered in the medulla. (Modified from Okamura 1934, 1935.)

Distribution: Japan; China.

(9) *Gelidium pluma* Loomis (Fig. 22)

Thalli crispate and cartilaginous, up to 20 cm high, one to several erect axes with upper portion distichously and plumosely branched, above cylindrical creeping axes with numerous short haptera that form a massive discoid holdfast. Erect fronds cylindrical to compressed, 1.1–1.5 mm wide, with a spatulate apex 0.7–1.2 mm wide, up to 0.4 mm thick. Margins of axes subentire to irregularly sinuous dentate or eroded dentate above, and distichously branched along the upper half. Primary branches lanceolate or spatulate to irregularly lanceolate and pinnately branched when mature, increasing in size basipetally, up to 3.5 mm long by 0.5 mm wide. Secondary branchlets shorter. Primary branches deciduous, especially in fertile thalli, leaving scars at both margins of the lower parts of the erect axes. External cortical cells ovoid in surface view, up to 6 μm long, and arranged without order, anticlinally elongated in transection, up to 10 μm high by 3 μm diam., becoming larger toward the medulla. Rhizoidal filaments abundant in the innermost cortical layer and sparse in the inner layers of the medulla. Tetrasporangia cruciate, 30 μm diam., arranged without order in sori on pinnately compound, somewhat twisted, and densely congested branches with undulate margins. They appear only on the terminal portions of primary branches and on the whole surface of secondary branches. Proximal parts of the primary branches usually sterile, appearing as a supporting axis for terminal and lateral tetrasporangial blades. Cystocarps on pinnately compound branches, normally ovoid, 0.5 by 0.7 mm in surface view, up to 0.5 mm thick, with one (more rarely, several) opening toward both surfaces of the frond. (After Santelices 1977.)

Distribution: Hawaiian Islands.

(10) *Gelidium purpurascens* Gardner (Fig. 24)

Thalli 8–15 (–30) cm high, mostly with rather regular distichous branching, sometimes markedly polystichous, alternate or opposite, with or without geniculate branching; axes basally nearly cylindrical or compressed, usually more compressed above; ultimate sterile branchlets occasionally terete, with acute apices; branching highly variable; lower axes unbranched, or with branching near base; distal branching sparse to dense; main axes 0.5–1.6 (–2) mm wide, 0.25–0.8 (–1.2) mm thick near base; ultimate branches 0.27–0.95 mm wide, 0.12–0.6 mm thick. (After Stewart 1976.)

Pacific Distribution: British Columbia, Canada to Baja California, Mexico.

(11) *Gelidium rex* Santelices et Abbott (Figs. 15–16) This is a new species described in the next paper in this volume.

(12) *Gelidium robustum* (Gardn.) Hollenberg et Abbott (Fig. 13)

Thalli to 40 (–100) cm high, branches mostly compressed, basal axes cylindrical; branching most frequently distichous, often strikingly geniculate, occasionally showing a more polystichous arrangement where lateral branchlets produce short unbranched branchlets from flattened surfaces; axes one to many times pinnate, often sparsely branched or unbranched proximally; axes 0.9–2.2 mm wide, 0.4–1.7 mm thick. (After Stewart 1976.)

Pacific Distribution: Washington, U.S.A. to Baja California, Mexico.

(13) *Pterocladia caerulescens* (Kützing) Santelices (Fig. 7)

Thallus erect, to 7 cm tall, light to dark green, or almost blackish; branched, ligulate axes rising at variable intervals from subcylindrical creeping axes, up to 250 μm diam., attached to the substratum by peg-like holdfasts. Erect axes subcylindrical below, up to 450 μm diam., flattened or ligulate above, up to 1.3 mm wide, 100 μm thick. Branching extremely variable, from quadripinnate in large specimens to almost none or simple alternate in smaller thalli. Branches similar in appearance to main axes but of smaller dimensions. External cortical cells anticlinally elongated in transection, 4–6 μm by 3–4 μm; two subcortical

Table 2. Comparison of Some Species of Pterocladia.

Features	*Pterocladia bulbosa*	*Pterocladia caerulescens*	*Pterocladia capillacea*
Axes	cylindrical at base, flattened above.	dark-green, lingulate, branched cylindrical at base.	cylindrical below, flattened above.
Branching	distichous, pertinate or opposite along both edges.	variable, ranging from quadripinnate to none or simple alternate.	up to 5 orders generally restricted to the upper 2/3 of the frond.
Shape of branches	short, 2–4 mm, cylindrical slightly clavate ending in rounded apex.	similar to main axis.	similar to main axis.
Fertile portions	on terminal parts of pectinate branches.	apex of axes and branches.	apex of axes and branches.
Size of plants and main axes	up to 4 cm high, up to 0.7 mm broad.	up to 7 cm high, up to 0.5 mm broad.	up to 18 cm high, up to 1.8 mm broad.
No. of layers of cortical cells	3	3	3
Size of external cortical cells	6–12 μm	4–6 x 3–4 μm	3 x 6 μm
Size of medullary cells	up to 30 μm	about 20 μm	about 20 μm
Rhizoidal filaments	moderately abundant surrounding medullary cells.	abundant in medulla.	varying in number and position.
Tetraspores	ovoid, 21 x 30 μm	spherical, up to 50 μm diam.	rounded up to 30 μm diam.
Arrangement of tetrasporangia	irregular	irregular	irregular
Cystocarps	globose, up to 0.5 mm diam.	as elongated swellings at the medial part of the branch with sterile margin.	up to 440 μm with peristome.

layers of sparser and ± periclinally elongate cells, up to 15 μm diam.; rhizoidal filaments surround medullary filaments. Tetrasporangia irregularly disposed in sori at apex of axes and branches, sometimes with sterile margins. Tetrasporangia spherical, cruciate, and up to 50 μm diam. Cystocarps unilateral, near the apex of fertile branches, appearing as elongate swellings at the medial part of the branch, sometimes with more than one ostiole, but always only on one surface of the frond; lacking prominent peristome but with evident sterile margins around the cystocarps. (After Santelices 1977).

Distribution: Hawaiian Islands; Guam (new record); Viet Nam.

(14) *Pterocladia capillacea* (Gmelin) Bornet et Thuret (Fig. 1)

Thalli 2–37 cm high, 1 to many distichously branched erect axes from a holdfast of entangled stolons; erect axes strongly flattened distally, equally or less compressed below; lower parts 0.35–2.0 mm wide, 50–900 μm thick; apices 0.2–1.3 mm wide, 50–700 μm thick, apical fronds in some plants attenuated to spatulate; branching irregularly alternate, or regularly pinnate on some branches, often opposite on terminal portions of branches, with 1 to several orders of branchlets; sometimes loose and open with wide intervals between, or dense and congested above; branchlets more or less constricted at point of branching; transection broadly or narrowly elliptical, medulla of thick-walled cells 12–20 μm diam. grading into pigmented cortex of about 3 layers, the outermost of cells slightly anticlinally elongated to 5.0–6.5 μm high, the medulla with few to many rhizoidal filaments which vary greatly in number and position with the part of the thallus sectioned. Tetrasporangial sori variable in appearance, elongate and extensive on terminal parts of the frond, further extending to branches below, or limited to short somewhat laterally swollen branchlets. Tetrasporangia cruciate, rounded, to 30 μm diam. Cystocarps unilateral, 500–600 μm diam., on distal part of a branch or branchlet, with a single rostrate ostiole. Spermatangial sori flat, relatively unpigmented, and elongated, superficial in a distal portion, extending frequently into the branch below. (After Stewart 1968.)

Pacific Distribution: Santa Barbara, California to Pacific Baja California; Gulf of California, México; Galápagos Islands; northern Peru; northwest New Zealand, southeastern coast of Australia; New Caledonia; Taiwan; Japan; China; Hawaiian Islands.

Table 3. Geographic distribution and selected references for species included in the "Key to Gelidiaceae." (Figures in brackets refer to illustrations herein, and numbers in parentheses refer to literature cited.)

Pacific Coast of North America and Gulf of California

Gelidium coulteri (4,20) [Fig. 12]
G. johnstonii (4,21) [Fig. 28]
G. nudifrons (4,20) [Fig. 25]
G. purpurascens (4,20) [Fig. 24]
G. pusillum (4,20,21) [Fig. 9]
Pterocladia capillacea (18,20,21) [Fig. 1]
G. robustum (4,20) [Fig. 13]
Gelidiella acerosa (4) [Fig. 6]

Chile

Gelidium chilense (14) [Fig. 10]
G. lingulatum (14) [Fig. 23]
G. rex (Santelices and Abbott, this volume) [Figs. 15–16]

Hawaiian Islands

Gelidiella acerosa (11,12) [Fig. 6]
Gelidium crinale (12,19) [Fig. 11]
G. pluma (12) [Fig. 22]
G. pusillum (12) [Fig. 9]
G. reediae (12)
Pterocladia bulbosa (12) [Fig. 8]
P. capillacea (12) [Fig. 1]
P. caerulescens (12) [Fig. 7]

Japan

Acanthopeltis japonica (6) [Fig. 3]
Beckerella subcostata (2,6,10) [Fig. 4]
Gelidiella acerosa (10) [Fig. 6]
Gelidium amansii (9,10,15) [Fig. 19]
G. crinale (8) [Fig. 11]
G. japonicum (1,7,9) [Fig. 20]
G. linoides (9,10) [Fig. 17]
G. pacificum (8,9) [Fig. 14]
G. pusillum (10) [Fig. 9]
G. tenue (9,10) [Fig. 18]
G. vagum (9,10) [Fig. 21]
Pterocladia capillacea (18) [Fig. 1]
Yatabella hirsuta (6) [Fig. 5]

Taiwan

Gelidium amansii (5,9,10) [Fig. 19]
G. japonicum (5,10) [Fig. 20]
G. planisculum (5,10) [Figs. 26-27]
G. pusillum (5) [Fig. 9]
G. vagans (10)
Pterocladia capillacea (18) [Fig. 1]

New Zealand

Pterocladia lucida (3) [Fig. 2]

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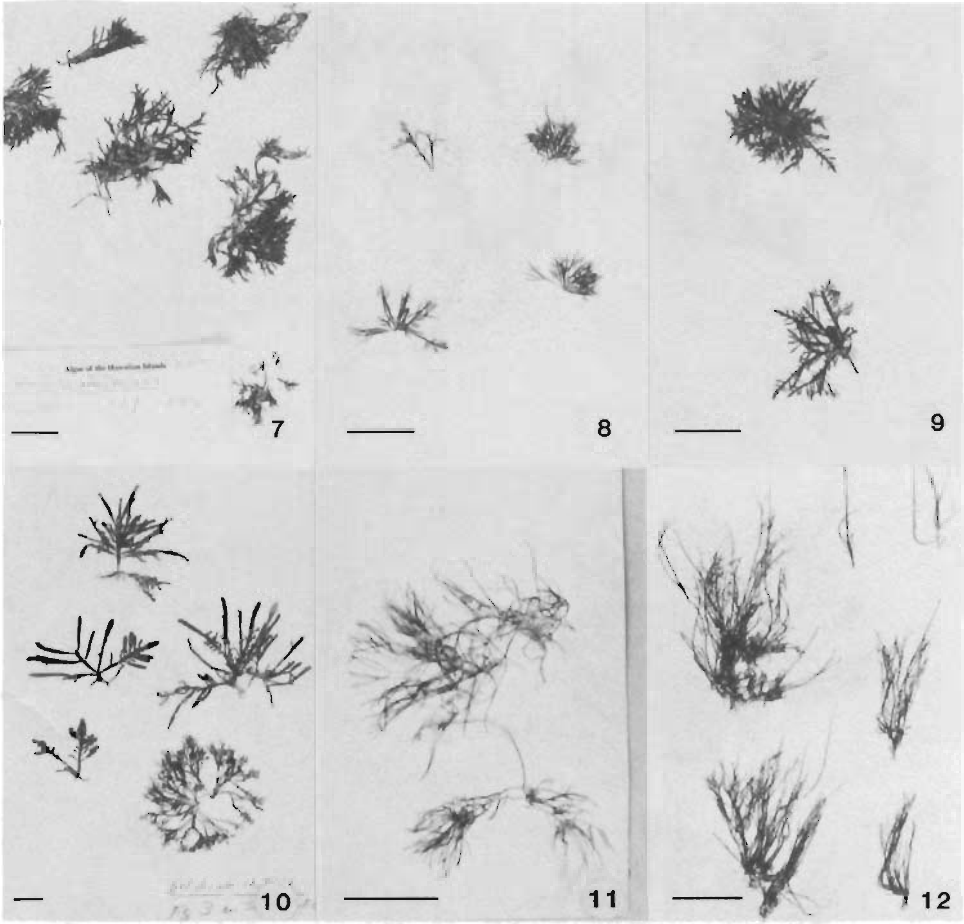
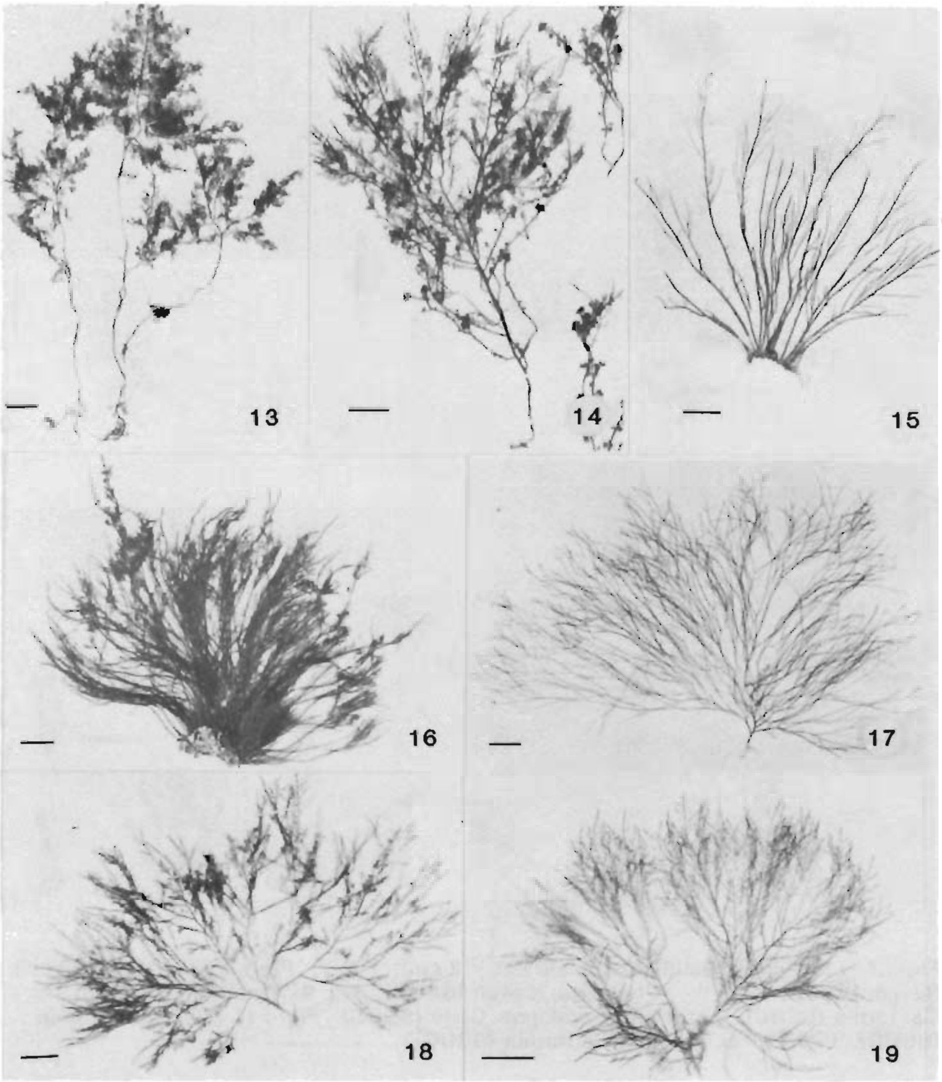
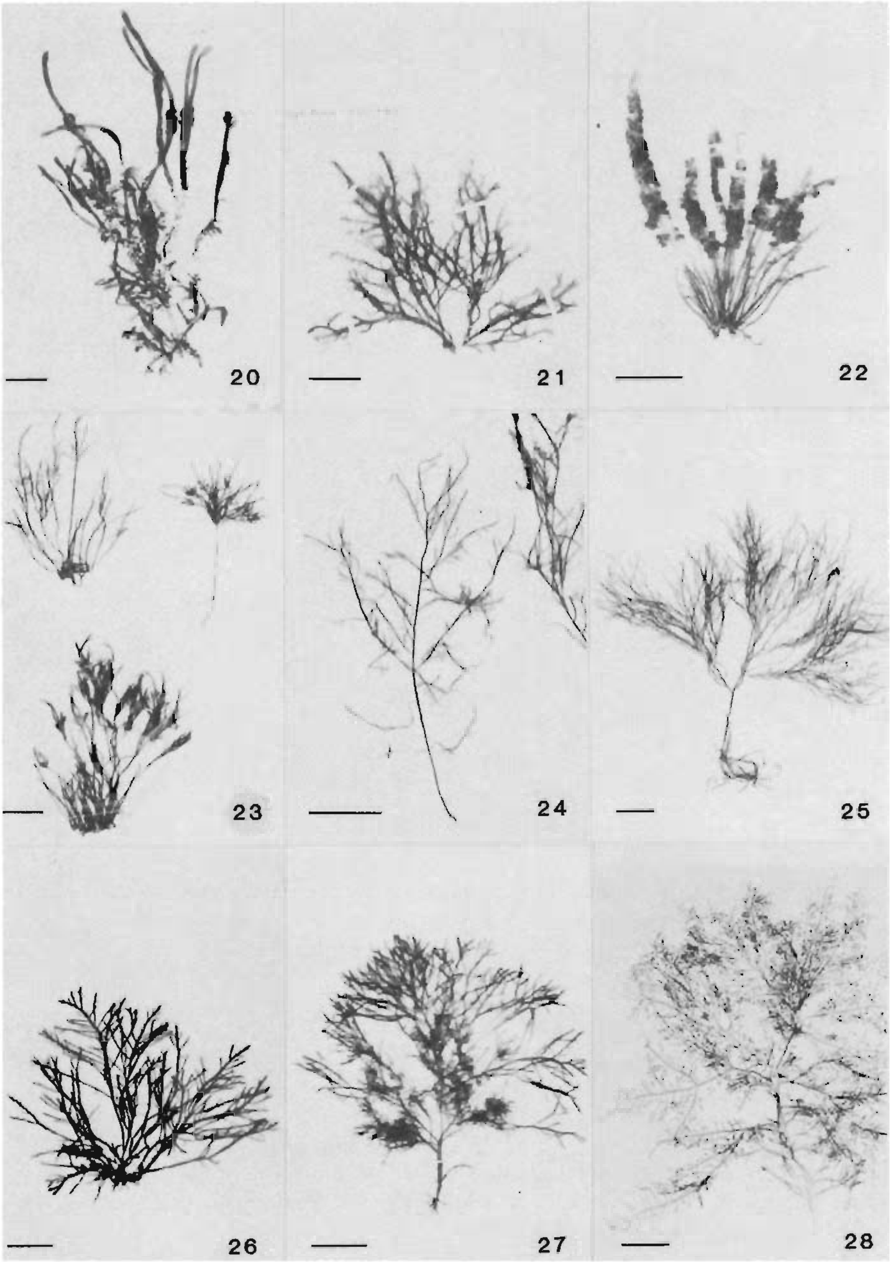


Figs. 7–12. Pacific Gelidiales (scale bar = 2 cm). Fig. 7. *Pterocladia caerulescens*, Hawaii (SSUC). Fig. 8. *P. bulbosa*, Hawaii (SSUC). Fig. 9. *Gelidium pusillum*, California (SSUC). Fig. 10. *G. chilense*, Chile (SSUC). Fig. 11. *G. crinale*, Japan (SSUC). Fig. 12. *G. coulteri*, California (SSUC).

Figs. 1–6. Pacific Gelidiales (scale bar = 2 cm). Fig. 1. *Pterocladia capillacea*, California (JSX). Fig. 2. *P. lucida*, New Zealand (SSUC). Fig. 3. *Acanthopeltis japonica*, Japan (SSUC). Fig. 4. *Beckerella subcostata* Japan (SSUC). Fig. 5. *Yatabella hirsuta*, Japan (SSUC). Fig. 6. *Gelidiella acerosa*, Guam (SSUC).



Figs. 13–19. Pacific Gelidiales (scale bar = 2 cm). Fig. 13. *Gelidium robustum*, Pacific Mexico (JSX). Fig. 14. *G. pacificum*, Japan (SAP). Fig. 15. *G. rex*, Chile (SSUC). Fig. 16. *G. rex*, Chile (SSUC). Fig. 17. *G. linoides*, Japan (JSX). Fig. 18. *G. tenue*, Japan (SSUC). Fig. 19. *G. amansii*, Japan (SSUC).



Figs. 20–28. Pacific Gelidiales (scale bar = 2 cm). Fig. 20. *Gelidium japonicum*, Taiwan (JSX). Fig. 21. *G. vagum*, Japan (SSUC). Fig. 22. *G. pluma*, Hawaii (SSUC). Fig. 23. *G. lingulatum*, Central Chile (SSUC). Fig. 24. *G. purpurascens*, California (SSUC). Fig. 25. *G. nudifrons*, California (SSUC). Fig. 26. *G. planisculum*, Taiwan (JSX). Fig. 27. *G. planisculum*, Taiwan (JSX). Fig. 28. *G. johnstonii*, Gulf of California (type specimen from Setchell and Gardner, 1924: Pl. 72).

GELIDIUM REX SP. NOV. (GELIDIALES, RHODOPHYTA) FROM CENTRAL CHILE

Bernabé Santelices and Isabella A. Abbott

Recent studies on the Gelidiaceae from central Chile have clarified the taxonomic status of several species previously reported for temperate Pacific South America (Santelices and Montalva 1983). A common species of *Gelidium* was omitted from that study because of the uncertainty of its position and is now described as a new species, *Gelidium rex*.

Description

Gelidium rex Santelices et Abbott, sp. nov.

Thallus rigidus, usque ad 30 cm altus; axes divisi in partes repentes et erectos; partes erecti cylindrici basi, complanati superne, ramis de partibus superis. Frondes marginibus conspicue dentatis. Fertiles ramuli lobati usque dentati. Cystocarpia in pinnatim compositis ramis dense congestis.

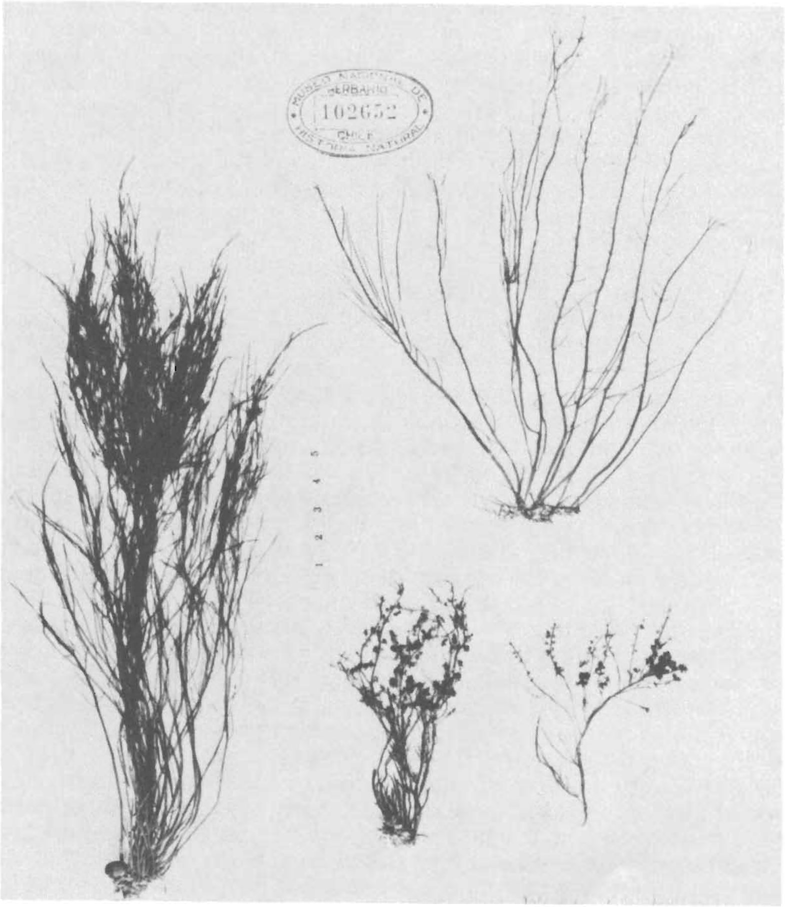


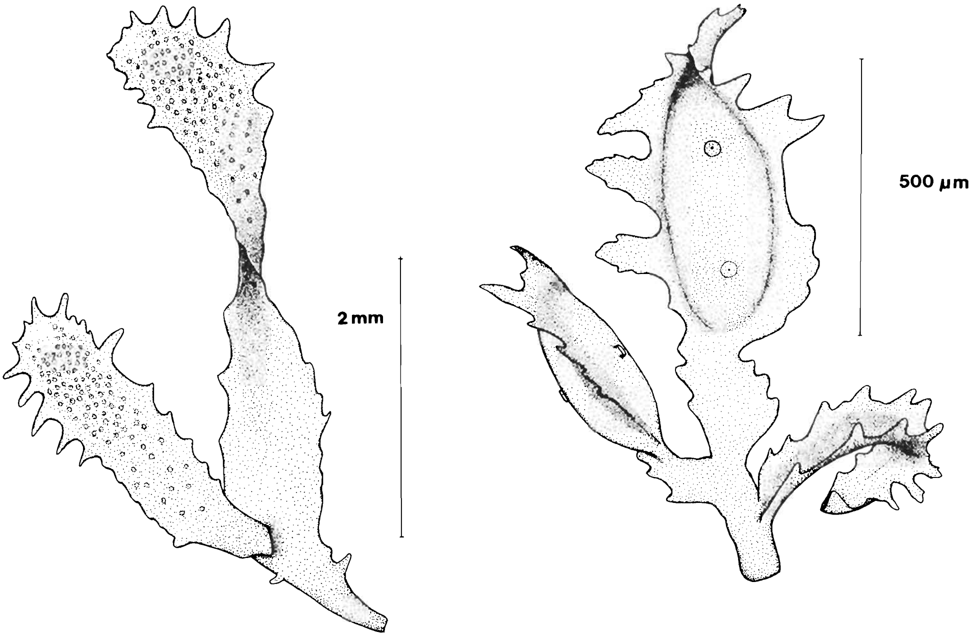
Fig. 1. Type sheet of *Gelidium rex*; holotype specimen is the large plant on the left (SGO #102652) (ruler = 5 cm).

Thallus rigid, crispate, and cartilaginous, up to 30 cm tall, consisting of one to several erect axes devoid of branches in the basalmost half and irregularly branched in the apical portion of the thallus (Fig. 1). Erect axes arising from cylindrical creeping axes with numerous short haptera that form a massive discoid holdfast. Erect axes cylindrical at the base, flattened above and slightly compressed at the apical end; to 2 mm wide, 0.8 mm thick at the cylindrical base. Margins of axes and branches conspicuously dentate, particularly in upper portion. Branches in young specimens and in sterile adult plants scarce, generally of one order, disposed alternately along the axis and externally similar to the erect axes. Fertile thalli abundantly branched in upper third of axes, from numerous elongated, bladelike branches, also with margins conspicuously dentate. Fertile branchlets lobate, or pinnately compound (Figs. 2–3). Cortex of erect axes of 4–6 pigmented cell layers; the most external cortical layer conspicuous, of cuboidal cells with rounded corners, to 12 μm high by 8 μm diam.; inner cortical cells increase slightly in size inwardly, surrounded by numerous, colorless, rhizoidal filaments. Medullary cells rounded and ovoid in transection, to 30 μm diam., with extremely thick cell walls; rhizoidal filaments scarce in inner medulla (Fig. 4).

Tetrasporangia cruciate, 20–40 μm diam., arranged without order in sori on single or pinnately compound fertile branchlets, with dentate margins (Fig. 2). Cystocarps on pinnately compound, somewhat twisted and densely congested branches; ovoid, about 0.5 mm in surface view, up to 0.7 mm thick, with one or, more rarely, several openings on both surfaces of the frond. Holotype: SGO #102652 in Herbarium of the Muséo Nacionál Historia Natural, Santiago, Chile (SGO). Collected with isotypes, June 10, 1977, among holdfasts of *Lessonia nigrescens* Bory at Pelancura (ca. 5 km north of San Antonio Port), Santiago Province, Chile on a wave-exposed rocky platform. Isotypes are in the Herbarium of the Sala de Sistematica, Pontificia Universidad Católica de Chile (SSUC), the Algal Collection of the U.S. National Herbarium, Smithsonian Institution, Washington, D.C. (US), and the Herbarium of the B. P. Bishop Museum, Honolulu (BISH).

The species name, *rex* ("king") reflects the fact that it is the largest of the species of *Gelidium* in Chile. Usually, it occurs in low intertidal habitats exposed to very heavy wave impact. According to our collections, the species extends from San Antonio (ca. 34° S) north to Coquimbo (ca. 30 ° S), but it also has been collected in southern Peru (J. Acosta, pers. comm.) and Valdivia, southern Chile (R. Westermeir, pers. comm.); therefore it probably occurs along most of temperate South America. In central Chile it is collected by fishermen and exported as raw material for agar production. It produces the strongest gel among all Chilean species of *Gelidium* (Santelices et al. 1981).

The description of this new species of *Gelidium* is made after reviewing representative specimens of 87 other *Gelidium* and *Pterocladia* species in various European herbaria (Museum National d'Histoire Naturelle, Paris; British Museum (Natural History), London; Herbaria at Goteborg University and Lund University, Sweden. From the other two species of large-sized *Gelidium* frequently occurring in central Chile (*G. chilense* Santelices et Montalva and *G. lingulatum* Kützing) it is easily distinguished by the external morphological features of conspicuous marginal dentition along the axes, the lack of branchlets along the main axes, and a rigid and crispate thallus. It also generally occurs in habitats different from the two other *Gelidium* species in Chile. Only *Gelidium chilense* can sometimes be found between holdfasts of *Lessonia nigrescens*, where it forms a low tuft, adopting a creeping habit which is distinct from the erect, rigid habit of *G. rex*. There are only two other species, *G. australe* J. Agardh from SE Australia, Tasmania, and Lord Howe I., and *G. microdon* Kützing



Figs. 2–3. *Gelidium rex*. Fig. 2. Tetrasporic branchlet. Fig. 3. Cystocarpic branchlet.

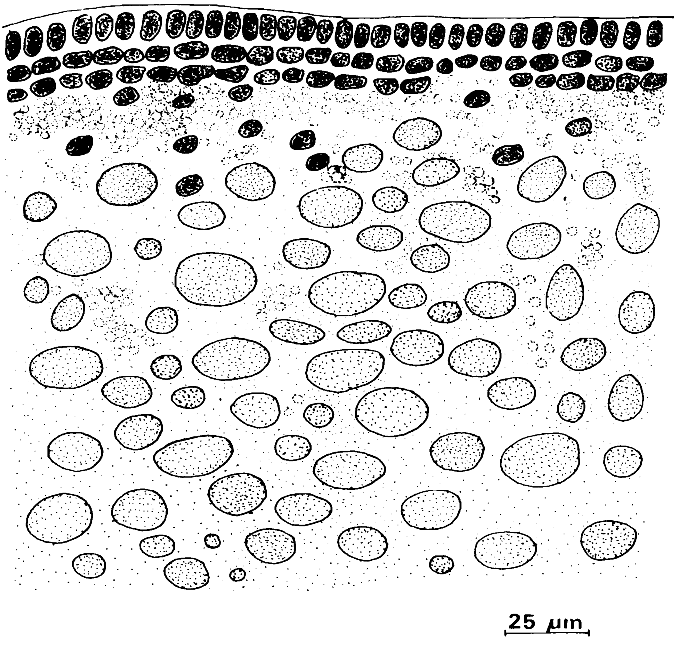


Fig. 4. *Gelidium rex*: transection of an erect axis.

[= *G. spinulosum* (C. Agardh) J. Agardh, according to Dixon, 1959] from the Atlantic coast of Spain and north Africa, that resemble *G. rex*. However, in *G. australe* the axes are much more compressed throughout, and branched to more orders than in *G. rex*. Branches are thinner, and a cross-section of *G. australe* shows the absence of thickened walls in the medullary cells and the presence of rhizoidal filaments abundant in both the inner cortex and in the medulla. A comparison of *Gelidium rex* with *G. microdon* shows our new species to be thicker and more rigid than *G. microdon*. The spines along the margins of the axes in *G. microdon* are longer and incurved, and the fertile branchlets occur along most of the length of the plant, while in *G. rex* they are concentrated in the upper half of the thallus.

Acknowledgements

We are grateful to the International Foundation for Science (Grant # G-112 to B. S.) and to Dirección de Investigación P. Universidad Católica de Chile (Grant # DIUC 87/83), which have supported much of the field work for this study. The examination of species in European herbaria was supported by a travelling fellowship awarded to the first author by the Division of Marine Sciences, UNESCO, Paris; we are grateful to UNESCO and especially Dr. Marc Staeyert for their significant help. The following persons and institutions kindly provided facilities for examination of critical herbarium specimens: Dr. Françoise Ardre, Museum National d'Histoire Naturelle, Paris; James Price and Steve Honey, British Museum (Natural History), London; the late Dr. Tore Levring, Goteborg University; Dr. T. von Wachenfeldt, Lund University, and J. Acosta, Universidad Mayor de San Marcos, Lima.

We are pleased to acknowledge the help of Meng Doty for the Latin description.

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SECTION III. Commercial Species of *Eucheuma*

EUCHEUMA ALVAREZII SP. NOV. (GIGARTINALES, RHODOPHYTA) FROM MALAYSIA

Maxwell S. Doty

Abstract

A new species, *Eucheuma alvarezii*, is established for the principal red alga currently farmed for its kappa-carrageenan content. *Eucheuma alvarezii* differs from other species of *Eucheuma* in its unique morphology and growth physiology. It grows distinctively and rapidly in a wide variety of environments to as much as 56 kg live weight and can be in some cases over 2 meters in length. Three varieties of this species are recognized: *E. alvarezii* var. *alvarezii*, *E. alvarezii* var. *tambalang*, and *E. alvarezii* var. *ajak-assi*. *Eucheuma alvarezii* var. *alvarezii* is thought to be the basic variety from which the other two varieties have been derived. This paper suggests a standardization of morphological terminology for *Eucheuma* (Solieriaceae) regarding the axes, its branching, and internal cellular and tissue differentiation.

Introduction

The 1974 take-off point in seaweed farming of the "cottonii types" (producers of the hydrocolloid kappa-carrageenan) in the Philippines was accompanied by the domestication (Doty and Alvarez 1975) in 1973 of a *Eucheuma* species, since referred to by a number of informal colloquial names. Taxonomy and nomenclature in this genus are in woeful confusion. However, this particular species has been studied extensively in the field and anatomically over the past few years and compared with the lectotype Species for *Eucheuma* J. Agardh, *E. denticulatum* (Burman) Collins et Hervey (1917). It has also been compared with the holotype and lectotype, respectively, for *E. cottonii* Weber-van Bosse (1913) and *E. striatum* Schmitz (1895). In comparison, this now-domesticated species has proven so distinctive physiologically (Glenn and Doty 1981) and morphologically that formal specific status is proposed.

Eucheuma alvarezii sp. nov.

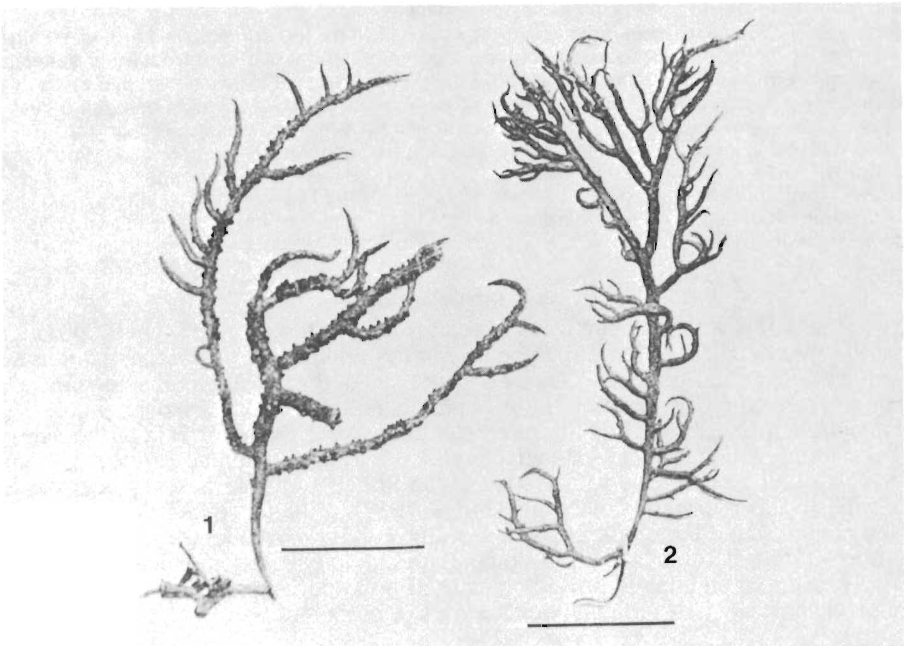
Thalli valde adfirmate crescentes ad lucem aperte dumales axibus 2 metris tenus et usque 3 cm diam. sunt. Fere omnes rami primarii indeteriminati et gradatim angustati a diametro maximo ad apices, paginae rasiles, irregulares origine et dispersi e basi ad apicem axis unde oriundi. Plerumque pauci rami secundarii sunt. Apicalia segmenta ramosa continentia irregularem centralem nucleum filamentorum omnium quae e cylindratis cellulis secondariis tenentibus relative tenues planos parietes extremos eadem crassitie quam lateralibus parietibus et tenentibus diametros circiter 1/5 eorum longitudinum consistent. Primariae cellulae medullosae pseudoparenchymatae saepe isodiametricae et ferentes thylles procurrentes in spatia intercellulosa. Paries cellulosus matricis large kappa carrageenan. Structurae reproductivae dispersae in segmentis axialibus.

Holotypus: In Herbario Pacifico B. P. Musei Bishop ferens numerum mandati auctoris 28727.

The type-specimen (MSD #28727, BISH) for *Eucheum alvarezii* was collected growing attached to calcareous solid materials of detrital origin near the channel west of Karindingan Island on Creagh Reef, south of Semporna, Sabah, Malaysia, 13-X-1978. Within 0.5 km of this same site paratype collections were made of similar specimens: 10-VII-1979, MSD #28800, #28801, and #28802; 25-X-1979, MSD #28882. (These are being distributed to BISH, US, and elsewhere.)

The thalli of *Eucheuma alvarezii* (Figs. 1–8) are multiaxial and otherwise of the nature of members of the Solieriaceae. Often over 60 percent of the wall substance is kappa-carrageenan. Several individual thalli have weighed between 20 and 56 kg.

The main axis of a simple thallus arises from a simple discoid holdfast (Figs. 1–2). Later, further new main axes may arise from the same base very near the primary axis or from the main axis itself below the basal primary branch.



Figs. 1–2. *Eucheuma alvarezii* var. *alvarezii* (scale bar = 5 cm). Fig. 1. Cystocarpic specimen, of holotype material mounted on one herbarium sheet (#MSD-28727, BISH). Fig. 2. Tetrasporic specimen, part of the holotype material mounted on one herbarium sheet (#MSD-28727, BISH).

The branches are irregular to unilateral in origin and, after turning toward the light (shortly after emerging from their bases), grow stiffly toward it, forming open, bushy thalli (Figs. 1, 2, 7). However, when growing in sufficiently consistent current they may trail, becoming over 2 m long. The branches are all essentially primary in nature (Figs. 1, 2, 7, 8), and tend to increase in diameter (often to 2.5 cm) a short distance above where they bend toward the light, tapering then very gradually from their maximum to their slender apices. There are usually no (or occasionally very few) natural secondary branches (Figs. 1, 2, 7, 8), and essentially no branch is determinate. The bending, the inflation, and the prolonged tapering of the very smooth primary branches superficially characterize the species.

Internally, both an inner and outer cortex are recognizable. The outer cortex is a small part of the diameter (Figs. 3–6), consisting of pigmented, radially elongated cells often 9–12 μm long and 3–4 μm diameter. The inner cortex (Figs. 5, 6) is of generally radially elongated, otherwise isodiametric, thick-walled cells bearing pit-plug connections to adjacent cells. Further inwards the cells are proportionately broader, much larger (> 400 μm), and more isodiametric.

The primary cells of the medulla are for the most part isodiametric in transections (Figs. 3–5), often over 400 μm to 1000 μm diameter, and in longitudinal views somewhat elongated parallel to the axis revealing their pseudoparenchymatous nature (Fig. 6). In the apical regions a central core of secondary cells is present in the medulla (Figs. 3–6). This core consists of filaments (Fig. 6) of cells (Figs. 3–5), mostly 30 to 90 μm diameter and initially 120 to 150 μm long with largely flat end walls, which in thickness, like their largely cylindrical lateral walls, are about one-tenth the diameter of the cell lumen or less. Below, the filaments become less conspicuous as their cells enlarge (Figs. 3–6). Below this region there are many intercellular spaces (Fig. 5). The primary cells of the medulla often have thylles that are solitary or in multicellular irregular clusters, with the thylles protruding into what would otherwise be intercellular spaces.

In transections, the apical segment of the core (Fig. 3) is relatively compact and irregular in outline. Note that the cells of the core are few, small, and relatively uniform in size. Towards the base (Figs. 4, 5) the core is successively more irregular, interrupted by large cells, with more cells involved, and its size range is greater and more random. Also, below, there often are outlying individual thylles, filaments, or groups of filaments visible (Fig. 5).

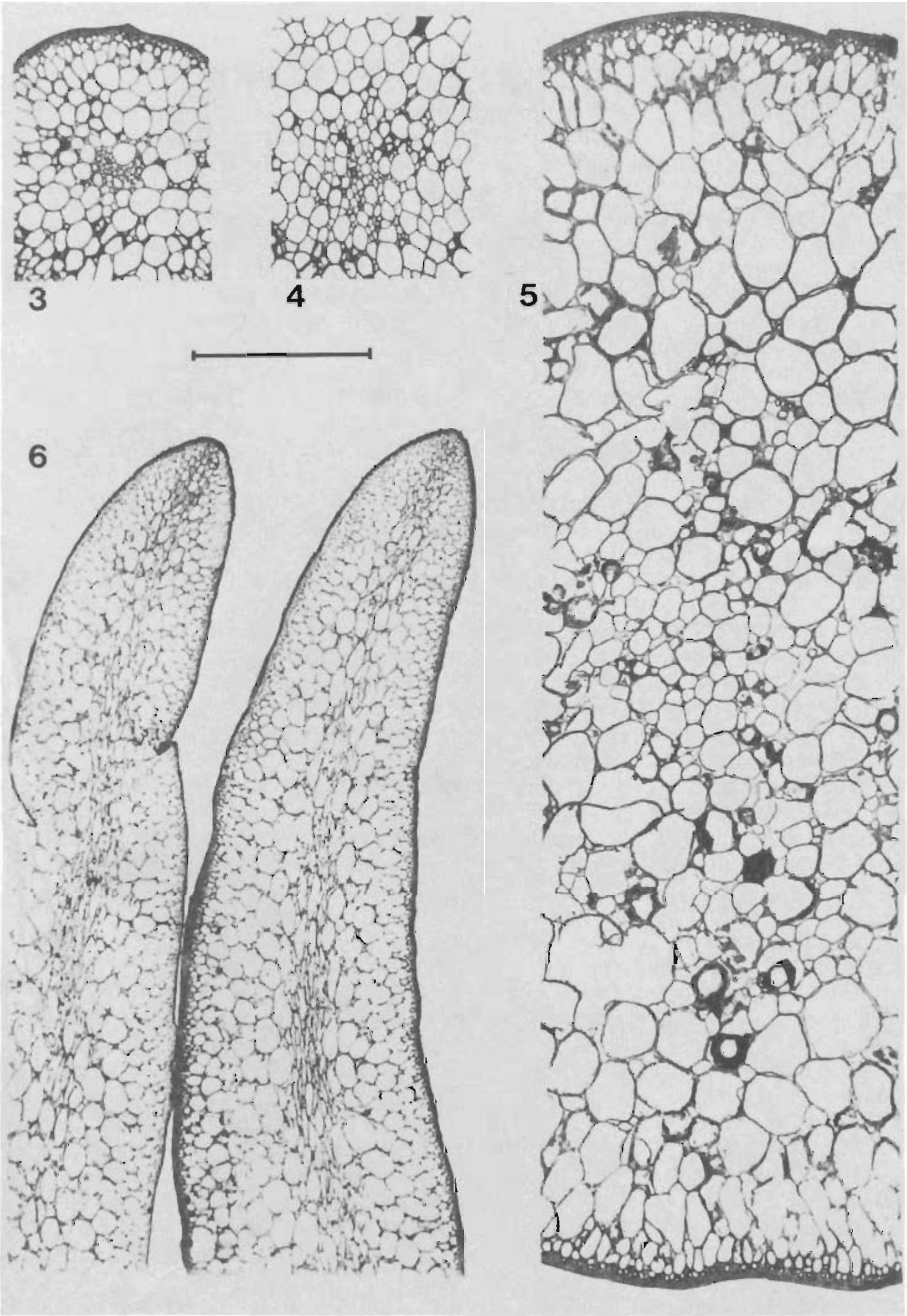
The reproductive structures are on or in the lateral surfaces of otherwise normal axial segments. The cystocarps are swollen from the cortex. The putative spermatangia are in indefinite superficial sori. The seriately divided tetrasporangia are embedded in the cortex. As shown by Weber-van Bosse (1928) for *Eucheuma striatum*, the cystocarps centrally come to display two types of cell groups radiating from a central fusion cell. One radiating type is of slender-celled vegetative filaments which outwardly merge with the pericarp; the other is of gonimoblast filaments. No consistent morphological or size difference between tetrasporangial and carpogonial thalli was observed.

The specific epithet honors Mr. Vicente B. Alvarez who was responsible initially for this species becoming widely farmed in the Philippines.

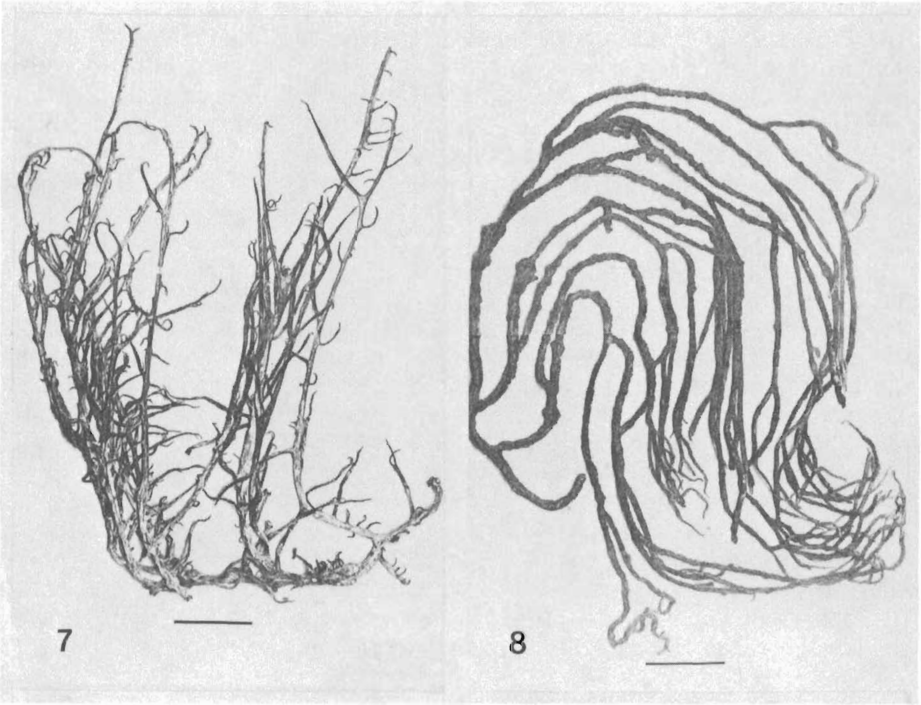
While several varieties have been isolated and grown from time to time, there are three principal varieties.

(1) *Eucheuma alvarezii* var. *alvarezii*

Eucheuma alvarezii var. *alvarezii* (Figs. 1, 2) is distinguished from the following varieties by its more open nature, simplicity, and smaller size. This simplest and smallest variety is often found reproductive, in a wide variety of sizes and degrees of simplicity, and naturally attached. Characteristically it



Figs. 3–6. *Eucheuma alvarezii* var. *alvarezii* (scale bar = 1 mm). Fig. 3. Transection of segment 5 mm from branch tip. Fig. 4. Transection of segment 1.5 cm from tip. Fig. 5. Transection of segment far below tip. Fig. 6. Longitudinal section of tip.



Figs. 7–8. *Eucheuma alvarezii* (scale bar = 5 cm). Fig. 7. *E. alvarezii* var. *tambalang*, holotype (#MSD-26618, BISH). Fig. 8. *E. alvarezii* var. *ajak-assi* holotype (#MSD-24492, BISH).

grows on limestone rock materials in the less sandy reef flat communities dominated by spotty or open stands of *Enhalus acoroides* on Creagh reef, bordering the west shore of the small island, Karindingan, southeast of the larger island, Semporna, Tawau Residency, Sabah, Malaysia. This is at the southernmost tip of the Sulu Archipelago.

(2) *Eucheuma alvarezii* var. *tambalang* var. nov.

Haec varietas distinguibilis a ceteris duobus nunc cognitis inclinatione dumali relative brevibus segmentis axialibus et proportione magna massae minoribus ramis indeterminatis.

Holotypus: In Herbario Pacifico B. P. Musei Bishop ferens numerum mandati auctoris MSD#26618.

The type specimen (Fig. 7) was collected from the seaweed farm of Mr. Vicente B. Alvarez at Calatagan, Batangas Province, Philippines. It was shipped to Honolulu, Oahu, Hawaii (imported under Board of Agriculture Permit #253), and after being grown for a time at the Anuenue Fisheries Research Center and at Coconut Island, Kaneohe Bay, Oahu Island, it was used in experiments and for anatomical study. This import has been exported elsewhere for farming purposes.

Eucheuma alvarezii var. *tambalang* is distinguished by its tendency to be bushy when farmed, having a large proportion of the total mass in smaller indeterminate axes with relatively short segments. Diameters of over 2 cm are common in old basal segments. Farmed material is often recognizable by the rather sharply different orientations of the basal and terminal youngest segments. It is generally found to be nonreproductive, although tetrasporangial individuals have been collected.

The original discovery of this variety was made near Omadal Island, Tawi Tawi Province, Philippines, in the Sulu Archipelago by a fisherman, Mr. Tambalang, whose name is widely applied informally to several of the forms most frequently farmed. From the stories of Mr. Tambalang's discovery, which is commemorated by this new varietal name, the original thallus was a loose mass on the bottom presumably without a primary holdfast.

(3) *Eucheuma alvarezii* var. *ajak-assi* var. nov.

Haec varietas distinguibilis a ceteris forma serpenti, longitudinibus et diametris segmenti longitudinibus et massa gravibus ubique quoque.

Holotypus: In Herbario Pacifico B. P. Musei Bishop ferens numerum mandati auctoris MSD#24492.

The holotype specimen (Fig. 8), selected from farmed material, lacks a primary discoid holdfast. A large portion of it weighed close to 20 kg and was about 2 meters long. A much smaller part of it, brought to Honolulu and dried to 16% moisture, weighed 1550 grams. Several isotypes (BISH, US) were prepared from it along with the holotype preparation.

Eucheuma alvarezii var. *ajak-assi* is distinguished from the others by its trailing growth form and concordantly impressively long main axis. It was growing on the *Eucheuma* farm of Mr. Assi where it was collected in company with Mssrs. Sapayani Ajak, Assi, Malik, Vicente B. Alvarez, and Florante Villanueva, about 1 km southwest of the southern tip of Tumindao Island, Sulu Archipelago, Philippines, 14-I-1972. The name honors both Mssrs. Ajak and Assi who have made significant contributions to the farming of this seaweed.

General Comments on the Species

The natural habitat for the species, *Eucheuma alvarezii*, appears to be the reef flats of easternmost Sabah and the most southern part of the Philippines (i.e., the southern Sulu Archipelago). *Eucheuma alvarezii* var. *tambalang* was brought live to Hawaii (under Hawaii State Department of Agriculture Permit Number 253, issued October 29, 1970) in 1971 from Mr. Alvarez's farm in Calatagan, Batangas Prov., Philippines. Mr. Alvarez's original stock came from Sitangkai, Tawi Tawi Province, Philippines. It has prospered (Doty 1978) locally in Hawaii but hardly spread (Russell 1983) from the sites where it has been planted. The Hawaiian populations have served as the source (Russell 1984) for many of the other Pacific distributions including laboratory use in California. It is known to have been transported by human endeavors and outplanted in many places. In the Pacific it has been spread to at least the reefs surrounding the high islands of Ponape in the Federated States of Micronesia; to Guam; to Christmas (Russell 1984), Fanning (Russell 1984), Tarawa and other atolls of Kiribati; to Fiji; Tonga; and French Oceania.

Adult *Eucheuma alvarezii* does not readily attach to other objects or to its own branches. Though it is not known to be farmed through the setting of spores on outplanted materials, this would seem to be easy since very small thalli are often seen growing on a wide variety of substrata in its native habitat. Plantings are instituted (Doty and Alvarez 1975) through outplanting of vegetative cuttings. The farming has produced as much as 25,000 dry tons in one year. In culture and on farms this species is almost always seen sterile and without a primary basal discoid attachment.

Morphological Terminology

Definition of the terms used in describing the vegetative features of *Eucheuma* is in order, as their terminology is critical in distinguishing the present species from its congeners.

Nearly all *Eucheuma* thalli have round, compressed, or flat axes. Constrictions or branches separate an axis into segments. These same features can be separated into tissue and cell levels of organization as Norris, Wollaston, and Parsons (1984) have suggested in the case of sympodial branching. The idea of distinguishing morphological tissue levels from cellular levels has long been an important concept in the animal world (see Buchsbaum 1976).

The apical segment, considered to be a critical feature of this and related species, is designated as that part of the axis projecting beyond the first primary branch (i.e., the branch nearest the tip of the thallus). The second axial segment would have the first primary branch at its top and the second primary branch at its base, the successive segments being sequentially numbered towards the base of the thallus.

In *Eucheuma* and perhaps all Solieriaceae, the branching is a tissue-level phenomenon. In *E. alvarezii* most of the branches seen are considered to be primary branches, i.e., they arise near the apex of the axis that bears them. They do not, as a rule, overgrow the height of the parent axis. However, damage to the main axis seems to result in overtopping (Figs. 1, 2) by primary branches. Often such damage is the result of fish grazing. In nature, upward growth may be terminated at some tide level and, thus, head-like or flat-topped thalli or populations may result.

Secondary branches appear after and between the primary branches when present. In *Eucheuma alvarezii* secondary branches are usually absent, while in *E. striatum* secondary branches are common.

Primary and secondary branches may be either determinate or indeterminate, though this status may be somewhat conditional or temporary. Adventitious branches appear where wound damage has healed. Unilateral or general adventitious branching on isolated segments, when present, is conspicuous.

The basal primary branch is the first branch that appeared on the oldest erect juvenile or primary axis. Indeterminate branches appearing below the most basal primary branch could be described as secondary axes rather than as secondary branches. There is often at least one present (Fig. 2). Sometimes such secondary axes arise from the holdfast.

Indeterminate branches of this genus look like the axis that bears them. Determinate branches are limited in growth, and in one way or another differ from the main axis and often bear dentations, spines, or protuberances. In the case of *Eucheuma denticulatum* (Burman) Collins et Hervey the whorls of spines are primary, and while initially determinate, one or more is often only ephemerally so. On old *E. denticulatum* thalli, short secondary determinate branches may appear and eventually cover the axes between the determinate primary branch whorls. In some other *Eucheuma* species such secondary branching is common, and these branches may be determinate on the brightly lighted portions of the thallus, while indeterminate in the shaded portions, or this relationship with light may be reversed as though some light dosage thresholds were being transgressed.

At the cellular level of organization, cells of *Eucheuma* thalli are primary cells (e.g., see Weber-van Bosse 1928) if they are in the cell families derived directly from the apical cells. A cell family is those cells related directly by cell division. Primary cell families lead directly to the superficial structure of the thallus.

The term "cell family" is used here, for despite the ontogeny leading to them, their cellular components are pseudoparenchymatous in appearance and may produce secondary cells from cells below their apical cells. These secondary cells may remain as solitary thylles, or may become irregularly branched systems or relatively simple descending filaments that can develop differently, depending on the species and conditions. To term them merely filaments could be misleading. In the tissues of the present species the secondary productions are the thylles and the axial filaments. Such secondary cellular features of vegetative branches do not appear in some genera otherwise similar in their internal appearance, e.g., *Gracilaria*.

The systematic position of *Eucheuma alvarezii* within the genus is not taken up here. Any definitive discussion of its systematic position would have to be based on disposal of several significant questions as to the application of the classical names to existing material.

There is a great deal of confusion in the nomenclature of *Eucheuma* species. However readily the history may be traced in the literature, associating names with taxa via the "type method" frequently is frustrated, for distinguishing the taxa so often requires some destructive analysis. Even if the necessary analysis of type specimens were permissible, the types for the earliest validly published species names are often not useful because of the degraded condition of the hydrocolloids in old specimens, the fact that no type specimen exists, or the putative type specimen cannot be placed taxonomically with certainty. When the application of the correct name cannot be determined on the basis of external morphology, the internal anatomy, or the original hydrocolloid nature of the type specimen, the application must rely on protologue illustrations and verbiage. When only the latter are available, the subjectivity wrought from the nature of the descriptions and figures in the taxonomic incunabulae can readily deny the purpose of the "type method." This is particularly serious in *Eucheuma*, and for this genus there is considerable merit in applying the epithet "nomina inquirenda" to names lacking existing protologue specimens.

The three varieties of *Eucheuma alvarezii* were originally found in rather different habitats, but all were habitants of the reef flat in the southern part of the Sulu Archipelago. Insofar as known, *E. alvarezii* var. *alvarezii* grows on reef flat limestone rock where seaweeds are few in kind, but abundant; *Enhalus acoroides* (a flowering plant) dominates and the community is interrupted here and there by slightly deeper small sandy areas. The rigid *Eucheuma alvarezii* var. *tambalang* grows in the more turbulent water of shallow reef flats. Sometimes it dominates shallow hollows in the reef flat; there it may produce very dense, stiffly erect thalli with longer than usual segments. The farmed material is often reoriented in planting or during growth. This history can, as a result of the positive light responses of this variety, become recognizable by the orientations of different parts of the branching systems. Sometimes the changes in direction of growth are so few and synchronous that they can be counted or may remind one of the sudden changes in direction of the swimming of a small school of fish. The lax *E. alvarezii* var. *ajak-assi* grows where there are similar light/fertilizer dosages and consistent current and has, in correlation, longer than usual segments, but they are trailing rather than erect.

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EUCHEUMA SPECIES (SOLIERIACEAE, RHODOPHYTA) THAT ARE MAJOR SOURCES OF CARRAGEENAN

Maxwell S. Doty and James N. Norris

Abstract

A practical key to 15 *Eucheuma* species is provided along with commentaries on some of the taxonomic problems within this commercially important genus. It is proposed that Weber-van Bosse's two sections of *Eucheuma* and others, such as those described as new herein, be defined by detailed morphological attributes and attention to cell wall matrix chemistry. The commercial species are found to have central cores of either rhizoidal or hyphal cellular strands, and some of them possess thylles. Using the presence or absence of these features and the carrageenan type produced, the commercial species of *Eucheuma* are rearranged in the following four sections: *E.* sect. *Eucheuma* [Type: *Eucheuma denticulatum* (Burman) Collins et Hervey]; *E.* sect. *Anaxiferae* Weber-van Bosse, emend. (Type: *Eucheuma arnoldii* Weber-van Bosse); and two proposed new sections, *E.* sect. *Gelatiformia* [Type: *Eucheuma gelatinae* (Esper) J. Agardh] and *E.* sect. *Cottoniformia* (Type: *Eucheuma alvarezii* Doty).

Introduction

Consistent distinction (taxonomy) of the *Eucheuma* species and application of their names (nomenclature) is of considerable practical value to producers and processors of this seaweed. Different species and species groups produce quite distinctive carrageenans; a specific species produces only one kind (Santos and Doty 1978). *Eucheuma* is a major carrageenan source for the world (Bixler 1979; Abbott and Cheney 1982). Thus it is not surprising that the world's supply has now shifted from the wild crop harvesting of several species to the farm production of a few. It is hoped that this publication will advance the taxonomic and nomenclature stability of these commercial species.

There has been no worldwide monograph of the genus published in the 20th century, but there are probably fewer species of *Eucheuma* than are implied by the 43 names appearing in the literature. *Eucheuma denticulatum* (Burman) Collins et Hervey is accepted as the type for the genus (Cheney and Dawes 1980; Gabrielson 1983). The taxonomy of *Eucheuma* J. Agardh (Solieriaceae J. Agardh; Gigartinales Schmitz) at the species level is covered in greatest detail by J. Agardh (1852, 1876, 1892), Schmitz (1895), Weber-van Bosse (1913, 1926, 1928), Yamada (1936), Børgesen (1943, 1950, 1951, 1953), Dawson (1961), Taylor (1960), and Cheney and Dawes (1980); and sometimes in reference to individual species by Kraft (1969, 1972), Gabrielson (1983), and Doty (this volume). Others have contributed to the literature on indexing (DeToni 1905, 1924), systematics (Kylin 1932, 1956), physiology (Cheney and Dawes 1980; Glenn and Doty 1981), or natural products (Santos and Doty 1978).

There is considerable confusion in the recognition and consistent naming of the different species by taxonomists and by the concerned business world. It is hoped that through use of the following key all readers may be able to separate consistently the species and understand the application of the names used in the discussion sections which follow. However, the authors are aware that this is a state-of-the-art effort.

Key to the Species and Species Groups in the Genus *Eucheuma*

(Two species of *Gracilaria* are included since they are often confused with *Eucheuma* in the commercial trade and sometimes in ecological studies or herbaria.)

1. Axes with whorls of spines someplace, *or* branching at predictable intervals along the axes where some of the whorled spines may have become indeterminate branches like their parent axes 2
1. No whorls of spines or branches present; major branches not appearing at predictable places 5

2. Spines bearing sharp points, curving toward the branch apex and determinate; spines of all whorls of about the same length; branches not regularly at predictable intervals and probably not the results of elongation of a spine in one of the mature whorls; presumably producing agar; Southern Africa .... *Gracilaria aculeata* (Hering) Papenfuss
2. Spines gradually tapered to slender points, some of them elongating into indeterminate branches; branches regularly appear at predictable places along an axis; producing an iota carrageenan 3

3. Spines rebranched, in discrete whorls or covering axis segments completely; anaxiferous; Southeast Asia .... *Eucheuma arnoldii* Weber-van Bosse
3. Spines simple, in whorls or widely spaced pairs someplace on the axis; axiferous 4

4. From the Indo-Pacific .... *Eucheuma denticulatum* (Burman) Collins et Hervey
4. From the Gulf of California .... *Eucheuma uncinatum* Setchell et Gardner
4. From the Atlantic and Caribbean .... *Eucheuma isiforme* (C. Agardh) J. Agardh

5. Thallus prostrate, decumbent, *or* of erect blades that are equally flat on the two sides 6
5. Thallus erect, cylindrical, and/or procumbent to erect with the two broader sides unequally compressed, and often segmented 12

6. Thalli prostrate or decumbent (often with constrictions at intervals, secondary attachments to the substratum present or forming rigid heads) 7
6. Thalli of erect apically flat blades .... *Eucheuma procrusteanum* Kraft

7. Thallus arising as a crust with no clearly defined branches (= *E. horizontale, E. striatum* forms, and *E. cottonii* forms) .... *Eucheuma crustiforme* Weber-van Bosse
7. Thallus arising from clearly defined branches which may be prostrate, compressed, and bilaterally ornamented, *or* the thallus forming a dense head 8

8. Thalli of flat or strongly compressed segments 9
8. Thalli merely compressed to nearly cylindrical; linear segments connected by cylindrical nodes, segments often recumbent and broader centrally; axiferous; producing a unique carrageenan; Southern Indian Ocean .... *Eucheuma odontophorum* Børgesen

9. Thallus generally of long somewhat deltoid segments which grow directly from, and gradually broadening from, the axis; anaxiferous; producing kappa-carrageenan; East Africa .... *Eucheuma platycladum* Schmitz
9. Thallus generally of linear segments; Old World 10

10. Thallus having traces of ventral or dorsal rows of spines in addition to the marginal spines; producing kappa-carrageenan; medulla axiferous and compressed, central axis with many flexuous filaments extending through all segments; Western Pacific .... *Eucheuma gelatinae* (Esper) J. Agardh
10. Thallus without rows of ventral or dorsal spines in addition to the sometimes presence of marginal teeth; medulla *not* as above 11

11. Cortex with small cells among the medullary cells; producing kappa-carrageenan; Southeast Asia and Guam .... *Eucheuma cottonii* Weber-van Bosse

11. Cortex without small cells among the medullary cells; producing an agaroid gel; warmer Pacific .... *Gracilaria eucheumoides* Harvey[1]

12. Proliferations from axis flattened or bilateral in origin; the main axis tending to be compressed and unequally flattened on the two broader sides; axiferous; producing a carrageenan 13

12. Proliferations from axis circular in transection, and scattered to irregular or unilateral in origin; the main axes round or angular in transection; producing kappa-carrageenan 14

13. Juvenile stage creeping or recumbent; erect fronds usually lacking segmentation, commonly branched, and with ten or fewer fronds arising from an expanding cushion-like holdfast; producing iota-carrageenan; Southeast Asia .... *Eucheuma serra* (J. Agardh) J. Agardh

13. No creeping or recumbent juvenile fronds known; erect fronds largely segmented, little-branched, commonly with up to fifty fronds arising from a flat prostrate disc-like holdfast; producing kappa-carrageenan; Western Australia .... *Eucheuma speciosum* (Sonder) J. Agardh

14. Segments tending to be smoothly cylindrical with the only branches defining them indeterminate; other kinds of branches usually absent or only denticulations (which, especially on the apical segments, may be but evidence of haploid fertility); branching generally open and the branch axiles sinusoid; branches generally shortly flexed upward, directed toward the light, characteristically inflated and thence tapered to their apices; secondary indeterminate branches generally neither conspicuous nor increasing the density of the branching at the thallus perimeter; medullary core of axial hyphae persisting to at least 10 cm below the apex of any indeterminate branch axis less than 5 mm in diameter 15

14. Segments tending to be roughened by determinate secondary branches which may be uniformly short rounded protrusions or acute denticulations sometimes obscuring the otherwise cylindrical segment nature; branching generally close and axiles angular; branches generally directed toward the light and plagiotropic, not inflated near their bases, often of uniform diameter to the apical quickly tapered tips; secondary indeterminate branches conspicuously arising from the shaded lower interior segments and often significantly increasing the density of the branching at the thallus perimeter; medullary core of axial hyphae tending to disappear in branches less than 5 mm diam. .... *E. striatum* Schmitz

15. East African and Southwestern Indian Ocean .... *E. inerme* Schmitz

15. Sulu Sea (Philippines) and elsewhere in this vicinity of the Old World .... *E. alvarezii* Doty (species described in this volume).

Discussion of the Key and Species

In using *Eucheuma denticulatum* (Burman) Collins et Hervey, a major nomenclatural confusion has been avoided. The often-seen species names, *E. spinosum* (Linnaeus) J. Agardh, *E. serra* (J. Agardh) J. Agardh, and *E. muricatum* (Gmelin) Weber-van Bosse, are not used; though each has at times been given as the type for the generic name, *Eucheuma* J. Agardh (1847). It is believed (Collins and Hervey 1917, pp. 106–108; Dixon 1962, pp. 249–250) that *Fucus denticulatus* Burman (March 1768), the basionym for *E. denticulatum*, was the first validly published name for any of these species or those distinguished in the above key. The more recent *F. spinosus* Linnaeus (1771), *F. muricatus* Gmelin (April 1768) and *Sphaerococcus serra* J. Agardh (1841) are considered later synonyms and use of the first name applied to the species is continued.

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[1] The original spelling of the specific epithet by Harvey (1859, p. 331) as "eucheumioides" does not conform to the International Code of Botanical Nomenclature; the Greek "o" is a connecting vowel, thus the spelling is accepted as *eucheumoides* following J. Agardh (1876, p. 442).

The commercial species are extremely responsive to their environments and correspondingly morphologically variable. Thus, in commercial shipments, as well as in the world's herbaria, a bewildering array of forms and sizes is found. Simple small scraps and juveniles weighing the dried equivalent of less than a gram, as well as samples from thalli that had live weights of over 50 kilograms, are found. The taxonomy is complicated by this high degree of morphological variation. Therefore in identifying the species it is helpful to have large numbers of specimens to understand the range of variability.

For the commercial species of *Eucheuma* the wet (live) to dry weight (unwashed field dry) ratios are often 6 to 10, and variable with the species and their growth rates or age. The carrageenan content (the matrix of the cell wall) ranges from 25 to about 70% of the salt-free dry weight. Salt (mostly over 95% KCl) is usually about 16% of the unwashed field-dried weight.

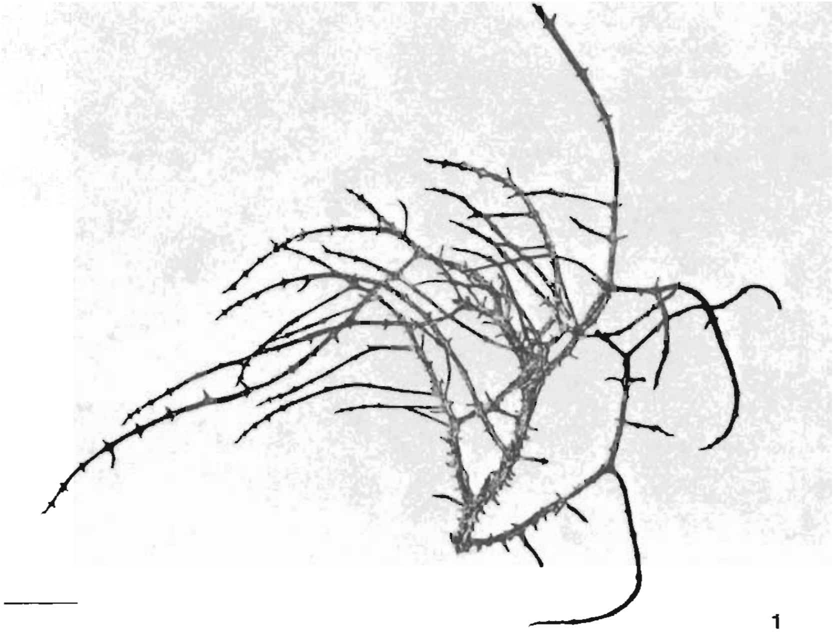
Once the salt is washed out of the thalli and they are redried, as often happens in the case of air-dried herbarium specimens, a subsequent resoaking can lead to the carrageenan wall matrix dissolving and the specimen being lost. This probably accounts for the paucity of type materials for the older species and the poor physical condition of those extant. Resoaking in 5% solutions of calcium (for iota-carrageenan forms) or potassium salts (for kappa-carrageenan forms) tends to prevent such losses in recently collected specimens. The high sulfur content of these matrix materials, in time, leads to such degradation that old dried specimens usually disintegrate when wetted and manipulated.

Almost none of the taxonomic treatments, with the notable exception of Weber-van Bosse (1928), takes into account morphological variations found within a given species. It is, thus, not possible to make a key to all the species that is readily useful without going into extensive details that are beyond the scope of this paper. Similarly it is impossible to key out correctly every specimen of some of the closely related, but rather geographically distinct, species such as those related to *Eucheuma denticulatum* or those in the *E. alvarezii/E. striatum* complex. Yet these, like the oft-mentioned *E. cottonii* Weber-van Bosse, may be distinguished by the infrared absorption spectra of their gels or by their cellular anatomy.

Investigations of type specimens and other materials related to the species names have led to the belief that many of the 43 specific epithets are probably synonyms applying mostly to a few of the commercial species. A few other species are believed to be separate entities but they are rare, relatively unknown, or are not commercially significant. Some, e.g., *Eucheuma crustiforme* Weber-van Bosse, are included in the key though we have little faith in their being a distinct taxon.

While all of the species in the key have been found in commercial lots of *Eucheuma*, there are only four species significantly utilized: *Eucheuma alvarezii* (see Doty this volume, figs. 1–8), *E. denticulatum* (Figs. 1–2), *E. gelatinae* (Fig. 3), and *E. striatum* (Fig. 4). Of these, *E. alvarezii* is the only kappa-carrageenan seaweed farmed for international commerce, but often with tiny amounts of *E. striatum* being included. In 1983 perhaps as much as 28,000 dry tons may have been produced and sold by the farmers. In the same period *Eucheuma denticulatum* provided most of the rest of the farmed *Eucheuma* crop and was used for its purely iota-carrageenan content.

Eucheuma gelatinae (Fig. 3) is used in international commerce for its distinctive, furcellaran-like carrageenan, but its commercial importance is minimal. In some years, 100 to 200 tons of it, all from Taiwanese or Philippine wild harvests, may have been sold for local use and exported in small lots (e.g., 10 to 20 tons) from the country of origin. Although this species is farmed to a minor extent on Hainan Island, China, neither this farmed seaweed nor its extractive are traded internationally insofar as we know.



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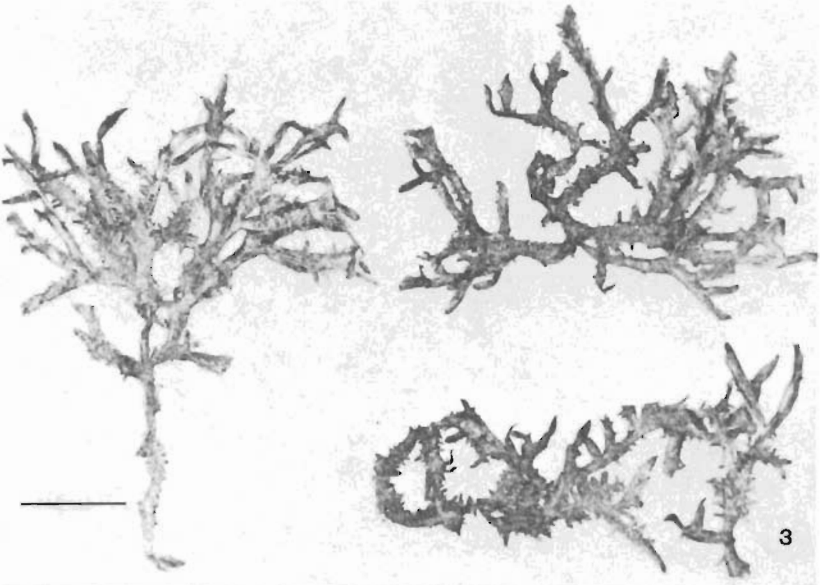
Figs. 1–2. *Eucheuma denticulatum* (scale line = 5 cm). Fig. 1. A simple cultured form from Hawaii (MSD #20869, BISH). Fig. 2. An unusually oppositely branched form from a farming effort in Indonesia (MSD #20676, BISH).



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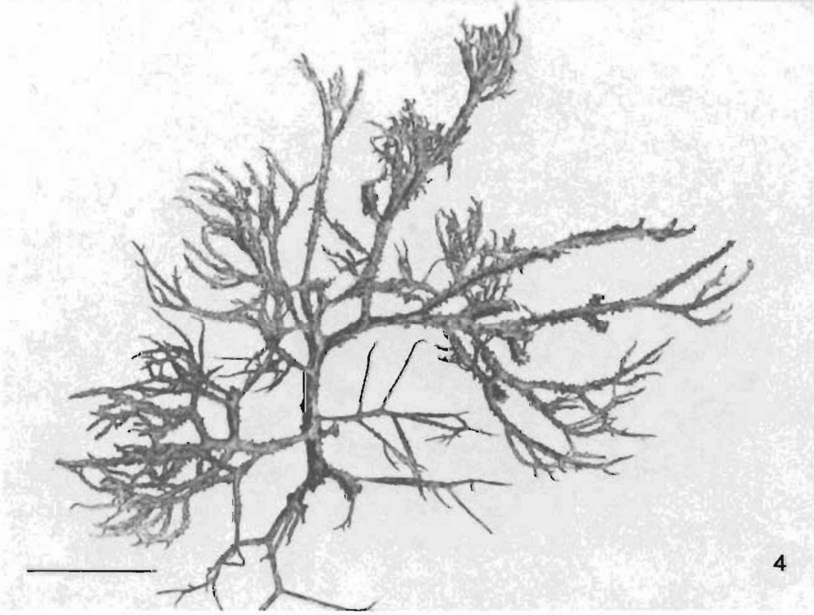

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Figs. 3–4. *Eucheuma* (scale line = 5 cm). Fig. 3. *E. gelatinae*; farm produced along the east coast of Hainan Island, China (MSD #31779, BISH). Fig. 4. *E. striatum*; an unusually light-sensitive spiny form from the southern Philippines but grown in Hawaii (MSD #32404, BISH).

The other species mentioned, with little exception, do not get into international commerce in significant quantities. When they do they are mixtures of one or more species from collected wild crops coming largely from Taiwan, Tanzania, or Indonesia.

Discussion of the Vegetative Basis for *Eucheuma* Taxonomy

Problems with the basis for taxonomy of the species met in constructing the above key have led to a reconsideration of the features used for subgeneric classification. Therefore, the following rather hypothetical discussion, often based on as little as one observation, focuses only on the principal commercial species.

Weber-van Bosse began recognizing (1913, 1926) two sections within *Eucheuma* based on vegetative criteria. In her key to the "Siboga" species (1928), if a species had a central axial core she placed it in "*E.* sect. *Axiferae*;" those without a core were *E.* sect. "*Anaxiferae*." Closer inspection of *Eucheuma* medullary cores, however, reveals the likelihood that Weber-van Bosse's subgeneric classification may be an oversimplification. As is, Weber-van Bosse's two sections are neither in correlation with the type of carrageenan contained nor, depending on interpretation or where in a thallus the anatomical evidence was seen, the presence of an axis. Other genera in the Solieriaceae, e.g., *Dicurella* Harvey ex J. Agardh and *Trematocarpus* Kützing, have also been found (Searles 1969) to have a range of filamentous to pseudoparenchymatous medullary tissues. Thus within these three genera it may well be acceptable to distinguish species or species groups on a vegetative basis.

The use of detailed vegetative cellular anatomy appears desirable, if only for its taxonomic utility. If the anatomical features are consistent, then species can be determined on nonreproductive material of any of the life forms. This has practical advantages for taxonomy since farmed commercial lots are often sterile and "if one doesn't get the taxonomy right, he doesn't know what he is talking about."

Weber-van Bosse shows such an awareness of the natures of the species occurring outside the "Siboga area" that it is quite possible she might have modified her two-subgeneric-group system if she had produced a monograph of the world's species. Thus the basic vegetative anatomy of *Eucheuma* is expanded upon below, avoiding reference to the multiaxial nature of the genus and the use of "filament" for anything other than for a row of related cells.

Weber-van Bosse (1928) recognized the axial medullary tissue of a *Eucheuma* as being made up of large primary cells and relatively small secondary cells. This presence of secondary small cells means that one can distinguish *Eucheuma* from *Gracilaria*. That is, in studying the microscopic medullary details there are large cells mixed with small ones in the conspicuously pseudoparenchymatous medulla of a *Eucheuma* that are not found in the species of other genera with which it otherwise might be confused by external appearance. For example, the presence of secondary cells in the medulla of *Eucheuma cottonii* distinguishes it from *Gracilaria eucheumoides*. The two are look-alikes and both are apt to be nonreproductive, abundant, and overlapping in distribution.

It appears there are at least three kinds of secondary cells, the thylles and two other kinds, which form axial filaments (Weber-van Bosse 1928). Kützing

(1868) and J. Agardh (1852) recognized that the cells in the central part of the medulla of a *Eucheuma* are not all alike. Weber-van Bosse developed the idea (1913, 1926, 1928) of their taxonomic use at the species level. Yet she may not have recognized the apparent differences between the axial filaments in the different species, although in her descriptions of "hyphae" she may have laid the basis for such distinctions.

Weber-van Bosse (1928) mentioned the core disappearing soon below the apex in some species and, in some such cases, she apparently thought it absent. In the case of *Eucheuma striatum* having axial filaments similar to those found in *E. inerme* and *E. gelatinae*, Weber-van Bosse (1928) placed the first of these three species in her subgeneric group *E.* sect. *Anaxiferae* and the last two in *E.* sect. *Axiferae*. *Eucheuma inerme* and *E. gelatinae* are very different from each other, and from both *E. denticulatum* and *E. isiforme*, on the basis of their phycocolloid gels and different aspects of their morphology. The axial filaments of the latter two species are very distinct from those of the first three.

Expanding Weber-van Bosse's (1928) usage of axial filaments, it is proposed that two kinds be recognized, axial rhizoids and axial hyphae. In addition, the thylles Weber-van Bosse (1928) described may either be solitary or in irregular groups or "strands." However, it is only axial rhizoids or axial hyphae that appear to accumulate, giving rise to the appearance of axial cores. While a strand is a single simple filament (i.e., a row of cells), a core is a longitudinally extensive accumulation of filaments at the center of the axis, whether or not it includes primary cells. At least one of the two kinds of axial filaments, either the axial rhizoids or axial hyphae, is present in the apical segments of every commercial *Eucheuma* species; thylles are in some.

Gabrielson (1983, figs. 2–3) describes and illustrates the axial rhizoids in *E. isiforme* as ascending or descending and bearing pits along their surfaces. Weber-van Bosse (1928) (and personal observation) shows these axial rhizoids have thick walls with the lumen less than one-fifth of the cell diameter in *E. isiforme, E. denticulatum*, and *E. uncinatum*. The lumen and its protein-rich content are often only about 2 μm in diam. and may have been incorrectly reported as cell diameter.

The second kind of axial filament, axial hyphae *sensu stricto*, is of thin-walled cells about five times as long as their diameters and has flat transverse walls. The lumens of axial hyphal cells are often five or more times as broad as the transverse and lateral walls are thick. Weber-van Bosse (1913) vaguely mentions this type of cell being present, e.g., in the apical segments of *Eucheuma cottonii*. She felt they enlarged below, and so, looking more and more like the primary cells, appear to have disappeared when sought still further below.

Thylles are well described by Weber-van Bosse (1928) and do not form axial cores. They develop as bubble-like outgrowths from the relatively large inner primary medullary cells. They appear to arise from an otherwise normal secondary wall pit, and resemble tyloses in flowering plants. However, thylles do not protrude into another cell through a pit; thus they are not inside cells but protrude into intercellular space. (Tyloses are inside a cell adjacent to the cell that produced them.) Thylles may in turn bear secondary, tertiary, etc., thylles with all thylles and other medullary cells forming interconnecting pits. Such chains of thylles sometimes branch and contain somewhat irregular cylindrical cells. These short filaments may wander irregularly in the intercellular spaces rather than form regular filaments of descending nature. In general, thylle-rich axes have considerable intercellular space.

Determination of the axial morphology[2] and nature of the secondary cells of a *Eucheuma* thallus is facilitated by studying longitudinal sections of the most apical 3 to 4 mm and transverse sections of the next 1 to 3 mm. Use of this most distal portion of the apex reduces the confusion that can result from using information based on random sections at different distances from the apex or due otherwise to ontogeny, age, or growth conditions. Often macerated material is useful from apical portions as is repeating the study of transverse sections from regions further down a thallus. These latter reveal the changes that are wrought in the secondary cells in time." The macerated materials supplement the longitudinal sections largely in respect to the origins and fate of the secondary cells.

Discussion of the Sections Proposed in the Genus *Eucheuma*

On the basis of their vegetative anatomy, secondary medullary cells, chemical type of phycocolloid contained, and other attributes, the principal commercial species seem to fall naturally into the sections described below (Table 1). Since this study is of today's commercial species, it makes no attempt to be monographic. The noncommercial *Eucheuma isiforme, E. uncinatum*, and *E. arnoldii* are included only to stabilize more fully Weber-van Bosse's (1928) separation of the species of *Eucheuma* into two taxonomic sections. The other species of the genus not included in Table 1 may or may not belong in the following four sections as now defined.

Table 1. The Sectional Classification of *Eucheuma*. The carrageenan type is shown in parentheses followed, in the same column, with a reference to illustrations for a species in each section. (See Doty, Figs. 1-8, elsewhere in this publication for illustrations of *E. alvarezii*.)

Section *Eucheuma* (Iota) Figs. 1-2	Section *Anaxiferae* (Iota) Kraft 1972	Section *Gelatiformia* (Kappa) Fig. 3	Section *Cottoniformia* (Kappa) Fig. 4
E. denticulatum	*E. arnoldii*	*E. gelatinae*	*E. alvarezii*
E. isiforme			*E. striatum*
E. uncinatum			

Eucheuma sect. *Eucheuma*

Synonym: *Eucheuma* sect. *Axiferae* Weber-van Bosse, as "Axifera," 1928, p. 404, includes the lectotype for the generic name, *E. denticulatum* (Burman) Collins et Hervey.

Lectotype: *Eucheuma spinosum* (Linnaeus) J. Agardh, as "*spinosa*" [= *Eucheuma denticulatum* (Burman) Collins et Hervey].

The species in this section differ from the others in the genus in having an axial core of rhizoids. The generally cylindrical axes bear whorls of primary branches which are initially determinate spines. Later one spine (Fig. 1) or more (Fig. 2) in a whorl may produce an indeterminate branch. Members of *Eucheuma* sect. *Eucheuma* produce iota-carrageenan.

The length of individual rhizoidal cells (seen in longitudinal section) usually exceeds ten times their diameter. The cell lumen is often several times smaller

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[2] Various authors have commented on the lack of herbarium materials of these common large algae. Risking redundancy, it seems worthwhile to say again that once a *Eucheuma* is dead and dried, in the absence of an excess of calcium ions in the case of the iota-carrageenan forms or potassium ions for kappa-carrageenan forms, its major wall materials (Table 1) are more or less water soluble (though the minor wall components such as cellulose fibers are not). Thus in examining air-dried specimens and preparing materials for microscope study, one should become aware of the carrageenan expected to be present. Correspondingly, then, any aqueous solutions used in making preparations of *Eucheuma* should contain as much as 5% calcium or potassium chloride. These salts may interfere with staining, but without them the wall structure may become a featureless gel between adjacent cell lumens.

than the cell's outside diameter; thus the walls are relatively thick. The end walls are difficult to distinguish in the rhizoids and seem to be more notable as constrictions in the outer wall profile in association with a narrowing of the cytoplasts of adjacent cells. There are often conspicuous pit-plug connections along the lateral surfaces of the rhizoids (Gabrielson 1983).

This section is the traditional "spinosum" of commerce. For that reason the authors were inclined initially to name this section "spinoformae." However, the International Code of Botanical Nomenclature requires (Voss et al. 1983) that the *E.* sect. *Axiferae* Weber-van Bosse ("Axifera" 1928, p. 408) be treated as a synonym of the autonym *E.* sect. *Eucheuma* since it included the lectotype of the generic name. Thus we use the tautonymical *Eucheuma* for the genus and *Eucheuma* for the section in which one would place *E. denticulatum.*

In the Linnaean Herbarium in London, England, the type specimen for *Eucheuma spinosum* is readily accessible. Figure 1 shows its general character well. The precise origin of this Linnaean specimen appears to be unknown. Since Linnaeus was in close correspondence with J. Burman (father) and N. L. Burman (son) and often identified their plant specimens (Stafleu and Cowan 1976, pp. 413-417), he may have named the algal materials of the son. N. L. Burman's (1768) algal specimens, including the one(s) for the specific epithet, *Fucus denticulatus*, have never been found. Linnaeus (1771) cites Burman's (1768) name as an earlier synonym of his own creation, *F. spinosus*, and Linnaeus did preserve his voucher specimens. Thus it is proposed here that the Linnaean specimen may actually be the Burman material and the type for both specific epithets (see Dixon 1962 for additional information).

Among the names often found associated with the species of this section are the more recent *Eucheuma muricatum, E. spinosum*, and *E. serra*. *Eucheuma serra* is a member of a different section and not now in international commerce; thus it is not treated here.

Currently the world's supply of purely iota-carrageenan comes from two species: the "*Gigartina radula*" of the trade, a wild crop seaweed from South America and not a *Eucheuma* in any sense, and *Eucheuma denticulatum.* There is perhaps no wild crop material of the latter in the trade any longer unless it comes from African or Indonesian sources.

The commercial use of *Eucheuma uncinatum* from the Gulf of California is incipient. Its gel is more reactive to calcium than that from *E. denticulatum.* Various efforts to produce *E. uncinatum* consistently in commercial quantities have been unsuccessful (Parker 1974), if for no other reason than its brief seasonal appearance. From time to time local or cottage industry use of *Euchuema isiforme* in the Caribbean is reported, but this species does not seem to be a part of international commerce.

The species or subspecies of this section are individually very variable, as seen in the case of *E. uncinatum* Setchell et Gardner (Dawson 1961; Norris, this volume). There are also wide ranges of form in *E. isiforme* (Caribbean), *E. jugatum* J. Agardh, and *E. horridum* J. Agardh (both Indian Ocean), but these no longer seem to get into commerce now that farming of *E. denticulatum* is doing well in the Philippines (Doty 1973, 1978, 1979; Doty and Alvarez 1975). Some forms of all these species are very similar superficially and may be characterized as being cylindrical and bearing whorls of spines at predictable intervals along their indeterminate primary branches. These species grow at different places around the world, and their iota-carrageenans differ to a minor extent. All members of this section in commerce are commonly called "spinosum."

Eucheuma sect. *Anaxiferae* Weber-van Bosse, emend.

Lectotype: *Eucheuma arnoldii* Weber-van Bosse (selected here from among the species given by Weber-van Bosse 1928, pp. 409-410).

Eucheuma section *Anaxiferae*, here emended, is recognized by the presence of whorls of spines on the indeterminate and determinate branches and by the gel-wall matrix materials of largely iota-carrageenan. There are no axial hyphae or rhizoids. Thylles are abundant and scattered in the medulla.

This species is rarely seen (even as a contaminant) in commercial lots of seaweed. It produces an iota-carrageenan.

There is much variability of this and related species; most of their forms are not common. Kraft (1972) has provided very adequate illustrations and a discussion of *Eucheuma arnoldii* and its forms, including its descriptive ecology and unusual mimicry of coelenterate corals. The senior author has found this species readily farmable in some shallow water, near surface habitats in the vicinity of coelenterate corals. Under these conditions it grew well and was a bright rosy pink.

Weber-van Bosse (1928) included several species in her *E.* sect. *Anaxiferae*. Among her original list was the currently commercial species, *E. striatum*, which is treated below and now recognized in another section.

Eucheuma sect. *Gelatiformia* sectio nova

Distinguibilis a sectionibus ceteris praecipae prostratis segmentis similibus loris quae dorso-ventraliter compressa sunt et inclinationem basicam producendi seriae proliferationum vel dentitionum, duorum lateralium, ventraliter unius, dorsaliter unius varie exprimunt. Funiculus axilis hyphae compressus est. Producens kappa carrageenan.

Typus: *Eucheuma gelatinae* (Esper) J. Agardh (Fig. 3).

Eucheuma section *Gelatiformia* is distinguished from the other sections by the species having principally prostrate, strap-like segments which are dorsiventrally compressed (especially when grown near the surface). The type expresses a basic tendency to produce four rows of proliferations or dentations, two bilaterally, one ventrally, and one dorsally. The axial core of hyphae is compressed. Members of this section produce a kappa carrageenan.

Material of *Eucheuma gelatinae* believed to be E. J. C. Esper's in the herbarium Institut für Allgemeine Botanik, University of Hamburg (HBG) has been studied. It has the general features of this section, including the axial hyphal core; thus, this material is designated the lectotype for the species. The core structure of *E. gelatinae* consists of sinuous strands differing largely in degree from those found in *E.* sect. *Cottoniformia*. Furthermore the frond of *E. gelatinae* is dorsiventrally flat. Its axial core is more impressive and sinuous with considerably more intercellular space than usually found in members of *E.* sect. *Cottoniformia*.

The gel produced by *Eucheuma gelatinae* is a kappa carrageenan with low (e.g., 20%) sulfate. Because of this and other attributes, it is described as furcellaran-like; furcellaran being the carrageenan found in the red algal genus *Furcellaria* Lamouroux (Furcellariaceae, Gigartinales). In the trade *Eucheuma gelatinae* is often confused with and called "serra," resulting in considerable confusion. Buyers have come to consider anything sold under either name likely to be unreliable, as both names have been applied to seaweeds containing iota- and kappa-carrageenan.

Some tonnages of *Eucheuma gelatinae* are farm-produced on the east coast of Hainan Island, South China Sea (Tseng 1981). As yet this Hainan material has not gotten into international commerce, but is utilized within China. Tonnages of wild crop that occasionally get into international commerce are usually from Taiwan or the Phillipines. Taiwan is believed to be the largest producer of *E. gelatinae*, but most of the material is said to be used domestically as wall sizing. Small shipments of less than 20 tons were found in international commerce some ten to twenty years ago. Perhaps as much as 100 dry tons have found application in a year.

Eucheuma sect. *Cottoniformia* sectio nova

Sectio Cottoniformia distinguibilis a ceteris in genere et recognita presentia non compressi funiculi irregularis parietum tenuium hypharum axialium orientium ad apicem et extensarum per segmentum apicale est. Lumina cellularum hyphae compluriens latiora carassitudine parietis cellulae sunt. Materiae matricis parietis cellulae magna ex parte kappa carrageenan est. Aetate vel quando pergens longe sub apice funiculus permixtio gradus cellularum magnarum et parvarum est.

Typus: *Eucheuma alvarezii* Doty, elsewhere in this volume.

Eucheuma section *Cottoniformia* is recognized by the presence of a core of irregular, thin-walled axial hyphae present below the apical segment, and by the cell wall matrix materials which are largely of kappa-carrageenan. The hyphal cell diameters are about one-fifth their length. The transverse walls are thin, like the cylindrical lateral walls. The lumens are from six to ten times thicker (i.e., broader in diam.) than the cell walls. With age or far below the apex the irregular core becomes a mixture of large and small cells. It is not known if the large cells represent primary or secondary cells. The primary branches tend to be indeterminate in growth and irregularly arranged unless inhibited by their environment. Secondary branches may arise irregularly between the primary branches, perhaps at random, though they may be concentrated in particular portions of the thallus. They are usually relatively indeterminate in their growth.

Illustrations of the three varieties of the type species are provided by Doty (earlier in this volume, figs. 1–8). His illustrations show the critical axial core anatomy. Figure 4 provides an illustration of one form of *Eucheuma striatum*, another member of this same section. Some *E. striatum* varieties are unique in tending to have segments that are squarish or angular in transection due to a somewhat linear arrangement and the size of the branches or cystocarps. In some strains, due to the light sensitivity of the many short determinate branches on the indeterminate axes, the axes may appear to bear a host of down-turned short proliferations that (even when dried) look like the thorns of a rosebush, each with its tip directed toward the base of the thallus.

Cystocarps are embedded in, or protrude from, the segment surface. The presence of a fusion cell in the center of the mature carpospore-producing gonimoblast is characteristic of this section.

The anatomical tissues of the members of this section also include thylles. Thylles are described for *E. striatum* by Weber-van Bosse (1928) in some detail.

Grazing scars and wounds of different kinds heal rapidly with formation of a thin but obvious callus from which adventitious branches usually arise. If the wounding removes a branch tip, as a rule only one central adventitious branch arises. It will resume the growth in length of the wounded axis, leaving a swollen ring-like callus around its base.

Eucheuma section *Cottoniformia* may contain the world's largest red algal species, though some crustose coralline algae may be heavier as a result of their calcium carbonate deposits. Thalli of this species weighing over a kilogram are common and some may be over 2 meters long. One live specimen of the Philippine *E. alvarezii* weighed a little over 56 kilograms, and even larger ones have been seen in the field.

Potentially the world's major source of kappa-carrageenan, this cluster of species is referred to as "cottonii" by the trade. There are, however, several distinct species involved. Early in farming "cottonii" most of the material produced was what would be identified as *E. striatum* (Doty 1973; Parker 1974). After the discovery of *E. alvarezii* var. *tambalang*, the species *E. alvarezii* soon became, and essentially still is, the only kappa-carrageenan species farmed (Doty and Alvarez 1975).

The section name *Cottoniformia* is derived from the traditional trade name, pronounced as "cotton eye," for members of this kappa-carrageenan–producing section and not from the species name *E. cottonii*. *Eucheuma cottonii* Weber-van Bosse (1928) (Figs. 5–6), for reason of its different axial anatomy and carrageenan, is not included in this section. It is relatively rare in commercial shipments of the wild crop seaweed and has never been farmed.

Acknowledgements

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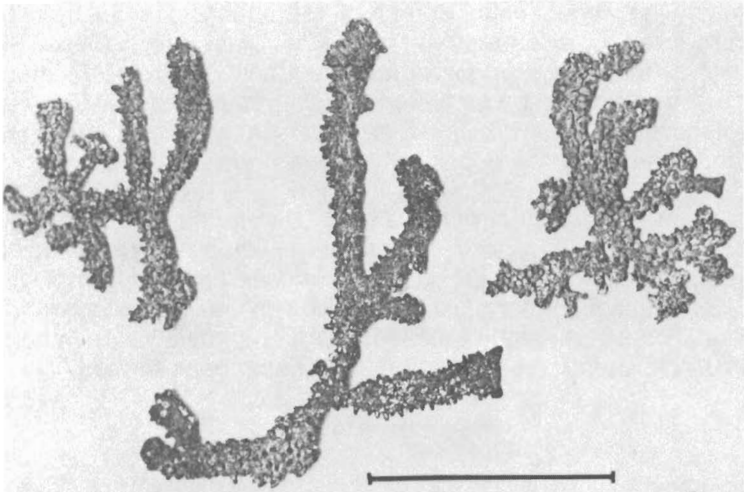

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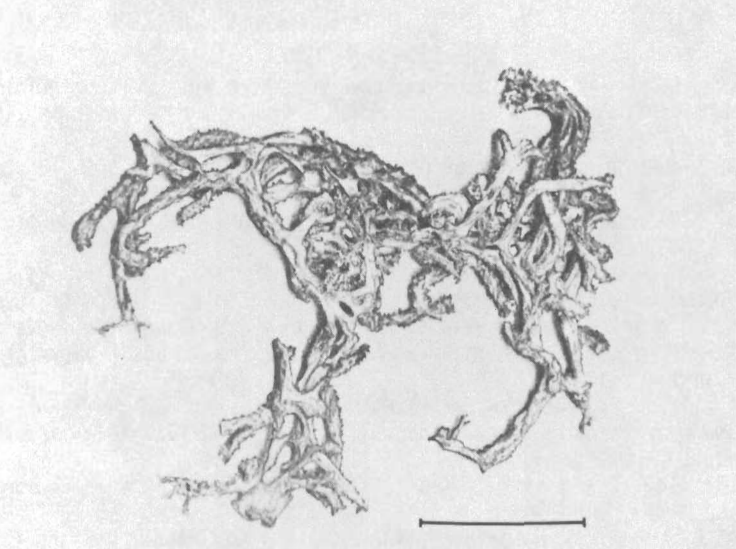

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Figs. 5–6. *Eucheuma cottonii* (scale line = 5 cm). Fig. 5. A non-imbricated form similar to the type; collected by Gerald T. Kraft at Cabulauan Island, Palawan Province, Philippines (MSD #531, BISH). Fig. 6. A simple imbricated form found in a commercial wild crop harvest from Tawi, Tawi Province, Philippines (MSD #14235, BISH).

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OBSERVATIONS ON *EUCHEUMA* J. AGARDH (SOLIERIACEAE, RHODOPHYTA) FROM THE GULF OF CALIFORNIA, MEXICO

James N. Norris

Most members of *Eucheuma* produce carrageenan, a natural product of commercial value which is extensively utilized by industry. There is one species, *E. uncinatum*, in the Gulf of California. A member of *E.* sect. *Eucheuma* (see Doty and Norris, this volume), it is an iota-carrageenan producer of economic potential that is not presently being exploited.

Eucheuma uncinatum Setchell et Gardner (Figs. 1–6)

Eucheuma uncinatum Setchell et Gardner 1924, p. 748, pls. 67–68; Dawson 1944, p. 288; 1961, p. 230, pl. 32; Norris 1973, p. 11.

Eucheuma johnstonii Setchell et Gardner 1924, p. 748, pl. 25, fig. 42, pls. 65–66.

Thalli cylindrical, and freely branched throughout, to 50 cm tall, arising from a discoid to conical holdfast. Primary axes abundantly branched, (3–)4–7(–10) mm diam. with slender, often long, branches with acute apices; most are sparsely to densely beset with simple or branched, short spinose proliferations. Medulla dense, a central cable-like strand of compacted longitudinal filaments, sometimes lacking in larger, older axes which appear centrally hollow; surrounded by parenchymatous cells, which become progressively smaller outwards to cortex of small cells.

Tetrasporangia zonate, 70–90 μm long, to 33 μm wide, the two end spores of each tetrad very greatly reduced in size (cf. Setchell and Gardner 1924, pl. 25, fig. 24), borne in slightly modified cortex, scattered over thallus. Cystocarps subspherical, large, 1.0–1.4 mm diam., protruding, near the base of lateral proliferations, either spread or clustered on the thallus; with a central parenchymatous sterile tissue, carposporangia in clusters within chambers with sterile filaments (no gonimoblast filaments present). Spermatangia narrowly elongate, anticlinally arranged in irregularly shaped superficial sori, on branch surfaces and proliferations; spermatia 2.5–3.0 μm diam.

Habitat: attached to rocks, from low intertidal to 12 m depths.

Distribution. Gulf of California: Puerto Peñasco to Guaymas. Pacific Mexico: Mazatlan, Sinaloa.

Type locality: Isla San Lorenzo del Norte, Gulf of California.

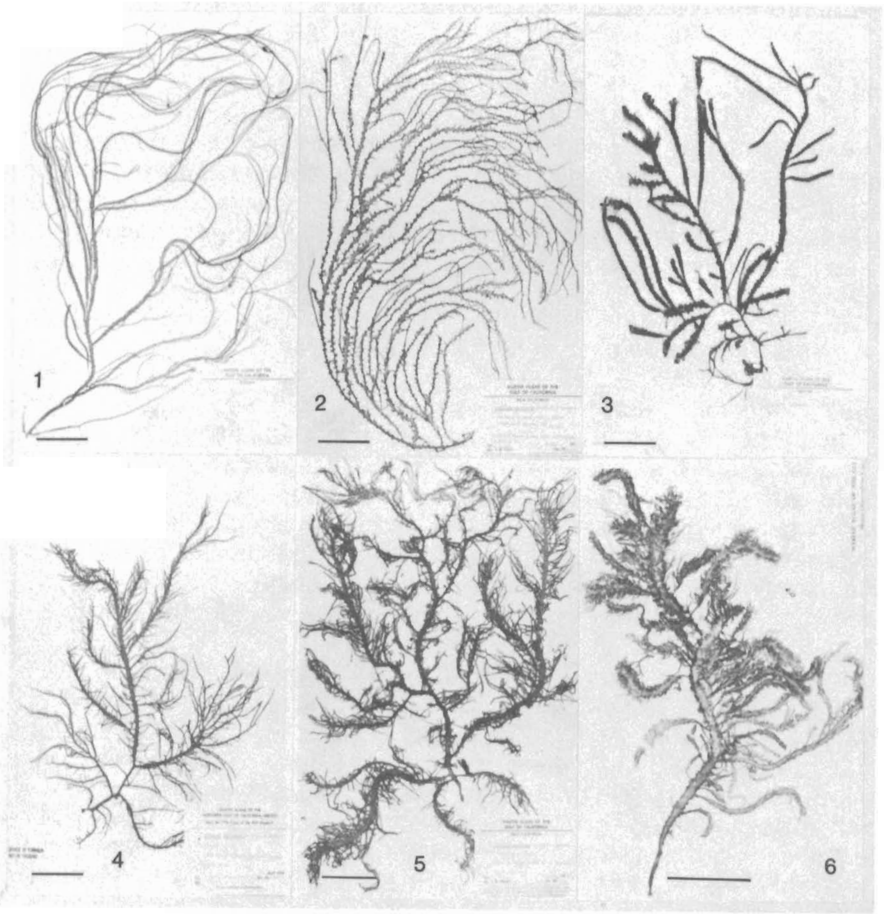
Type specimen: I. M. Johnston no. 86 (CAS #1349, now UC).

Discussion

Eucheuma uncinatum is an annual species, attaining its largest size in late spring and early summer, and is usually not present in fall. Setchell and Gardner (1924, pp. 748–749) originally described two species, separating *E. johnstonii* from *E. uncinatum* on the numerous, branched (rarely branched in cystocarpic specimens), acute, uncinate "ramuli" (= proliferations). Dawson (1944, p. 288) reported overlapping variation of the "fructiferous ramuli" (= proliferations), questioned the differences between the type specimens, and placed *E. johnstonii* in synonymy with *E. uncinatum*. As currently interpreted (cf. Dawson 1961), *E. uncinatum* exhibits a dazzling array of morphological forms (Figs. 1–6).

Eucheuma uncinatum is similar in external morphology to *E. isiforme* (C. Agardh) J. Agardh from the western Atlantic (Taylor 1960; Cheney and Dawes 1980). They differ in the nature of their mature cystocarps (parenchymatous sterile tissue vs. single solid fusion cell) and isoenzyme differences seen in electrophoretic analysis (D. Cheney, personal communication).

The construction of the mature cystocarp of *E. uncinatum* is similar to *Sarcodiotheca furcata* (cf. Setchell et Gardner 1903, pl. 24; fig. 41; Dawson



Figs. 1–6. Morphological variability of Gulf of California *Eucheuma uncinatum* (scale bar = 5 cm). Fig. 1. *E. uncinatum*, tetrasporangial thallus, Desemboque de San Ignacio, Sonora (#JN-5174, US). Fig. 2. *E. uncinatum*, Puertecitas, Baja California del Norte (#JN-5988, US). Fig. 3. *E. uncinatum*, cystocarpic thallus, Cabo Tepopa, Sonora (#JN-7078, US). Fig. 4. *E. uncinatum*, Punta Willard, Bahía San Luis Gonzaga, Baja California del Norte (#JN-5415, US). Fig. 5. *E. uncinatum*, Punta La Gringa, Bahía de Los Angeles, Baja California del Norte (#JN-3052, US). Fig. 6. *E. uncinatum*, spermatangial thallus, Punta Colorado (vic. Guaymas), Sonora (#EYD-1800, US).

1961, pl. 31, fig. 1) in that both have a central parenchymatous sterile tissue. However, pericarp and carpospore development appear to be very different (for *Sarcodiotheca furcata*, see Gabrielson 1982, figs. 23–28). The kind of cystocarp seen in *E. uncinatum* also resembles that of *E. gelidium* (J. Agardh) J. Agardh (cf. Cheney and Dawes 1980), but differs in that the carposporangia do not develop on gonimoblast filaments (which are lacking).

Based on electrophoretic (Cheney and Babbel 1978) and anatomical studies, Cheney and Dawes (1980) pointed out two distinct groups of *Eucheuma* in Florida, and suggested that those with the parenchymatous tissue in the cystocarp (i.e., *E. acanthocladum* (Harvey) J. Agardh, *E. echinocarpum* Areschoug, *E. gelidium*, and *E. schrammii* (P. et H. Crouan in Schramm et Mazé) be removed from the genus. In the absence of adequate specimens of the generic type, *E. spinosum* (Linnaeus) J. Agardh [= *E. denticulatum* (Burman) Collins et Hervey] (see Cheney and Dawes 1980, p. 623; Doty and Norris, this volume), Cheney and Dawes (1980) and Gabrielson (1982) have accepted the cystocarpic features of *E. isiforme* (C. Agardh) J. Agardh, with its single solid fusion cell and gonimoblast filaments, as representative of the genus.

The distinctive cystocarp construction and unusual tetrasporangia of *E. uncinatum* raise the interesting question of its generic placement. The construction of the cystocarp of *E. uncinatum* is quite different from the central single fusion cell seen in *E. isiforme*, which also has gonimoblast filaments present (cf. Cheney and Dawes 1980; Gabrielson 1983, figs. 12–15). I suggest with P. Gabrielson and D. Cheney that the Gulf's *E. uncinatum* is a distinct genus, and together in a separate study we hope to resolve its generic status.

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SECTION IV. *Gracilaria*

Part 1

Keys, Lists and Distributions of the Common Economically Important Species

THE RED ALGA *GRACILARIA* GREVILLE (GRACILARIACEAE, GIGARTINALES): INTRODUCTION

Isabella A. Abbott, Young Meng Chiang, Suzanne Fredericq, James N. Norris,
Roy T. Tsuda, Xia Bangmei, and Hirotoshi Yamamoto

Though the subgeneric features of *Gracilaria* Greville (1830), principally based upon locations of spermatangia (Yamamoto 1978), divide the genus, repeated studies recently made on a number of species of the genus (e.g., Bird and McLachlan 1982) have not unequivocally illuminated features that can be used reliably for purposes of species discrimination.

The *Gracilaria* specialists at the workshop were by far the largest working group as a result of the numerous poorly known species of this economically important genus. To elucidate each species clearly, material was brought by each person, and together anatomical features and whole-plant morphologies were compared. The specialists found it possible to resolve the definition of several widespread species, e.g., *G. lemaneiformis* (Bory) Weber-van Bosse and *G. salicornia* (C. Agardh) Dawson, and to refine the definition of the genus *Polycavernosa* Chang et Xia.

The construction of the keys that follow also reflects the clarification of species concepts by the authors. It thus becomes helpful to use each key (on a geographically limited group of species) to narrow the choice of species, and in fact to recognize the same species from the keys of two or more areas. All keys share with at least one other region at least one species; some regions share several taxa.

Our greatest difficulty is with the entity known as "*G. verrucosa*," which is recorded from "everywhere" with the widest kinds of ecological conditions. Some of the descriptions or specimens in general match those from the English coast (type locality), but critical comparisons show differences in details of the gonimoblast, pericarp, or spermatangia. The Japanese and Chinese specimens referred to *G.* "*verrucosa*" were found to be a similar taxon, but taxonomically not the same as the English *G. verrucosa*. Further, it is different from the Taiwan specimens under that name (Yang and Chiang 1982) especially in the gonimoblast structure. Also different were specimens from California called "*G. verrucosa*" (Abbott and Hollenberg 1976). Clearly, it is necessary to understand the features and their variation by which the British topotype material of *G. verrucosa* is to be recognized.

The distinctions that supposedly separate *Gracilaria blodgettii* Harvey from *G. cylindrica* Børgesen are equally confusing. Both have their type locality in the Caribbean basin, in Key West, Florida, and the Virgin Islands, respectively. The type specimens will need to be examined and compared with more recently collected and adequate material from the type localities.

Not one of the *Gracilaria* specialists would hazard a guess as to the identification of species without making many sections (of all specimens on a sheet!). The paper contributed by Fredericq and Norris (this volume) on the ontogeny of cystocarps, spermatangia, and tetrasporangia goes beyond these routine sections and reveals the foundation reflected in what is seen in sections of mature plants. These studies clarified and placed greater emphasis on the basal "nutritive filaments" that Chang and Xia showed in *Polycavernosa* (Chang and Xia 1963, pl. 1, figs. 7, 8). The origin and probable function of the basal absorbing filaments are totally different from the origin and purported function of "nutritive filaments" (called "absorbing filaments" in this volume) that connect the gonimoblast to the pericarp in some species.

Finally, many taxonomic features used in *Gracilaria* would probably not be noticed in other taxa, but no feature seems too inconsequential to examine in species as variable as these. We call attention to the shapes of cells that make up the pericarp, and follow Chang and Xia's (1984) recognition of several types. They must be correlated with other features that are used to distinguish species. With this kind of attention to detail, it seems possible to separate taxa and to mark the taxonomic boundaries by which they may be recognized.

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GRACILARIA SPECIES FROM BOTH CHINA AND JAPAN: KEY, LIST AND DISTRIBUTION OF COMMON AND ECONOMICALLY IMPORTANT SPECIES

Xia Bangmei and Hirotoshi Yamamoto

Key to the Economic Species

I. Fronds blade-like, margins entire .... *G. textorii* (Suringar) DeToni

II. Fronds cylindrical or slightly compressed, or complanate

  A. Fronds prostrate, complanate, fleshy, branching irregular or pinnate .... *G. eucheumoides* Harvey

  B. Fronds erect 1

1. Branches not constricted at bases; branching dichotomous, alternate, or unilateral; spermatangia in shallow conceptacles .... *G. bursa-pastoris* (Gmelin) Silva

1. Some or all branches slightly constricted at bases; branching alternate or unilateral

  (1) Fronds red, turning dark red when dried, holdfast remaining purplish-red; spermatangia superficial

    (a) Fronds slender, 0.5–2 mm thick, medullary cells 115–400 μm diam. .... *G. lemaneiformis* (Bory) Weber-van Bosse

    (b) Fronds robust, 3–5 mm thick, medullary cells 600–830 μm diam. .... *G. chorda* Holmes

  (2) Thalli slender, fronds pale to dark brown to brownish with some yellow-green

    (a) Many orders of branching, the lower order elongate; cystocarps semiglobose, non- or slightly rostrate; non- or slightly constricted at bases; spermatangia in deep, oval conceptacles .... *G. "verrucosa"*[1]

    (b) Few orders of branches, the final orders similar to main axes; cystocarps elongate spheres, markedly rostrate and constricted at base; spermatangia in shallow conceptacles .... *G. tenuistipitata* Chang et Xia

  (3) Fronds blackish or purplish brown; sometimes vermiform; last branching order tending toward slender unilateral laterals .... *G. vermiculophylla* Ohmi

  (4) Fronds olive-green in color; branches markedly constricted at bases and often appearing to be on small stalk; elongate, with few laterals; spermatangia in deep conceptacles .... *G. hainanensis* Chang et Xia

List and Distribution of Common Species

G. chorda Holmes. (Figs. 1–3)

Distribution: Hokkaido, Honshu, Shikoku, Kyushu (Okamura 1918, p. 41; Ohmi 1958, p. 50; Yamamoto 1978, pp. 119–121); Hainan Is., China (Chang and Xia 1976, p. 140).

G. blodgettii Harvey. (Figs. 10, 11)

Distribution: Fujian Province, Guandong Province, China (Tseng 1945, p. 161; Chang and Xia 1976, p. 129); Ryukyu Islands, (Ohmi 1958, p. 13; Yamamoto 1978, pp. 122–123).

G. "verrucosa." (Figs. 5–8)

Distribution: Yellow Sea and China Sea, except Hainan and Xisha Islands (Tseng et al. 1962, p. 137; Chiang and Xia 1962, p. 190; 1976, p. 125); all main islands of Japan and Okinawa (Ohmi 1958, p. 6; Yamamoto 1978, pp. 129–130).

G. arcuata Zanardini. (Fig. 18)

Distribution: Hainan and Xisha Islands; Dongsha Islands (Chang and Xia 1962, p. 190; 1976, p. 109); southcentral Japan (Ohmi 1958, p. 23); Okinawa (Yamamoto 1978, pp. 131–132).

G. bursa-pastoris (Gmelin) Silva. (Figs. 14, 16)

Distribution: Zhejiang and Fujian provinces; Hainan Is., China (Tseng et al. 1962, p. 140; Chang and Xia 1962, p. 190); central Japan (Ohmi 1958, p. 18; Okamura 1927, p. 160, as *G. compressa*).

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[1] *G. verrucosa* is placed in quotes since, as a result of the workshop, it is clear that while the Japanese and Chinese specimens under this name are similar, they are not identical with the British species. Further studies will be needed to solve this problem.

G. textorii (Suringar) DeToni. (Figs. 24, 27–30)

Distribution: Shandong and Liaoling provinces, China (Tseng and Chang 1952, p. 73; 1959, p. 45; Tseng and Cheng 1954, p. 107; Tseng et al. 1962, p. 141; Chang and Xia 1962, p. 196; 1964, p. 204); west coast of Hokkaido through main islands of Japan and Okinawa (Ohmi 1958, p. 40; Yamamoto 1978, p. 123).

G. eucheumoides. (Figs. 20, 21)

Distribution: Hainan and Xisha Islands, China (Chang and Xia 1962, p. 190; 1976, p. 134; Tseng et al. 1962, p. 141; Okinawa (Yamamoto 1978, p. 136).

G. tenuistipitata Chang et Xia. (Fig. 6)

Distribution: Locally abundant in Fujian and Guangdong provinces, China (Chang and Xia 1976, p. 102).

G. lemaneiformis (Bory) Weber-van Bosse (as *G. sjoestedtii*). (Fig. 34)

Distribution: Locally abundant in Shandong Province, China (Chang and Xia 1976, p. 135).

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GRACILARIA FROM CHINA: KEY, LIST AND DISTRIBUTION OF THE SPECIES

Xia Bangmei

Key to the Species

Translated and modified from a key in Chinese in Chang and Xia, 1976.

I. Thallus flat and leafy

- A. Thallus with denticulate or spiny outgrowths on the margins .... *G. denticulata* (Kützing) Weber-van Bosse
- B. Thallus with entire (smooth) margins .... *G. textorii* (Suringar) DeToni

II. Thallus cylindrical or more or less compressed

- A. Branches constricted at bases
  - 1. Some or all branches slightly constricted at bases; branching alternate or secund
    - a. Thallus red, turning dark red when dried; holdfast remaining purplish red; medulla of thin-walled cells; spermatangia superficial, arranged continuously or in patches; mature cystocarps may be taller than the diameter of the branch that bears them .... *G. lemaneiformis* (Bory) Weber-van Bosse
    - b. Thallus and holdfast purplish brown or brownish with some yellow-green color, turning dark brown or brownish, or yellowish pink when dried; medulla of thick-walled cells; spermatangia in deep conceptacles; height of mature cystocarp less than the branch diameter .... *G.* "*verrucosa*"[1]
  - 2. Branches markedly constricted at bases and often appearing to be on small (cylindrical) stalks
    - a. Thallus rigid, with gradual transition between medulla and cortex; no absorbing filaments between gonimoblast and pericarp .... *G. firma* Chang et Xia
    - b. Thallus fleshy, with abrupt transition between medulla and cortex; medullary cells large; with absorbing filaments between the gonimoblast and pericarp.
      - z) Small plants (5–10 cm tall), branches many and branching frequent .... *G. blodgettii*[2]
      - y) Large plants, about 15 to 45 cm tall; branches simple, elongated, up to 30–40 cm long .... *G. hainanensis* Chang et Xia
  - 3. Only some branches constricted at bases
    - a. Axes slender, 0.5–1.0 mm diam.; constrictions restricted to young branches .... *G. rubra* Chang et Xia
    - b. Thallus axes coarse, up to 5 mm diam., thick and succulent; constrictions occurring at bases of long branches .... *G. gigas* Harvey

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[1] *Gracilaria* "*verrucosa*," as explained elsewhere, requires restudy as it is clear that the Chinese specimens are not identical to those from Britain.

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[2] Dr. Yamamoto and I agreed at the workshop that what he and I have identified as *G. blodgettii* should be compared with type or topotype material in order to be certain of the identification.

B. Branches not constricted at their bases

1. Thallus succulent, sometimes soft or fragile; branch bases wide and apices slender; medulla of thin-walled cells .... *G. parvispora*[3]
2. Thick and fleshy thalli

   a. Branches compressed, prostrate; branchlets distichous; in culture resembling *Eucheuma gelatinae* .... *G. eucheumoides* Harvey
   b. Branches cylindrical, 3–4 mm diam., lateral branches irregularly pinnate; main axes gradually curved .... *G. arcuata* Zanardini

3. Mostly dichotomously branched; branches mostly originating from upper portion of thallus, giving an umbrella shape to thallus; branches 1.5–2 mm diam. .... *G. coronopifolia* J. Agardh

C. Thallus gradually tapering toward base; branching simple or complex

1. Main axis distinct; tips of branches frequently with bushlike rebranchings .... *G. chorda* Holmes
2. No distinct main axis, without bushlike small branches .... *G. tenuistipitata* Chang et Xia

D. Some or all branches with distinct nodes and internodes

1. Internodes obcuneate; branch apices each with a depression in its truncate surface

   a. No main axis apparent

      z) Segments constricted throughout the thallus with 3–4 branches, sometimes only 2, per node .... *G. salicornia* (C. Agardh) Dawson
      y) Segments never constricted from base to apex (if present, usually in upper parts); thallus generally matted; brittle .... *G. crassa* Harvey ex J. Agardh

   b. With main axis distinct in lower portion of thallus

      z) Main axis not constricted into nodes; with branching irregular; slightly or not constricted at the bases of branches .... *G. cacalia* (J. Agardh) Dawson

      y) Main axis with branching opposite or alternate; branch bases markedly constricted .... *G. minor* (Sonder) Durairatnam

2. Internodes cylindrical and segments curved, not enlarged at their tips; branches constricted 1– to several times; branching irregularly dichotomous, or lateral .. .. *G. articulata* Chang et Xia

E. Branches in upper portion of thallus tapering toward the bases; carpospores up to 40–50 μm diam. .... *G. megaspora* (Dawson) Papenfuss

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[3] *Gracilaria parvispora* (new species, this volume) has been identified as *G. bursa-pastoris* in China, but an examination of Dr. Abbott's material from Hawaii shows that the Chinese material is identical, and both differ from the European, especially in the structure of the pericarp.

Table 1. Vegetative Comparison of *Gracilaria* Species from China.

Species	Habit	Medulla	Cortex
G. chorda Holmes	terete, main axes ± distinct and elongated; several branches frequently arise from a single branch apex.	600-700 μm diam.	cortical cells 5-8 μm; cell transition ± abrupt.
G. "verrucosa"	terete, percurrent main axes; branching irregular; most branch bases slightly constricted.	166-365 μm; cell walls 10-30 (-40) μm thick.	cell transition gradual.
G. bursa-pastoris (Gmel.) Silva (= *G. parvispora* Abbott)	terete, sometimes slightly compressed in middle portions, fleshy texture; branching alternate, subsecund or divaricate, with patent axils; branches brittle when fresh; branch base not constricted.	700-1000 μm; cell wall 2-3 μm thick.	cell transition abrupt.
G. "blodgettii"	terete; branch bases markedly constricted.	500-615 (-1000) μm; cell wall 2-5 μm thick.	cell transition abrupt.
G. arcuata Zanardini	terete, fleshy and robust, axes frequently curved; branching irregularly alternate, dichotomous, or secund; branches constricted at bases, attenuated towards apex.	340-820 μm; cell wall 3–8 μm thick.	cell transition abrupt.
G. textorii (Sur.) DeToni	flat, foliose; branching dichotomous or subdichotomous; branch margins entire or proliferous.	150-282 μm; cell wall 5-9 μm thick.	cell transition abrupt.
G. coronopifolia J. Ag.	terete axes, bushy; branching subdichotomous, dense above with wide rounded angles.	183-365 μm; cell wall 6-9 μm thick.	cell transition gradual.
G. eucheumoides Harv.	compressed, ± prostrate, thick and fleshy; branching irregular or pinnate.	130-332 μm; cell wall 3-6 μm thick.	cell transition gradual.
G. crassa Harv. ex J. Ag.	terete, fleshy, repent; axes articulato-constricted in lower parts (not always in upper portions).	332-365 (-450) μm; cell wall 7-12 μm thick.	cell transition gradual.
G. denticulata (?)	foliose; branching subdichotomous; blade margins with spinose laterals.	ca. 132 μm; cell wall 6 μm thick.	cell transition abrupt.
G. firma Chang et Xia	terete, robust and rigid; branches markedly constricted at base.	230-360 (-500) μm; cell wall 10-20 μm thick.	cell transition gradual.
G. tenuistipitata Chang et Xia	terete, slender and elongated; gradually tapering from lower axis to holdfast.	225-390 μm; cell wall 13-16 μm thick.	cell transition abrupt.
G. lemaneiformis (Bory) Weber-v. Bosse	terete, elongate; main axis distinct; branching sparse and irregular; many thalli arising from a spreading holdfast.	215-400 μm; cell wall 3-8 μm thick.	cell transition abrupt.
G. rubra Chang et Xia	terete, very slender and elongated; branchlets abruptly constricted at base.	250-350 μm; cell wall 3-5 μm thick.	cell transition abrupt.
G. hainanensis Chang et Xia	terete, succulent; branches similar in shape to the axis, abruptly constricted at base.	500-550 (-950) μm; cell wall 7-10 μm thick.	cell transition abrupt.
G. articulata Chang et Xia	terete, succulent; articulations club-shaped, arcuate, 10-20 times as long as wide; lateral branches present.	ca. 1030 μm; cell wall 3-7 μm thick.	cell transition abrupt.
G. salicornia (C. Ag.) Daws.	terete, fleshy; articulations obcuneate, straight, > 8 times as long as wide; no lateral branches present.	ca. 540 μm; cell wall 2-6 μm thick.	cell transition gradual. gland cells abundant.

Table 2. Reproductive Comparison of *Gracilaria* Species from China.

Species	Center of Gonimoblast	Absorbing Filaments	Base and Shape of Cystocarp	Pericarp Layer	Spermatangia Type
G. chorda Holmes	small cells	–	conspicuous, semiglobose.	ca. 155 μm thick, undifferentiated tissue; cells horizontally oblong with rounded corners, in distinct order, with dense contents having ± extended arms.	Chorda
G. "*verrucosa*"	slightly large cells	+ (sometimes scarce)	conspicuous, semiglobose; usually not constricted or rostrate, or if so, only slightly.	115–250 μm thick, undifferentiated tissue; cells ± invisible anticlinal and radially arranged, with star-shaped contents.	Verrucosa; oval conceptacles, 80–90 μm deep.
G. bursa-pastoris (Gmel.) Silva (= *G. parvispora* Abbott)	isodiametric large and empty	+ (abundant)	small, conical -semiglobose	132–166 μm thick, undifferentiated tissue; cells mostly slightly compressed with distinct cell walls, not orderly arranged, cell contents occasionally remaining and having extended arms.	Textorii; shallow, 19–29 μm deep.
G. "*blodgettii*"	few large cells	+	globose	100–132 μm thick, differentiated into two tissues; cells elongated in outer layer, horizontally elliptical in inner, with obscure cell walls, ± distinct order, few contents remaining.	shallow or oval; 38–64 μm deep.
G. arcuata Zanardini	few large cells	+	globose, rostrate	250–280 μm thick, differentiated into two ± distinct layers; cells cuboid to elongated in outer layer, oblong with rounded corners in inner, with distinct cell walls, in slight anticlinal order, with dense contents in outer layer and few contents in inner.	
G. textorii (Sur.) DeToni	isodiametric	+	conspicuous, semiglobose to globose.	215–332 μm thick, undifferentiated cells; cells ± round with distinct cell walls, in slight anticlinal order, few contents remaining.	Textorii, 23–26 μm deep.
G. coronopifolia J. Ag.	few large cells	+	conspicuous	undifferentiated cells, cells roundish—elliptical with distinct cell walls, in slight anticlinal order, some cells with dense contents having short arms.	Verrucosa; 33–60 μm deep.
G. eucheumoides Harv.	isodiametric	+	globose, rarely constricted at base.	215–365 μm thick, differentiated into two layers, cells not distinct, in anticlinal order, cell contents irregular star-shaped in outer layer, flat star-like with bilateral longer arms in inner.	
G. crassa Harv. ex J. Ag.	isodiametric	+	semiglobose	215–280 μm thick, differentiated into two layers, cells elongate in outer layer, bricklike in inner with distinct cell walls, in distinct order, dense contents remaining	oval conceptacles
G. denticulata (?)	small cells	+	conspicuous, globose	332–415 μm thick, undifferentiated; cells not distinct, ± in distinct order, dense contents irregular, occasionally with extended shorter arms.	shallow conceptacles
G. firma Chang et Xia	smallest cells	-	conical or semiglobose	83–95 μm thick, undifferentiated, cells horizontally elliptical, ± distinct order, with distinct cell walls and some cell contents remaining	oval conceptacles, 66–116 μm deep.
G. tenuistipitata Chang et Xia	large cells	+ (rare)	semiglobose, rostrate, markedly constricted at base	72–102 μm thick, undifferentiated; cells roundish to ± horizontally elliptical, with distinct cell walls, irregular order, few cell contents remaining.	shallow conceptacles, 19–23 μm deep.
G. lemaneiformis (Bory) Weber-v. Bosse	small cells	-	globose or semiglobose, sometimes slightly rostrate or constricted	116–182 μm thick, undifferentiated, cells roundish to horizontally elliptical, with obscure cell wall, ± in distinct order, dense contents, compressed or nearly star-shaped.	superficial
G. rubra Chang et Xia	isodiametric, large	+ (abundant)	globose or semiglobose	82–170 μm thick, undifferentiated, cell roundish to compressed, with obscure cell walls, ± in distinct order, dense contents occasionally with extended short arms.	oval conceptacles, 33–43 μm deep
G. hainanensis Chang et Xia	isodiametric	+	conical	90–120 μm thick, undifferentiated, cells bricklike or horizontally oblong, with distinct cell walls, in distinct order, cell contents obscure	oval conceptacles, 39 μm deep
G. articulata Chang et Xia	large cells (few)	+	semiglobose	60–85 μm thick, undifferentiated; cells cuboid, horizontally oblong or elliptical, with distinct cell wall, in distinct order, few cell contents remaining.	oval conceptacles, 41 μm deep
G. salicornia (C. Ag.) Daws	isodiametric	+	globose	180–265 μm, differentiated into two layers, cells elongated in outer layer, bricklike in inner, with distinct cell walls, arranged in distinct order, with dense cell contents	oval conceptacles, 43 μm deep

List and Distribution of *Gracilaria* in China

Gracilaria arcuata Zanardini (Fig. 18)

Distribution: Hainan I. and Xisha Is., Guangdong Prov. (Chang and Xia 1962, 1976; Tseng et al. 1983).

Gracilaria articulata Chang et Xia

Distribution: Hainan I., Guangdong Prov. (Chang and Xia 1976; Tseng et al. 1983).

Gracilaria blodgettii Harvey (Fig. 11)

Distribution: Fujian Prov.; mainland and Hainan I., Guangdong Prov. (Tseng 1945; Chang and Xia 1976; Tseng et al. 1983).

Gracilaria bursa-pastoris (Gmelin) Silva (Fig. 14)

Distribution: Zhejiang, Fujian Prov.; mainland and Hainan I., Guangdong Prov. (Tseng 1936; Tseng et al. 1962, 1983; Chang and Xia 1962, 1976).

Gracilaria chorda Holmes (Fig. 1)

Distribution: Hainan I., Guangdong Prov. (Chang and Xia 1976; Tseng et al. 1983).

Gracilaria coronopifolia J. Agardh (Fig. 48)

Distribution: Taiwan and Hainan I., Guangdong Prov. (Chang and Xia 1962, 1976; Tseng et al. 1983).

Gracilaria crassa Harvey ex J. Agardh

Distribution: Taiwan; mainland and Hainan I., Guangdong Prov. (Chang and Xia 1962, 1976; Tseng et al. 1983).

Gracilaria eucheumoides Harvey (Fig. 21)

Distribution: Hainan I. and Xisha Is., Guangdong Prov. (Chang and Xia 1962, 1976; Tseng et al. 1962, 1983).

Gracilaria firma Chang et Xia

Distribution: Guangdong Province (Chang and Xia 1976; Tseng et al. 1983).

Gracilaria hainanensis Chang et Xia (Fig. 15)

Distribution: Hainan I., Guangdong Province (Chang and Xia 1976; Tseng et al. 1983).

Gracilaria rubra Chang et Xia

Distribution: Hainan I., Guangdong Province (Chang and Xia 1976; Tseng et al. 1983).

Gracilaria salicornia (C. Agardh) Dawson

Distribution: Guangdong (mainland and Hainan I.) Province (Chang and Xia 1962, 1976; Tseng et al. 1983).

Gracilaria lemaneiformis (Bory) Weber-van Bosse (Fig. 34)

Distribution: Shangdong Province (Chang and Xia 1976; Tseng et al. 1983), both as *G. sjoestedtii* Kylin.

Gracilaria spinulosa (Okamura) Chang et Xia

Distribution: Hainan I., Guangdong Province (Chang and Xia 1976).

Gracilaria tenuistipitata Chang et Xia (Fig. 6)

Distribution: Guangdong and Guangxi provinces (Chang and Xia 1976; Tseng et al., 1983).

Gracilaria textorii (Suringar) DeToni

Distribution: Huanghai, Shangdong, and Liaolin provinces (Tseng and Li 1935; Tseng 1936; Tseng and Chang 1952; Tseng et al. 1962, 1983; Chang and Xia 1962, 1976).

Gracilaria cacalia (J. Agardh) Dawson

Distribution: Hainan I., Guangdong Province (Chang and Xia 1962, 1976).

Gracilaria minor (Sonder) Durairatnam

Distribution: Naozhou I. and Hainan I., Guangdong Province (Chang and Xia 1962, 1976).

Gracilaria gigas Harvey

Distribution: Guangdong Province, excepting Hainan I. and Xisha Is. (Chang and Xia 1976).

Gracilaria megaspora (Dawson) Papenfuss

Distribution: Fujian Province (Chang and Xia 1976).

Gracilaria "*verrucosa*" (Fig. 8)

Distribution: Mainland China, excepting Hainan I. and Xisha Is. (Tseng et al. 1962; Chang and Xia 1962, 1976).

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GRACILARIA FROM JAPAN: VEGETATIVE AND REPRODUCTIVE KEYS AND LIST OF THE SPECIES

Hirotoshi Yamamoto

[Editors' Note: This key and the one that follows replace those on pp. 117–119 of Yamamoto (1978): Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish., Hokkaido University, vol. 25, no. 2, pp. 97–152.]

Vegetative Key to the Species

I. Fronds cylindrical or slightly compressed
  - A. Fronds prostrate throughout 2
  - B. Fronds partly prostrate or wholly erect
    - 1. Fronds partly prostrate, often articulated .... *G. crassa* Harvey ex J. Agardh
    - 1. Fronds erect, not articulated
      - a. Branch bases markedly constricted
        - + Fronds more than 50 cm long; cortical layer consisting of 2–3 cells .... *G. chorda* Holmes
        - + Fronds less than 50 cm long; cortical layer consisting of 1–2 cells .... *G. "blodgettii"*[1]
      - b. Branch bases slightly constricted
        - + Fronds more than 3 mm diam. .... *G. gigas* Harvey
        - + Fronds less than 3 mm diam.
          - x. Fronds vermiform, blackish or purplish-brown .... *G. vermiculophylla* (Ohmi) Papenfuss
          - x. Fronds slender, pale or dark brown .... *G. "verrucosa"*[2]
      - c. Branch bases not constricted
        - + Fronds fleshy, more than 3 mm thick .... *G. arcuata* Zanardini
        - + Fronds rigid, less than 3 mm thick .... *G. edulis* (Gmelin) Silva
        - + Fronds tender, branching dichotomous to unilateral, mid-portions sometimes compressed .... *G. bursa-pastoris* (Gmelin) Silva
        - + Fronds sometimes slightly compressed, ultimate branchlets dichotomous or spinous .... *G. coronopifolia* J. Agardh
    - 2. Fronds complanate, prostrate throughout .... *G. eucheumoides* Harvey

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[1] It would be desirable to examine type material or material from the type locality of *G. blodgettii* and of *G. cylindrica* since they appear to be closely related.

[2] I agree with my colleague Xia Bangmei that the Chinese and Japanese specimens of "*verrucosa*" are the same, and that they are different from *G. verrucosa* from Britain.

II. Fronds flattened

A. Margins entire

1. Fronds more than 5 cm long

a. Fronds curved and twisted, fleshy .... *G. incurvata* Okamura
b. Fronds not as above, leathery

\+ Medullary cells less than 600 μm maximum diam. .... *G. textorii* (Suringar) DeToni
\+ Medullary cells more than 600 μm maximum diam. .... *G. sublittoralis* Yamada et Segawa

2. Fronds less than 5 cm long .... *G. punctata* (Okamura) Yamada

B. Margins dentate

1. Fronds usually more than 3 mm wide, having cylindrical stalk .... *G. denticulata* (Kützing) Weber-van Bosse
2. Fronds usually less than 3 mm wide .... *G. ?purpurascens* (Harvey) J. Agardh

Table 1. Vegetative Comparison of *Gracilaria* Species from Japan.

Species	Habit	Medulla	Cortex
G. chorda Holmes	terete, to 150 (–200) cm long and to 5 mm diam.; branching alternate or all sides at irregular intervals; branch base slightly to considerably constricted, sometimes fasciated.	590–830 μm diam.	cortical cells 8–14 μm x 4.5–5.0 μm; cell transition abrupt.
G. "verrucosa"	terete, 8–50 cm long and to 2 mm diam.; branching irregularly alternate, sometimes secund; branch base slightly constricted.	400–540 μm x 270–400 μm	cortical cells 8.4–17 μm x 4–6 (–7.5) μm; cell transition abrupt.
G. gigas Harvey	terete, sometimes slightly compressed, to 30 cm tall, 4–7 mm wide; branching alternate and secund; branch base slightly constricted.	560–1138 μm x 437–910 μm	cortical cells 5.5–13.5 (–18) μm x 5.5–9.5 μm; cell transition abrupt.
G. bursa-pastoris (Gmel.) Silva	terete, sometimes slightly compressed, soft in texture; branching more or less dichotomous; branch bases not constricted.	440–560 μm x 320–480 μm	cortical cells 6–11 μm x 4–6 μm; cell transition abrupt.
G. "blodgettii"	terete, to 30 cm tall and 2.7–3.0 mm diam.; branching alternate or irregular; branch bases slightly constricted.	490–660 μm x 360–600 μm	cortical cells 6.7–11 (–13) μm x 6–8 μm; cell transition abrupt.
G. vermiculophylla (Ohmi) Papenf.	terete, 20–60 cm long and 2.5–3.0 mm diam.; branching alternate or irregular, branch bases slightly constricted.	400–490 μm x 270–365 μm	cortical cells 9–16 μm x 4.5–6.0 μm; cell transition abrupt.
G. arcuata Zanardini	terete or slightly compressed, 6–10 cm tall and 3–4 mm wide; branching alternate or dichotomous, sometimes secund; branches attenuated towards bases.	660–760 μm x 490–660 μm	cortical cells 6.7–13.5 μm x 5.5–8.8 μm; cell transition abrupt.
G. textorii (Sur.) DeToni	flat, 5–20 cm tall, 1–2 cm wide, 500–800 μm thick; branching irregularly dichotomous.	200–310 μm x 150–270 μm	cortical cells 9.5–13.5 (–16) μm x 6.5–11 μm; cell transition abrupt.
G. denticulata (Kütz.) Weber-v. Bosse	flat, 5–8 cm tall, 3–8 mm wide, above a long and terete stipe; branching dichotomous or irregular, with dentate margins.	100–167 μm x 100–159 μm	cortical cells 8.3–15 μm x 6.6–11 μm; cell transition abrupt.
G. coronopifolia J. Ag.	terete axes, sometimes anastomosing in young plants, becoming a loosely entangled mass; branching dichotomous or secund.	310–470 μm x 270–410 μm	cortical cells 6.7–10.8 (–13.5) μm x 6.8–8.0 μm, cell transition abrupt.
G. eucheumoides Harv.	compressed, growing + prostrate, to 15 cm long and 7–10 mm wide, 2.0–3.5 mm thick; branching regular or pinnate; branch bases somewhat constricted.	240–300 μm x 160–220 μm	cortical cells 7–13.5 μm x 4.5–9.0 μm; cell transition gradual.
G. crassa Harv. ex J. Ag.	terete, constricted at intervals of 0.4–1.0 cm, 2–3 cm tall and to 3.5 mm diam.; branch bases constricted.	270–440 μm x 250–340 μm	cortical cells 6.5–13.5 μm x 6.5–15 μm; cell transition comparatively gradual.

Reproductive Key to the Species
(see vegetative key for authors of binomials)

I. Spermatangia superficial, scattered continuously over frond surface; cystocarps destitute of absorbing filaments .... *G.* subgen. *Gracilariella* Yamamoto

A. Fronds cylindrical, large 60–150 (200) cm long, 2–5 mm diam., generally sparingly branched, sometimes provided with abundant short branchlets .... *G. chorda*

II. Spermatangial conceptacles depressed, spermatangia covering floor of conceptacle; cystocarps provided with absorbing filaments .... *G.* subgen. *Textoriella* Yamamoto

A. Fronds cylindrical

1. Branch bases markedly constricted .... *G.* "*blodgettii*[3]
2. Branch bases generally slightly constricted .... *G. gigas*
3. Branch bases not constricted, branching often unilateral and dichotomous .... *G. bursa-pastoris*

B. Fronds flattened

1. Frond margins entire

a. Fronds less than 5 cm long .... *G. punctata*
b. Fronds more than 5 cm long
\+ Fronds curved and twisted; fleshy .... *G. incurvata*
\+ Fronds not curved and twisted; leathery .... *G. textorii*

2. Frond margins dentate

a. Fronds usually more than 3 mm wide .... *G. denticulata*
b. Fronds usually less than 3 mm wide .... *G. ?purpurascens*

III. Spermatangial conceptacles deeply pot-shaped, spermatangia covering entire inner surface of conceptacles; cystocarps provided with many or few absorbing filaments .... *G.* subgen. *Gracilaria*

A. Fronds cylindrical

1. Fronds more than 3 mm wide, fleshy .... *G. arcuata*
2. Fronds less than 3 mm wide, abundantly branched

a. Fronds vermiform, blackish or purplish-brown; absorbing filaments infrequent .... *G. vermiculophylla*
b. Fronds slender, pale to dark brown; absorbing filaments abundant .... *G.* "*verrucosa*"[4]
c. Fronds rigid, pale or yellowish brown .... *G. edulis*

B. Fronds flattened .... *G. sublittoralis*

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[3] See note 1.

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[4] See note 2.

Table 2. Reproductive Comparison of *Gracilaria* Species From Japan.

Species	Center of Gonimoblast	Absorbing Filaments	Carposporangia	Base and Shape of Cystocarp	Spermatangia Type
G. chorda Holmes	30–50 μm x 6–30 μm	–	in chains	to 1.7 mm tall, to 2.0 mm wide.	Chorda
G. "verrucosa"	80–170 μm x 30–60 μm	+ (abundant)	in chains	0.9–1.3 mm tall, 1.3–1.6 mm wide.	Verrucosa, 100–120 μm deep, 56–83 μm wide.
G. gigas Harvey	170–260 μm x 80–140 μm	+	in chains	1.9–2.2 mm tall, 2.3–2.5 mm wide.	Textorii, 21–35 (–40) μm deep, 26–40 μm wide.
G. bursa-pastoris (Gmel.) Silva		+	in chains		Textorii, 26–36 μm deep, 24–32 μm wide.
G. "blodgettii"	230–340 μm x 80–135 μm	+	in chains	to 1.7 mm tall, to 1.7 (–2.0) mm wide.	Textorii, 33–56 μm deep, 33–43 μm wide.
G. vermiculophylla (Ohmi) Papenf.	80–100 μm x 23–35 μm	+ (rare)	in chains	to 1.5 mm tall, to 1.8 mm wide.	Verrucosa, 100–150 μm deep, 60–100 μm wide.
G. arcuata Zanardini		+			Verrucosa, 80–100 μm x 55–80 μm wide.
G. textorii (Sur.) DeToni	140–230 μm x 130–165 μm	+	in chains	to 1.8 mm tall, to 2.0 mm wide.	Textorii, 20–30 μm deep.
G. denticulata (Kütz.) Weber-v. Bosse	56–90 μm x 19–33 μm	+	in chains	to 1.7 mm tall, to 2.0 mm wide.	Textorii, 23–33 μm deep, to 35 μm wide.

List of the Japanese Species

(The following list is given mostly to aid in identifying the accompanying illustrations and is not meant to be exhaustive. Eds.)

Gracilaria arcuata Zanardini	
Gracilaria "blodgettii"	(Fig. 11)
Gracilaria bursa-pastoris (Gmelin) Silva	(Fig. 16)
Gracilaria chorda Holmes	(Fig. 2–3)
Gracilaria coronopifolia J. Agardh	(Fig. 44)
Gracilaria crassa Harvey ex J. Agardh	
Gracilaria denticulata (Kützing) Weber-van Bosse	(Fig. 25)
Gracilaria edulis (Gmelin) Silva	
Gracilaria eucheumoides Harvey	(Fig. 20)
Gracilaria gigas Harvey	(Fig. 38)
Gracilaria incurvata Okamura	
Gracilaria punctata (Okamura) Yamada	
Gracilaria ?purpurascens (Harvey) J. Agardh	
Gracilaria sublittoralis Yamada et Segawa	
Gracilaria textorii (Suringar) DeToni	(Figs. 24, 27–30)
Gracilaria vermiculophylla Ohmi	(Fig. 12)
Gracilaria "verrucosa"	(Figs. 5, 7)

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GRACILARIA FROM TAIWAN: KEY, LIST AND DISTRIBUTION OF THE SPECIES

Young Meng Chiang

I. Key to the Species

1. Branches cylindrical 2
1. Branches flat or compressed (at least in part) 7

    2. Branches with occasional constrictions, at least in some parts of thallus 3
    2. Branches without constrictions, or if there are any, only at the bases of branches 4

3. Plants erect; branch constrictions occur upward from the base of the thallus .... *G. salicornia* (C. Agardh) Dawson
3. Plants prostrate; branch constrictions infrequent, only in upper parts of the thallus .... *G. crassa* Harvey ex J. Agardh

    4. Plants partly prostrate 5
    4. Plants entirely erect 6

5. Branches slender, less than 1 mm diam.; profusely branched .... *G. coronopifolia* J. Agardh
5. Branches coarse, more than 1 mm diam. when fresh; branches few .... *G. arcuata* Zanardini

    6. Branches fine, less than 1 mm diam., with or without constrictions at base of branches .... *G. "verrucosa"*[1]
    6. Branches coarse, more than 1 mm diam., with distinct constriction at bases of branches .... *G. "blodgettii"*[2]

7. Thallus flat, foliaceous, and erect .... *G. denticulata* (Kützing) Weber-van Bosse
7. Thallus compressed and prostrate .... *G. eucheumoides* Harv.

Table 1. Vegetative Comparison of Taiwan Species of *Gracilaria*.

Species	Habit	Medulla	Cortex
G. salicornia (C. Ag.) Daws.	terete to slightly compressed; constricted throughout the thallus.	grading slightly outward; 63–115 μm diam., cell wall 2.5–5 μm thick.	1–2 layers; 3.8–15 μm x 6.4–12.5 μm.
G. "verrucosa"	terete and slender, < 1.0 mm diam.	gradual change outward; 150–400 μm diam., cell wall 10–40 μm thick.	3–5+ layers; 5–10 x 5–7 μm.
G. crassa Harv. ex J. Ag.	prostrate, terete to compressed; constrictions rare and only in upper parts.	gradual change outward; to 450 μm diam., cell wall 4–13 μm thick.	1–3 layers; 6–8 x 7–10 μm.
G. eucheumoides Harv.	prostrate and compressed.	100–200 μm diam., cell wall 3–5 μm thick.	1–2 outer cortical layers, 5–9 x 5–6 μm; 2–3 inner cortical layers, 15–33 μm diam.
G. "blodgettii"	terete, branches with distinct constrictions at base.	350–500 μm diam., 18–22 μm thick; abrupt change outward.	1–2 outer cortical layers, 5–10 x 2.5–5 μm; 2–3 inner cortical layers.
G. coronopifolia J. Ag.	terete, profusely branched.	gradual change outward; 100–225 μm diam., cell wall 10 μm thick.	2–3 outer cortical layers, 5–9 x 5–17 μm; 2–3 inner cortical layers.
G. denticulata (Kütz.) Weber-v. Bosse	flat, foliose, 370–440 μm thick.	abrupt changes; 44–154 μm diam.	1–2 outer cortical layers, 5–8 x 2–5 μm.

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[1] A comparison of material at the workshop showed that Taiwan specimens identified as "*G. verrucosa*" (Yang and Chiang 1982) differed from both the British specimens and from the Chinese and Japanese material as well.

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[2] I agree with Xia and Yamamoto that the Chinese, Japanese, and Taiwanese material identified by us as *G. blodgettii* is the same, but the question as to their identity with Caribbean and type specimens is still to be resolved.

Table 2. Reproductive Comparison of *Gracilaria* Species from Taiwan.

Species	Center of Gonimoblast	Absorbing Filaments	Base and Shape of Cystocarp	Pericarp Layer	Spermatangial Type
G. salicornia (C. Ag.) Daws.	slightly large cells.	+	nearly globose, not constricted at base.	10–12 layers	oval conceptacles.
G. "*verrucosa*"	slightly large cells.	+ (scarce)	semiglobose to globose, unconstricted to slightly constricted at base.	7–12 layers	
G. crassa Harv. ex J. Ag.	slightly large cells.	+	semiglobose	11–15 layers	deep conceptacles.
G. "*blodgettii*"	slightly large cells.	+	globose, slightly constricted at base.	8–10 layers	
G. denticulata (Kütz.) Weber-v. Bosse	very large cells, ± lobate in shape.	+	semiglobose to globose, constricted at base.	10–11 layers	

II. Descriptions of Economically Important *Gracilaria* from Taiwan

1. *Gracilaria* "*blodgettii*" (Fig. 10)

Thallus erect, solitary or in clumps, about 5–22 cm high; axis not percurrent; branches many, cylindrical, 1–3 mm diam., irregular to secund in arrangement with acute apices and usually basally constricted. Medullary layer composed of large, polygonal parenchymatous cells 350–500 μm diam., with cell walls 18–22 μm thick; medullary layer composed of 2 or 3 layers of cells; cortical layer 1 or 2 cells, irregular in shape, 5–10 x 2.5–5 μm diam.; cells increasing abruptly in size from the outside cortical layer to the medullary layer.

Tetrasporangia scattered over thallus (except in old portions), embedded in the cortical layer, spherical to oval, 20–40 x 15–27 μm, and cruciately divided. Cystocarps prominent, spherical, with slightly constricted base, 0.44 x 0.8 mm diam.; pericarp composed of 8–10 layers of cells, 100–130 μm thick; center of the gonimoblast composed of small parenchymatous cells; absorbing filaments present; carposporangia borne in chains. Spermatangial conceptacles elliptical in cross section, deeply embedded in the cortex.

2. *Gracilaria* "*verrucosa*" (Fig. 4)

Thallus erect, solitary, usually becoming a large, bushy clump when growing in brackish water ponds, up to 25 cm high; irregular to alternately branched but sometimes secund or dichotomous; cylindrical, slender, less than 1 mm diam., tapering toward the apex; with or without constricted bases. Medullary layer composed of more or less spherical cells of 150–400 μm, cell wall 10–40 μm thick, grading through 3 or 5 or more layers of small cells; cortical cells oval or elliptical, 5–10 x 5–7 μm.

Tetrasporangia scattered over the surface of the frond (except not in basal and apical portions), cruciately divided. Cystocarps prominent, spherical, about 1 mm high, 0.9 mm diam., base not constricted; absorbing filaments usually present, but sometimes absent; center of the gonimoblast composed of large parenchymatous cells; pericarp composed of 7–12 cell layers, 100–125 μm thick; carposporangia borne in chains. Spermatangial conceptacles oval, embedded deeply in tissue.

III. List of the Species with Their Geographic Distribution

1. *Gracilaria "verrucosa"* (Fig. 4)
   as *G. verrucosa* in Yang and Chiang 1982.
   Distribution: Taiwan (Yang and Chiang 1982, p. 57).
2. *Gracilaria crassa* Harvey ex J. Agardh
   Distribution: China including Taiwan (Chang and Xia 1976, p. 119; Yang and Chiang 1982, p. 58); Japan (Ohmi 1958, p. 25); Guam, Philippines, Malay Archipelago, Vietnam, Indonesia, Thailand, Ceylon, India, Red Sea (Dawson 1954b, p. 438).
3. *Gracilaria salicornia* (C. Agardh) Dawson
   Distribution: China including Taiwan (Chang and Xia 1976, p. 116; Yang and Chiang 1982, p. 62); Japan (Ohmi 1958, p. 27; Yamamoto 1978, p. 135); Philippines (Cordero 1981, p. 132; Dawson 1954a, p. 4).
4. *Gracilaria eucheumoides* Harvey
   Distribution: China including Taiwan (Chang and Xia 1976, p. 134; Yang and Chiang 1982, p. 62); Japan (Okamura 1936, p. 634; Yamamoto 1978, p. 136); Philippines, Indonesia, Malay Archipelago, Vietnam (Dawson 1954b, p. 438); Solomon Islands (Womersley and Bailey 1970, p. 317).
5. *Gracilaria coronopifolia* J. Agardh
   Distribution: China including Taiwan (Chang and Xia 1976, p. 132; Yang and Chiang 1982, p. 66); Ryukyu Islands (Yamamoto 1978, p. 133); Hawaiian Islands (Dawson 1949, p. 22).
6. *Gracilaria arcuata* Zanardini
   Distribution: China including Taiwan (Chang and Xia 1976, p. 109); Japan (Yamamoto 1978, p. 131).
7. *Gracilaria "blodgettii"* (Fig. 10)
   (as *G. blodgettii* in Yang and Chiang 1982, p. 66).
   Distribution: China including Taiwan (Yang and Chiang 1982, p. 66); Japan (Yamamoto 1978, p. 122).
8. *Gracilaria denticulata* (Kützing) Weber-van Bosse
   Distribution: Taiwan (Yang and Chiang 1982, p. 68); Japan (Yamamoto 1978, p. 126).

[Eds. Note: *Gracilaria denticulata* of Schmitz ex Mazza applies only to a South African taxon (Papenfuss 1951, p. 177), whereas Kützing's *Sphaerococcus denticulatus* from New Caledonia is a different species, transferred to *Gracilaria* by Weber-van Bosse and a later homonym. If the material from Taiwan and Japan are the same, they should have a new name.]

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GRACILARIA FROM HAWAII: KEY, LIST AND DISTRIBUTION OF THE SPECIES

Isabella A. Abbott

I. Key to the Species

1. Erect or upright plants 2
1. Low or prostrate plants 5

    2. Plants usually less than 15 cm tall 3
    2. Plants usually more than 15 cm tall 4

3. Branch intervals regular and numerous; bushy plants crisp, with rounded (corymbose) tops .... *G. coronopifolia* J. Agardh
3. Branch intervals irregular to distant; brittle plants in dense clumps .... *G. epihippisora* Hoyle

    4. Robust, coarse plants, frequently the main axes more than 2 mm diam.; branches few, the last orders usually unilateral (secund); plants never with rounded tops .... *G. parvispora* Abbott (new species, this volume).
    4. Slender, delicate plants, main axes rarely more than 1 mm diam., usually branching from near the base or along a percurrent axis; sporophytes and cystocarpic plants more branched than spermatangial plants .... *G. lemaneiformis* (Bory) Weber-van Bosse

5. Prostrate to semi-erect plants making ball-like mats with free ends erect; axes and branches cylindrical to flattened, brittle, regularly to irregularly constricted .... *G. salicornia* (C. Agardh) Dawson
5. Low, tufted plants in clusters 6

    6. Slender; wiry, erect fronds arising from rose-colored lower portion; rarely more than 5 cm tall, with relatively few branches .... *G. dotyi* Hoyle
    6. Compressed; bladelike, with tufts of terminal, finely dissected branchlets (in nature, with the aspect of a species of *Rhodymenia*) .... *G. abbottiana* Hoyle

II. List of Hawaiian Species of *Gracilaria* with Their Geographic Distribution and References

(Species marked with an asterisk are important food plants in the Hawaiian markets.)

Gracilaria abbottiana Hoyle (Fig. 49)

Distribution: Black Point, Oahu Island, Hawaii (type locality) (Hoyle 1978, pp. 299–303).

**Gracilaria coronopifolia* J. Agardh (Figs. 45, 47)

Distribution: Oahu Island, Hawaii (type locality); on all major Hawaiian Islands; Ryukyus (Yamamoto 1978); Hainan Is., China (Chang and Xia 1976); Philippines (Trono and Put 1982). See also Micronesia and Taiwan list of *Gracilaria* (this volume).

Gracilaria dotyi Hoyle (Figs. 50–51)

Distribution: Kahanahaiki, Oahu Island, Hawaii (type locality, Hoyle 1977a); Maili, Oahu Island; Lawai-kai, Kauai Island (new records).

Gracilaria epihippisora Hoyle (Figs. 52–53)

Distribution: Hilo Bay, Hawaii Island, Hawaii (type locality).

Gracilaria lemaneiformis (Bory) Weber-van Bosse (Fig. 35)

Gigartina lemaneiformis Bory 1828, p. 151; Weber-van Bosse 1928, p. 435; Abbott (this volume).

Distribution: Widely distributed in the Pacific (see under California species); in Hawaii on northeast and northwest coasts of Oahu Island; on east coast of Molokai Island.

**Gracilaria parvispora* Abbott (Figs. 13, 36–37)

Abbott (new species, this volume).

Distribution: South and northeast coasts of Oahu Island; northeast coast of Molokai Island, Hawaii. (May be more widely distributed in the Pacific, specimens under the name of *G. bursa-pastoris* should be re-examined.)

Gracilaria salicornia (C. Agardh) Dawson

Distribution: Philippines (type locality); Hawaii Island at Hilo Bay; Oahu Island at Kaneohe Bay, Kaloko, Waikiki, Ala Moana Park. See also distribution records under China, Taiwan and Japan.

III. The Common Species of Hawaiian *Gracilaria*

There is only one common species of *Gracilaria* in Hawaii, *G. coronopifolia* J. Agardh. This species favors somewhat sandy areas, and is frequent near mouths of streams or around freshwater springs in the marine environment. Oahu Island is the type locality of this species.

Gracilaria coronopifolia J. Agardh (Figs. 45–47)

J. Agardh 1852, pp. 592–3; Dawson 1949, pp. 22–24.

Thallus 3.5–15 cm tall, terete to infrequently compressed, branches 750–1500 μm diam., axis from a small, discoid holdfast, soon repeatedly branching to 5–6 orders; bushy, corymbose; no essential differences in branching pattern among the gametophytes and sporophytes, though some spermatangial plants are loosely branched and twice as tall as the female gametophytes in the same populations. Medullary cells with thick walls, grading gradually to 1- to 2-celled pigmented cortex; cystocarps with large, conspicuous absorbing filaments; center of cystocarp with large cells; carpospores in chains. Tetrasporangial thalli more common than gametophytic; tetrasporangia relatively small, 20–24 μm diam.; spermatangial plants with spermatangia in oval conceptacles (*Verrucosa*-Type), 60–80 μm deep.

Distribution: Reported from: Ryukyu Islands, Hainan Island, Philippine Islands, Palau, Ponape, and Guam. Specimens have not been critically examined from these locations. From comparisons made at the workshop, there seems to be a strong overlap of vegetative and perhaps reproductive features (not quantitatively evaluated) with *G. edulis* (Gmelin) Silva.

The Hawaiian name for this alga, one of the favorite food species in Hawaii, is "limu manauea" (Abbott 1984, p. 29).

Verrucosa-Type spermatangia are those described as occupying "pits" (Dawson 1949) or "conceptacles" (Yamamoto 1978); they are "pot-like" (Yamamoto 1978), resemble "crypts" (Bird and McLachlan 1982), or are "cup-like." Inasmuch as these words bring different images of shapes to those of different cultures, e.g., a Chinese or Japanese (tea) cup is invariably a different shape from an American coffee mug, or a cup of English or French bone china, it would appear that a more standard or uniform description that would accurately reflect the conceptacles should be sought. Such a shape as ovoid or obpyriform as illustrated in Hawksworth et al. (1983, pl. 16) would be satisfactory. For the cavities themselves, conceptacle is to be favored because of its use among other groups of algae and because the cavities have both the dimensions and complexities of some other algal conceptacles.

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GRACILARIA FROM THE PHILIPPINES: LIST AND DISTRIBUTION OF THE SPECIES

Isabella A. Abbott

This list is necessitated by the illustrations of specimens of *Gracilaria* species from the Philippines that were brought to the Guam workshop by Maxwell S. Doty. The captions bear Dr. Doty's identifications; I have not studied any of the specimens reported herein. This list is compiled from the literature available to me, and is incomplete since I do not have all of it.

Gracilaria arcuata Zanardini (Fig. 17).
  Weber-van Bosse 1928, p. 429; Velasquez et al., 1972, p. 146; Trono and Ganzon-Fortes, 1980, p. 95; Cordero 1981, p. 124; Trono et al. 1983, p. 32.
  Distribution: From north central Philippines (Pangasinan to Batangas), and Sulu archipelago.

Gracilaria arcuata var. *snackeyi* Weber-van Bosse (Fig. 17)
  This variety and two of its forms are recognized by Trono et al. 1983, p. 32.

Gracilaria canaliculata (Kützing) Sonder (Fig. 43)
  Cantoria et al. 1951, p. 187; Velasquez et al. 1972, p. 146.
  Distribution: North central Philippines.

Gracilaria compressa (C. Agardh) Greville
  Howe 1932; Meñez 1961; Velasquez et al. 1972, p. 146.
  Distribution: North central Philippines.

Gracilaria "*confervoides*"
  Montagne 1844; Velasquez 1952, 1953; Velasquez et al. 1972, p. 146.
  Distribution: "Philippines."

Gracilaria coronopifolia J. Agardh (Fig. 46)
  Galutira and Velasquez 1963, p. 508; Trono and Ganzon-Fortes 1980, p. 89; Cordero 1981, p. 127; Trono and DeLara 1981, p. 18; Trono and Put 1982, p. 19; Trono et al. 1983, p. 20.
  Distribution: From northern Philippines through central islands to Palawan.

Gracilaria crassa Harvey ex J. Agardh
  Domontay 1961, p. 291; Velasquez et al. 1972, p. 146; Saraya and Trono 1982, p. 41.
  Distribution: Central Luzon.

Gracilaria dactyloides Sonder
  Dickie 1876; Velasquez et al. 1972, p. 146.

Gracilaria disticha J. Agardh (Fig. 56)
  Illustrated material from: Sibuyan Island, Romblon Prov., central Philippines.

Gracilaris edulis (Gmelin) Silva (Figs. 55, 58)
  Cordero 1981, p. 128.
  Illustrated material from: Sabang, Guimaras Island, central Philippines.

Gracilaria eucheumoides Harvey
  Dickie 1876; Domontay 1961, p. 290; Velasquez et al. 1972, p. 146; Reyes 1970, p. 155; Trono and Bina 1973, p. 9; Trono and Ganzon-Fortes 1980, p. 93; Cordero 1981, p. 129; Trono and DeLara 1981, p. 18; Trono and Put 1982, p. 19.
  Distribution: North central to southwestern (Palawan) Philippines.

Gracilaria gigas Harvey (Fig. 39)
  Trono et al. 1983, p. 31.
  Distribution: Bulasan, Luzon (central Philippines).

Gracilaria lacinulata (Vahl) Børgesen
  Weber-van Bosse 1928, p. 434; Velasquez et al. 1972, p. 146.
  Distribution: Sulu Archipelago (southern Philippines).

Gracilaria lichenoides (Linne) Harvey
  Howe 1932; Cantoria et al., 1951, p. 187; Domontay 1961, p. 290; Velasquez et al. 1972, p. 146.
  Distribution: Central Philippines.

Gracilaria salicornia (C. Agardh) Dawson (Fig. 42)
  Galutira and Velasquez 1963, p. 506; Reyes 1970, p. 155; Trono 1973, p. 18; 1974, p. 90; Velasquez et al. 1972, p. 146; Trono and Ganzon-Fortes 1980, p. 93; Cordero 1981, p. 132; Trono and DeLara 1981, p. 18; Trono et al. 1983, p. 23.
  Distribution: Throughout the Philippines from Ilocos Norte to the Sulu Archipelago.

Gracilaria textorii (Suringar) DeToni (Fig. 26)
Cordero 1981, p. 135.

Gracilaria turgida Dawson
Saraya and Trono, 1982, p. 40
Distribution: Pacific Mexico and north central Philippines.

Gracilaria "verrucosa" (Fig. 9)
Galutira and Velasquez 1963, p. 507; Reyes 1970, p. 155; Velasquez et al. 1972, p. 146; Cordero 1981, p. 135; Trono et al. 1983, p. 17.
Distribution: Northern Philippines to Palawan.

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GRACILARIA FROM MICRONESIA: KEY, LIST AND DISTRIBUTION OF THE SPECIES

Roy T. Tsuda

I. Key to the Species

1. Thallus prostrate, low growing 2
1. Thallus erect 4

    2. Thallus conspicuously compressed, smooth, and at times with dentate margins .... *G. eucheumoides* Harvey
    2. Thallus cylindrical 3

3. Thallus cylindrical and segmented throughout .... *G. salicornia* (C. Agardh) Dawson
3. Thallus cylindrical, segmented near apices (or not at all), forming tight clumps in intertidal zone .... *G. crassa* Harvey ex J. Agardh

    4. Branches irregularly dichotomous, often not distinct from main axis; base more than 3 mm diameter .... *G. arcuata* Zanardini
    4. Branches short, irregularly arranged on main branches; base less than 2 mm diameter .... *G. edulis* (Gmelin) Silva[1]

Of the five species of *Gracilaria* listed in this key, only *G. edulis* may be different in Guam and Saipan from the remaining taxa as recognized in the regional keys (China including Taiwan, and Japan). A description of Guam and Saipan specimens is provided here.

Gracilaria edulis (Gmelin) Silva

Silva 1952, p. 293. *Fucus lichenoides* Gmelin 1768, p. 113. *Gracilaria lichenoides* (L.) Harvey

Thallus solitary, erect, cylindrical throughout, arising from a small discoid holdfast; main branches dichotomous, up to 14 cm high and less than 1.5 mm diam., with up to five orders of short branches less than 10 mm long toward the apices; branches irregularly arranged, acuminate; lower portions brown to purple; cartilaginous. Cortical layer of 1 or 2 rows of cells; outermost cells slightly elongated parallel to the surface, 4.6–9.2 μm long and 9.2–10.5 μm wide; medulla of 4–5 rows of polygonal cells increasing in diameter toward the center; outer medullary cells about 60 μm diam., increasing to 300 μm toward the center; transition between cortex and medulla abrupt.

Distribution within Micronesia: Guam and Saipan.

II. List and Distribution of *Gracilaria* within Micronesia

Gracilaria arcuata Zanardini (Fig. 19)

Distribution: Palau, Caroline Islands (Kanda 1944).

Gracilaria cacalia (J. Agardh) Dawson

Distribution: Saipan, Marianas Islands (Okamura 1904); Palau (Okamura 1916), Yap (Okamura 1904), Caroline Islands.

Gracilaria coronopifolia J. Agardh

Distribution: Palau (Kanda 1944), Ponape (Yamada 1941), Caroline Islands; Funafuti, Kiribati (Chapman 1955).

Gracilaria crassa Harvey ex J. Agardh (Fig. 40)

Distribution: Ponape and Kosrae, Caroline Islands (Trono 1969).

Gracilaria edulis (Gmelin) Silva (Fig. 54)

Distribution: Guam (Bryan 1974), Saipan (new report, here), Marianas Islands.

Gracilaria eucheumoides Harvey (Figs. 22–23)

Distribution: Palau (Kanda 1944), Yap (Trono 1969), Caroline Islands.

Gracilaria minor (Sonder) Durairatnam

Distribution: Palau (Kanda 1944; Okamura 1904; Tokida 1939), Yap (Reinbold 1901;

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[1] At the present time, there appears to be more than one species in the taxon referred to as *G. edulis* in Guam and Saipan; further critical studies are required for resolution.

Tokida 1939), Ponape (Glassman 1952), Caroline Islands.

Gracilaria radicans Hauck

Distribution: Saipan, Marianas Islands (Okamura 1916).

Gracilaria salicornia (C. Agardh) Dawson (Fig. 41)

Distribution: Guam (Bryan 1974; Safford 1905), Anatahan (Tsuda and Tobias 1977), Marianas Islands; Palau, Caroline Islands (Trono 1969).

Gracilaria "*verrucosa*"

Distribution: Guam (Safford 1905).

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GRACILARIA FROM THE GULF OF CALIFORNIA: KEY, LIST AND DISTRIBUTION OF THE COMMON SPECIES

James N. Norris

Key to the Species

1. Thallus essentially cylindrical throughout, or in part slightly compressed 2
1. Thallus distinctly complanate or flattened 6

2. Thallus cylindrical, lax throughout, irregularly branched from a percurrent axis up to 2 mm diam. .... *G. lemaneiformis* (Bory) Weber-van Bosse
2. Thallus cylindrical to more or less compressed, rigid and erect, variously branched mostly more than 2 mm diam. 3

3. Branching subdichotomous, subsecund or more or less pinnate; axes terete to slightly compressed 4
3. Branching dichotomous, irregular or multifarous; axes terete 5

4. Thallus not brittle, branching subdichotomous, sometimes secund and repeated; axes terete to compressed, up to 3 mm diam. .... *G. subsecundata* Setchell et Gardner
4. Thallus crisp and brittle, branching more or less pinnate from distinct, slightly compressed (oval) axes 3–7 mm diam. .... *G. pinnata* Setchell et Gardner

5. Small, erect (to 6 cm high) dichotomously branched plants with robust axes 1.5–3 mm diam. and more or less uniform diameter throughout .... *G. pachydermatica* Setchell et Gardner
5. Middle-sized plants (8–15 cm tall) with thick, turgid, secondary branches usually of equal length; axes 2–5 mm diam. .... *G. turgida* Dawson

6. Thallus less than 1 cm wide, with abundant spinose and/or dentate margins .... *G. crispata* Setchell et Gardner
6. Thallus over 1 cm wide with smooth margins or with proliferous lateral outgrowths on margins only, i.e., not spinose or dentate 7

7. Thallus thick (750–800 μm) usually with abundant marginal laterals or proliferations; cystocarps less than 900 mm diam. .... *G. rubrimembra* Dawson
7. Thallus thinner than 750 μm, usually without marginal proliferations; cystocarps 1–1.5 mm diam. .... *G. textorii* (Suringar) DeToni

List of the Common Gulf of California Species of *Gracilaria* with Their Geographic Distribution and References

Gracilaria crispata Setchell et Gardner
Dawson 1949, p. 26; 1961, p. 205; Norris, this volume, fig. 6.
Distribution: Puerto Peñasco to Cabeza Ballena.

Gracilaria lemaneiformis (Bory) Weber-van Bosse (Fig. 33)
Guaymas (Dawson 1949, p. 40; 1961, p. 206, as *Gracilariopsis sjoestedtii*; Abbott 1983, p. 561; Norris, this volume, figs. 9–10.
Distribution: Puerto Peñasco to Guaymas.

Gracilaria pachydermatica Setchell et Gardner
Dawson 1949, p. 18; 1961, p. 206; Norris, this volume, fig. 3.
Distribution: Puerto Peñasco to Cabeza Ballena.

Gracilaria pinnata Setchell et Gardner
Setchell and Gardner 1924, p. 751; Norris, this volume, fig. 4.
Distribution: Isla Angel de la Guarda to Bahía de las Animas.

Gracilaria rubrimembra Dawson
Dawson 1949, p. 32; 1961, p. 208; Norris, this volume, fig. 2.
Distribution: Puerto Peñasco to Guaymas.

Gracilaria subsecundata Setchell et Gardner
Dawson 1949, p. 20; Norris, this volume, fig. 7.
Distribution: Puerto Peñasco to Bahía Agua Verde

Gracilaria textorii (Suringar) DeToni (Fig. 31)
Dawson 1961, p. 211; Norris, this volume, fig. 1.
Distribution: San Felipe to Guaymas; Puerto Escondido to Isla Espiritu Santo.
Gracilaria turgida Dawson
Dawson 1949, p. 14; 1961, p. 213; Norris, this volume, fig. 5.
Distribution: Puerto Peñasco; Bahía de las Animas.

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Table 1. Habit and Vegetative Comparison of Gulf of California *Gracilaria* Species.

Taxon	Habit	Axis	Medulla	Cortex
G. crispata Setch. et Gardn.	clumps of several complanate blades, 4–7 cm tall.	flattened, re-divided into segments which become smaller and attenuated upwards to almost terete or spinose ultimate segments, margins with minute sharp dentation along lower portions and somewhat "crisped" in upper portions.	3–5 layers of isodiametric cells, to 200 μm diam.	outer: 2–4 cells in anticlinal rows, outermost surface cell anticlinally elongated. Inner: 2–3 cells.
G. pachydermatica Setch. et Gardn.	clumps of several terete dichotomously branched axes, arising above a small discoid holdfast.	terete, rigid, 1.5–3.0 mm diam., dichotomous branching regular and repeated to 5 times, branches becoming closer upwards. Surfaces without proliferations.	large, thin-walled rotund cells, to 200 μm diam., becoming successively smaller outwards.	outer: single row anticlinal elongated cells, about 10 x 5 μm. Inner: cells becoming larger towards the medulla.
G. pinnata Setch. et Gardn.	pinnately branched from more or less distinct axis, cartilaginous and brittle in texture, slightly compressed, to 25+ cm tall.	slightly compressed, 3–4 (–7) mm diam., segments narrowing upwards to acuminate apices.	large colorless cells, becoming smaller outwards.	2 layers of small cuboidal cells.
G. rubrimembra Dawson	one to few complanate blades, branched dichotomously, subflabellately borne above a short stipe and attached by a discoid holdfast.	complanate blades, branched in one plane, 700–850 μm thick. Upper portions-congested and overlapping, middle-broadest, to 2.5 cm wide, lower-becoming cuneate towards base, margins with numerous short, divided, pointed or lobed lateral proliferations.	large thin-walled cells, 120–160 μm diam., becoming smaller towards cortex.	1–2 cell layers, cells variously shaped, 8–15 μm diam.
G. subsecundata Setch. et Gardn.	bushy, several terete to compressed branches, to 25 cm tall, above a discoid holdfast.	terete to compressed, to 3 mm diam., branching pseudodichotomous and repeated, sparse to dense, to 6–7 orders, sometimes secund, internodes from a few to 6 cm.	large rotund cells, to 200+ μm diam., becoming smaller outward.	mostly 2 cells, angular to elliptic, 10 x 5–8 μm, tending to be anticlinally arranged.
G. textorii (Suringar) DeToni	foliose, 1 to few irregularly dichotomous to flabellate blades, to 35 cm tall, discoid holdfast.	branches in one plane, to 5 cm wide, membranous to coriaceous, with round to attenuated apices, most with smooth margins, some with simple or branched proliferations, 250–600 (–750) μm diam. thick.	large thin-walled cells, 250–500 μm diam.	single layer of small cells, becoming distromatic in older portions.
G. turgida Dawson	1 to several terete, turgid, robust, sparsely branched axes, to 15 cm tall.	terete, usually once or twice branched with blunt apices.	large thin-walled cells, becoming smaller outward.	small anticlinally elongated cells.
G. lemaneiformis (Bory) Weber-Van Bosse	few to several long cylindrical branches, up to 2 m long, above discoid holdfast usually associated with prostrate branches.	slender, terete, (0.5–) 1.5–3.5 mm diam., irregularly and sparingly branched, mostly with abundant short laterals.	large cells.	small cells.

Table 2. Reproductive Comparison of Gulf of California *Gracilaria* Species.

Taxon	Fusion Cell	Center of Gonimoblast	Absorbing Filament	Carposporangia	Base and Cystocarp	Pericarp Layer	Spermatangia Type	Tetrasporangia Origin
G. crispata Setch. et Gardn.		large, irregular cells.	+	in irregular chains.	not constricted, dome-shaped, 750–800 μm diam.		textorii	terminal from cortical bearing cell.
G. pachydermatica Setch et Gardn.		very large, irregular cells.	+	uniform in size, in irregular, short chains.	slight basal constriction, spherical, 750–1000 μm diam., rostrate.	thick walled, irregular, >7 cell layers at highest point.	textorii	terminal, flanked by unmodified anticlinal cortical cells.
G. pinnata Setch. et Gardn.	relatively small, gonimoblast arising straight from fusion cell.	relatively few, large, irregular cells.	+	not uniform in size, in irregular chains.	not basally constricted, dome shaped, prominent to 1.8 mm diam.	elongate, linear, > 13 cell layers at highest point.	textorii	terminal, flanked by 2–3 celled narrow cortical cells.
G. rubrimembra Dawson		large, irregular cells.	+	in irregular chains.	not basally constricted, projecting, dome shaped, to 900 μm diam., slightly rostrate.	elongate, roundish, > 15 cell layers at highest point.	textorii	terminal
G. subsecundata Setch. et Gardn.		large, irregular cells.	+	uniform in size, in irregular chains.	not basally constricted, dome shaped.	elongate, > 15 cell layers at highest point.	monoecious? small textorii	terminal
G. textorii (Suringar) DeToni	prominent, relatively small.	narrow, high, irregular cells.	+	relatively small, uniform, in irregular, short chains.	not basally constricted, globose, prominent 1.2–1.6 mm diam., slightly rostrate.	roundish to squarish towards surface, > 20 cell layers at highest point.	textorii	terminal, flanked by 2–3 celled narrow cortical cells.
G. turgida Dawson	prominent, large.	very few large, irregular cells.	+	not uniform in size, in irregular chains.	somewhat basally constricted, globose, prominent, 700–900 μm diam.	elongate, bricklike, >12 cell layers at highest point.	textorii	terminal
G. lemaneiformis (Bory) Weber-Van Bosse		isodiametric cells.	–	in irregular chains.	not basally constricted.	flat, horizontal, > 8 cell layers at highest point.	chorda, superficial and very small pits.	

GRACILARIA FROM CALIFORNIA: KEY, LIST AND DISTRIBUTION OF THE SPECIES

Isabella A. Abbott

I. Key to the Species

The following key is revised from the one appearing in "Marine Algae of California" (Abbott and Hollenberg, 1976, Stanford University Press), a key originally constructed by George J. Hollenberg.

1. Branches essentially cylindrical throughout or only slightly flattened 2
1. Branches distinctly flattened 6

    2. Erect branches mostly less than 15 cm tall 3
    2. Erect branches mostly 30+ cm tall 5

3. Erect branches stiff but not turgid, 1–1.3 mm diam., arising from compact, semi-stoloniferous base .... *G. papenfussii* Abbott (= *G. andersonii*)
3. Erect branches turgid, to 5 mm diam. in thickest part arising from discoid base 4

    4. Branches pale, irregularly branched, crisp to brittle .... *G. turgida* Dawson
    4. Branches deep burgundy red, 4–5 times subdichotomously branched, turgid but not brittle .... *G. robusta* Setchell

5. Branching pyramidal, of 3 or 4 orders; spermatangia in small, nonconfluent pits .... *G. pacifica* Abbott (new species, this volume, = *G. verrucosa* of Abbott and Hollenberg 1976).
5. Branching mostly basal, mostly of 2 orders; spermatangia in continuous, superficial layer .... *G. lemaneiformis* (Bory) Weber-van Bosse (= *G. sjoestedtii* Kylin)

    6. Plants 6–8 cm tall; tetrasporangia distributed in cortex .... *G. veleroae* Dawson[1]
    6. Plants 10–20 cm tall; tetrasporangia in nemathecioid areas .... *G. textorii* var. *cunninghamii* (Farlow) Dawson

II. List of California Species of *Gracilaria*

Gracilaria lemaneiformis (Bory) Weber-van Bosse (Figs. 32, 59–65)
Abbott (1983); Dawson (1949) as *Gracilariopsis sjoestedtii.*

Distribution: Chile northward to British Columbia (Paita, Peru, the type locality) (Abbott 1983); also Indonesia (Weber-van Bosse 1928); Shandong Prov., China (as *G. sjoestedtii,* Chang and Xia 1976); Hawaii (new record). Possibly more widespread (e.g., *G. sjoestedtii* has been reported in the Caribbean by Taylor 1960, p. 449) but those specimens not examined.

Gracilaria pacifica Abbott
Abbott (this volume). Abbott and Hollenberg (1976) as *Gracilaria verrucosa.*

Distribution: Southern British Columbia to Baja California (Pacific Mexico).

Gracilaria papenfussii Abbott
Abbott (1983); Kylin (1941) as *Gracilaria andersonii.*

Distribution: San Francisco Bay; Santa Barbara, California south to Punta Maria, Baja California (Mexico).

Gracilaria robusta Setchell

Distribution: Monterey Peninsula and off Santa Cruz Island, California (Abbott and Hollenberg 1976).

Gracilaria textorii var. *cunninghamii* (Farlow) Dawson (Dawson 1961).

Distribution: Central California (San Luis Obispo) to Isla Magdalena, Baja California (Mexico) (Abbott and Hollenberg 1976).

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[1] Schneider (1975) has placed *G. veleroae* Dawson in synonymy with *G. mammillaris* (Montagne) Howe, a move with which Norris (this volume) disagrees; Dr. Norris's judgment will be followed in this account.

Gracilaria turgida Dawson

Distribution: Newport Harbor, California to Bahía Magdalena, Baja California (Mexico) (Abbott and Hollenberg 1976), into Gulf of California (Norris, this volume).

Gracilaria veleroae Dawson

Distribution: La Jolla, California to Baja California (Mexico) and into the Gulf of California (Abbott and Hollenberg 1976).

Most Common *Gracilaria* Species in California

Both *Gracilaria lemaneiformis* (= *G. sjoestedtii*) and *G. pacifica* are common in California. On the Monterey Peninsula, California, where populations of both taxa have been examined for many years, plants of the two species grow side by side, even at the type locality of *G. sjoestedtii*, accounting for the long and frustrating taxonomic and nomenclatural confusion. *Gracilaria pacifica* is newly named in this volume for what has been known (Abbott and Hollenberg 1976, p. 500, fig. 447) as *G.* "*verrucosa*" in California. A description of *G. lemaneiformis* as it occurs in California is given here to permit comparison. *Gracilaria lemaneiformis* (Bory) Weber-van Bosse (Figs. 59–65) (Weber-van Bosse 1928, p. 435; Abbott 1983). Basionym: *Gigartina lemaneiformis* Bory (1828, p. 151). Synonyms: *Gracilaria sjoestedtii* Kylin (1930, p. 55); *Gracilariopsis sjoestedtii* (Kylin) Dawson (the type species of *Gracilariopsis*) (1949, p. 40); *Cordylecladia lemaneiformis* (Bory) Howe (1914, p. 128).

In sheltered bays and occasionally in more open situations, fronds are slender to almost delicate, the plants with a central basal region from which as many as 14 branches may arise, these more or less uniform in size, the plants becoming bushes, 30–70 cm tall with each axis having 2–3 orders of branching. In areas of lower salinity, specimens are shorter with at most 2 orders of branching; the second order mostly less than 1 cm long. In open coastal areas or regions where there is a constant flush of water and accumulation of coarse sand, plants tend to be less bushy, with fewer laterals and each erect axis thicker in diam. (up to 3 mm thick when fresh), and rarely 2 m long. Fresh thalli terete, becoming compressed on drying.

Medulla of large cells with thick walls, grading gradually into the subcortex; cortex of 2 (rarely 3) layers of deeply pigmented cells (Fig. 59), followed inwardly by a subcortex (Fig. 60) of 3–5 layers of regularly arranged cells, frequently as pigmented as the outer cortical layers.

Tetrasporangia irregularly produced in the cortical layer with adjoining cortical cells elongate (as seen in transection); cruciately divided, though often they apparently remain in the bisporangial phase for some time before the final division (may be seasonal?). Cystocarps up to 2 mm diam., in some populations wider than the axis bearing them, occasionally occurring densely radially clustered; pericarp generally domoid, occasionally rostrate; cells of the pericarp cuboidal to horizontally elongate; shape of the cystocarp somewhat narrow throughout, with thin-walled parenchyma in the center (Fig. 61) of the gonimoblast. Material from the type locality of *G. sjoestedtii* (Mussel Point, Pacific Grove, California) and from the type locality of *G. lemaneiformis* (Paita, Peru) shows no absorbing filaments between the carpospore mass and the pericarp in the majority of specimens. When present, they are conspicuous to inconspicuous. Spermatangial plants generally of 1–2 orders of branching (frequently only one), the spermatangia occurring in continuous or discontinuous superficial sori (Fig. 62).

Representative specimens: The specimens that have been selected fall into three categories—(1) those that resemble the type specimen of *Gigartina lemaneiformis* Bory (basionym of *Gracilaria lemaneiformis*) from the Laboratoire de Cryptogamie Herbarium, Paris (PC); (2) those similar to the type specimen of

Gracilaria sjoestedtii Kylin in the Botanical Museum, Lund (LD); and (3) those that have the important diagnostic anatomical features of this species, but externally do not resemble morphologically either of the first two categories. These particular kinds of specimens are deposited in the Gilbert M. Smith Herbarium, Hopkins Marine Station of Stanford University (GMS). Similar specimens will be distributed to the University of California, Berkeley (UC); Algal Collection, U.S. National Herbarium, Smithsonian Institution (US); Hokkaido University, Sapporo (SAP); Institute of Oceanology, Academia Sinica, Qingdao, China (AST); and Laboratoire de Cryptogamie Herbarium, Paris Museum (PC).

Gracilaria lemaneiformis, (specimens all GMS): *PB-A* 384a,b, (as *G. confervoides*), Monterey, California, leg. C. P. Nott and W. A. Setchell; Mussel Point, Pacific Grove, California (type locality of *Gracilaria sjoestedtii* Kylin) GMS #13514, 13592, 5146 and 13559; dredged off Monterey in 8–10 m depth, GMS 3981; Asilomar Point to Middle Reef of Moss Beach (near Pacific Grove), GMS 1868, 13543 and 13644; Stillwater Cove, Pebble Beach, (type locality of *G. pacifica*), GMS 13642; and finely branched almost black specimens characteristic of harbors, GMS 13365, Upper Balboa Harbor, leg. G. J. Hollenberg 3183 and 8685; Elkhorn Slough, Monterey County, leg. J. Norris 821; Abbott 13552, 13415, 13799 and 13812.

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GRACILARIA AND *POLYCAVERNOSA* FROM THE CARIBBEAN AND FLORIDA: KEY AND LIST OF THE SPECIES OF ECONOMIC POTENTIAL

James N. Norris

Key to the Species

1. Thallus compressed, very thick and brittle; prostrate with marginal lobes extending into terete to compressed branches .... *P. crassissima* (P. et H. Crouan) Fredericq and Norris, this volume
1. Thallus erect, terete to flat 2
    2. Thallus terete throughout 3
    2. Thallus flat or subterete with flat portions 5
3. Thallus lax, axes with branches abruptly constricted at their bases .... *G. cylindrica* Børgesen
3. Branches not basally constricted, but broad or tapering at base 4
    4. Thallus coarse, cartilaginous, sparsely and irregularly branched, 3–6 mm diam. ... . *P. debilis* (Forsskål) Fredericq and Norris, this volume
    4. Thallus soft, slender, often repeatedly branched, 0.5–2.0 mm diam. .... *G. "verrucosa"*
5. Thallus flat throughout 6
5. Thallus subterete with flat portions 7
    6. Axes and main branches distinctively flat and strap-like, marginally branched, sometimes more or less pinnate .... *G. domingensis* Sonder ex Kützing
    6. Axes compressed, sparingly to repeatedly and irregularly branched throughout .... *G. foliifera* (Forsskål) Børgesen
7. Axes mostly subterete and sometimes flattened at branch dichotomies; branching more or less regular .... *G. tikvahiae* McLachlan
7. Axes subterete below and flattened above; branching more or less pinnate to divaricate .... *G. cervicornis* (Turner) J. Agardh

List and References to Some Caribbean Species of *Gracilaria* That Have Economic Potential

G. cervicornis (Turner) J. Agardh (Fig. 69)
  Taylor 1960, p. 445; Oliveira et al. 1983, p. 3003.
P. crassissima (P. et H. Crouan) Fredericq and Norris, this volume. (Fig. 72)
  Taylor 1960, p. 443
G. cylindrica Børgesen
  Børgesen 1920, p. 375; Taylor 1960, p. 446.
P. debilis (Forsskål) Fredericq and Norris, this volume. (Fig. 71)
  Børgesen 1932, p. 7; Taylor 1960, p. 442.
G. domingensis Sonder ex Kützing (Fig. 67)
  Taylor 1960, p. 446; Oliveira et al. 1983, p. 3000.
G. foliifera (Forsskål) Børgesen (Fig. 70)
  Børgesen 1932, p. 7; Taylor 1960, p. 446.
G. tikvahiae McLachlan (Fig. 68)
  McLachlan 1979, p. 19.
G. "verrucosa" (Fig. 66)
  Taylor 1960, p. 441.

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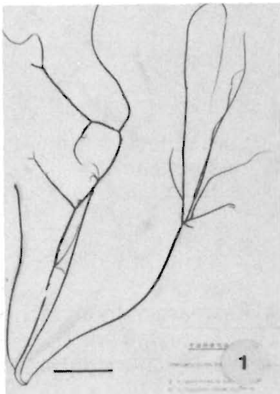
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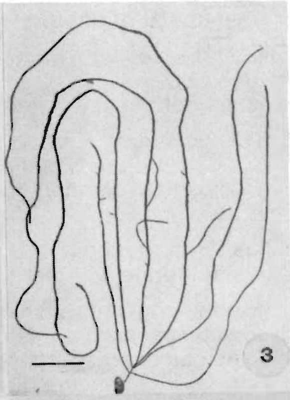
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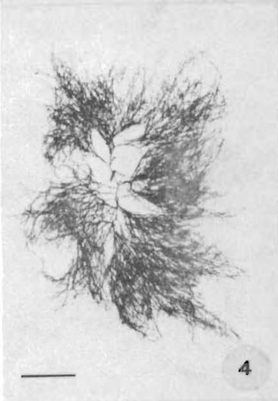
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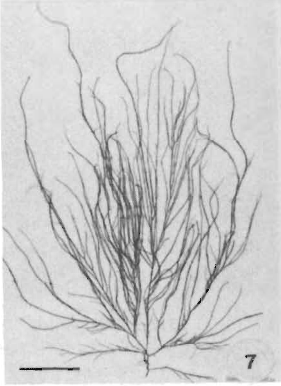
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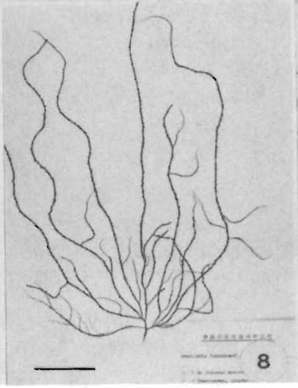
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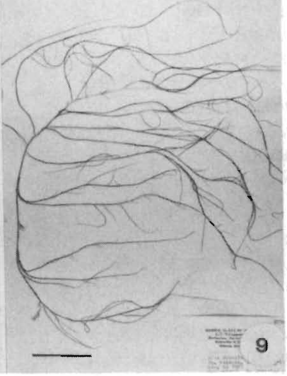
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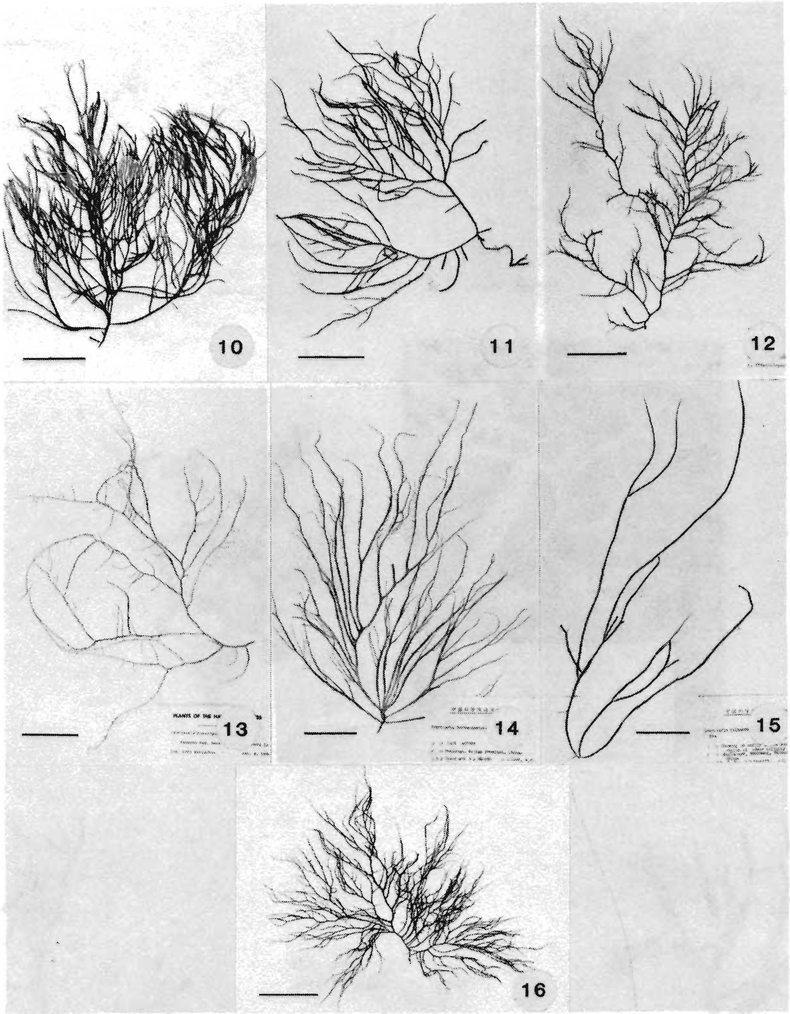
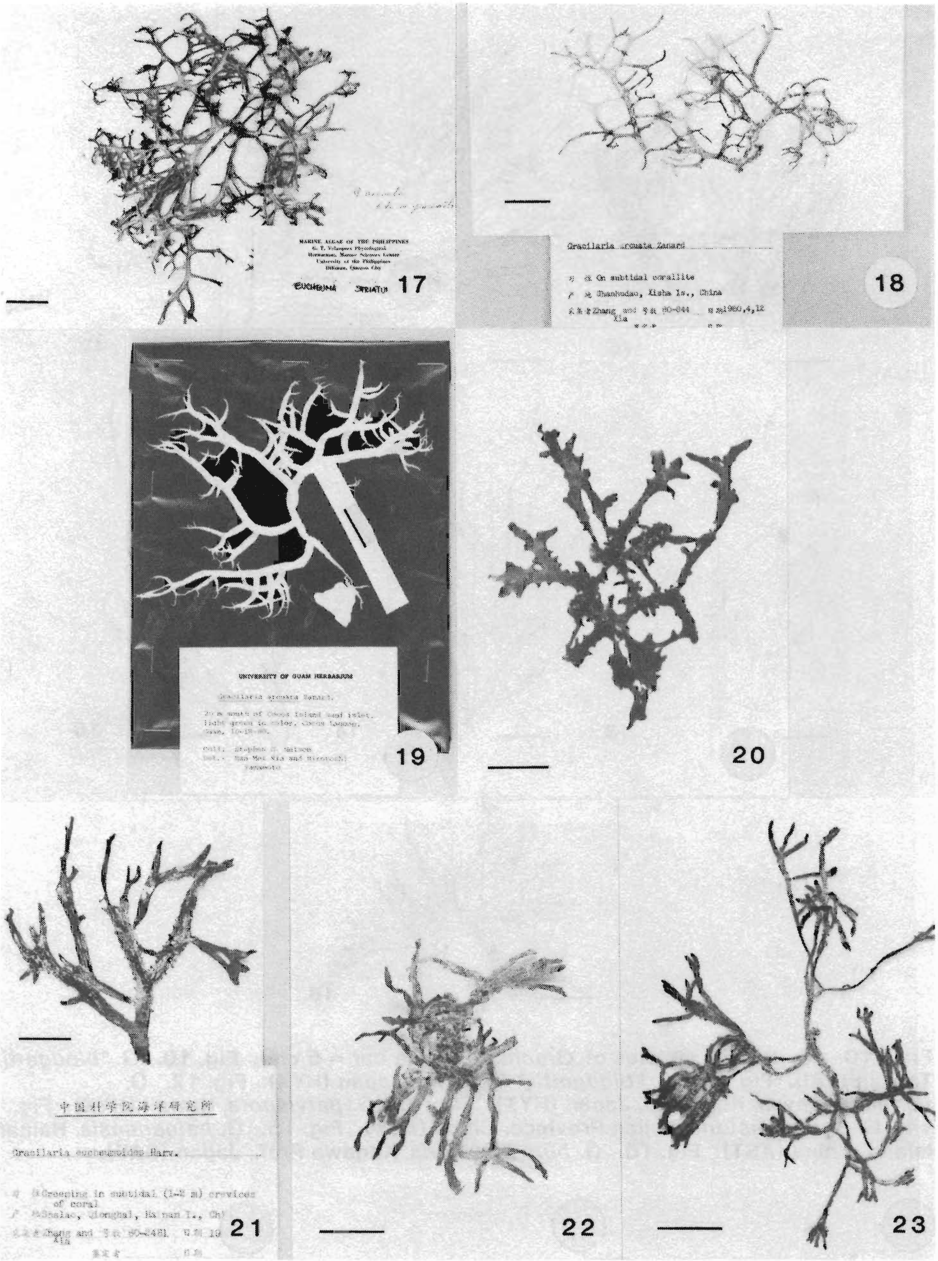
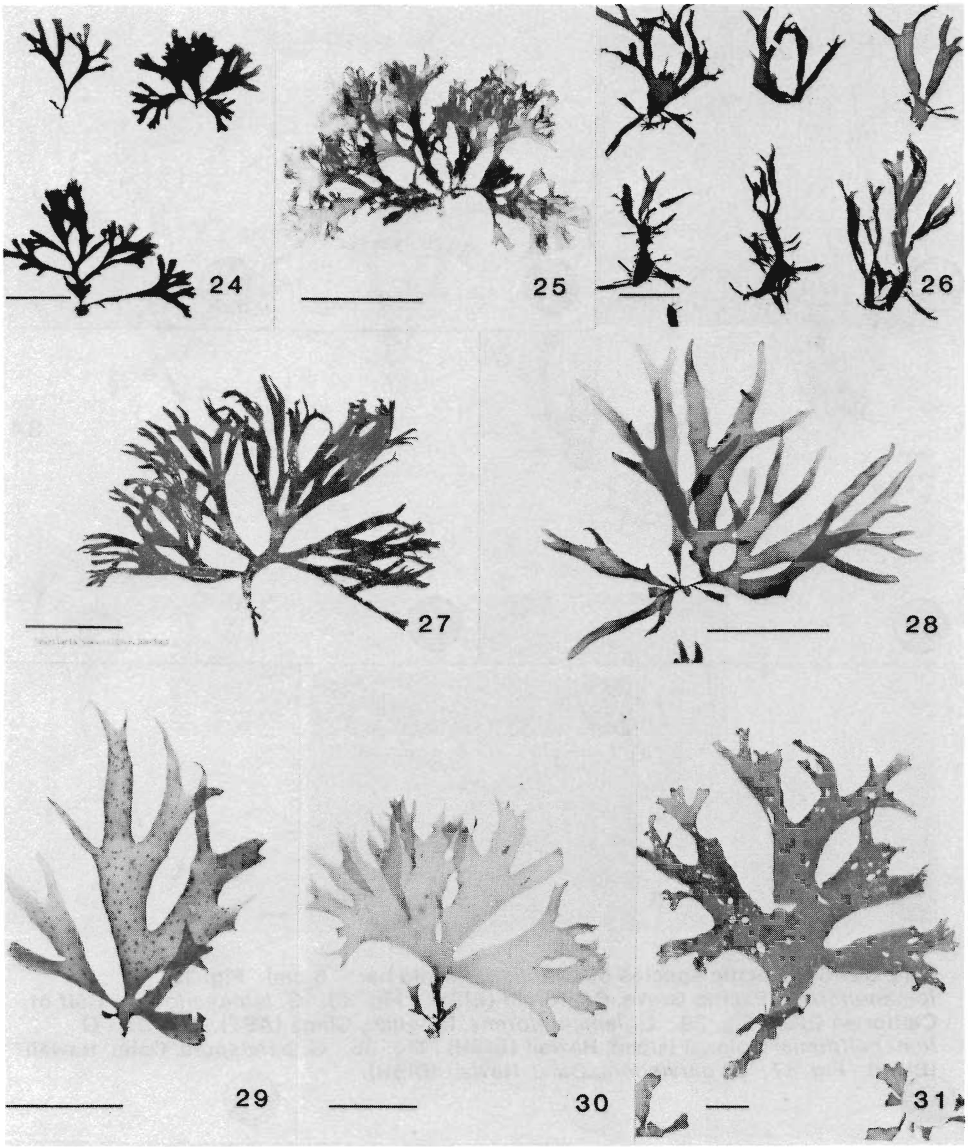


Figs. 10–16. Pacific species of *Gracilaria* (scale bar = 5 cm). Fig. 10. *G.* "*blodgettii*," Taiwan (TAI). Fig. 11. *G.* "*blodgettii*," Okinawa, Japan (HYX). Fig. 12. *G. vermiculophylla*, Hokkaido, Japan (HYX). Fig. 13. *G. parvispora*, Hawaii (HYX). Fig. 14. *G. bursa-pastoris*, Fujian Province, China (AST). Fig. 15. *G. hainanensis*, Hainan Island, China (AST). Fig. 16. *G. bursa-pastoris*, Kagawa Pref., Japan (SAP).

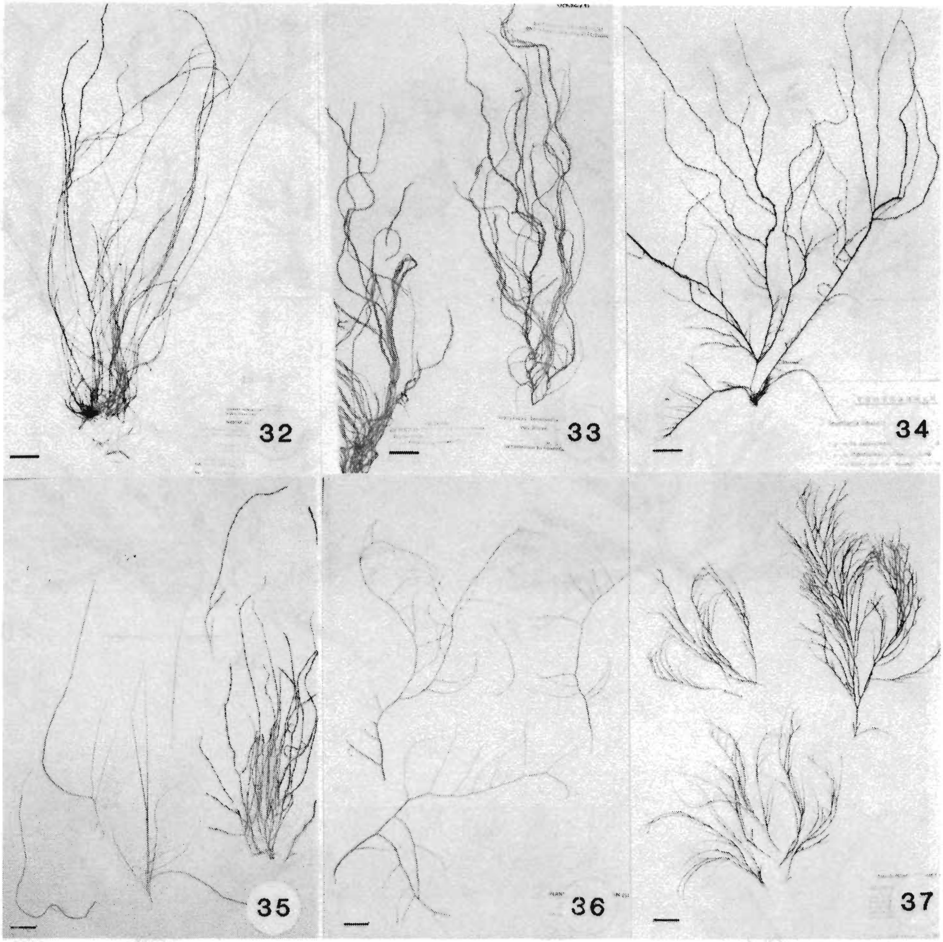
Figs. 1–9. Pacific species of *Gracilaria* (scale bar = 5 cm). Fig. 1. *G. chorda*, Hainan Island, China (AST). Fig. 2. *G. chorda*, Kyushu, Japan (SAP). Fig. 3. *G. chorda*, Japan (SAP). Fig. 4. *G.* "*verrucosa*," Taiwan (TAI). Fig. 5. *G.* "*verrucosa*," Japan (HYX). Fig. 6. *G. tenuistipitata*, Hainan Island, China (AST). Fig. 7. *G.* "*verrucosa*," Japan (HYX). Fig. 8. *G.* "*verrucosa*," Quingdao, China (AST). Fig. 9. *G.* "*verrucosa*," Philippines (BISH).



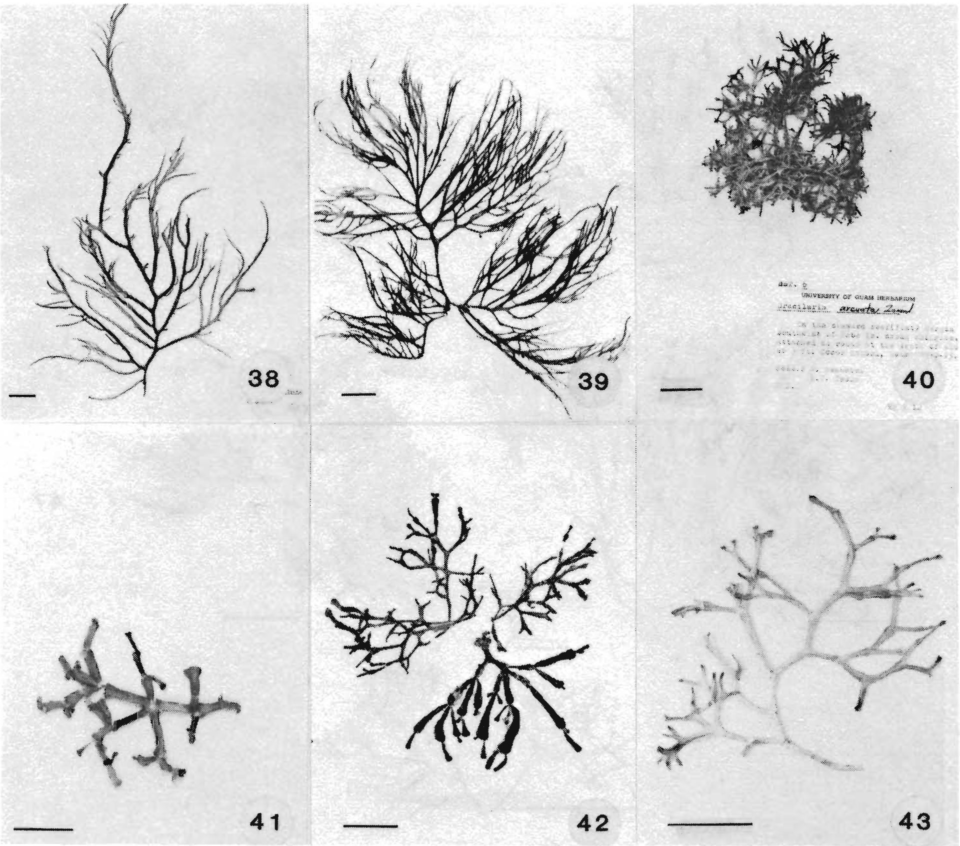
Figs. 17–23. Pacific species of *Gracilaria* (scale bar = 2 cm). Fig. 17. *G. arcuata*, Philippines (BISH). Fig. 18. *G. arcuata*, Xisha Island, (AST). Fig. 19. *G. arcuata*, Guam (AST). Fig. 20. *G. eucheumoides*, Okinawa, Japan (SAP). Fig. 21. *G. eucheumoides*, Hainan Island, China (AST). Fig. 22. *G. eucheumoides*, Guam (AST). Fig. 23. *G. eucheumoides*, Guam (AST).



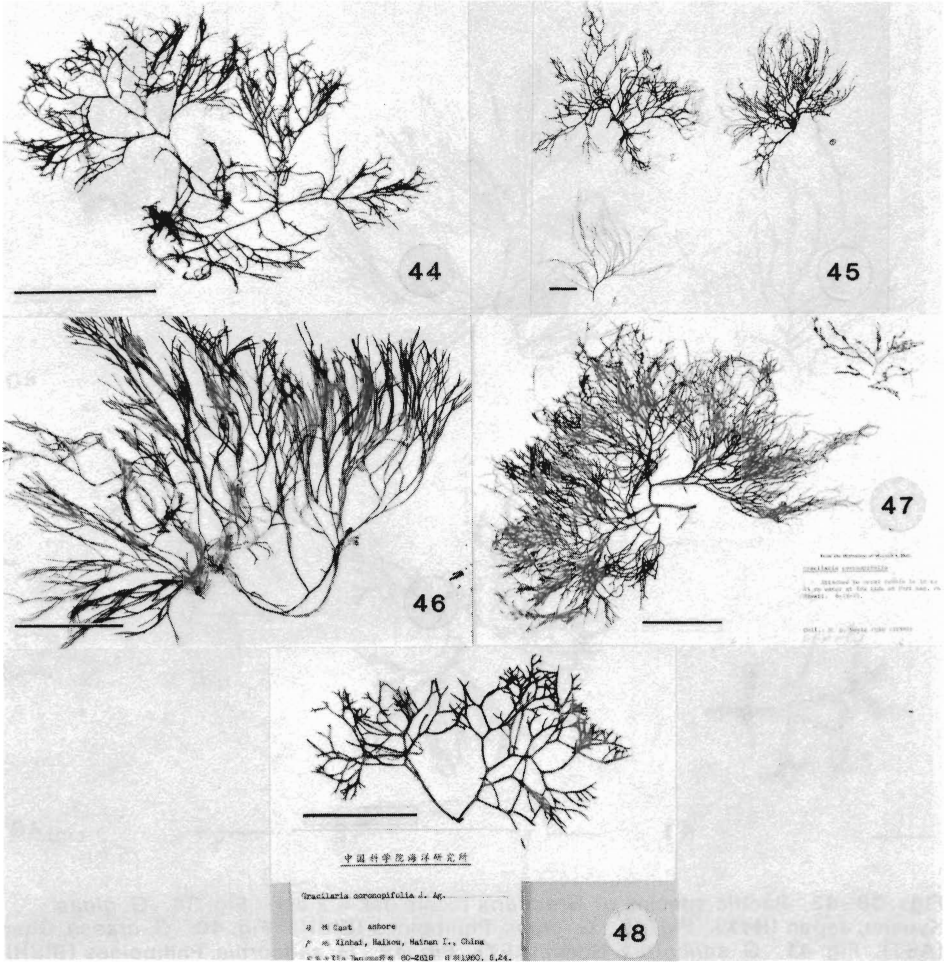
Figs. 24–31. Pacific species of *Gracilaria* (scale bar = 5 cm). Fig. 24. *G. textorii*, near Hakodate, Japan (SAP). Fig. 25. *G. denticulata*, Okinawa, Japan (HYX). Fig. 26. *G. textorii*, Philippines (BISH). Fig. 27. *G. textorii*, Qingdao, China (AST). Fig. 28. *G. textorii*, Kyushu, Japan (SAP). Fig. 29. *G. textorii*, Kyushu, Japan (SAP). Fig. 30. *G. textorii*, Kyushu, Japan (HYX). Fig. 31. *G. textorii*, Gulf of California (US).



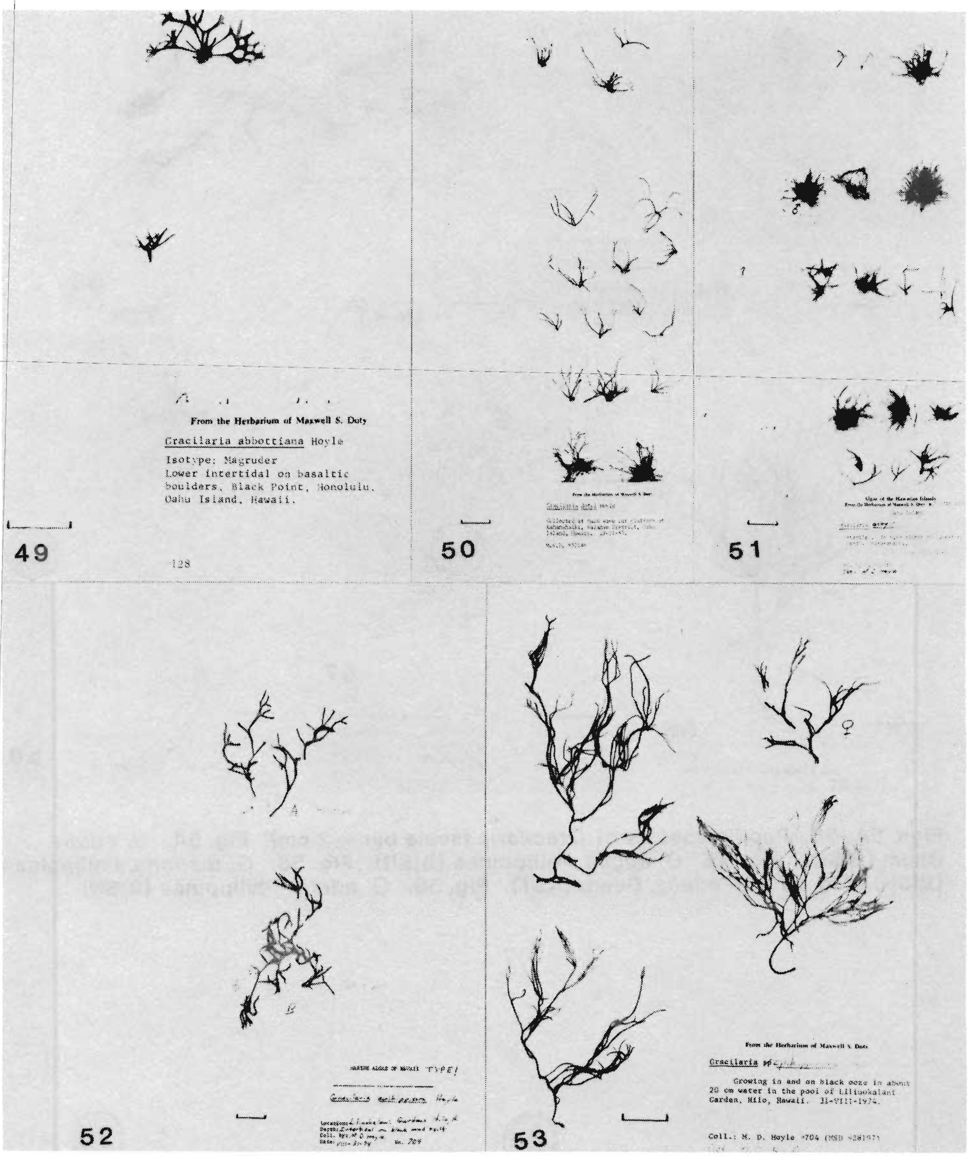
Figs. 32–37, Pacific species of *Gracilaria* (scale bar = 5 cm). Fig. 32. *G. lemaneiformis*, Pacific Grove, California (BISH). Fig. 33. *G. lemaneiformis*, Gulf of California (US). Fig. 34. *G. lemaneiformis*, Qingdao, China (AST). Fig. 35. *G. lemaneiformis*, Molokai Island, Hawaii (BISH). Fig. 36. *G. parvispora*, Oahu, Hawaii (BISH). Fig. 37. *G. parvispora*, Oahu, Hawaii (BISH).



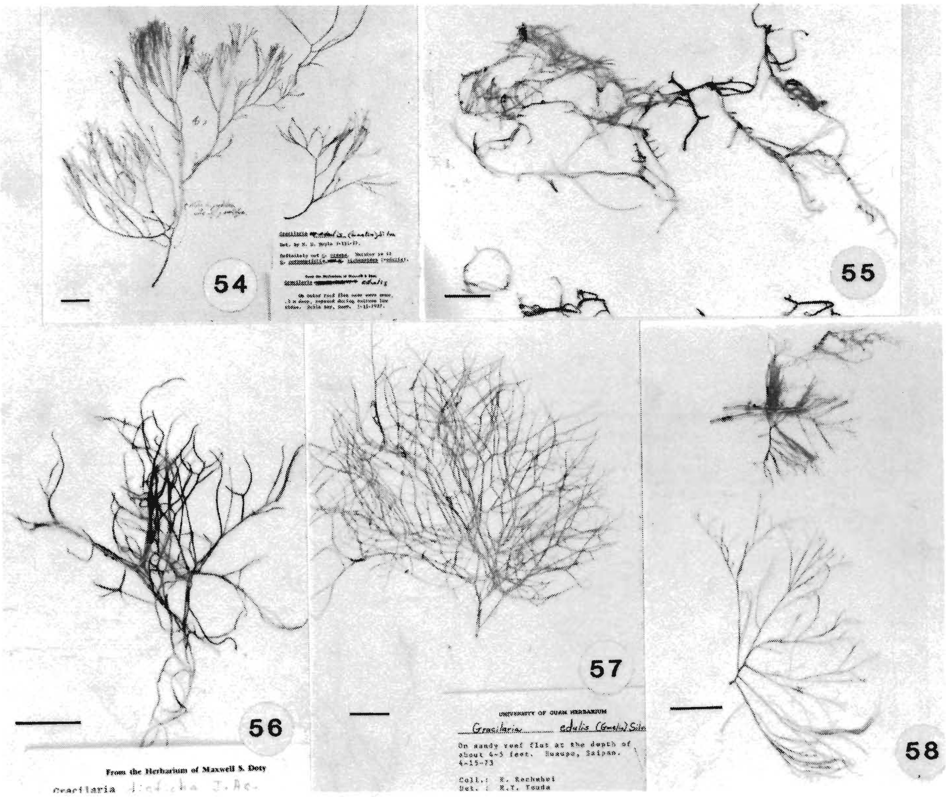
Figs. 38–43. Pacific species of *Gracilaria* (scale bar = 2 cm). Fig. 38. *G. gigas*, Kyushu, Japan (HYX). Fig. 39. *G. gigas*, Philippines (BISH). Fig. 40. *G. crassa*, Guam (AST). Fig. 41. *G. salicornia*, Guam (AST). Fig. 42. *G. salicornia*, Philippines (BISH). Fig. 43. *G. canaliculata*, Philippines (BISH).



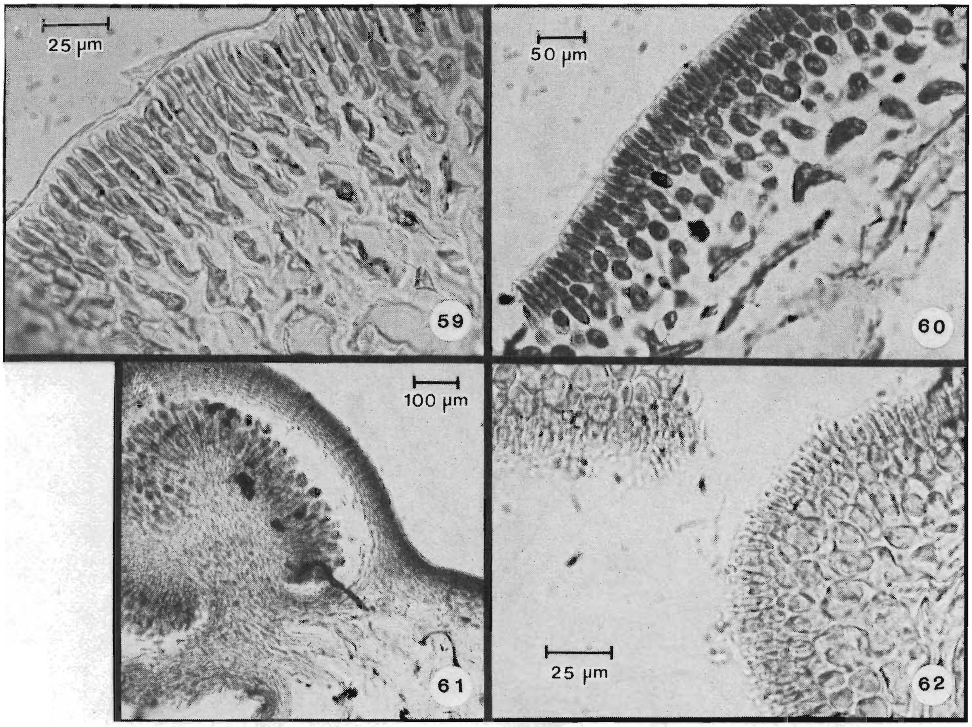
Figs. 44–48. Pacific species of *Gracilaria* (scale bar = 5 cm). Fig. 44. *G. coronopifolia*, Japan (HYX). Fig. 45. *G. coronopifolia*, Oahu, Hawaii (BISH). Fig. 46. *G. coronopifolia*, Philippines (BISH). Fig. 47. *G. coronopifolia*, Hawaii (BISH). Fig. 48. *G. coronopifolia*, Hainan Island, China (AST).



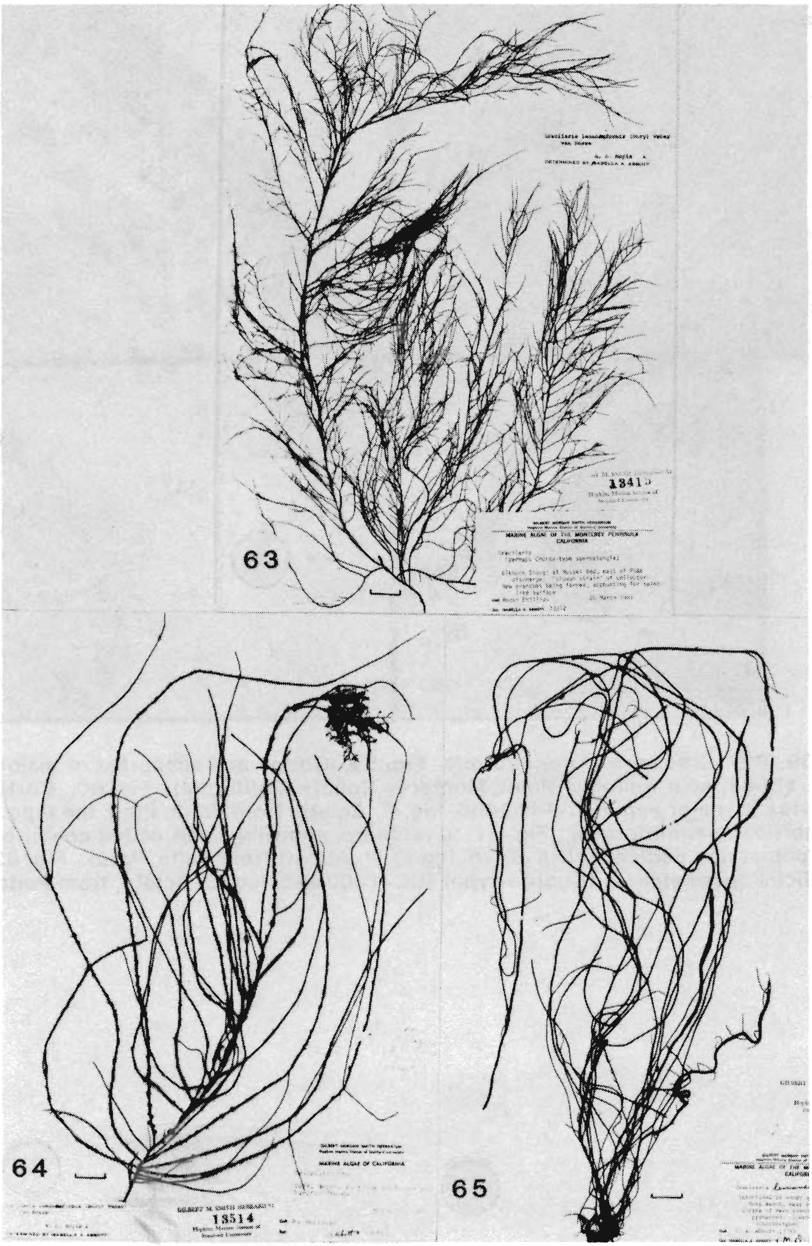
Figs. 49–53. Habits of some Hawaiian species of *Gracilaria* (scale bar = 2 cm). Fig. 49. *G. abbottiana* Hoyle, isotype, from Black Point, Honolulu, Hawaii, leg. W. H. Magruder (BISH). Fig. 50. *G. dotyi* Hoyle (#MSD-32146, BISH), and Fig. 51. *G. dotyi* Hoyle (#IAA-4325, BISH) both from Kahanahaiki, Oahu Island, Hawaii. Fig. 52. *G. epihippisora* Hoyle, holotype from Liliuokalani Gardens, Hilo Bay, Hawaii Island, Hawaii (BISH). Fig. 53. *G. epihippisora* Hoyle, from the same locality as Fig. 52 (BISH).



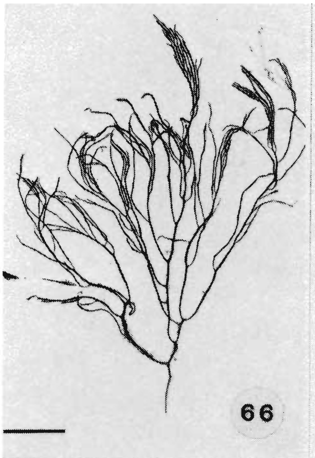
Figs. 54–58. Pacific species of *Gracilaria* (scale bar = 2 cm). Fig. 54. *G. edulis*, Guam (BISH). Fig. 55. *G. edulis*, Philippines (BISH). Fig. 56. *G. disticha*, Philippines (BISH). Fig. 57. *G. edulis*, Guam (AST). Fig. 58. *G. edulis*, Philippines (BISH).



Figs. 59–62. *Gracilaria lemaneiformis*. Fig. 59. Cortex and subcortex of major axis (#IAA-15561, near Asilomar Point, Monterey County, California). Fig. 60. Cortex and subcortex of major axis (UC-1402496, leg. C. Acleto, from Paita, Peru, the type locality of *Gigartina lemaneiformis*). Fig. 61. Cystocarp, showing small-celled center of gonimoblast and pedicel (#IAA-6716, leg. D. P. Abbott from Paita, Peru). Fig. 62. Superficial spermatangia (Chorda-type) (UC-1402496, leg. C. Acleto, from Paita, Peru).



Figs. 63–65. *Gracilaria lemaneiformis* (scale bar = 2 cm). Fig. 63. Habit of spermatangial plant from Elkhorn Slough, California, typical of estuarine plants (#IAA-13812, leg. Roger Phillips, GMS). Fig. 64. Habit of plant from Mussel Point, Pacific Grove, California, the type locality of *G. sjoestedtii* Kylin (IAA-13686a, GMS). Fig. 65. Habit of spermatangial plant from Middle Reef of Moss Beach, near Pacific Grove, California (#IAA-13793, leg. I. Abbott, GMS).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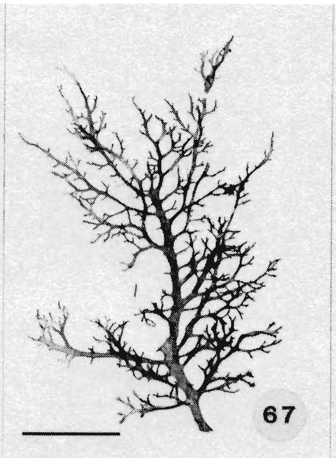
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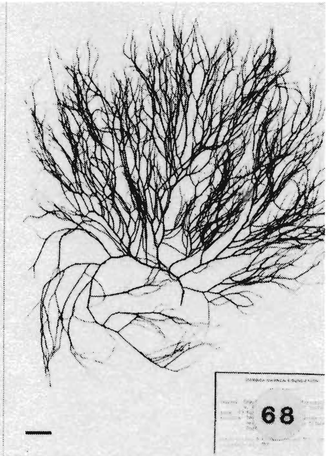
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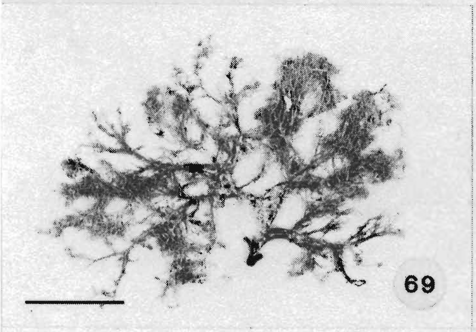
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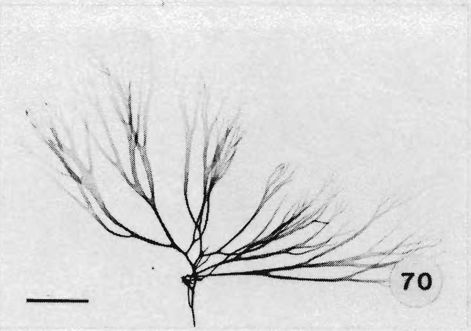
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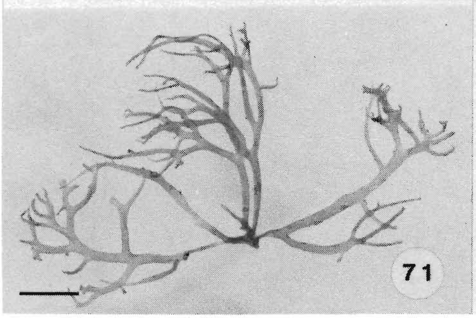
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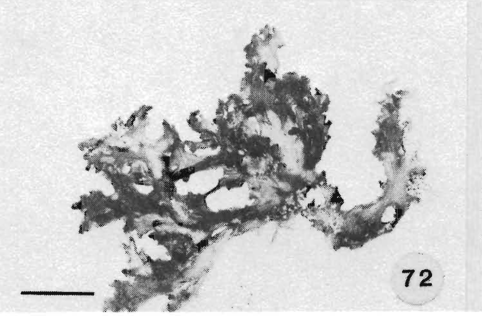
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Figs. 66–72. Caribbean species of *Gracilaria* and *Polycavernosa* (scale bar = 2 cm). Fig. 66. *G.* "*verrucosa*," British West Indies (US). Fig. 67. *G. domingensis*, Caribbean Panama (US). Fig. 68. *G. tikvahiae*, Indian River, Florida (US). Fig. 69. *G. cervicornis*, Santo Domingo, Dominican Republic (US). Fig. 70. *G. foliifera*, North Carolina (US). Fig. 71. *P. debilis*, South Water Cay, Belize (US). Fig. 72. *P. crassissima*, Carrie Bow Cay, Belize (US).

SECTION IV. *Gracilaria*

Part 2

Taxonomic and Morphological Studies

NEW SPECIES OF *GRACILARIA* GREV. (GRACILARIACEAE, RHODOPHYTA) FROM CALIFORNIA AND HAWAII

Isabella A. Abbott

When Abbott (1983) described *Gracilaria papenfussi* from southern California, she distinguished it from the commoner and morphologically similar species of *Gracilaria* that occurs from Chile northward to British Columbia by anatomical details of the cortex, cystocarp, and spermatangia. However, this common species, *G. lemaneiformis* (Bory) Weber-van Bosse (= *Gracilaria sjoestedtii* Kylin), was not distinguished from an equally prevalent taxon in California known as *G. verrucosa sensu* Abbott et Hollenberg (1976, p. 500). The latter name could not continue to be used since the California specimens did not agree with specimens of *G. verrucosa* from England (the type locality), and some critical morphological details were lacking. *Gracilaria verrucosa*, like *Ulva lactuca*, has been reported or described from every kind of temperature range and habitat in the earth's seas, but it has only recently been realized that "*verrucosa*" could not be applied to all of these specimens. The first step in clearing this situation was to examine true *G. verrucosa* (Hudson) Papenfuss from England, which has been possible owing to generous gifts of plants from C. J. Bird (Halifax, Nova Scotia) and M. D. Guiry (Galway, Ireland).

Materials and Methods

Specimens of *Gracilaria verrucosa* (Hudson) Papenfuss were collected at Church Reef, Wembury, Devon, 16 May 1979, leg. and det. C. J. Bird and G. T. Boalch, and at Finavarra, Co. Clare, Ireland in spring 1983 by M. D. Guiry. The living, 5% Formalin/seawater liquid-preserved or air-dried material of the California *G.* "*verrucosa*" was available to Abbott at Gilbert M. Smith Herbarium, Hopkins Marine Station of Stanford University in Pacific Grove, California (now deposited US).

From material either preserved in Formalin or dried, microscope slides were made, stained in 1% aqueous aniline blue, fixed with 2% HCl, and mounted in 50% corn syrup with phenol added.

Results

The salient features describe the detail that must be observed for the discrimination of these two taxa, which are morphologically so similar. Externally, the sizes of the Pacific coast plants are 3 to 4 times those of Britain and Ireland, but size is not a reliable taxonomic character for species of *Gracilaria*.

Table 1. Main taxonomic features of *Gracilaria verrucosa* from the British Isles and *G.* "*verrucosa*" from California.

Species	Cortex Transition	Cystocarp Center	Absorbing Filaments	Spermatangial Conceptacles
G. verrucosa	gradual	columnar; fusion cell	weak to moderate	ca. 60 μm deep; oval
G. "*verrucosa*"	abrupt	columnar; no fusion cell	weak	ca. 100 μm deep; pyriform

While large populations of *G. verrucosa* were not examined, enough material from different localities was studied to confirm these observations. Large numbers of the California *G.* "*verrucosa*," principally from the Monterey Peninsula, were examined. Additional comparisons with respect to the cystocarp may be noted from the pericarp construction. In *G. verrucosa* the pericarp is made up of nearly linear rows of oval cells, whereas in the California material, the pericarp shows nearly cuboidal to relatively flat cells.

The gradual transition of cell sizes between the medulla and cortex in *G. verrucosa* from England appears to be a notable feature of this species, infrequently seen in Pacific species under study.

Description of a California Species

Gracilaria pacifica Abbott, sp. nov. (Figs. 2–8)

Thallus firmus, plerumque axe percurrenti, tres usque complanatus, 1–3 mm diam.; ramificatio flagelliformis usque unilateralis, rami patentes, plerumque longi quan lati ut axis. Cystocarpia columna cellularum sterilium in centro; massa sporarum relative parva inconspicuis filis absorbentibus. Spermatangia in discretis conceptaculis pyriformibus usque late obovatis, concepta-culis 100 μm alta x 50–60 μm lata.

Thallus sparingly irregularly branched, from percurrent axes 30–90 cm tall, 1–2.5 mm thick in sheltered bays; in open coastal situations, plants frequently unbranched (spermatangial or tetrasporangial) or of 1–2 orders (spermatangial, tetrasporangial or cystocarpic), main axes 1.5–3.5 mm thick. Branches of tetrasporangial plants most often formed below the middle of the plant, and becoming nearly as long as the axes. Medulla of cells 150–250 μm diam., with walls 3 μm up to an exceptional 10 μm thickness; cortex of 2 layers of heavily pigmented cells, with a disorganized subcortex, the transition to cells of the medulla abrupt.

Tetrasporangia numerous, in main axes and laterals, disrupting the cortex, in young plants encircling the base of laterals in a thick, raised nemathecium but quickly spreading into the distally developing tissue. Cystocarps usually few, mostly less than 1 mm, sometimes up to 2 mm diam.; center of gonimoblast of large cells with thin walls, columnar in median longitudinal section, rich in protoplasm; absorbing filaments weakly developed and usually lateral to the carpospore mass. Pericarp of bricklike cells. Spermatangial conceptacles usually (more than 55% of 100 counted) obovate, the remainder somewhat oval, up to 125 μm deep.

Type locality: Midway to southwest end of Stillwater Cove, Pebble Beach, Monterey County, California. Holotype: Abbott #16141, leg. I. A. Abbott, 8 July 1982, about 0.0 ft tide level near *Rhodoglossum californicum* flats (cystocarpic). Other material: Abbott 15596, west end of Stillwater Cove, landward of *Phyllospadix* bed on rock covered with sand, leg. I. Abbott, 2 July 1981

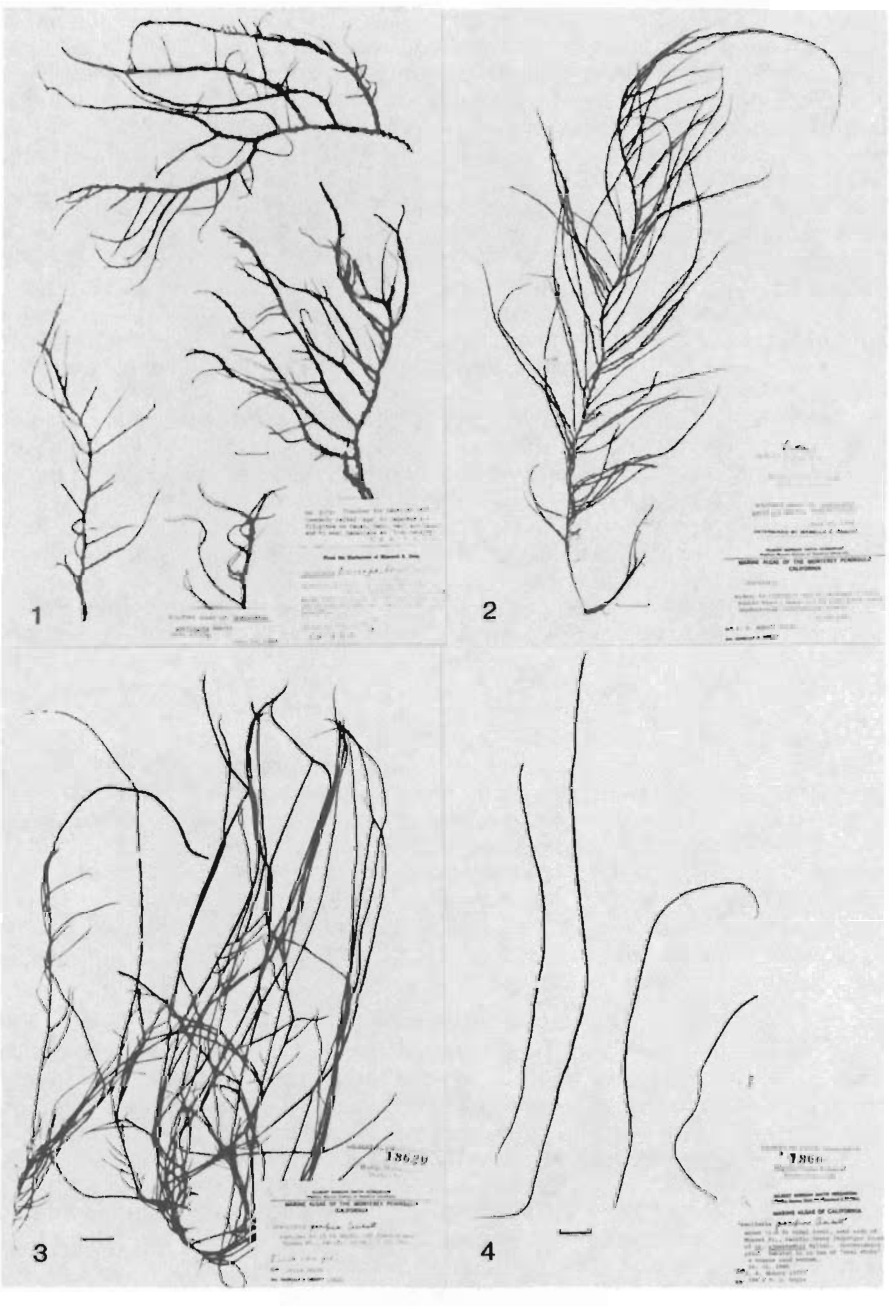


Fig. 1. Holotype of *Gracilaria parvispora* Abbott from Kaneohe Bay, Oahu Island, Hawaii (BISH). Figs. 2–4. *Gracilaria pacifica* (scale bar = 2 cm). Fig. 2. Holotype of *G. pacifica* Abbott, from Stillwater Cove, Pebble Beach, California (UC). Fig. 3. Habit of cystocarpic plant (#IAA-15620, leg. Celia Smith, AST). Fig. 4. Habit of spermatangial plant, (#IAA-13777 from Mussel Pt., Pacific Grove, Calif., AST).

(tetrasporangial); Abbott 13771, southwest end of Stillwater Cove, in sand, about 2.0 ft tide level, leg. I. Abbott, 14 June 1980 (spermatangial). These specimens have been filed in the Herbarium of the University of California, Berkeley (UC). Others are deposited in the Algal Collection of the U.S. National Herbarium, Smithsonian Institution (US): Abbott 16137, from the Middle Reef of Moss Beach, near Pacific Grove, June 22, 1982; Abbott 16146 from 0.5 km north of Santa Cruz, California leg. M. Wolcott (spermatangial); Abbott 15596, from Stillwater Cove (cystocarpic); Herbarium of Hokkaido University, Sapporo (SAP): duplicates of Abbott numbers 15596, 16146, and 16134, from 0.5 km north of Santa Cruz, California, June 20, 1982, leg. M. Wolcott; Algal Herbarium Institute of Oceanology, Academia Sinica, Qingdao (AST): Abbott numbers 15620 (cystocarpic) from Mussel Pt., Pacific Grove, leg. Celia Smith; 13777 (spermatangial and tetrasporangial) from Mussel Pt., leg. I. Abbott and M. Hoyle; 15615 from Middle Reef of Moss Beach; and 16142 from Stillwater Cove, Pebble Beach.

The following specimens (grouped by geographic location on the Monterey Peninsula, Monterey County, and adjacent Santa Cruz County, California) are in the Hopkins Marine Station of Stanford University Herbarium (GMS) in Pacific Grove: Abbott 16133; 16146 from north of Santa Cruz city; Abbott, *s.n.* collected Mar. 17, 1966; Abbott, *s.n.* collected July 7, 1966; 3363; 13777 (3 sheets); 13794; 13815, from Mussel Point, (Hopkins Marine Station of Stanford University), Pacific Grove (the type locality of *Gracilaria sjoestedtii* Kylin), Abbott 3037; 5388; 13789; 13790; 13791; 16135, from between the Middle Reef of Moss Beach and Asilomar Point (near Pacific Grove); Abbott, *s.n.*, collected June 9, 1967; Abbott, *s.n.*, collected July 14, 1967; 3036 (spermatangial; first record of *G.* "*verrucosa*" for Monterey County); 3365; 13771; 13772 (3 sheets); 14697; 15596; 15604; 16142 (2 sheets) from Stillwater Cove, Pebble Beach (chosen in this paper as the type locality for *G. pacifica*).

From frequently look-alike thalli of *G. lemaneiformis* (for description see Abbott, this volume), especially when growing side by side in open coastal areas, *G. pacifica* is commonly the more robust of the two taxa, has spermatangia in pits as opposed to being borne superficially, and shows absorbing filaments in the cystocarp. In southern California where *G. papenfussii* (= *G. andersonii*) is more common, *G. pacifica* shows single axes arising separately, even when growing in a tuft, whereas *G. papenfussii* has an intricate, much branched base. The plants of the latter species are usually shorter and more slender than *G. pacifica*, and lack absorbing filaments in the cystocarp.

Description of a Hawaiian Species

In Hawaii, the species of *Gracilaria* that is used most commonly as food is "*G. bursa-pastoris*," commonly called *ogo* after the Japanese common name *ogo-nori*. It is preferred by fishmongers who use it, chopped, with raw fish, claiming that sales are increased with the addition of this seaweed. Although the native *G. coronopifolia* J. Agardh, called *limu manauea* by Hawaiians (Abbott 1984) is more common in the field, it is used as a substitute for *ogo* when the latter is scarce, there being a price differential in these two species in the marketplace. Although this is a well-known, commercial species in Hawaii, this species has been incorrectly named and is described herein.

Hoyle (1978b) described the gel strength of the agar from this new species (as *G. bursa-pastoris*) as being superior to that of *G. coronopifolia*.

Description

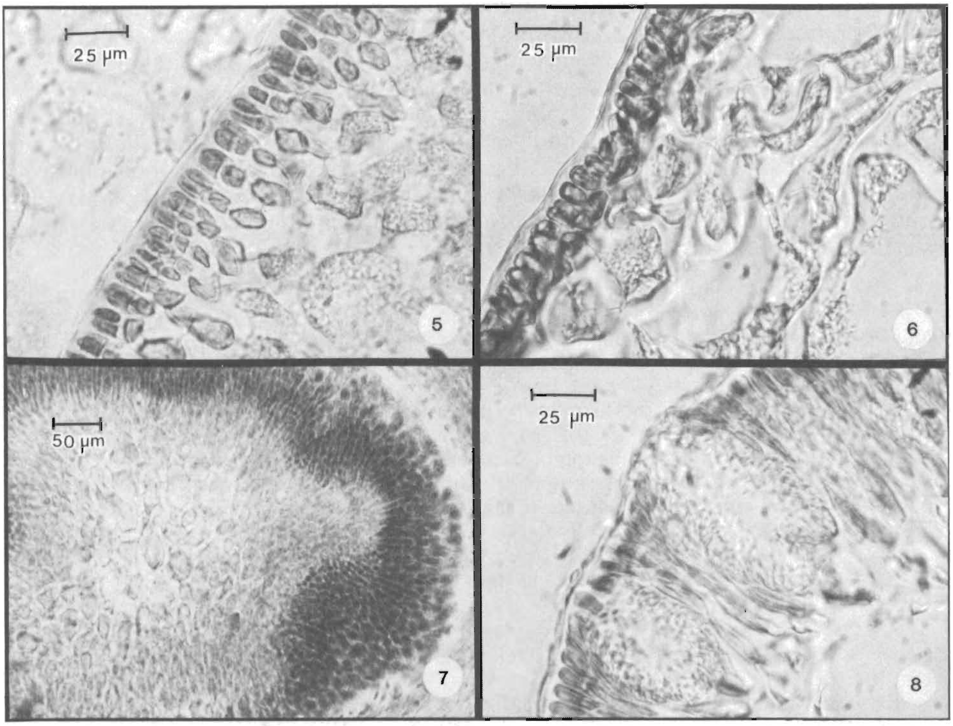
Gracilaria parvispora Abbott, sp. nov. (Fig. 1)

Gracilaria bursa-pastoris sensu Hoyle 1978; Abbott and Williamson 1974; Abbott 1984; Magruder and Hunt 1978; Fortner 1978 [*non G. bursa-pastoris* (Gmelin) Silva, 1952].

Thallus grossus, plerumque compressus prominentibus ramificationibus unilateralibus. Cystocarpia magnis, cellulis tenuimarginatis sub massa sporam absorbentia fila conspicua, conjungentis ad stelliformes cellulas pericarpii. Spermatangia in conceptaculis ovalibus, 60 μm altis x 30 μm latis, plerumque confluentibus.

Thalli coarse, commonly compressed, with prominent (and frequently wholly) unilateral branching; axes usually percurrent, 0.8–3.5 mm diam., orders of branching rarely more than 3; if more, the last order short, slender, and spine-like. Thalli commonly 30 cm tall, frequently taller. Medulla thick-walled, grading gradually in sizes of cells to a 1- to 2-celled cortex.

Cystocarps 2–3 mm diam., internal spore mass relatively small, not filling the cavity, spherical to somewhat flattened, the center with large thin-walled cells below the spore mass; absorbing filaments conspicuous; pericarp of small cells with conspicuous lateral and vertical pit connections making the contents appear star-shaped. Spermatangia in shallow depressions ("Textorii-Type" of Yamamoto 1978), 35 μm deep by 20–35 μm wide, frequently confluent.



Figs. 5–8. *Gracilaria pacifica*. Fig. 5. Cortex of major axis (#IAA-13779, Mussel Pt., Pacific Grove, California). Fig. 6. Cortex of minor axis (#IAA-13914a, Mussel Pt., Pacific Grove). Fig. 7. Longitudinal section through cystocarp showing large parenchymatous cells in center (#IAA-13777, Mussel Pt., Pacific Grove, Calif.). Fig. 8. Spermatangial pits (#Hoyle-10558, from Humboldt County, California).

Holotype: From Kaneohe Bay, Oahu Island, Doty 20710 (with letter *a* to distinguish it from 5 other sheets bearing the same number), a sheet that contains 4 cystocarpic thalli, collected October 3, 1970 (BISH).

Paratypes: Spermatangial thalli (Hoyle 704 and 705) should be noted (though not type material) as well as tetrasporangial thalli (especially Hoyle 642) collected from Fort Kamehameha, Oahu Island, which was selected by Jack Fisher who has worked on economic algae with Prof. M. S. Doty for many years and who thought that this number was particularly typical of the habit of the species. Other specimens, all from localities on Oahu Island, Hawaii (BISH): Waikiki, Doty (14043, 14143; Honolulu Harbor area, Doty 20597; Hoyle 20, 369; Keehi Lagoon and Fort Kamehameha area, Hoyle 704, 705 (both spermatangial); Doty 26949, 28676, 28767, 28994; Kahuku, Doty 28942; Kaneohe Bay, Doty 20710 (5 sheets); 28376; 31336 (3 sheets); 31747.

A certain difference in branching pattern is evident between the cystocarpic plants, which are heaviest and coarsest (up to 3.4 mm diam.) and with conspicuous unilateral branching, and the spermatangial plants, which are more slender and bushy and do not show the strong unilateral branching that the female gametophyte shows. Moreover, the female plants are twice or slightly taller than the male plants. In height and branching, tetrasporangial plants resemble the spermatangial ones. The most conspicuous differences from the European *G. bursa-pastoris* (Gmelin) Silva are in the small cells of the pericarp (Renfrew 1983) and their star-shaped contents together with the large cells of the gonimoblast (65 x 150 μm, Renfrew 1983, p. 185).

Small cells of the pericarp with star-shaped contents are also characteristic of *G. coronopifolia*, whose primary distinction from *G. parvispora* otherwise is the possession of Verrucosa-Type spermatangia.

Under certain ecological conditions (e.g., lower water motion, lower salinity) the thalli are very bushy, repeatedly dichotomously branched, branches rarely more than 1 mm diam. and plants about 10 cm high, and hence superficially resembling *G. coronopifolia*. Under these conditions, spermatangial plants of each of these taxa retain their different spermatangial types, i.e., Textorii- and Verrucosa-Types.

Acknowledgements

Many students over the years have helped to make the *Gracilaria* collection at Hopkins Marine Station not only large but geographically comprehensive as well. I am grateful to them for their interest, especially Marjorie Zimmerman, Celia Smith, Robert Sellers, and Roger Phillips. The outstanding northern Santa Cruz collection by Michael Wolcott helped to develop an understanding of Grunow's opinion of *Cordylecladia andersonii*, which was originally described from Santa Cruz. I am thankful also to Dr. Mitchell Hoyle who substantially helped in the formation of opinions of the limits of California *Gracilaria* species.

I thank Dr. M. S. Doty for allowing me to examine specimens of Hawaiian material in his herbarium. I am especially grateful to Meng Doty for aid with the Latin translations. I thank Earl Zablackis for furnishing fresh material for examination. Finally, I am pleased to acknowledge the financial support of the Hawaii Sea Grant College Program for my participation in the Guam Workshop and for subsequent research funds.

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STUDIES ON *GRACILARIA* GREV. (GRACILARIACEAE, RHODOPHYTA) FROM THE GULF OF CALIFORNIA, MEXICO

James N. Norris

The genus *Gracilaria* Greville (1830) was first reported in the Gulf of California by Howe (1911) in describing a new species, *G. vivesii* (= *G. textorii*). Studies of Setchell and Gardner (1924) on Gulf marine algae reported 12 *Gracilaria* taxa, of which 8 were new. Dawson's account of Gulf algae (1944) included 16 species of *Gracilaria*, 3 described as new. In his detailed monograph on northeast Pacific Gracilariaceae, Dawson (1949) recognized 12 *Gracilaria* species (5 as new) and 2 in his new genus, *Gracilariopsis* (Dawson 1949, p. 40), in the Gulf. Subsequently, in his treatment of Pacific Mexico Gigartinales, Dawson (1961a) added one new species, *G. ascidiicola*, to the Gulf's marine flora.

The present study, based on collections made in the Gulf of California between 1972 and 1976, provides a key to the Gulf species and descriptions for each, including new morphological information and, for some, first descriptions of reproductive material and new distribution extensions. Sixteen species of *Gracilaria* and one uncertain record are currently recognized from the Gulf.

Seven of the species, *G. ascidiicola, G. marcialana, G. pinnata, G. ramisecunda, G. rubrimembra, G. spinigera*, and *G. subsecundata*, are presently considered to be endemic to the Gulf of California. *Gracilaria megaspora* is known only from the Gulf of California and China; *G. textorii* is reported from the Gulf, Japan and China; and *G. lemaneiformis* from the Pacific coast of North and South America, in the Gulf, Hawaii, and China. The remainder of the species, *G. crispata, G. pachydermatica, G. tepocensis, G. turgida*, and *G. veleroae*, also occur elsewhere in the Pacific.

Key to the Species

(Numbers in parentheses refer to species descriptions that follow.)

1\. Thallus essentially cylindrical throughout, or in part slightly compressed 2
1\. Thallus distinctly complanate or flattened 10

2\. Thallus cylindrical, lax throughout, irregularly branched from a percurrent axis 3
2\. Thallus cylindrical to ± compressed, rigid, and erect; variously branched; most without a distinct main axis 5

3\. Thallus delicate, under 500 μm diam. throughout; carpospores ca. 50 μm diam. .... (5) *G. megaspora* (Dawson) Papenfuss
3\. Thallus coarse, mostly over 1000 μm diam., or only with some branches 500 μm diam.; carpospores ca. 30 μm diam. 4

4\. Thallus relatively small; axes less than 2 mm diam.; cystocarps mostly under 1 mm diam.; spermatangia in pits throughout upper portions of thallus .... (16) *G.* "*verrucosa*"
4\. Thallus relatively large, longer, coarser; axes usually more than 2 mm diam.; cystocarps mostly over 1 mm diam.; spermatangia superficial, covering thallus surface .... (3) *G. lemaneiformis* (Bory) Weber-van Bosse

5\. Thallus compressed, branching irregular, subsecund, or pinnate 6
5\. Thallus cylindrical, branching dichotomous, irregular, or multifarious 7

6\. Branching variable, irregular to subsecund; main axes 2–3 mm diam. .... (11) *G. subsecundata* Setchell et Gardner
6\. Branching ± pinnate; main axes 3–4 (–7) mm diam.; brittle when fresh .... (7) *G. pinnata* Setchell et Gardner

7. Thallus irregularly branched, very robust and turgid, axes 2–5 mm diam. . . . . (14) *G. turgida* Dawson
7. Thallus subdichotomously to dichotomously branched, robust but not turgid; axes 1.5–3.0 mm diam. 8

   8. Thallus dichotomously branched, robust, stiff; axes 1.5–3.0 mm diam.; individuals ± uniform diam. throughout . . . . (6) *G. pachydermatica* Setchell et Gardner
   8. Thallus not uniform diam., either more robust in mid-portion or in lower portions 9

9. Thallus subdichotomously branched, more robust (1.5–3.0 mm) in mid-portions; cystocarps small compared to its branch diam. . . . . (4) *G. marcialana* Dawson
9. Thallus dichotomously branched below to irregularly subsecund above; robust (1.5–2.0 mm) only in lower portions; cystocarps large compared to its branch diam. . . . . (8) *G. ramisecunda* Dawson

   10. Thalli associated with a compound ascidian . . . . (1) *G. ascidiicola* Dawson
   10. Thalli free, not closely associated with an invertebrate animal 11

11. Thalli with abundant short, spinose, or dentate protuberances on margins and/or on blade surfaces 12
11. Thalli with smooth and entire margins, or with proliferous outgrowths on margins only (but, if present, outgrowths are not spinose or dentate) 13

   12. Thallus thick, fleshy; with spinose protuberances on blade surface and margins . . . . (10) *G. spinigera* Dawson
   12. Thallus thin; spinose and dentate protuberances restricted to margins . . . . (2) *G. crispata* Setchell et Gardner

13. Thallus with narrow ligulate branches, 1.5–3.0 mm wide, upper segments tapering to attenuated, subacute apices . . . . (12) *G. tepocensis* (Dawson) Dawson
13. Thallus broad, wider than 5 mm wide, some over 1 cm or wider; apices mostly rounded 14

   14. Thallus relatively short, to 8 cm tall, 5–7 mm wide, with rounded apices; tetrasporangia within unmodified cortex, scattered over blade . . . . (15) *G. veleroae* Dawson
   14. Thallus relatively large, over 9 cm tall, over 1 cm wide (some to 5 cm wide); tetrasporangia in modified cortex 15

15. Thalli normally with abundant finely divided marginal proliferations; ultimate segments sharply reduced in width over middle portions; cystocarps under 900 μm diam. . . . . (9) *G. rubrimembra* Dawson
15. Thalli usually without marginal proliferations, but relatively coarse if present; upper segments gradually reduced in width upwards from middle portions; cystocarps 1.0–1.5 mm diam. . . . . (13) *G. textorii* (Suringar) DeToni

Gulf of California Species of *Gracilaria*

1. *Gracilaria ascidiicola* Dawson

(Fig. 8)

Dawson 1961a, p. 203, pl. 14.

Thalli forming sessile balls, 8–10 cm diam., in association with a grey-white ascidian (Didemnidae), a bryozoan (*Bugula*) and the red alga, *Gelidiopsis*; generally overgrown by the ascidian, with upper portions protruding 1–2 mm; thallus flat, much-branched or a dissected ± contorted blade, 2.5–4 (–5) mm wide, with segments 4–5 mm long, broadly rounded apices, margins entire, slightly lobed or undulate. Transection 300–400 μm thick; medulla of isodiametric cells about 100 μm diam. in center, becoming smaller outward to 30–40 μm diam. below thin cortex; cortical layer of 1–2 periclinally elongated cells, 7–16 μm long.

Reproduction not found. (After Dawson 1961a.)

Habitat: muddy bottom of shallow lagoon, 1–2 m depth.

Distribution. Gulf of California: Puerto Escondido.

Type locality: innermost lagoon, Puerto Escondido, Baja California del Sur, Gulf of California.

This species can resemble some forms of *G. crispata*, but differs in lacking marginal teeth, and in having a less thick transection with smaller medullary cells and thinner cortical layer. Reproductive material is needed to verify its generic placement.

2. *Gracilaria crispata* Setchell et Gardner

(Fig. 6)

Gracilaria crispata Setchell et Gardner, 1924, p. 753; Dawson 1949, p. 26; 1959, p. 26; 1961a, p. 205; 1961b, p. 415; 1966a, p. 21.

Gracilaria lacerata Setchell et Gardner, 1924, p. 755, Dawson 1944, p. 293.

Thalli clumped, of several variably branched complanate blades, 4–7 cm tall, attached by a small discoid holdfast. Blades divided into few to several flattened main axes; these re-divided into smaller segments which become progressively smaller and attenuated upwards to narrow, almost terete or spinose ultimate segments; margins with minute, sharp dentation along lower portions and somewhat "crisped" in upper portions. Medulla of 3–5 layers of isodiametric cells, to 200 μm diam.; inner cortex of 2–3 smaller subcortical cells, merging somewhat abruptly with outer cortex of anticlinal rows of 2–4 cells, with the outermost surface cells anticlinally elongated; basal cells with hairs, to 500 μm long, sometimes present.

Tetrasporangia isolated, scattered throughout cortex, over entire blade. Cystocarps protruding, dome-shaped, 750–800 μm diam., with a small rostrum, scattered over upper portions of blades; carpospores in chains; gonimoblast of parenchymatous cells, with absorbing filaments to pericarp, developing from a large ramified cell. Spermatangia (Textorii-Type) borne in small, shallow depressions or pits, 15–25 μm diam., separated by rows of elongated cortical cells, throughout upper blade segments.

Habitat: on rocks, mid-tidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific Coast: Bahía Topolobampo, Sinaloa to Acapulco, Guerrero. El Salvador.

Type locality: Rancho Eureka (near Punta Soledad), Bahía de Las Palmas, Baja California del Sur, Gulf of California.

The minute, whitish to yellow, "parasite," *Gracilariophila gardneri* Setchell (1923) has been reported on *G. crispata* by Dawson (1949) from Bahía Bocochibampo (Dawson 1949) and Puerto Peñasco (Dawson 1966a; JN-3163 and 5866c).

3. *Gracilaria lemaneiformis* (Bory) Weber-van Bosse

(Figs. 9–10)

Gigartina lemaneiformis Bory, 1828, p. 151 (as lemanaeformis).

Gracilaria lemaneiformis Weber-van Bosse, 1928, p. 435; Abbott 1983, p. 561; Abbott, this volume.

Gracilariopsis lemaneiformis (Bory) Dawson, Acleto et Foldvik, 1964, p. 59 (as lemanaeformis).

Gracilaria sjoestedtii Kylin, 1930, p. 55; Dawson 1944, p. 296; 1961a, p. 218; Papenfuss 1967, p. 98; Norris 1973, p. 12; Abbott and Hollenberg 1976, p. 498.

Gracilariopsis sjoestedtii (Kylin) Dawson, 1949, p. 40; 1966a, p. 22.

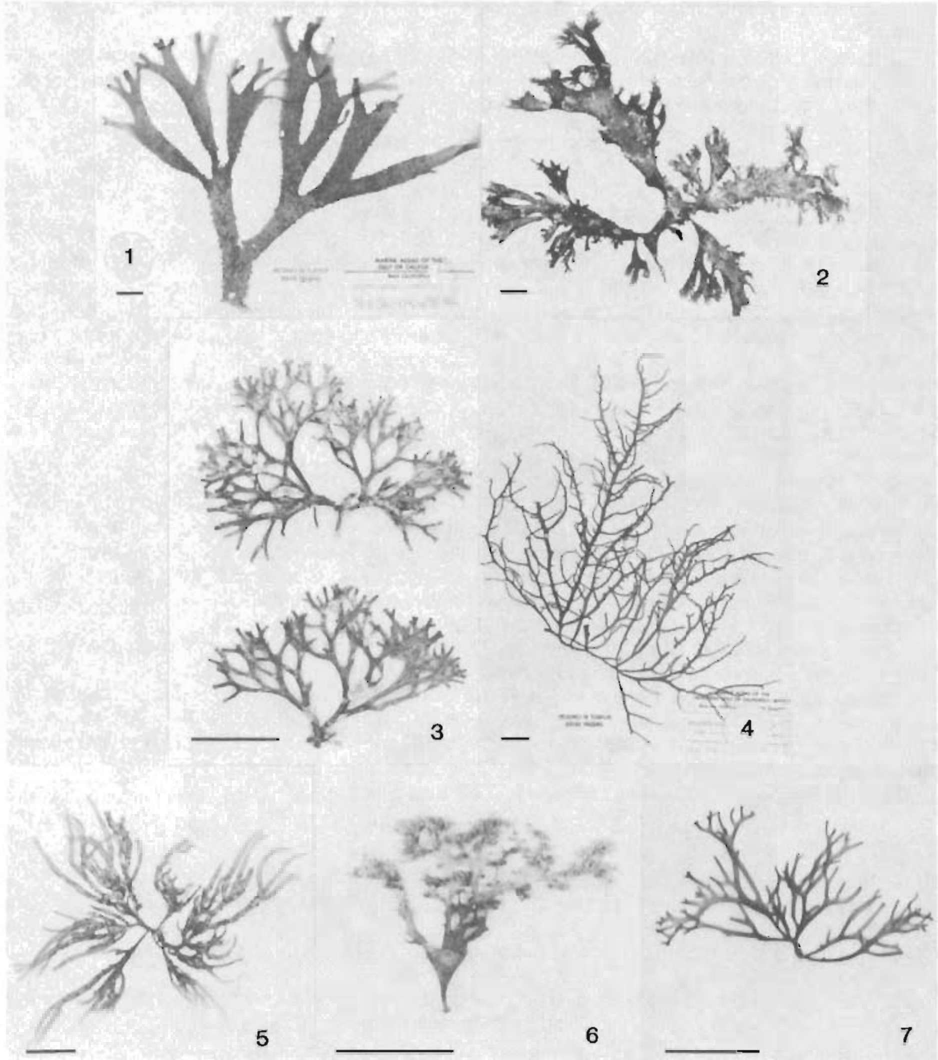
Thalli of few to several long, slender terete branches, up to 2 m long, arising from a discoid holdfast usually associated with prostrate branches. Erect cylindrical branches, (0.5–) 1.5–2.5 (–3.5) mm diam., irregularly and sparingly branched, mostly with abundant, short laterals. Medulla of large cells becoming progressively smaller outwards and grading into the small-celled cortex, often with intact hairs above their basal cells.

Tetrasporangia ellipsoidal, to 38 μm long, embedded in slightly modified cortex of anticlinally elongated cells, scattered throughout the cortex of the branches. Cystocarps dome-shaped, 800–1800 μm diam., protruding and scattered over branch surfaces; carpospores borne in chains, to about 28 μm diam.; gonimoblast of small cells, no absorbing filaments present. Spermatangia in superficial layer (Chorda-Type) arising from the cortex, covering branch surface.

Habitat: usually growing on sand-covered rocks, and generally found midtidal to shallow waters of bays and estuaries; occasionally on midtidal to low tidal rocks elsewhere.

Distribution. Gulf of California: Puerto Peñasco to Guaymas. Pacific Coast: British Columbia to Costa Rica; Peru. China.

Type locality: Paita, Peru.



Figs. 1–7. Gulf of California species of *Gracilaria* (scale bar = 2 cm). Fig. 1. *G. textorii*, Punta La Gringa, Bahía de Los Angeles (#JN-2966, US). Fig. 2. *G. rubrimembra*, Punta La Gringa, Bahía de Los Angeles (#JN-3032, US). Fig. 3. *G. pachydermatica*, Punta Pelicano, vic. Puerto Peñasco (#JN-3953, US). Fig. 4. *G. pinnata*, Puerto Refugio, Isla Angel de la Guarda (#JN-5334, US). Fig. 5. *G. turgida*, estero Bahía de las Animas (#JN-3212, US). Fig. 6. *G. crispata*, Playa Hermosa, Puerto Peñasco (#JN-3258, US). Fig. 7. *G. subsecundata*, Bahía Cholla, vic. Puerto Peñasco (#JN-4990, US).

4. *Gracilaria marcialana* Dawson

Gracilaria marcialana Dawson 1949, p. 15; 1961a, p. 205.

Thalli cylindrical, to 5.5 cm tall, of 2–6 axes attached by an irregular, semi-pulvinate discoid holdfast, 2–3 mm diam.; axes 1.5–2 (–3) mm diam., infrequently branched, 1–2 subdichotomous orders, terete to acute apex, often with a few short, sometimes spinose, branchlets; cystocarpic plants more robust and turgid than tetrasporangial or spermatangial plants. Transection with a broad medulla of large, thin-walled cells, 250–300 μm diam., which extend to within 80 μm of outer margin and merge with subcortical cells, 40–70 μm diam.; cortex 1–2 cell layers, of irregularly shaped cells, about 10 μm diam. (these sometimes further divided by cell walls in various planes), often with only bases of hair cells.

Tetrasporangia cruciate, ovate, 30–35 μm diam., scattered through a very slightly modified cortex. Cystocarps protruding, globose, 750–800 μm diam., often with slight basal constriction, nonrostrate; gonimoblast of large, elongated cells radiating from a prominent fusion cell and connected to the pericarp by numerous absorbing filaments; carpospores about 30 μm diam., with a conspicuous stellate central body. Spermatangia (Textorii-Type) in irregular shallow depressions, 20–40 μm diam., which are separated by 1–2 rows of elongated cortical cells; spermatia 3–4 μm diam., produced on slender clavate cells which arise from concave floor of the depression. (After Dawson, 1961a.)

Habitat: on coral fragments, 16–30 m depths.

Distribution. Gulf of California: Punta San Marcial to Canal de San Lorenzo (Isla Espiritu Santo).

Type locality: reef (vicinity of Roca San Marcial), about 1¼ miles north-northeast of Punta San Marcial (south of Bahía Agua Verde), Baja California del Sur, Gulf of California.

This species resembles *G. turgida* in general appearance; it also has similar tetrasporangia and spermatangia. *Gracilaria marcialana* is smaller, and is known only from deep-water reefs; in contrast *G. turgida* is found in shallow, mud bottom lagoons. Anatomically it differs in the shape of the gonimoblast cells and the size of the carpospores (Dawson 1949).

5. *Gracilaria megaspora* (Dawson) Papenfuss

Gracilariopsis megaspora Dawson 1949, p. 45; 1961a, p. 217.
Gracilaria megaspora (Dawson) Papenfuss, 1967, p. 100.

Thalli cylindrical, to 20 cm long, thin, less than 500 μm diam. throughout, main axes abundantly branched to 2–3 orders, above a small discoid holdfast; branches 5–35 mm long. Medulla of large cells, to 100 μm diam., with abrupt change to subcortex of 2–3 cell layers, 20–35 μm diam.; cortex one layer of anticlinally arranged cells, about 10 μm diam., with abundant short hairs above their basal cells.

Tetrasporangia unknown. Cystocarps projecting, globose, about 500 μm diam., slightly constricted base and barely rostrate; gonimoblast of small, densely massed cells, rich in protoplasm, and arising from a distinct fusion cell; lacking any absorbing filaments; carpospores ovoid, in chains, unusually large, to 50 μm long, with a distinct stellate central body. Spermatangia unknown. (After Dawson 1949, 1961a.)

Habitat: floating in shallow sandy lagoon.

Distribution. Gulf of California: Bahía San Carlos, Sonora. China.

Type locality: lagoon, Bahía San Carlos, Sonora, Gulf of California.

This species, known in the Gulf only from the type collection, has also been reported in China (Chang and Xia 1976). Though similar to *G. lemaneiformis*, it differs in having abundant, short, stubby basal cells of hairs in the cortex, and smaller cystocarps with very large carpospores. Future collections from the type locality should reveal tetrasporangial and spermatangial material, necessary to clarify the status of this taxon.

6. *Gracilaria pachydermatica* Setchell et Gardner

(Fig. 3)

Gracilaria pachydermatica Setchell et Gardner, 1924, p. 753; Dawson 1944, p. 294; 1949, p. 18; 1959, p. 26; 1961a, p. 206; 1966a, p. 22.
Gracilaria guaymasensis Dawson, 1944, p. 298.
Gymnogongrus sinicola Dawson, 1944, p. 300.

Thalli clumped, of few to several rigid, terete, dichotomously branched axes, arising from a discoid holdfast. Axes 1.5–3.0 mm diam., regularly, repeatedly dichotomously branched, to 5 times; branches closer upwards; surfaces without proliferations. Medulla of large, thin-walled, rotund cells to 200 μm diam., becoming successively smaller outwards to subcortex of small cells, 10 μm diam.; outer cortical layer of a single row of cells, anticlinally elongated, about 10 μm long, 5 μm wide, often with hairs above basal cells which are larger and of different shape than other cortical cells.

Tetrasporangia ovoid, 30–35 μm long, borne in little modified cortex, scattered over upper branches. Cystocarps spherical, 750–1000 μm diam., with slight basal constriction, ostiolate, rostrate, borne on upper branches; carpospores 13–15 μm diam.; gonimoblast of parenchymatous cells, with abundant absorbing filaments to pericarp, developing from a large fusion cell (which remains visible in mature cystocarp). Spermatangia in sunken confluent pits, (Textorii-Type) separated by elongated cortical cells, over thallus surface.

Habitat: on rocks, midtidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific Mexico: Isla Cedros; Bahía Vizcaino; Isla Magdalena.

Type locality: Isla de Tortuga, Gulf of California.

7. *Gracilaria pinnata* Setchell et Gardner

(Fig. 4)

Gracilaria pinnata Setchell et Gardner, 1924, p. 751; Dawson 1944, p. 294.

Gracilaria subsecundata sensu Dawson, 1949, p. 20 (in part); Dawson 1961a, p. 209 (in part) (*non G. subsecundata* Setchell et Gardner, 1924, p. 755).

Thalli rose red, pinnately branched from more or less distinct axes, slightly compressed, cartilaginous, brittle in texture, attachment unknown. Fronds to 25 cm tall or more, 3–4 (–7) mm wide, segments narrowing upwards to acuminate apices, short marginal laterals present. Medulla of large thick-walled cells, (110–) 200–350 (–400) μm diam., grading gradually outward to a 2-layered cortex of small cuboidal to anticlinally elongated cells, 10–12 μm long, (3–) 5–10 μm diam.

Tetrasporangia ovoid, (30–) 40–65 μm long by 25–40 μm wide, deep in subcortex surrounded by 3–4 anticlinally elongated cortical cells. Cystocarps dome-shaped, prominent, to 1000 μm diam., scattered over thallus; gonimoblast of parenchymatous cells, with absorbing filaments to pericarp; carpospores (18–) 22–30 μm diam. Spermatangia in shallow depressions (Textorii-Type) 20–22 μm wide by 12–15 μm diam. deep, separated by anticlinally elongated cells, scattered over upper portions of thallus.

Habitat: clumps of entangled fronds found free-living and on sand bottoms; subtidal, 5–23 m depths.

Distribution. Gulf of California: Puerto Refugio, Isla Angel de la Guarda to Bahía de las Animas.

Type locality: Bahía de Los Angeles, Baja California del Norte, Gulf of California.

Dawson (1949, p. 20) had concluded that *G. subsecundata* Setchell et Gardner and *G. pinnata* were a single species. However, collections (JN-5334, JN-5814) from the R/V *Dolphin* cruise (Norris and Bucher 1976) to the northern Gulf of California, including type locality material (JN-2971, JN- 2997), were identical with the type and have led me to believe that the two are distinct species. I suspect that Setchell and Gardner (1924) may have described their plant from dried herbarium material, for fresh specimens are not flat as they noted, but slightly compressed and oval in transection. The pinnate branching, bright rose red color when fresh, oval transection, and the rigid but brittle nature serve to distinguish it from all other Gulf species.

The largest specimens measured 25 cm tall (JN-5334) and 7 mm diam. (JN-3214), but some were probably larger since these plants are so brittle when fresh that they easily break into pieces. When collecting the plants subtidally it was impossible to place specimens into collecting bags without breakage.

8. *Gracilaria ramisecunda* Dawson

(Fig. 14)

Gracilaria ramisecunda Dawson, 1949, p. 32; Dawson 1959, p. 26; 1961a, p. 208; 1966a, p. 22; 1966b, p. 64.

Thalli cylindrical to compressed, cartilaginous, 6–8 cm tall, to 2 mm diam. below and tapering gradually to upper portions of 400–1000 μm diam., with blunt apices; usually a single main axis above a discoid holdfast, branching to 3–4 orders, first and second orders irregularly dichotomous with acute angles and long internodes, third and fourth irregular, tending to secund. Medulla in transection of 8–10 rotund to ovoid cells, > 100 μm diam., decreasing gradually outwardly to a single layer cortex of anticlinally elongated cells, (6–) 10–15 μm diam.; basal cells of hairs observed; in longitudinal section a 2-layer subcortex of isodiametric cells is distinct from longitudinally elongated medulla cells.

Tetrasporangia ovoid, 25–35 μm diam., in slightly modified cortex of anticlinal elongate cells; scattered on upper branches. Cystocarps protruding, subglobose, 600–1200 μm diam., with a slight basal constriction, slightly rostrate, ostiolate, carpospores 14–17 μm diam.; gonimoblast of parenchymatous cells, with absorbing filaments to pericarp, developing from a conspicuous fusion cell. Spermatangia (Textorii-Type in small sunken depressions separated by anticlinally elongated cortical cells.

Habitat: low intertidal rocks and tide pools.

Distribution. Gulf of California: Puerto Escondido to Cabeza Ballena.

Type locality: Cabeza Ballena (east of Cabo San Lucas), Baja California del Sur, Gulf of California.

9. *Gracilaria rubrimembra* Dawson

(Fig. 2)

Gracilaria rubrimembra Dawson 1949, p. 32; Dawson 1961a, p. 208; 1966a, p. 22; 1966b, p. 64.

Thalli of one to few closely dichotomously, subflabellately branched, complanate blades, borne on a short stipe, attached by a discoid holdfast. Blades branched in one plane, upper portions congested and overlapping, middle portions broadest, to 2.5 cm wide, lower portions narrowing basally to a very short compressed stipe, 1 mm diam.; margins with numerous short, divided, pointed, or lobed lateral proliferations. Transection 700–850 μm thick; medulla of large, thin-walled cells, 120–160 μm diam., grading to smaller inner cortical cells, 20–25 μm diam., in turn to outer cortex of 1–2 layers of small variously shaped cells, 8–15 μm diam.

Tetrasporangia 20–30 μm diam., embedded within inner cortex, surrounded by 2–4 filamentous cells (which are modified inner and outer cortical cells). Cystocarps dome-shaped, projecting, to 900 μm diam., ostiolate, slightly rostrate, scattered over upper portion of blade surfaces; gonimoblast of parenchymatous cells above a dome of medullary cells, with numerous absorbing filaments to pericarp, developing from a ramified fusion cell. Spermatangia unknown.

Habitat: on rocks, midtidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Guaymas.

Type locality: Ensenada de San Francisco (near Guaymas), Sonora, Gulf of California.

This species may be confused with *G. textorii* since it is difficult to separate the small, broadly proliferous forms of both of these species. In such cases, the marginal proliferations of *G. rubrimembra* appear to be more finely divided and dentate than those of *G. textorii*. The cystocarps are larger and more prominent in *G. textorii*. Detailed studies on the variation within each species and on the overlapping characteristics is needed to evaluate the distinctions of these two taxa.

10. *Gracilaria spinigera* Dawson

(Fig. 15)

Gracilaria spinigera Dawson, 1949, p. 24; Dawson 1959, p. 26; 1961a, p. 208.

Thalli of several branched, complanate blades, to 15 cm tall, attached by a small discoid holdfast. Blades broad in upper portions, (3.5–) 5.0–12.0 mm wide, narrowing downward to a cuneate to stipe-like or abruptly contracted basal portion. Primary branching subdichotomous, often closely set; apical portion with several spinose terminal segments. Secondary branches short, marginal spinose branchlets, 4–12 mm long. Transection 600–1500 μm thick; medulla of large cells, 150–180 μm diam., grading into subcortical layer of cells, 25–50 μm diam.; outer cortex a single layer of small, anticlinally elongated cells.

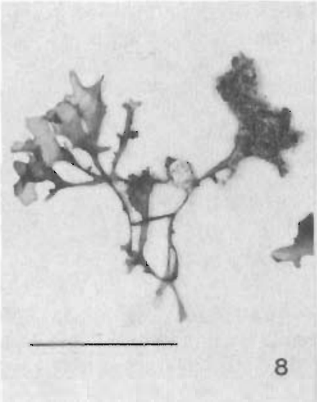
Tetrasporangia 20–25 μm diam., embedded in little modified cortex of anticlinal oblong cells, 10–14 μm long, scattered over blade. Cystocarps globose, barely rostrate, 1200–1500 μm diam., scattered on blade surfaces, or clustered and 400–600 μm diam. among spines of branchlets; gonimoblast of large parenchymatous cells, with numerous absorbing filaments to thick pericarp. Spermatangia in closely spaced ovoid cavities (Verrucosa-Type) in blade surfaces, 35–60 μm deep and 28–45 μm diam., with a surface opening to 20 μm diam.

Habitat: on rocks, low intertidal to shallow subtidal.

Distribution. Gulf of California: Bahía de Los Angeles to Puerto Escondido.

Type locality: Ensenada de San Francisco, Sonora, Gulf of California.

This species differs from other Gulf species by its "*Gigartina*-like" appearance, and the deep spermatangial cavities.



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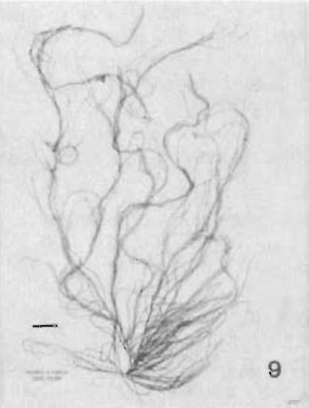

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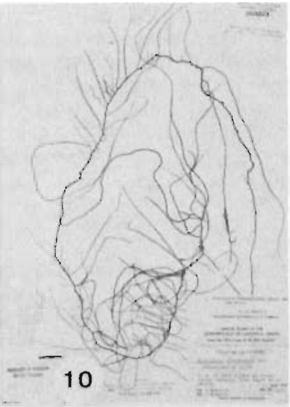

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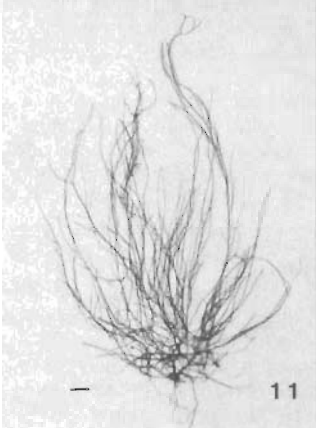

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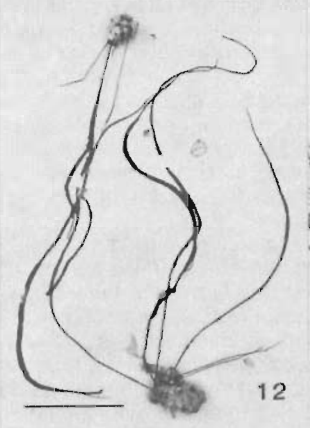

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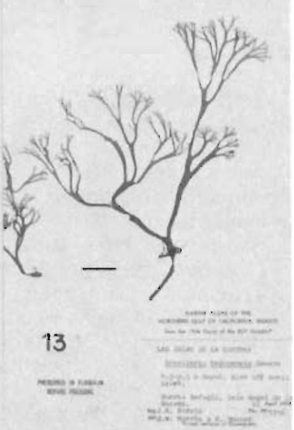

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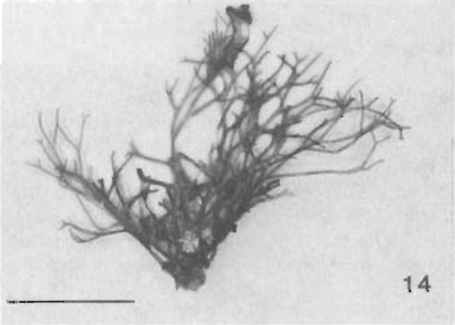

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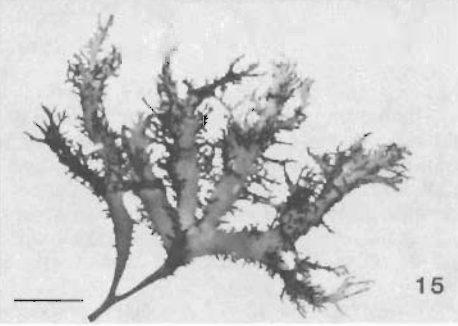

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Figs. 8–15. Gulf of California species of *Gracilaria* (scale bar = 2 cm). Fig. 8. isotype of *G. ascidiicola*, Puerto Escondido (#EYD-3215, US). Fig. 9. *G. lemaneiformis*, estero, Bahía de las Animas (#JN-3215, US). Fig. 10. *G. lemaneiformis*, Puerto Refugio, Isla Angel de la Guarda (#JN-5825, US). Fig. 11. *G. "verrucosa,"* Bahía Cholla, vic. Puerto Peñasco (#JN-4987, US). Fig. 12. *G. rhodotricha*?, Bahía de San Lucas (#EYD-6847, US). Fig. 13. *G. tepocensis*, Puerto Refugio, Isla Angel de la Guarda (#JN-5356, US). Fig. 14. *G. ramisecunda*, Cabeza Ballena (#EYD-6767, US). Fig. 15. *G. spinigera*, Ensenada de San Francisco, vic. Guaymas (#EYD-1903, US).

11. *Gracilaria subsecundata* Setchell et Gardner
(Fig. 7)

Gracilaria subsecundata Setchell et Gardner, 1924, p. 755; Dawson 1944, p. 294; 1949, p. 20; 1959, p. 26; 1961a, p. 209; 1966a, p. 22; Norris 1973, p. 13.

Gracilaria compressa sensu Dawson, 1944, p. 296 (in part) [*non G. compressa* (J. Agardh) Greville, 1830, p. 125].

Gracilaria pinnata sensu Dawson, 1961a, p. 209 (in part) (*non G. pinnata* Setchell et Gardner, 1924, p. 751).

Thalli bushy to more or less lax, of several subcylindrical to compressed branches, to 15 cm tall, to 2 (–3) mm diam., arising from a small discoid holdfast. Branching pseudodichotomous, distichous, and repeated to 6–7 orders, attenuating upwards to acute tips; sparse to dense, often more or less secund; internodes variable with size and age, from a few mm to 6 cm in larger thalli. Medulla of large rotund cells, about 200 μm diam. or more, grading into inner, radially elongate subcortical cells, 25 μm diam., outer cortex of ± anticlinal rows of 3–4 cells, to 10 μm long, 5–8 μm wide; conspicuous hairs or only basal cells of hairs sometimes present.

Tetrasporangia usually cruciate and ovoid, but in some divided periclinally to produce bispores, 25–30 (–45) μm diam., borne in modified cortex of irregular, small cells in anticlinal rows of 3–4 cells, scattered over branch surfaces. Cystocarps dome-shaped, ostiolate, scattered over upper portions of thallus; gonimoblast broad-based of parenchymatous cells, with many absorbing filaments to pericarp, developing from a large fusion cell. Spermatangia in sunken depressions (Textorii-Type), 14–17 μm diam., separated by bands of cortical cells, and grouped together in patches over branch surfaces.

Habitat: on rocks, or sand-covered substrate from midtidal to shallow subtidal. Often found in bays and estuaries.

Distribution. Gulf of California: Puerto Peñasco to Bahía Agua Verde.

Type locality: Guaymas, Sonora, Gulf of California.

Re-examination of tetrasporangial plants is necessary in order to verify the reported (Dawson 1949, p. 22) bispores.

12. *Gracilaria tepocensis* (Dawson) Dawson
(Fig. 13)

Rhodymenia? *tepocensis* Dawson, 1944, p. 307.

Gracilaria tepocensis (Dawson) Dawson, 1961a, p. 211; 1961b, p. 415; 1966b, p. 64; Norris and Bucher 1976, p. 17.

Gracilaria crockeri Dawson, 1949, p. 30.

Thalli lax, of few to several narrow complanate pseudodichotomously branched blades, to 25.5 cm tall and 2–3 (–5.5) mm wide, attached by a small discoid holdfast. Blades repeatedly branched in one plane, to 3–4 orders, at intervals of 1–2 (–6) cm; margins entire, smooth; upper branches reduced in width upwards to a blunt apex, or apex of two or more digitate segments. Transection (150–) 200–300 μm thick; medulla of two layers of large cells, 100–200 μm diam., abruptly adjoined to a narrow, completely or partially developed subcortical layer of smaller cells; outer cortex usually a single layer of periclinally elongated cells, 7–10 (–20) μm diam.

Tetrasporangia to about 20 μm diam., in slightly modified cortex of two-celled anticlinal filaments (not always evident), scattered over thallus. Cystocarps globose, to 500 μm diam., rostrate, marginal or superficial over thallus surface; gonimoblast of radially elongated parenchymatous cells, with numerous absorbing filaments to pericarp, developing from a large fusion cell. Spermatangia (Textorii-Type) in small, partially sunken, irregularly confluent sori, and bordered by little-modified to anticlinal elongate cortical cells, spermatia 3–4 μm diam.

Habitat: on rocks, 4.5–10.6 m depths (also reported from dredged depths of 21 m and 113 m).

Distribution. Gulf of California: Puerto Refugio, Isla Angel de la Guarda to Isla Estanque. Pacific Coast: El Salvador; Costa Rica; Perú.

Type locality: Bahía Tepoca, Sonora, Gulf of California.

Previously known in the Gulf only from dredged material taken at 21 m depths, Bahía Tepoca and from Isla Estanque at 113 m depth (Dawson 1944; 1961a), and more recently from Agiabampo, Sonora (Dawson 1966b). Our recent diving surveys (Norris and Bucher 1976) contributed several collections from 1 to 10.6 m depths at Puerto Refugio, Isla Angel de la Guarda (JN-5356) and off Isla Estanque (JN-5606), which make suspect the dredged depths (particularly the 372 ft. depth reported by Dawson 1961a) as being correct for attached, intact specimens. This alga has also been reported from El Salvador (Dawson 1961b) and Perú (Acleto 1973).

13. *Gracilaria textorii* (Suringar) DeToni

(Fig. 1)

Sphaerococcus textorii Suringar, 1868, p. 259; J. Agardh 1876, p. 426.

Gracilaria textorii (Suringar) DeToni, 1895, p. 27; Dawson 1959, p. 26; 1961a, p. 211; Norris 1973, p. 13; Yamamoto 1978, p. 123.

Gracilaria vivesii Howe, 1911, p. 503; Dawson 1949, p. 34.

Gracilaria johnstonii Setchell et Gardner, 1924, p. 752.

Gracilaria sinicola Setchell et Gardner, 1924, p. 752.

Gracilaria vivipara Setchell et Gardner, 1924, p. 750.

Thalli foliose, of one to few irregularly dichotomous flabellate blades, to 35 cm tall, and to 5 cm wide, attached below by a discoid holdfast. Blades branched in one plane, thick, membranous to coriaceous, with round to attenuate apices; most with smooth, entire margins, but some with abundant simple or branched proliferations. Transection (350–) 400–600 (–800) μm thick; medulla of large thin-walled cells, 250–500 μm diam.; cortex usually a single layer of small cells, becoming 2 layers in larger, older portions.

Tetrasporangia ovate to elongate, 15–22 μm diam., in modified cortex, surrounded by anticlinally elongated cortical cells, over thallus surface. Cystocarps globose, 1.2–1.6 mm diam., prominent, ostiolate, slightly rostrate, scattered over thallus; gonimoblast of parenchymatous cells with numerous absorbing cells to pericarp, developing from a large fusion cell. Spermatangia (Textorii-Type) in individual to confluent cup-shaped cavities, surrounded by modified cortical cells, over thallus surface.

Habitat: on rocks, low intertidal to shallow subtidal.

Distribution. Gulf of California: San Filipe to Guaymas; Puerto Escondido; Isla Carmen; Isla Espiritu Santo. Pacific Baja California: Bahía Tortuga to Punta Pequeña. Galápagos Archipelago. Japan. China.

Type locality: Japan Sea.

This species is very variable in size and shape. The red to greenish-red blades are found more frequently in the subtidal of the northern Gulf, but also have been collected occasionally in the southern Gulf. Many of the forms exhibited by Gulf material overlap (Dawson 1949) with those found in Japan (cf. Yamamoto 1978).

14. *Gracilaria turgida* Dawson

(Fig. 5)

Gracilaria turgida Dawson, 1949, p. 14; Dawson 1961a, p. 213; 1966a, p. 22; 1966b, p. 63; Abbott and Hollenberg 1976, p. 498.

Thalli of one to several terete, turgid, robust, sparsely branched axes, to 15 cm tall, arising from a discoid holdfast. Axes once or twice branched, with terete, blunt apices. Medulla of large thin-walled cells, grading outwards to the cortex of small, anticlinally elongated cells; numerous, deciduous hairs present in cortical layer.

Tetrasporangia in more or less modified cortex, scattered throughout thallus. Cystocarps globose, 700–900 μm diam., prominent, ostiolate, somewhat basally constricted, scattered on upper thallus; carpospores 18–20 μm diam.; gonimoblast of large vacuolate cells, with numerous absorbing filaments to pericarp. Spermatangia borne in depressions (Textorii-Type) of cortical layer, separated by modified, anticlinally elongated cortical cells.

Habitat: on shells or rocks, of mud flats and estuaries, often in drainage channels.

Distribution. Gulf of California: Bahía Cholla (vicinity of Puerto Peñasco); estuary Bahía de las Animas. Pacific Coast: Newport Harbor, southern California to Bahía Magdalena, Baja California del Norte. Philippines.

Type locality: mud flat, upper Newport Harbor, Newport-Balboa, Orange County, California.

15. *Gracilaria veloroae* Dawson

Gracilaria veleroae Dawson, 1944, p. 297; Dawson 1945, p. 83; 1949, p. 28; 1961a, p. 214; Abbott and Hollenberg 1976, p. 499.

Gracilaria tenuifolia Taylor, 1945, p. 234.

Thalli complanate, membranous, of irregularly dichotomously branched flabellate blades to 8 cm tall, which narrow downwards, forming cuneate fronds above a small discoid holdfast. Blades 5–7 mm wide, with entire smooth margins and rounded apices. Transection usually less than 250 μm thick (occasionally to 400 μm thick); cortex a single layer of periclinally flattened cells, 5 (–9) μm tall by 12 (–13) μm wide.

Tetrasporangia spherical, 25–35 μm diam., borne in scarcely modified cortex, scattered over thallus. Cystocarps, usually near blade margins, dome-shaped, to 1 mm diam., slightly rostrate, gonimoblast developing from a large fusion cell, of large parenchymatous cells, with numerous absorbing filaments to pericarp. Spermatangia in shallow depressions (Textorii-Type), sometimes partially confluent, separated by anticlinally elongate cells, scattered over blade surfaces; spermatia 2.5–3 μm diam.

Habitat: on rocks, usually subtidal to 30 (–79) m depths; rare low intertidal.

Distribution. Gulf of California: Punta Peñasco to Cabeza Ballena. Pacific Coast: La Jolla, California to Baja California; Revilla Gigedo Islands; Acapulco, Guerrero; Galápagos Islands.

Type locality: off the southern end of Isla Tiburon (near Isla Turner), Gulf of California.

Some specimens of *Gracilaria veleroae* resemble smaller examples of *G. textorii*. *G. veleroae* is typically thinner in transection (usually less than 250 μm thick) and membranous, whereas *G. textorii* is thicker (400–750 μm), tending towards coriaceous. The tetrasporangia of *G. veleroae* are larger and spherical (25–35 μm diam. vs. 15–22 μm diam. of *G. textorii*) and are not borne in modified cortex as in *G. textorii* (Dawson 1949; 1961a).

Schneider (1975) considered *G. veleroae* to be a synonym of *G. mammillaris* (Montagne) Howe based on comparisons with North Carolina specimens; unfortunately neither type-specimen, type-locality nor northern Gulf of California material were examined (i.e., all localities listed by Schneider, 1975, pp. 645-646, are outside the Gulf of California, except one from Isla Carmen). Until critical studies are made on type material of both Gulf *G. veleroae* and Caribbean *G. mammillaris* (Montagne) Howe (1918) (basionym: *Rhodymenia mammillaris* Montagne, 1842, p. 252; type-locality: Martinique), I recognize these as two separate taxa.

16. *Gracilaria "verrucosa"*

(Fig. 11)

Gracilaria verrucosa sensu Dawson, 1961a, p. 214 (with reference to Gulf of California specimens only); Dawson 1966a, p. 22; Norris 1973, p. 13 [*non G. verrucosa* (Hudson) Papenfuss, 1950, p. 195].

Thalli of several cylindrical axes, to 30 cm long and 0.5–1.0 (–2.0) mm diam., irregularly and sparsely to repeatedly branched, arising from a small conical holdfast. Branching mostly alternate, usually with numerous lateral proliferations. Medulla of large cells, 300–450 μm diam.; cortex 2–3 layers of small cells; basal cells in hairs to 1 mm, deciduous and protruding from outer cortical layer on upper portions of thallus.

Tetrasporangia oval, 30–33 μm long by 20–30 μm diam., in unmodified cortex, scattered over the thallus surface. Cystocarps dome-shaped to globose, protruding, scattered over thallus; gonimoblast of very large parenchymatous cells, with numerous absorbing filaments to pericarp, developing from a conspicuous fusion cell. Spermatangia in small non-confluent pits, (Verrucosa-Type) throughout upper portions of thallus.

Habitat: on rocks, midtidal to shallow subtidal.

Distribution. Gulf of California: Puerto Peñasco to Santa Rosalia.

It is difficult to distinguish some forms of this species from similar forms of *G. lemaneiformis*. When such overlapping forms are encountered they are easily separated by spermatangial plants. The spermatangia are in separated pits in Gulf *G. "verrucosa"*; in *G. lemaneiformis* they are superficial and continuous over the thallus surface (Abbott, this volume).

Uncertain Record

Gracilaria rhodotricha (Dawson) Papenfuss

(Fig. 12)

Gracilariopsis rhodotricha Dawson, 1949, p. 47; 1961a, p. 217.

Gracilaria rhodotricha (Dawson) Papenfuss, 1967, p. 100.

There is one collection tentatively referred to this species (E. Y. Dawson #6847, *US*, specimens dredged from 20 m, Bahía de San Lucas, Baja California del Sur). Originally described from Isla Clarión and reported from other Revilla Gigedo Islands (Dawson 1949; 1961a), its presence in the Gulf needs confirmation based on the finding of gametangial plants.

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MORPHOLOGICAL STUDIES ON SOME TROPICAL SPECIES OF *GRACILARIA* GREV. (GRACILARIACEAE, RHODOPHYTA): TAXONOMIC CONCEPTS BASED ON REPRODUCTIVE MORPHOLOGY

Suzanne Fredericq and James N. Norris

Abstract

Taxonomic features used to distinguish selected *Gracilaria* species from the tropical-subtropical Western Atlantic were investigated. Two groups are recognized based upon reproductive morphological differences shown by the female reproductive structures, and differences in the origin of spermatangial conceptacles and tetrasporangia. *Group 1* consists of *G. debilis* (Forsskål) Børgesen and *G. crassissima* P. et H. Crouan; *Group 2* of *G. tikvahiae* McLachlan and *G. cervicornis* (Turner) J. Agardh. *Group 1* is distinguished by the following features: the gonimoblast does not originate directly from the fusion cell; the direction of cystocarp development occurs principally horizontally; the number and shape of the pericarp layers is fixed prior to the formation of the fusion cell; the cystocarp cavity is present prior to the appearance of gonimoblast initials; the fusion cell becomes highly ramified and not distinguishable; the gonimoblast originates early in development from inner pericarp cells connected to the fusion cell; absorbing filaments connecting gonimoblast and upper pericarp are absent, but basal connections are formed between the inner pericarp and placenta; spermatangia originate from cortical, subcortical, or medullary cells; the tetrasporangia originate either basally or laterally from cortical cells. In contrast, *Group 2* is characterized by: a gonimoblast that originates directly from the fusion cell; the direction of the cystocarp development occurs principally vertically; the pericarp is formed concomitantly with the formation and expansion of the fusion cell; the cystocarp cavity is formed after the appearance of gonimoblast initials; the fusion cell is prominent and solid; the gonimoblast develops late and originates from cells cut off from the fusion cell; absorbing filaments are present that only connect the gonimoblast and upper pericarp; spermatangia originate only from cortical cells; the tetrasporangia originate only basally from cortical cells. These two groups are suggested to form the basis of two distinct genera.

Introduction: Historical Review of Reproductive Structures

Members of the genus *Gracilaria* Grev. (Greville 1830, p. lvi), *nomen conserv.* (Gigartinales Schmitz, Gracilariaceae Nägeli, *fide* Silva 1980, p. 83) are widespread from sub-boreal to tropical waters. The taxonomy of this economically important agar-producing genus is confused by the high degree of morphological and anatomical variation exhibited within species (e.g., Chapman et al. 1977), which has complicated recognition of species. As Dawson (1949) noted, although *Gracilaria* is a very polymorphic genus vegetatively, it has remarkably constant reproductive structures. Species limits are ill-defined and the genus is in need of major revision (e.g., Papenfuss 1953, 1967; Bird and McLachlan 1982, 1984).

Taxonomic and floristic treatments of *Gracilaria* in the tropical—subtropical Western Atlantic are by Taylor (1960, 1969) and Oliveira et al. (1983), and regionally from Puerto Rico (Diaz-Piferrer and Caballer de Perez 1964; Ortiz Sotomayor 1976; Ortiz Sotomayor and Almodovar 1982; Vélez Villamil 1981), and the northwestern Atlantic (McLachlan 1979).

Recent studies from other areas that involve reproductive morphology in *Gracilaria* have been undertaken by Bodard (1964, 1967), Chang and Xia (1964, 1976); Oliveira (1969); Oza (1976); Kraft (1977); Yamamoto (1978); Edelstein et al. (1978); Yang and Chiang (1982); Delivopoulos and Tsekos (1983); Abbott (1983); Bird and McLachlan (1984); and Hoyle (1984). Ecological studies on *Gracilaria* reproduction are few. The only studies of reproductive seasonality of tropical species of *Gracilaria* are those of Umamaheswara Rao (1973), Hoyle (1978), Trono and Azanza-Corrales (1981), and Hay and Norris (1984). Hay and

Norris (1984) found six sympatric species of Caribbean Panama *Gracilaria* to be fertile throughout the year, with no spatial or temporal isolation of reproduction, and suggested chemical or structural differences may be important in preventing hybridization.

Sjöstedt (1926) was the first to recognize carpogonial branches in *Gracilaria*. His interpretation of those structures was confirmed by Dawson (1949). The carpogonial branch develops from a transformed cortical cell that functions as the primordium (see Sjöstedt 1926; Yamamoto 1978). The primordium cuts off a supporting cell and an apical cell. This apical cell divides transversely forming a two-celled carpogonial branch, the lower cell becoming the hypogynous cell and the upper cell becoming the carpogonium bearing the trichogyne (see Sjöstedt 1926; Yamamoto 1978). Before development of the carpogonial branch is completed, the supporting cell also cuts off one or two cells which retain their vegetative character as sterile lateral branches (Sjöstedt 1926; Yamamoto 1978). Johnson (1888) commented on the presence of carpogonial branches originating after pericarp formation in *G. verrucosa* (Huds.) Papenfuss [as *G. confervoides* (L.) Grev.]; however, Sjöstedt (1926) felt Johnson's study was "fragmentary and in part inaccurate."

In describing the Gracilariaceae, Kylin (1930) noted that the family is distinguished by the occurrence of a large irregular fusion cell from which the gonimoblast develops after enlargement of the fertilized carpogonium and its fusion with several neighboring cells. Several interpretations exist regarding presence or absence of an auxiliary cell in *Gracilaria*. Sjöstedt (1926), later corroborated by Oliveira (1969), assumed that *Gracilaria* never shows an auxiliary cell and considered the carpogonium to be the starting point for the fusion cell. Sjöstedt further stated that the function of the auxiliary cell is taken over by the multinucleate basal cells of the sterile branches and that none of these cells becomes the typical auxiliary cell detectable before fertilization, with the carpogonium not degenerating after fertilization. More recently, Oza (1976) reported that in *G. corticata* J. Ag. an auxiliary cell is absent, and the fertilized carpogonium fuses with the hypogynous cell, the supporting cell, and the surrounding sterile cells. In studying *G. tikvahiae* McLachlan, Edelstein et al. (1978, as *G.* species) could not detect connections between the carpogonium, the hypogynous cell, and the supporting cell, but noted that the latter two cells increase in size while the carpogonium shrivels. They regarded further fusion to result in a single large cell which became irregularly shaped and strongly lobed as the fusion progressed. In contrast, Greig-Smith (1954) reported that the carpogonium in *G. foliifera* (Forsskål) Børg. (as *G. multipartita* J. Ag.) develops a short filament that connects to the auxiliary cell. This auxiliary cell is borne directly on the supporting cell and later develops the fusion cell. (If this is the case, it suggests that it does not belong in the Gigartinales.)

In a more detailed account Yamamoto (1978) described for Japanese *Gracilaria* species a connecting tube that emerges from the inflated basal portion of the carpogonium after fertilization. The connecting tube then makes a connection with the basal cell of a sterile branch. Assuming that the diploid nucleus in the carpogonium entered the basal cell, he considered it to be the auxiliary cell. After completion of the ephemeral connection between carpogonium and auxiliary cell, the carpogonium finally degenerates (Yamamoto 1978). Occasionally the pit-connection between the carpogonium and the hypogynous cell gradually widens, allowing the diploid nucleus to move into the hypogynous cell. In this case, it is the hypogynous cell that forms a connection with the auxiliary cell (Yamamoto 1978). The auxiliary cell then unites with a neighboring cortical cell and with the supporting cell through a wide pit-connection. In this case, the auxiliary cell serves as the starting point of a big fusion cell, which involves the hypogynous and supporting cells and eventually produces the gonimoblast at its periphery (Yamamoto 1978).

In summary, three sites of origin for the fusion cell have been proposed: (1) a typical auxiliary cell (Greig-Smith 1954; Yamamoto 1978), (2) the carpogonium (Sjöstedt 1926; Kylin 1930; Oliveira 1969), and (3) fusion among the hypogynous, supporting, and neighboring cells (Yamamoto, 1978).

Thuret and Bornet (1878) illustrated elongated, concentric cells within the cystocarp, which they thought originated either from the pericarp or from the gonimoblast. Sjöstedt (1926) suggested a nutritive function for those cells, naming them "nutrient tubular cells," capable of taking nutrients from the cortical cells and transferring them to the gonimoblast parenchyma. Dawson (1949) coined the term "nutritive filaments," which was subsequently accepted by Børgesen (1950) and Ohmi (1958). Sjöstedt (1926), later corroborated by Dawson (1949), described two kinds of cystocarps in *Gracilaria*. One type was based on the absence of nutritive filaments and the presence of a gonimoblast parenchyma which consists of a highly nutritive-rich multicellular tissue of small cells. The other type was based on the presence of nutritive filaments with a gonimoblast parenchyma of relatively few, though larger, and comparatively nutritive-poor elongated cells. Ohmi (1958a) further correlated a broad-based gonimoblast parenchyma with the presence of nutritive filaments and a small-based one with the absence of those filaments. Dawson (1949) recognized two genera on these features. Based on the cystocarps without nutritive filaments, he described a new genus, *Gracilariopsis* Dawson [generic type: *Gracilariopsis sjoestedtii* (Kylin) Dawson], segregating it from *Gracilaria* Grev., which had cystocarps with nutritive filaments.

Oliveira (1969) mentioned that occasionally in *Gracilaria verrucosa* (Huds.) Papenfuss he was unable to observe "nutritive filaments," suggesting that the filaments may not possess any systematic value. Earlier, Bodard (1967) had also considered the use of this character for generic separation to be weak. Both authors were apparently unaware that Papenfuss (1967) had reduced the genus *Gracilariopsis* Dawson to taxonomic synonymy with *Gracilaria* Grev. after having examined the British material of *Gracilaria verrucosa* (Huds.) Papenfuss [lectotype: *G. confervoides* (L.) Grev.]. He reported that the presence of nutritive or "connecting" filaments could not always be confirmed, and that the size of the placental cells did not differ fundamentally from the ones of *G. sjoestedtii*.

Yamamoto (1975, 1978) tentatively used the term "nutritive filaments" awaiting a better understanding of their function. Kraft (1977) preferred the use of a purely neutral descriptive term and suggested "traversing filaments." Børgesen (1950) noted that with large and vacuolated gonimoblast cells, typical for some *Gracilaria*, connecting filaments penetrate the gonimoblast tissue from below in *G. millardetii* (Mont.) J. Ag. Umamaheswara Rao (1972) observed the same phenomenon in some Indian species of *Gracilaria*. Yamamoto (1975) regarded the "nutritive filaments" as subsidiary in any systematic treatment of the genus. In order to use a consistent, uniform terminology, we will refer to "nutritive," "connecting," or "traversing" filaments as "absorbing" filaments throughout this study (and this volume) as used by Mikami (1965) and Abbott (1972).

Dawson (1949) first demonstrated the taxonomic importance of the shape and origin of spermatangial conceptacles. Ohmi (1958a), in his monograph on Japanese *Gracilaria* species, stressed that they were the most important characters to distinguish species. Later, Yamamoto (1975) divided the genus into three subgenera based on the three different types of male organs: (1) *Gracilariella*—with superficial spermatangia, scattered continuously over the thallus surface, e.g., *G. chorda* Holmes; (2) *Textoriella*—with spermatangia in shallowly depressed concave conceptacles in the cortex, with each spermatangial mother cell primordium forming a branch system covering the floor of the conceptacle at maturity, e.g., *G. textorii* (Sur.) DeToni; and (3) *Gracilaria*—with spermatangia in deep cup-shaped conceptacles within the cortex, with each spermatangial mother cell primordium forming a branch system covering the entire inner surface of the conceptacle at maturity, e.g., *G. verrucosa*. Yamamoto (1975) considered the superficial spermatangial formation of the *Chorda*-Type to be the most primitive, and the other two types (i.e., *Textorii* and *Verrucosa*) in which spermatangial branch systems and conceptacles are formed, more advanced. He found a correlation between the presence of absorbing filaments in the cystocarp and the three types of male organs. The *Chorda* male type always had cystocarps devoid of absorbing filaments, while the *Textorii* male type appeared exclusively in species having cystocarps with absorbing filaments. With the *Verrucosa* male the absorbing filaments were either present or lacking.

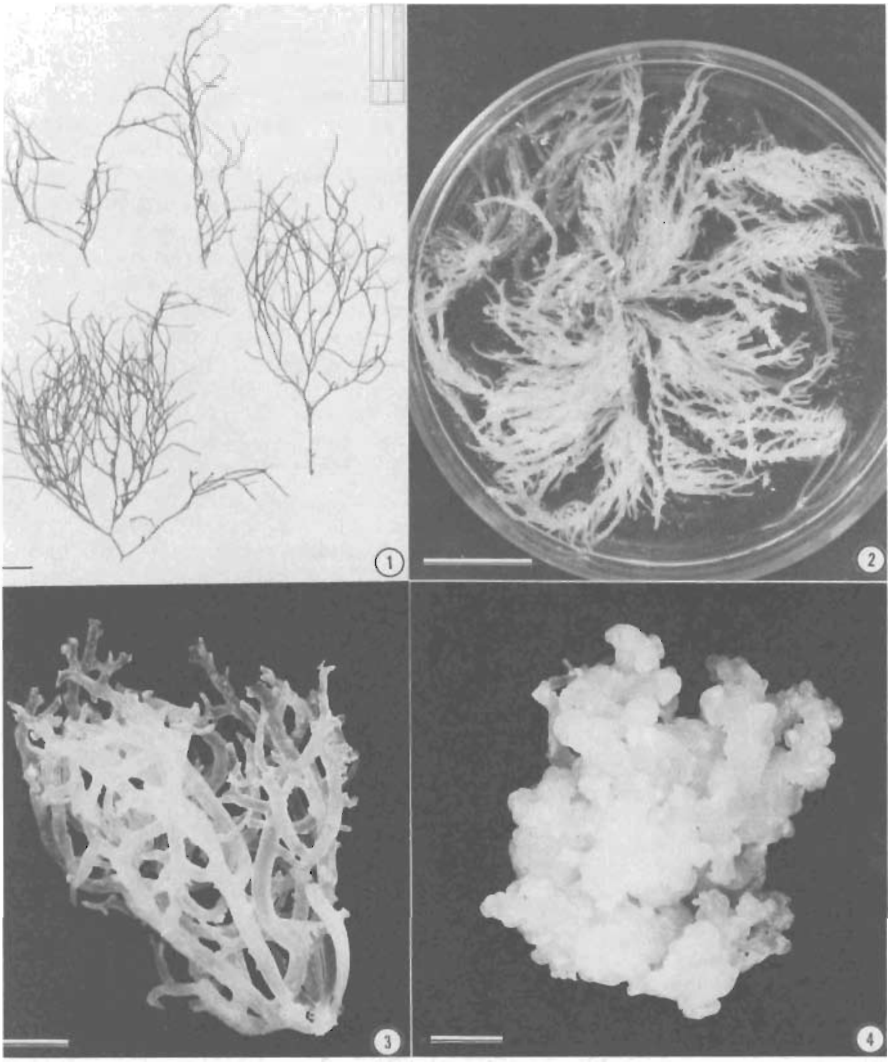
Tetrasporangia develop from primary cortical cells (Sjöstedt 1926; Kylin 1930) and are scattered throughout the cortical layers of the thallus. The meiotic cell divisions in the tetrasporangium result in a cruciate pattern with the tetrasporangium surrounded by narrowly elongated and inwardly curved vegetative cells (Yamamoto 1978).

Materials and Methods

Four species were studied: *Gracilaria tikvahiae* McLachlan, 1979, p. 19 (Fig. 1), *Gracilaria cervicornis* (Turner) J. Agardh, 1852, p. 604 (Fig. 2), *Gracilaria debilis* (Forsskål) Børgesen, 1932, p. 7 (Fig. 3), and *Gracilaria crassissima* P. et H. Crouan in Mazé and Schramm 1878, p. 218 (Fig. 4). The taxonomy of Taylor (1960) and McLachlan (1979) was followed.

Specimens were collected by skin- and scuba-diving, and liquid preserved in 5% Formalin—seawater buffered in borax. Some portions of each specimen were dried and pressed on herbarium sheets and cross-referenced to the liquid preserved material. Transverse sections were made through critical developmental stages of carpogonial, cystocarpic, tetrasporangial, and spermatangial structures of each species. All sections were made by hand with a stainless steel single-edge razor blade under a Wild M-5 stereomicroscope at 10X magnification, stained with 1% aqueous aniline blue (following the method of Papenfuss 1937), and permanently mounted on microscope slides in glycerin or in a mixture of 50% Karo Syrup/distilled water with 1% phenol added. Microscopic preparations were examined with a Zeiss Universal or a Leitz Ortholux Microscope. Photographs were taken on the Zeiss Universal Microscope. Specimens studied are deposited in the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C. (US).

Specimens studied. *G. tikvahiae*—Florida: Indian River, just north of Link Port Channel jetty, Link Port, 1 m depth, entangled with other algae, coll. J. N. Norris, JN-11627 (female, tetrasporic), 22 Jan 83 (US 94137). *G. cervicornis*—Belize: Carrie Bow Cay, reef flat off north end of island, on coral rubble and shell fragments in sand, depth 0.1—1 m, coll. S. Fredericq and S. M. Lewis, *s.n.* (female), 11 Apr 83 (US 94140). *G. debilis*—Belize: South Water Cay, 1.5—2 m depth, on coral rubble, coll. J. N. Norris and K. E. Bucher, JN-7351 (female, tetrasporic), 30 Apr 79 (US 94149); coll. R. H. Sims, D-45, 19 Apr 80 (US 94159); coll. J. N. Norris and M. M. Littler, JN-10032, 16 Nov 80 (US 94150); coll. S. Fredericq. G-18 (male), 18 Apr 83 (US 94145); west of reef crest off N.E. side of Cay, 0.3—1.6 m depth, coll R. H. Sims, G-5 (tetrasporic), 8 Mar 83 (US 94148). Curlew Bank, on coral rubble, 0.4 m depth, coll. S. Fredericq, G-15, 7 Apr 83 (US 94160). Tobacco Reef, between Tobacco Cay and South Water Cay,



Figs. 1–4. Habits of *Gracilaria* species studied. Fig. 1. *Gracilaria tikvahiae* McLachlan (cystocarpic; US 094137). Fig. 2. *Gracilaria cervicornis* (Turner) J. Agardh (cystocarpic; US 094140). Fig. 3. *G. debilis* (Forsskål) Børgesen (US 094160). Fig. 4. *Gracilaria crassissima* P. et H. Crouan, note parts of anastomosing thallus (US 094157).

0.5–1.7 m depth, on coral rubble, coll R. H. Sims, 6 Mar 83 (US 94151) and 13 Mar 83 (US 94152). *G. crassissima*—Belize: Curlew Bank, along SE side adjacent to sandy beach, on coral rubble, 0.5–1.3 m depth, 20 Jan 82, coll. R. H. Sims and S. Fredericq (US 94155, tetrasporic; US 94156). South sandbores near Carrie Bow Cay, 0.3 m depth, 8 Jun 1983, coll. S. M. Lewis (US 94146, female; US 94147, female; US 94157, tetrasporic; US 94158, female). Carrie Bow Cay, lagoon side of reef crest, 2 m depth, 11 Mar 83, coll. R. H. and L. Sims (US 94154).

Results

1. Carpogonial Branch and Carposporophyte Development

a. *Gracilaria tikvahiae* and *G. cervicornis*

In *G. cervicornis*, the carpogonial branch arises at the thallus surface from a transformed terminal cortical cell that cuts off a two-celled carpogonial branch and a sterile branch of initially one to two cells on each side of the carpogonial branches. In *G. tikvahiae*, once the carpogonial branch expands in volume, becoming distinguishable among its neighboring cortical cells, the outer cortical cells start anticlinal and periclinal divisions which result in a pericarp consisting of several cell layers (Figs. 5–6). In the carpogonial branch, then situated centrally at the base of the developing pericarp, the carpogonium becomes the largest cell (Fig. 6). Cortical branches arising from the supporting cell continue to grow apically to form a cell row terminally and show indeterminate growth, compared to the "typical" sterile branches as reported by Edelstein et al. (1978). Those cell rows contribute to the formation of the pericarp. When the carpogonium has reached a certain size (av. width = 10 μm), one of the cortical cells at one side of the carpogonium, and the lower part of the carpogonium bend towards each other and form a small connection (Fig. 6). This connection widens and the sterile cells fuse with the carpogonium. Connections between the cortical cells enlarge, resulting in subsequent local fusions that apparently can take place between any cortical cell in close proximity to the carpogonial branch.

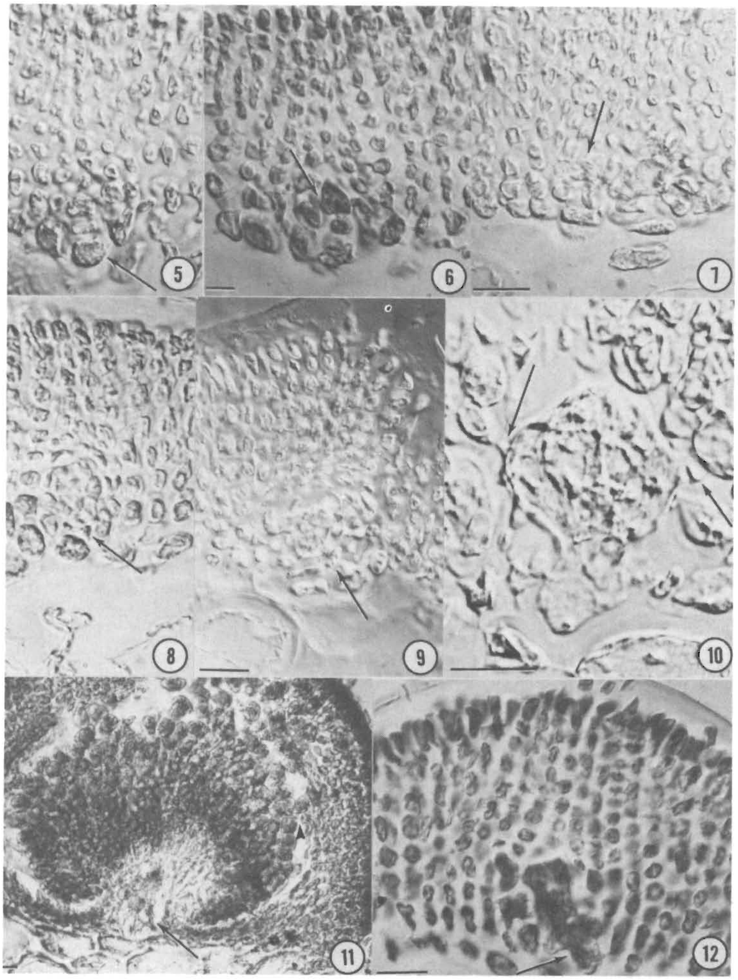
A difference exists between the way the incipient connection of the carpogonium and cortical cells proceeds in *G. tikvahiae* versus *G. cervicornis*. In *G. tikvahiae*, the first fusion movement initiates from a cortical cell in the cell row situated at nearly the same level and height as the carpogonium (Fig. 6). Then the carpogonium further incorporates adjacent cortical cells of the sterile branch laterally and makes extensions towards cells of the pericarp (Fig. 7). A

Figs. 5–9. Carpogonial branch and carposporophyte development in *G. tikvahiae*. Fig. 5. Two-celled carpogonial branch consisting of carpogonium and hypogynous cell on supporting cell (arrow). Note short sterile branches are absent, but vegetative cells cut off by the supporting cell grow indeterminately and contribute to pericarp formation (US 094137, slide 4047). Scale bar = 10 μm. Fig. 6. Two-celled carpogonial branch in which the carpogonium expands and makes contact (arrow) with terminal cell of two-celled sterile branch cut off by the supporting cell. Note basal cell of sterile branch cuts off a cell that grows indeterminately, contributing to pericarp formation (US 094137, slide 4046). Scale bar = 10 μm. Fig. 7. Incipient fusion cell formed by expansion of carpogonium and incorporation of cells of sterile branch cut off by supporting cell; hypogynous cell not detectable due to fusion to basal cell of sterile branch; fusion cell makes extensions horizontally (arrow) (US 094137, slide 4052). Scale bar = 20 μm. Fig. 8. Incorporation of cells of the sterile branch which are cut off by the supporting cell into the expanding fusion cell. The hypogynous cell (arrow) has not fused with the basal cells of the sterile branch (US 094137, slide 4049). Scale bar = 15 μm. Fig. 9. Incorporation of basal cell of sterile branch (arrow) fusing with hypogynous cell into expanding fusion cell (US 094137, slide 4050). Scale bar = 20 μm.

Figs. 10–11. Carposporophyte development in *G. tikvahiae*. Fig. 10. Young gonimoblast initials cut off at several places from the globose fusion cell (arrows) (US 094137, slide 4048). Scale bar = 25 μm. Fig. 11. Carposporophyte consisting of fusion cell (arrow), gonimoblast cells (placental cells) with carposporangia at the periphery, and absorbing filaments (arrowhead) (US 094137, slide 4052). Scale bar = 20 μm.

Fig. 12. Carposporophyte development in *G. cervicornis*: supporting cell and hypogynous cell not distinguishable and seemingly fused. Note extensive fusions at basal cells (arrow). Vegetative cells have fused to each other before becoming part of fusion cell (US 094140, slide 4055). Scale bar = 40 μm.

multinucleate fusion cell forms, which continues to expand until no more cortical cells are incorporated; the hypogynous and supporting cell remain distinct (Fig. 8). Occasionally, the basal cell of the sterile branch fuses with the hypogynous cell, and this fused structure is incorporated into the expanding fusion cell (Fig. 9). Once it has reached its maximum expansion size, the fusion cell begins cutting off gonimoblast initials at different places (Fig. 10). In contrast, it is most likely a basal cell of the sterile branch in *G. cervicornis* that will reach towards and fuse partly with the carpogonium (Fig. 12). Also, several cells are cut off from the supporting cell and form the base of a cell row that expands in diameter and, in fusing with each other, are finally incorporated with the carpogonium. In a more advanced stage, the prominent basal fusions are still recognizable in *G. cervicornis* (Fig. 13). Another difference is found in the fusion cell. It is generally more compact in shape in *G. cervicornis* than in *G. tikvahiae*, because of more fusions among cortical cells which result in the enlargement of the fusion cell. In *G. tikvahiae*, there are relatively fewer fusions between cortical cells, while the input of the carpogonium to the fusion cell is apparently greater.



A cystocarp cavity between pericarp and gonimoblast arises only after the fusion cell has generated gonimoblast initials. The few-celled gonimoblast initials are cut off obliquely from the fusion cell, growing and expanding outwardly. Several subsequent cell divisions form a dense cluster of vacuolate gonimoblast cells (Fig. 10). The expansion of gonimoblast cells proceeds in an irregular fashion. Rows of carposporangia of different sizes, also cut off irregularly, are formed at periphery of these vacuolate cells (Fig. 11). Absorbing filaments originate from the same vacuolate gonimoblast cells that can also cut off carposporangia. There are no absorbing filaments at the base of the cystocarp cavity connecting cortical and placental cells in either *G. cervicornis* or *G. tikvahiae*. The number of pericarp layers increases with the development and expansion of the carposporophyte. The development of the cystocarp in both species is vertical. Because the number of pericarp layers is variable, and not established at the time of carposporophyte initiation, they continue to increase with time, and hence cystocarps of different heights protrude above the thallus surface. An ostiole is not always present in seemingly mature cystocarps.

b. *Gracilaria debilis* and *G. crassissima*

Numerous carpogonial branches were observed immersed at the base of the pericarp in both *G. debilis* and *G. crassissima* (Fig. 14). No cystocarp cavity has developed at this stage, but a distinct boundary line is distinguishable between two zones. The part above the zone of the carpogonial branches is to become the cavity, and distally the pericarp in a strict sense is defined before the development of the gonimoblast. The part below the zone of carpogonial branches is the area below the future cystocarp cavity and is termed the "inner pericarp" following Kraft (1977).

A cortical cell is transformed into a supporting cell which cuts off a carpogonial branch consisting of two cells, the hypogynous cell and the carpogonium. The supporting cell also cuts off sterile branches that flank the carpogonial branch and consist initially of one to two cells (Fig. 15). The inner pericarp, of several layers of small cortical cells (Fig. 16), will play an important role in the development of the gonimoblast. The outer pericarp is present and

Fig. 13. Carposporophyte development in *G. cervicornis*: solid fusion cell has incorporated all but the terminal cells of the sterile branch (arrow). Note extensive fusion of vegetative cells at base of fusion cell (US 094139, slide 4054). Scale bar = 30 μm.

Figs. 14–17. Carpogonial branches and carposporophyte development in *G. debilis* and *G. crassissima*. Fig. 14. Carpogonial branches (arrow) in *G. debilis* shown at boundary of pericarp and inner pericarp (US 094144, slide 4060). Scale bar = 30 μm. Fig. 15. Carpogonial branch apparatus in outer cortex, consisting of a two-celled carpogonial branch cut off by the supporting cell (arrow) and flanked by sterile branches (US 094143, slide 4059). Scale bar = 20 μm. Fig. 16. Progressive splitting of pericarp from inner pericarp resulting in the appearance of a cystocarp cavity prior to the presence of gonimoblast initials. Fusion cell (arrow) is embedded in and connected to inner pericarp cells (US 094141, slide 4057). Scale bar = 100 μm. Fig. 17. Close up of a fusion cell (an irregular shaped syncytium) connecting (arrow) and fusing to inner pericarp cells (US 094142, slide 4058). Scale bar = 30 μm.

Fig. 18. Carposporophyte development in *G. crassissima*. Young gonimoblast originating from inner pericarp cells connected to the fusion cell underneath the cystocarp cavity (arrow). Note the separation of the pericarp from the inner pericarp (US 094138, slide 4053). Scale bar = 70 μm.

Fig. 19. Carposporophyte development in *G. debilis*: fusion cell (arrow) connected to inner pericarp cells from which the sporogenous pseudoparenchyma is being cut off forming carposporangia at its periphery. Note that the development of the cystocarp is horizontal (US 094149, slide 4066). Scale bar = 30 μm.

begins to develop prior to the development of the gonimoblast initials or before a fusion cell is distinguishable (Fig. 16). However, a pericarp is not always present when carpogonial branches can be seen (Fig. 15). Although a sterile cell was observed next to the carpogonium, the origin of the fusion cell could not be detected. The fusion cell is an irregularly ramified multinucleate syncytium which expands laterally and connects in several directions to a multitude of adjacent inner pericarp cells (Figs. 16–17). Previous to the splitting of the pericarp, the inner pericarp cells are linked to cells of the pericarp proper. With the appearance of a cystocarp cavity (Fig. 16), the inner pericarp cells become free apically and start to lengthen and expand. Each inner pericarp cell is secondarily pit-connected to other neighboring inner pericarp cells. Each of these cells has the potential to cut off a pseudoparenchymatous tissue thallus-outward. In turn, the pseudoparenchymatous cells cut off more cells, and the whole cell mass results in a sporogenous pseudoparenchyma. We make a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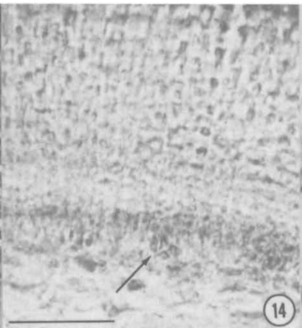
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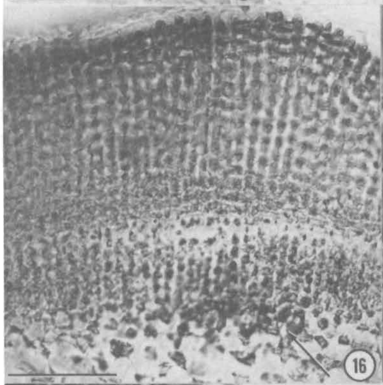
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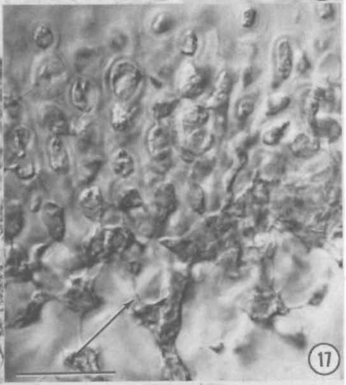
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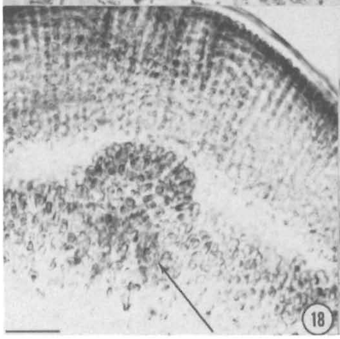
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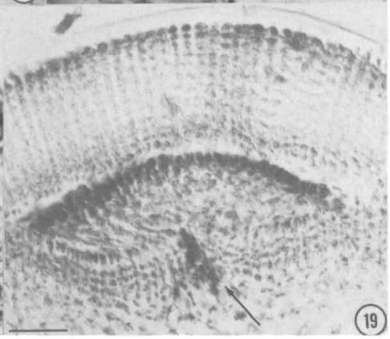
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distinction between the term "sporogenous pseudoparenchyma" and "placenta." We call placenta the gonimoblast arising directly from the fusion cell and capable of fusing secondarily with vegetative cells; and sporogenous pseudoparenchyma, the gonimoblast originating indirectly from the fusion cell but from inner pericarp cells which in turn are connected to a fusion cell.

The greater the separation between the pericarp and inner pericarp, the more inner pericarp cells are freed apically to further cut off pseudoparenchyma cells, and the greater the space for gonimoblast expansion (Fig. 18). The gonimoblast originates very early and indirectly from the fusion cell, which is connected to cells of the inner pericarp (Fig. 18). The pseudoparenchyma is of uniform cell size and shape and arises progressively from the inner pericarp cells. On the periphery of this cell mass, short regular rows of carposporangia develop (Fig. 21) without any indication of absorbing filaments connecting to the pericarp (Fig. 19). Proximal to the rows of carposporangia, the pseudoparenchyma is secondarily pit-connected. Short densely staining filaments were frequently present at the base of inner pericarp (Fig. 20) connected to the sporogenous pseudoparenchyma. After the splitting of the pericarp, the pericarp cell layers do not lengthen or increase in height. The number of layers seems to be fixed in early development, at about 13 cell layers. Anticlinal pericarp growth stops and pericarp layers remain constant from the time of carposporophyte initiation until full maturity, so that cystocarp heights in *G. crassissima* and *G. debilis* remain uniform. Since the development of the carposporophyte is principally expansion in width (Figs. 18–19), cystocarps protrude very little above the thallus surface. The gonimoblast develops on a broad base (Fig. 19). An ostiole in the pericarp is only occasionally present, and can be seen in either young or mature cystocarps.

2. Tetrasporangia

a. *Gracilaria cervicornis* and *G. tikvahiae*

In both species the tetrasporangial mother cell is always cut off terminally from a cortical cell and has basal pit-connections. Incurved branchlets encircling the tetrasporangia are common (Fig. 22).

b. *Gracilaria debilis* and *G. crassissima*

In these two species, the tetrasporangial mother cell is cut off by a cortical cell. The bearing cell can either be a cell of the cortical cell row or a cell at the dichotomy of a cell row. Usually if a tetrasporangial mother cell is borne laterally, having been cut off by a subapical cell, it will have lateral pit-connections (Fig. 23). When the tetrasporangial mother cell is borne terminally, it will have basal pit-connections. The tetrasporangial mother cell, at first quite elongate and thin, expands in diameter as it matures. The cleavage in the tetrasporangium develops in a cruciate manner. Mature tetrasporangia are bright red and ovate in shape.

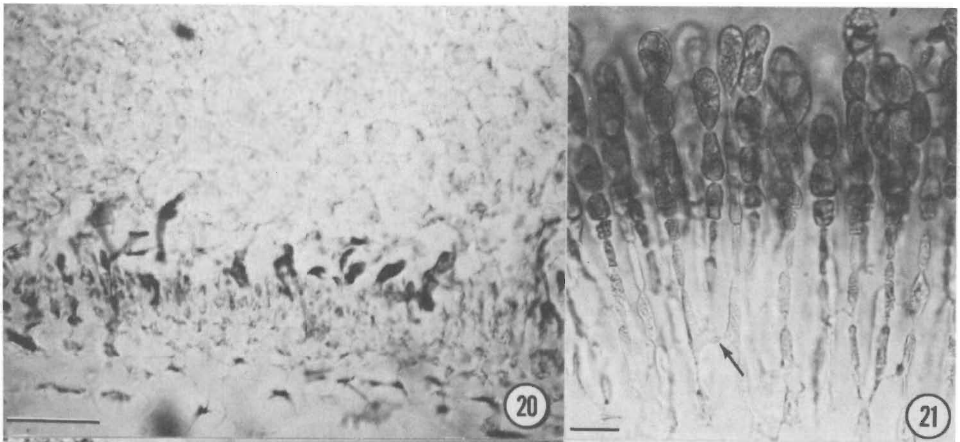
3. Spermatangia

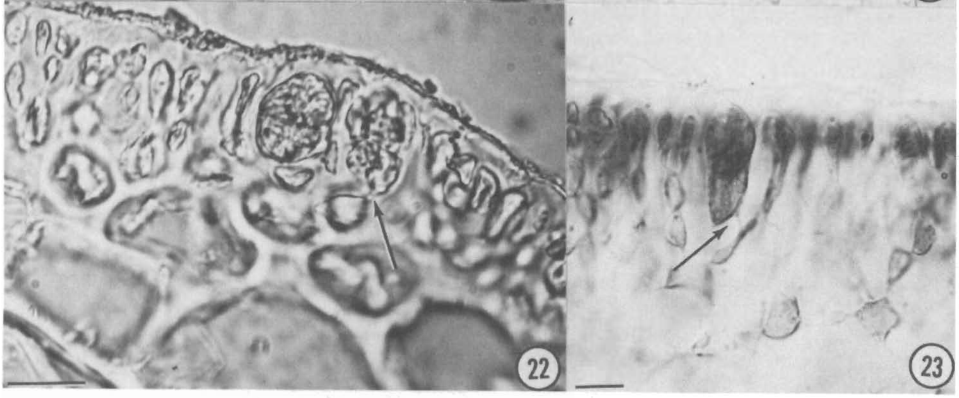
a. *Gracilaria cervicornis*

Spermatangial conceptacles are of the "Textorii-Type" and are formed by the partial conversion of outer cortical cells into spermatangial mother cells. A cortical cell divides, with the resulting outer cell functioning as the spermatangial mother cell. Many such cells, arranged in a horizontal plane, form a shallow depression (Fig. 24). Cortical cells that do not divide into spermatangial mother cells retain their original shape and form the barrier between each conceptacle (Fig. 24). Each spermatangial mother cell cuts off a cell terminally, the spermatangium (Fig. 24). The spermatangial conceptacles are relatively shallow; a surface view shows both spermatangial and cortical cells in the same focal depth.

b. *Gracilaria debilis* and *G. crassissima*

In these species, the cortical cell rows divide, with some transforming into





Figs. 20–21. Carposporophyte development in *G. crassissima*. Fig. 20. Short connecting filaments connect inner pericarp cells to sporogenous pseudoparenchyma (US 094146, slide 4063). Scale bar = 20 μm. Fig. 21. Sporogenous pseudoparenchyma is secondarily pit-connected (arrow), but not the rows of carposporangia (US 094147, slide 4064). Scale bar = 25 μm.

Figs. 22–23. Tetraspore development in *G. cervicornis* and *G. crassissima*. Fig. 22. Tetrasporic cortex in *G. cervicornis*. Tetrasporangium after the transverse division is cut off terminally from the tetrasporangial mother cell (arrow) (US 094138, slide 4053). Scale bar = 30 μm. Fig. 23. Young tetrasporangium originating laterally in *G. crassissima* from cortical bearing cell (arrow) (US 094148, slide 4065). Scale bar = 10 μm.

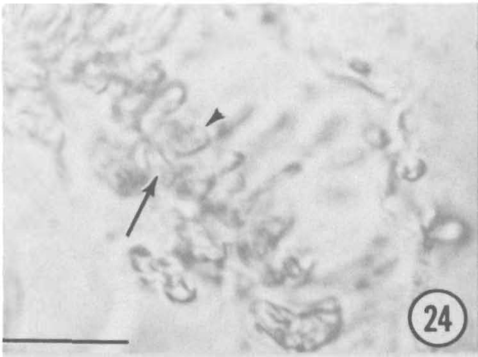
small rows of spermatangial mother cells all of which initially are connected to each other (Fig. 26). It appears that any cortical, subcortical, or medullary cell may be capable of dividing and being transformed into a spermatangial mother cell. However, the growth and shape of the conceptacles when they originate deep inside the thallus is restricted to the outline and shape of the medullary cells. The medullary cells are connected to each other in a cuboidal or pentagonal pattern, which forms the configuration of the conceptacles (Fig. 25). The configuration of male conceptacles embedded in the cortex, subcortex, or medulla is extremely variable. When several pentagonal-shaped medullary cells cut off simultaneously in close proximity small cells that function as spermatangial mother cells, then adjacent, compound internal spermatangial conceptacles are formed (Fig. 26). If all the cortical cells outward of the developing conceptacle divide and are transformed into the spermatangial mother cells, an outer cortical cell layer will be absent (Fig. 25, right). However, when these cortical cell layers are not dividing, they enclose the outside of the spermatangial conceptacle (Fig. 25, left). Eventually, the outer cortical cell layers divide, thus opening a space that functions as a pore through which the mature spermatangia may be released. In a surface view, when a pore is present, the spermatangial conceptacles are differentiated from the surrounding cortical cells by the presence of deep holes. In contrast, if the pore is absent, only cortical cells will be distinguishable, concealing the maturing conceptacle underneath. Because of this cryptic manner of conceptacle development in the young phases, male plants are difficult to identify in these species.

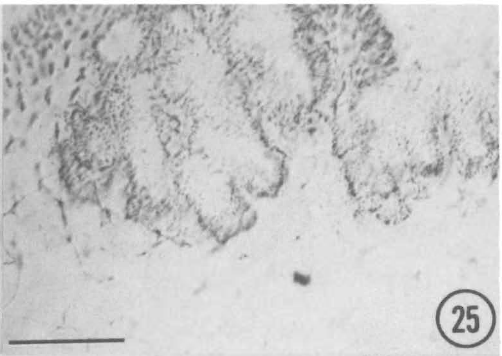
Discussion

An interesting taxonomic problem about the development of the pericarp reemerges. Johnson's (1888) interpretation that pericarp formation in *Gracilaria* occurred *before* fertilization of the carpogonium has been considered incorrect (e.g., Sjöestedt 1926; Oliveira 1969). However, in this study, carpogonial branches were observed at the boundary of pericarp and inner pericarp in *G. debilis* and *G. crassissima* without any detection of having been fertilized, thus supporting Johnson's conclusion based on his work on *G. confervoides*. In order to insure transfer of nutrients from the fusion cell to the carposporangia, it appears that either a large centralized fusion cell is necessary, or a very diffuse, ramified fusion cell that is pit-connected to a multitude of neighboring cells. The first pathway is shown in *G. cervicornis* and *G. tikvahiae*, and the second in *G. debilis* and *G. crassissima*. The result in both cases, though from different origins, is a rich gonimoblast.

Ohmi (1958) made the correlation that with a broad-based gonimoblast, absorbing filaments were absent, and that these absorbing filaments were mostly present with a narrow-based gonimoblast. [However, *G. lemaneiformis* has a *narrow* base and *no* absorbing filaments (I. A. Abbott, personal communication).] Ohmi's observations are corroborated in this study; *Gracilaria debilis* and *G. crassissima* have a broad-based gonimoblast devoid of absorbing filaments. In contrast, *G. tikvahiae* and *G. cervicornis* have a narrow-based gonimoblast with absorbing filaments. Ohmi did not, however, document the development of the fusion cell.

The nature of the fusion cell is the prime reproductive feature around which the other features, such as presence or absence of absorbing filaments, are formed. It has been generally assumed that the absorbing filaments have a nutritive function of connecting the assimilatory layers and conveying the photosynthetic products to the developing gonimoblast. (This assumes that they originate in the pericarp.) In *G. crassissima* and *G. debilis* such absorbing filaments are absent. If a nutritive role is assumed for the absorbing filaments, then no specialized supplementary means to transfer nutrients to the developing gonimoblast would be necessary: the small filaments connecting inner pericarp cells to the sporogenous pseudoparenchymatous tissue in *G. debilis* and *G. crassissima* probably are sufficient for nutrient transfer to the developing carposporangia. Because of the early progressive splitting of the pericarp, the cystocarp cavity is not spatially restricted in width for liberation of carpospores. In contrast, in *G. cervicornis* and *G. tikvahiae*, absorbing filaments are present and always originate late in the development of the cystocarps. Another possible role of the absorbing filaments could be biochemical. The absorbing filaments (if they originate in the gonimoblast) may produce a chemical, perhaps an enzyme,





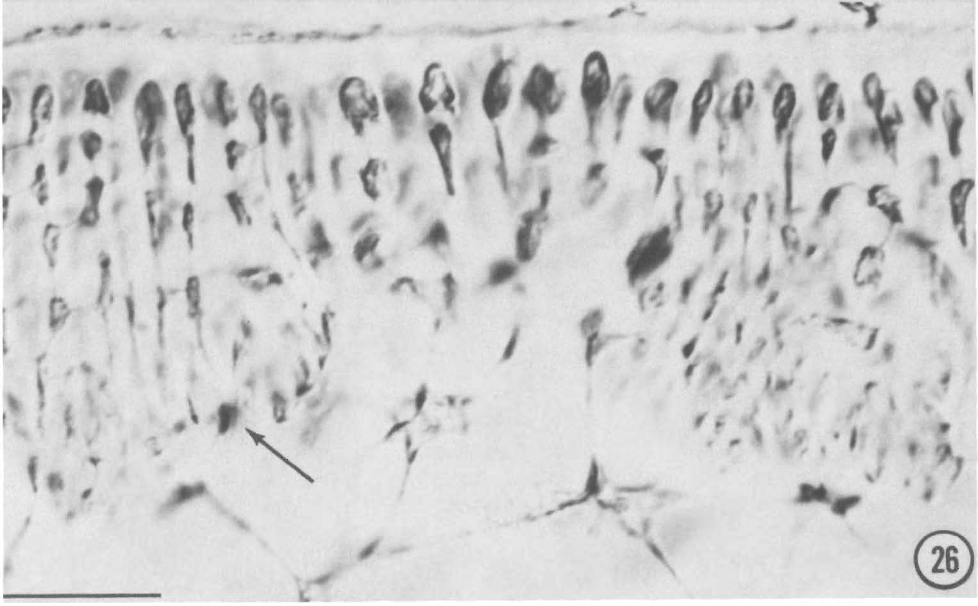


Fig. 24. Spermatangia of *G. cervicornis*, immersed in shallow conceptacles flanked by cortical cells. Spermatangial mother cells (arrow) and spermatangia (arrowhead) are distinguished (US 094139, slide 4054). Scale bar = 30 μm.

Fig. 25. Deeply immersed spermatangial conceptacles of *G. debilis*: cortical cells above conceptacles have completed division (right) while those on the left have not yet divided. Thus, a pore (right) is present or absent (left) (US 094145, slide 4062). Scale bar = 60 μm.

Fig. 26. Spermatangial mother cells of *G. crassissima* and *G. debilis* (arrow) do not originate from one outer cortical cell, but from a string of deep cortical–medullary cells (e.g., *G. debilis*, US 094145, slide 4061). Scale bar = 30 μm.

which, upon penetrating the pericarp, could stimulate the expansion of the pericarp, thus widening a space between the sporangial mass and the pericarp. This would provide enough space for carposporangial enlargement and release through the ostiole. It is possible that, as the cystocarp develops in height, space is needed for the carposporangia to grow upward since there is no space available for the gonimoblast to expand further laterally. Absorbing filaments are prevalent in cystocarps when the height of the cystocarp exceeds the width (e.g., *G. cervicornis* and *G. tikvahiae*), and tend to be absent when the width exceeds the height (e.g., *G. debilis* and *G. crassissima*).

Since the absorbing filaments originate from gonimoblast tissue, it can be assumed that a specific cystocarp will not have both types of filaments. Only one type is present, such as the "classic" absorbing filaments connecting gonimoblast to pericarp, or the other type, in which short filaments connect the inner pericarp cells to sporogenous pseudoparenchymatous tissue (see also Chang and Xia, 1963, fig. 7). In the specimens studied, presence or absence of absorbing filaments can be predicted based on the nature of gonimoblast origin: if the gonimoblast originates directly from the fusion cell, and immediately starts developing outward from the thallus prior to the occurrence of a cystocarp cavity, absorbing filaments will be present. On the other hand, if the gonimoblast originates indirectly from the fusion cell as sporogenous pseudoparenchyma from the inner pericarp cells, and the cystocarp cavity originates very early, then short filaments between the inner pericarp cells penetrating the pseudoparenchyma can be expected. A third option is that neither absorbing filaments nor "basal absorbing filaments" (the latter type are on the inner pericarp cells) are present [see e.g., *Gracilariopsis sjoestedii* (Kylin) Dawson, 1949, pl. 17, fig. 5].

A cortical cell in the region of developing tetrasporangia has the potential to cut off cells terminally as well as cutting off another cell laterally. For example in *G. debilis* and *G. crassissima*, if a tetrasporangial mother cell originates laterally from its bearing cell, cortical cells can originate terminally from the same bearing cell. This is apparently the first report in *Gracilaria* of lateral development of tetrasporangia from bearing cells. In another family of the Gigartinales, the Solieriaceae, a lateral or terminal origin of tetrasporangia was a prime character used for segregating major tribes (Gabrielson and Hommersand, 1982a,b).

Similarly, if a carpogonial branch is cut off terminally from a cortical cell, then that cortical cell will only cut off carpogonial branch initials and adjacent sterile cells. If, however, the carpogonial branch initial is cut off more laterally from a bearing cell, then that bearing cell can still cut off a cell row terminally. The result is that the carpogonial branches may not appear terminally immersed in the outer cortex, but rather in the subcortex. The carpogonial branches can then be present at the base of the pericarp or just underneath the cystocarp cavity, as was observed in *G. debilis* and *G. crassissima*.

When cells are cut off laterally in the development of spermatangia in *Gracilaria*, compound spermatangial conceptacles can be expected. Børgesen (1953) commented on the fact that an ostiole was absent in the compound, deeply imbedded conceptacles of *G. multifurcata* Børg. [= *Polycavernosa multifurcata* (Børg.) Chang et Xia, 1963]. Ohmi (1958b) found the same aberrant spermatangial (as "antheridial") conceptacles in *G. henriquesiana* Hariot from the Gold Coast, Africa. This type of spermatangial conceptacle was the primary basis for segregation of a new genus, *Polycavernosa* Chang et Xia (1963, p. 120), based on *P. fastigiata* Chang et Xia. This unusual development of spermatangia, which does not arise from one terminal cortical cell, was observed in our specimens of *G. debilis* and *crassissima*, and is fundamentally different from the "Textorii-Type" shown by *G. cervicornis*.

The inherent plasticity in the nature of cell divisions (anticlinal vs. periclinal) and the implications for cutting off various types of reproductive cells (e.g., carpogonial branch, tetrasporangium, or spermatangia) are derived from a differential capacity of cells to form secondary pit-connections with neighboring cells. All *Gracilaria* species in this study formed secondary pit-connections. However, the degree to which species have potential and plasticity to form secondary pit-connections must be tested as a basis for taxonomic evaluation of species groupings. It is obvious that the ability of *G. debilis* and *G. crassissima* to form secondary pit-connections is greater than that of *G. tikvahiae* or *G. cervicornis*. There is probably greater fertilization efficiency from an array of vegetative cells that have the ability to connect very closely either to other cortical cells or to a carpogonium (resulting in a large fusion cell), without the need for auxiliary cell filaments as seen in other families of Gigartinales (e.g., Solieriaceae J. Agardh). The phylogenetic affinities of the Gracilariaceae at the familial and ordinal levels remain to be clarified.

Summary

Developmental sequences of post-fertilization events reveal two developmental patterns within the genus *Gracilaria*, which are proposed to represent two distinct groups: *Group 1—G. debilis* and *G. crassissima*, and *Group 2—G. cervicornis* and *G. tikvahiae*.

Table 1. Comparison of Reproductive Features of *Gracilaria* Group 1 (=*Polycavernosa*) vs. Group 2 (=*Gracilaria*).

	GROUP 1: *G. debilis* (Forssk.) Børg. and *G. crassissima* P. et H. Crouan	GROUP 2: *G. cervicornis* (Turn.) J. Ag. and *G. tikvahiae* McLachlan
Timing and Origin of the Gonimoblast	develops early, from inner pericarp cells connected to the fusion cell; i.e., *indirect* from the fusion cell; space forms between pericarp and future gonimoblast *before* fusion cell incorporates adjacent cortical cells.	develops late, *direct* from the fusion cell; no space between pericarp and future gonimoblast until *after* fusion cell incorporates adjacent cortical cells.
Direction of Cystocarp Development	mainly horizontal; thus cystocarp growth is in width.	mainly vertical; thus cystocarp growth is in height.
Mature Cystocarp Shape	low, wide, and ± flat.	tall and ± pyramidal.
Nature of Pericarp	present before expansion of fusion cell; number of pericarp cell layers apparently fixed in early development; cystocarps ± uniform in height.	formed concomitant with development and expansion of fusion cell; number of pericarp cell layers not fixed; cystocarps of various heights.
Cystocarp Cavity	present *before* development of gonimoblast initials.	present, only *after* appearance of gonimoblast initials.
Fusion Cell Shape	ramified, spreading; not easily distinguished.	unbranched, appears "solid"; prominent.
Absorbing Filaments	absent	present
Origin of Spermatangia	from cortical or subcortical/ medullary cells.	only from cortical cells.
Origin of Tetrasporangia	terminal or lateral from a cortical cell.	only terminal from a cortical cell.

This generic complex of taxa is unique in having both a fusion cell and placental or pseudoparenchymatous cells in their respective cystocarps. Based on the material studied, there has been a significant divergence in the gonimoblast origin and in the developmental sequence shown by these two groups. Presence or absence of the other secondarily developed cystocarp features seem to develop around this basic difference in gonimoblast origin. Once the gonimoblast origin is established, the subsequent development can be predicted in the tropical and subtropical western Atlantic species we studied.

In the "classic" *Gracilaria* concept of Sjöstedt (1926) the gonimoblast originates directly from the fusion cell. This direct origin was found in *Group 2, G. cervicornis* and *G. tikvahiae*. In *Group 1, G. debilis* and *G. crassissima*, the gonimoblast does not originate directly, but rather indirectly from the fusion cell. The uniqueness of *Group 1* lies in the fact that a space forms between the pericarp and the future gonimoblast before the fusion cell incorporates adjacent cortical cells. Fundamental differences useful for taxonomic separation of the two groups are summarized in Table 1. The taxonomic significance of these differences in reproductive morphology was considered. At this point we suggest that the two distinct developmental pathways of these two groups represent two separate genera. A thorough investigation of reproductive structures and their developmental origins and sequences must be studied in the generic types of *Gracilaria, Gracilariopsis*, and *Polycavernosa* to reveal where *Group 2* belongs. We recognize that the species of *Group 2* are more closely aligned with the "classic" concept of *Gracilaria* (*sensu* Sjöstedt 1926). Studies are now in progress comparing developmental patterns of the reproductive structures of *Polycavernosa fastigiata* (from type locality) with our *Group 1*. At this time, based on our observations on the type and origin of the spermatangial conceptacles and the features of the mature cystocarps in our Caribbean specimens of *G. debilis* and *G. crassissima* being the same as described for *Polycavernosa* by Chang and Xia (1963), we propose the following new combinations:

Polycavernosa debilis (Forsskål) Fredericq et J. Norris, comb. nov. Basionym: *Fucus debilis* (Forsskål) 1775, p. 191. Synonym: *Gracilaria debilis* (Forsskål) Børgesen 1932, p. 7.

Polycavernosa crassissima (P. et H. Crouan) Fredericq et J. Norris, comb. nov. Basionym: *Gracilaria crassissima* P. et H. Crouan *in* Mazé and Schramm 1878, p. 218 (date of publication *fide* Stafleu and Cowan 1981, p. 392).

The recognition of these two groups is a contribution that we believe will help to clarify generic concepts and species limits in a taxonomically difficult but economically important group of red algae. We encourage that detailed studies be undertaken of type locality material of *Gracilaria* taxa to avoid nomenclatural problems and misidentifications.

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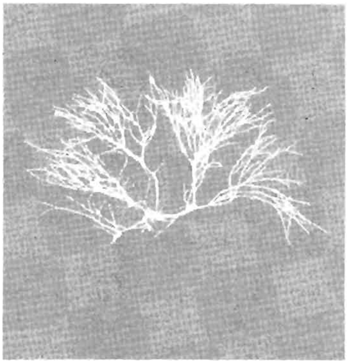
SECTION V. The Red Algal Genus *Polycavernosa*



THE GENUS *POLYCAVERNOSA* CHANG ET XIA (GRACILARIACEAE, RHODOPHYTA): A COMPARISON WITH *GRACILARIA* GREV., AND A KEY TO THE SPECIES

Xia Bangmei and Isabella A. Abbott

The recognition of *Polycavernosa* Chang et Xia (1963) as a taxon separate from *Gracilaria* Greville (Gracilariaceae, Gigartinales) has been slow to be made, largely because the paper describing this genus did not become available to the West until fairly recently, or about 15 years after its publication. The primary distinguishing features were: (1) the occurrence of spermatangia in multiple cavities, and (2) the appearance of darkly staining, irregularly shaped, conspicuous basal "nutritive filaments" emerging from the bottom of the gonimoblasts (Chang and Xia 1963, pl. 1, figs. 1–4, 7–8). Bird and McLachlan (1982) suggested that the spermatangia were possibly only a modification of the Verrucosa-type (Yamamoto 1978), or the so-called cup-shaped or pot-shaped spermatangial conceptacles, and withheld generic recognition until further studies had been made. However, they did not comment upon the basal "nutritive filaments," called *absorbing filaments* in this paper and throughout the workshop contributions of this volume.

Yamamoto (1984) suggested that the *Polycavernosa*-type of spermatangia might be grouped within *Gracilaria* as a subgenus on the same basis as *Gracilaria* subgenus *Gracilaria* (with pot-shaped spermatangial conceptacles), *G.* subgen. *Gracilariella* (with superficial spermatangia), and *G.* subgen. *Textoriella* (with shallow saucer-shaped conceptacles). He also suggested that if the *Polycavernosa*-type of spermatangia were actually an aggregation of the Verrucosa-type, that they should be named the "Henriquesiana-type," but also implied (Yamamoto 1984, table 1) that *Polycavernosa* might be maintained as a separate genus.

Materials and Methods

Dried herbarium materials, and small portions of these specimens that had been preserved in 5% buffered Formalin seawater were examined. Sections for microscope examination were cut by hand or by using a freezing microtome, stained in 1% aqueous aniline blue, fixed with 1% HCl, washed in distilled water, and mounted in clear glucose syrup (Karo, a brand name of Corn Products, Inc.). Specimens used have been deposited in the Herbarium of the B. P. Bishop

Museum (BISH) in Honolulu, with duplicates deposited in the Algal Collection of the U.S. National Herbarium, Smithsonian Institution (US), and at the Institute of Oceanology, Academia Sinica, Qingdao, China (AST).

Morphology and Development

Vegetative comparisons among species assigned to *Graciiaria* and *Polycavernosa* are difficult to make because they reflect the range of morphological variation displayed by thallus form within *Gracilaria* itself, e.g., axes nearly 11 mm diam. to those less than 1 mm. Thallus sizes and branching patterns sometimes are duplicated in taxa of the two genera. The most common thallus form in *Polycavernosa* is that of the slender plants of the type species, *P. fastigiata* (Fig. 5). However, the blade-like thallus form of some species of *Gracilaria* such as *G. textorii* has not yet been observed in *Polycavernosa*.

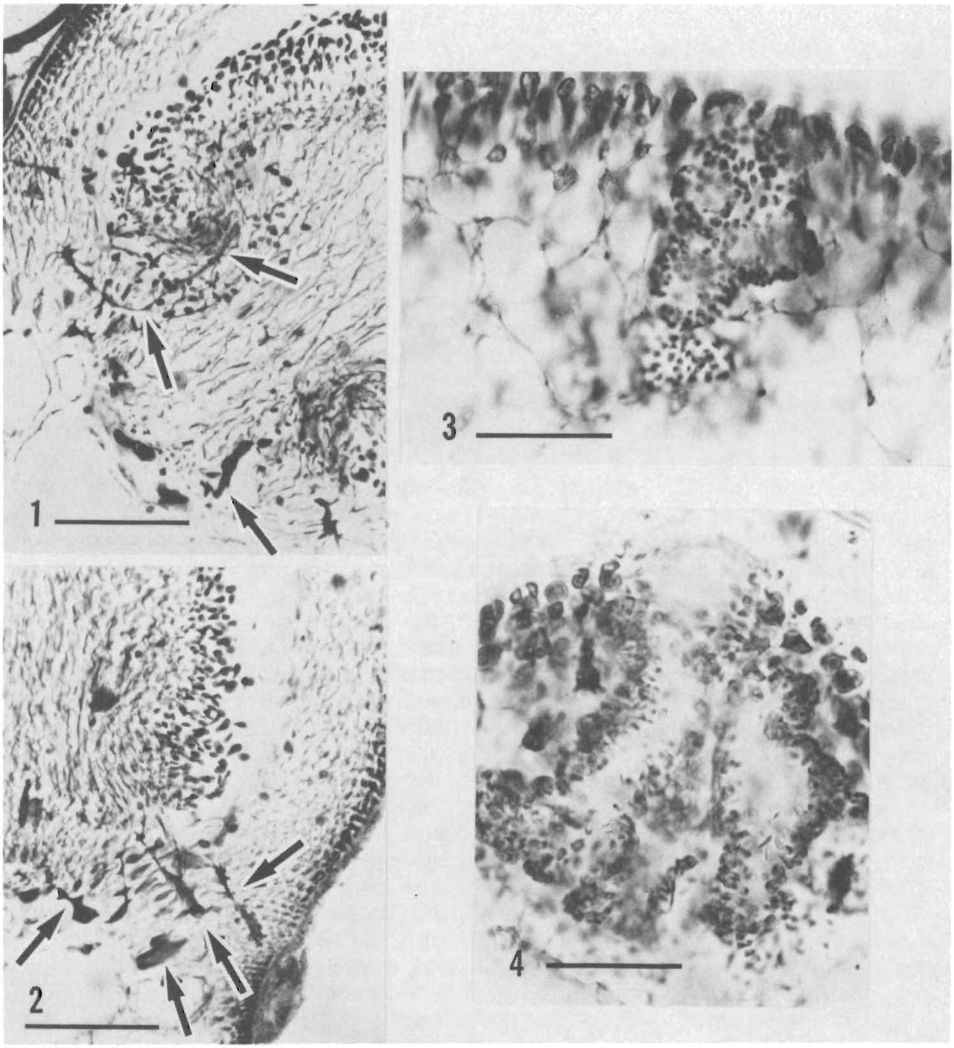
The main differences between *Gracilaria* and *Polycavernosa* are found in reproductive structures—first in the different locations of spermatangia, as mentioned above, and in their ontogenetic development as mentioned below, and second, in the appearance of the mature cystocarp (Chang and Xia 1963) and its ontogenetic development, as elucidated by Fredericq and Norris (this volume). Two kinds of attachment of tetrasporangia were observed in two Caribbean *Polycavernosa* species studied by Fredericq and Norris (this volume). However, our examination of many other species of *Gracilaria* and *Polycavernosa* shows that species of both genera have tetrasporangia borne laterally or basally from cortical cells.

Ontogeny of the female reproductive structures is the emphasis furnished in the paper by Fredericq and Norris (this volume), and we are in substantial agreement with their observations. Additionally, as shown by Zhang and Xia (1984) for *Gracilaria*, there appears to be a difference in the cellular arrangement in the pericarp in some species of *Polycavernosa*. As examples, in *Polycavernosa fastigiata*, the type species for the genus, the pericarp arrangement shows cells with elongated pit connections ("cobwebby"), whereas the pericarp cells of *P. debilis* (Fig. 19 of Fredericq and Norris, this volume) shows rows of brick-like cells. Figures 1 and 2 show the basal absorbing filaments at the base of the cystocarp in an undescribed species (Doty #32423) from Malaysia.

The basal absorbing filaments are scarce in the two Caribbean species studied, *P. crassissima* and *P. debilis*, but abundant and very conspicuous in the material from the western Pacific and adjacent seas. They are primarily at the base of the cystocarp, outside of the gonimoblast proper and below the inner pericarp, but in some specimens of the yet undescribed species from Malaysia, they occasionally extend along the lateral walls of the cystocarps, to as much as 25% of the height of the cystocarp. They are elongate, with many projecting arms principally in the vertical axis, and stain darkly, resembling schlereids in leaves of some terrestrial plants. We have not studied their ontogeny since we do not have any adequately preserved material of the western Pacific taxa.

The more commonly occurring absorbing filaments that are in the upper and terminal portions of the gonimoblasts of many species of *Gracilaria* are rarely seen in western Pacific species of *Polycavernosa*, and when seen are not in all specimens of the same taxon. These kinds of absorbing filaments may not be related to the more elaborate basal ones described for the genus *Polycavernosa*.

The development of the spermatangia of *Polycavernosa* is based upon examination of material of *P. fastigiata* (AST 80-2335), *P. debilis* (US #94145), and an unnamed species from Penang, Malaysia (Doty #31541a in Herb. BISH). Except for fewer or more caves of spermatangia, and one or more pores over the caves (this variation may be a reflection of age or development), there are no



Figs. 1–4. *Polycavernosa* species. Fig. 1. Median longitudinal section through cystocarp showing basal absorbing filaments (arrowheads) (Doty #32423 from Malaysia, BISH). Fig. 2. Lateral view of basal absorbing filaments (same specimen as Fig. 1, different cystocarp). (Scale bars of both figures = 50 μm.) Fig. 3. *Polycavernosa debilis*. Developing multiple spermatangial cavities (Belize, US). Fig. 4. *Polycavernosa fastigiata*. Mature spermatangial caves (Hainan Island, China, AST 80-2335). (Scale bars of both figures = 25 μm.)

essential differences in development of the spermatangial caves among these species.

The spermatangial groups are initiated by subcortical cells that divide off adjacent to intercellular spaces, forming spermatangial mother cells which either directly form spermatangia or form daughter cells in short uniseriate filaments, the latter in turn producing spermatangia on their lateral faces. If the first

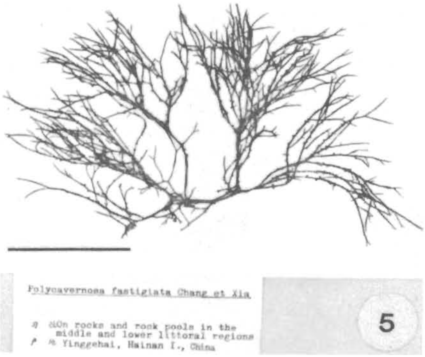


Fig. 5. ***Polycavernosa fastigiata*, Hainan Island (type locality), China (AST). (Scale bar = 1.5 cm.)**

divisions arise from cortical cells immediately internal to the outer layer, the divisions are at right angles to the surface, and small clusters of cells soon form, filling the spaces between the cortical cells. By continuous similar divisions, the masses of small cells (each less than 1 μm diam.) are pushed downward and inward, making small caves (Fig. 3) whose boundaries are formed by the spermatangial mother cells. If the first divisions are from inner cortical cells, small outwardly directed clusters of filaments of spermatangial mother cells soon become crowded with spermatangia, and these and adjacent developing clusters become the foci of the multiple caves. The mature caves disrupt (Fig. 4) the subcortex and outer medulla, and some of them raise the surface slightly. The developing groups of spermatangia may look superficially like the Verrucosa-type, but in that type, the internal surfaces of the conceptacles are lined throughout by spermatangial mother cells, giving rise to single layers of spermatangia toward the interior of the conceptacle. In *Polycavernosa*, in contrast, the spermatangial mother cells are loosely filamentous and do not line a cavity, and because of this, spermatangia are produced in more than one direction; they are at once more numerous and smaller than their counterparts in *Gracilaria*. In very thin transections, the cortical cells are seen as a cover over the multiple caves except where the sections traverse a small and relatively inconspicuous pore. During the course of their development, the caves may show thin walls separating the cavities; it is difficult to see whether they retain their shape as the spermatangia mature and are liberated, and how they change their shape as each cave is incorporated into newly developing caves, since the caves seem to develop gradually and may not reach their maximum size for some time after their initiation.

Discussion

The developing groups of young spermatangia may sometimes look superficially like the Verrucosa-type, but in that type, the internal surfaces of the conceptacles are formed from the invagination of outermost cortical cells (Yamamoto 1975) which become lined throughout by spermatangial mother cells, giving rise to single layers of spermatangia. In surface view, they appear as single pock marks. In *Polycavernosa*, in contrast, the arrangement of the spermatangial mother cells in surface view resembles irregular circles around a focus, with varying depths and widths (as much as 150 μm deep in lateral view, compared to 50–100 μm depth of most Verrucosa-type conceptacles).

Table 1. Comparison of Some Characteristics of *Polycavernosa*.[1]

Species	Habit	Medulla	Cortex	Cystocarp	Spermatangia
Polycavernosa fastigiata Chang et Xia	terete, fastigiate	abrupt, transition, medulla cell 180–330 μm in diam., thin walled cells 6 μm.	2–3 layers, 3.3–6.6 μm x 3–4 μm.	globose, rostrate, constricted at base, gonimoblast consisting of large cells, basal absorbing filament present, robust with many branches all below the gonimoblastic tissue, pericarp 230 μm thick, 9–11 layers cells.	spermatangial caves are nearly globular consisting 4–10 cavities, or more, each cavity 33–99 μm x 16–33 μm.
P. ramulosa Chang et Xia	terete; branching with short intervals (0.5–3 mm), rather dense above.	abrupt transition, 230–400 (–465) μm, 5–6 μm.	2–3 layers, 6.6–10 μm x 4–6 μm.	globose, rostrate, constricted at base, with a parenchymatous gonimoblast, absorbing filament present, robust with many branches all below the gonimoblastic tissue. Pericarp 200–215 μm thick, 10–12 layers.	
P. henriquesiana Chang et Xia	subterete to compressed.				spermatangial caves globular, 3–6 cavities.
P. multifurcata (Børg.) Chang et Xia	compressed	abrupt, 150 μm, 3–4 μm.	10–12 μm.		spermatangial caves globular, 6–16 cavities.

[1] See Fredericq and Norris (this volume, Table 1) for *P. debilis* and *P. crassissima*.

Finally, the *Polycavernosa*-type of spermatangial arrangements, because of their internal cortical origin, do not fit within the phylogenetic scheme proposed for *Gracilaria* by Yamamoto (1975) since the three main types of spermatangial arrangements he recognizes in *Gracilaria* all have their origin in the outermost cortical layer. Together with a difference in the origin of the gonimoblast—directly from a fusion cell in *Gracilaria* and from tissue formed from the fusion cell in *Polycavernosa* (see Fredericq and Norris, this volume)—the origin of the spermatangial caves adds an ontogenetic feature that merits genus level recognition.

Key to the Species

1\. Thalli cylindrical 2
1\. Thalli compressed or flattened 3

    2. Branches fastigiate in general outline; branching intervals long (0.2 to 2 cm) .... *P. fastigiata* Chang et Xia (Fig. 5).
    Distribution: Hainan Island, China
    2. Branches not fastigiate; branching intervals short (0.3 to 1 cm) .... *P. ramulosa* Chang et Xia
    Distribution: Hainan Island, China

3\. Plants erect, caespitose to freely branched 4
3\. Plant decumbent, subterete to strongly compressed, lobed to marginally branched .... *P. crassissima* (P. et H. Crouan) Fredericq et Norris (this volume).
Distribution: Bermuda, Florida, into the Caribbean Sea.

4\. Branches generally in one plane, frequently fanlike 5
4\. Branches irregularly alternate, frequently secund, the last order short, acute .... *P. debilis* (Forsskål) Fredericq et Norris (this volume).
Distribution: Egypt (the type locality); Florida through the Caribbean to Brazil.

5\. Branches irregularly pinnately or irregularly dichotomously divided; plants in low tufts . ... *P. multifurcata* (Børgesen) Chang et Xia
Distribution: Mauritius.
5\. Branches irregularly dichotomously divided, frequently fanlike and proliferous .... *P. henriquesiana* (Hariot) Chang et Xia[1]
Distribution: Ghana (West Africa).

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[1] If *Gracilaria dentata* J. Agardh as interpreted by Lawson and John (1982) proves to be the same species as *P. henriquesiana*, its transfer to *Polycavernosa* should be made and that binomial used as it will be the earlier name.

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SECTION VI. Taxonomic Index