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TAXONOMY OF ECONOMIC SEAWEEDS

With reference to some Pacific and Caribbean species Volume II

Isabella A. Abbott, Editor

A Publication of the
California Sea Grant College Program

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Rosemary Amidei,
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TAXONOMY OF ECONOMIC SEAWEEDS

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Volume II

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Results of an international workshop sponsored by the California Sea Grant College Program and the Institute of Oceanology of the Academia Sinica of the People's Republic of China in cooperation with the Pacific Sea Grant College Programs of Alaska, Hawaii, Oregon and Washington and hosted by the Institute of Oceanology in Qingdao, September 22 to 25, 1986.

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Preface

James J. Sullivan
Director, California Sea Grant College Program

This is the second volume on the taxonomy of commercially important sub-tropical and tropical seaweeds that California Sea Grant has published in cooperation with the Pacific Sea Grant College Program. We are especially pleased to have co-sponsored the workshop on which this book is based with the Academy of Science (Academia Sinica) of the People's Republic of China.

As I related in the first volume in this series, the need for these workshops was first suggested to me by Roy Tsuda, vice president of Academic Affairs of the University of Guam. According to Dr. Tsuda, confusion in the taxonomy of economically important tropical and subtropical algae remains the single greatest obstacle to progress in Pacific seaweed aquaculture and marine natural products chemistry—both topics of importance to the programs that constitute Pacific Sea Grant.

As a result of his observation, I asked Isabella Abbott of the University of Hawaii if she would convene an international group of specialists. The result was a working conference hosted by the University of Guam in June 1984, followed in 1985 by publication of a proceedings of that workshop entitled, *Taxonomy of Economic Seaweeds (with Reference to Some Pacific and Caribbean Species)*, edited by Dr. Abbott and by Dr. James N. Norris of the Smithsonian Institution in Washington, D.C. We were gratified that this volume was awarded first place in the "Book for Technical Audience" category by the National Association of Government Communicators.

That first meeting was tremendously productive, but it also served to highlight how many problems of nomenclature and systematics remained in the groups selected. We were all most pleased, therefore, when Dr. C. K. Tseng, director emeritus of the Institute of Oceanology in Qingdao and a participant in the workshop, suggested that China's Academia Sinica would like to co-sponsor a second workshop on the topic with us.

That second conference was held in Qingdao in September 1986, with Isabella Abbott and C. K. Tseng serving as co-convenors. The results appear in this volume. Our Chinese hosts could not have been kinder. I wish especially to thank Dr. Tseng for his hospitality and Xia Bangmei, who accompanied us for the two weeks that we were in China, serving not only as friend and colleague, but also as interpreter and guide.

On behalf of the directors of the programs that constitute the Pacific Sea Grant College Program, I also wish to thank all of the participants for their contributions to the success of this workshop. I believe this volume attests to their enthusiasm and to their hard work.

Introduction

Isabella A. Abbott
Workshop Co-convener and Editor

Because the kind and quality of a seaweed product is announced with its correct name, the taxonomic base on which the name rests furnishes the basis for proper valuation of seaweed crops. Used as food staples in many nations, including China and Japan, seaweeds are more commonly encountered in the West in food processing and biomedical products.

At the first California-sponsored international workshop on economically important algae, held in Guam in 1984, 12 taxonomists, representing the United States, Japan, China, Chile, and Taiwan, decided 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 were *Gracilaria, Polycavernosa, Eucheuma, Sargassum*, and the Gelidiales (including *Gelidium, Pterocladia, Gelidiella, Yatabella*, and *Acanthopeltis*).

We had hoped to include even more taxonomists in our second workshop, but several who had expressed interest were unable to attend. As a consequence, the number of taxa we examined and the scope of our studies had to be reduced. We chose to continue work on the groups selected at the first workshop, and to add *Laurencia*, in which agar has recently been found to occur.

Sargassum subgenus *Sargassum* (containing the bulk of the species of the genus) from the western Pacific was tackled by five of the participants, *Gracilaria* and *Polycavernosa* by three, and *Laurencia* by two.

Subsequent to the workshop, Dr. Santelices from Chile came to Hawaii to work on the Gelidiales of China, and Dr. Maxwell Doty contributed a paper that will help to clarify some of the difficulties in the problem-full genus *Eucheuma*. At Dr. Doty's instigation and with his help, we are also including a paper by Donald P. Cheney on *Eucheuma isiforme* from the western Atlantic and Florida; this will bring together information that will be valuable later when the type species of the genus, *E. denticulatum* (Burm. f.) Coll. & Hervey, is re-examined.

Visiting the herbarium at the Institute of Oceanology in Qingdao proved to be a real bonanza for several of us. This was especially true for Tadao Yoshida, who had the opportunity there to examine samples of species of *Sargassum* that have been reported from both China and Japan; he was, as a consequence, able to determine that a few species appear to be endemic to Japan. Karla McDermid found that a fairly common Hawaiian species of *Laurencia*, to which the name *Laurencia surculigera* had been applied, did not resemble specimens from the type locality, Hong Kong. (Indeed, on comparing Hawaiian and Chinese species of *Laurencia* it was found that very few species are in common.) I had brought with me specimens and a description of a "new species" of *Gracilaria* from Thailand, only to find that my Chinese counterparts Zhang Junfu and Xia Bangmei had decided that similar plants represented a new variety of a species that they had previously described as *G. tenuistipitata*. Obviously, the benefits of traveling multiply rapidly when one is able to share experiences with other specialists!

Most specimens studied in this workshop are deposited in the following herbaria: Academia Sinica, Institute of Oceanology, Qingdao, People's Republic of China (AST); Department of Botany, B. P. Bishop Museum, Honolulu, Hawaii (BISH); Herbarium of Faculty of Science, Department of Botany, Hokkaido University, Sapporo, Japan (SAP). In addition to the Bishop Museum, some specimens of Thai *Gracilaria* and *Polycavernosa* species will be shared with the algal collection of the U.S. National Herbarium, Smithsonian Institution, Washington, D.C. (U.S.) and with Katsetsart University Herbarium, Bangkok, Thailand. Other herbaria mentioned are those at Lund University (LD), Sweden; British Museum, Natural History (BM); and the State Herbarium of the Netherlands at Leiden (L). Abbreviations are from *Index Herbariorum* (Holmgren, P. K., Keuken, W. and Schofield, E. K. 1981. 7th ed. vii + 452 pp. Utrecht: Bohn, Scheltema & Hoikkema).

In this second workshop, we have demonstrated once again that small groups of specialists working together in a concentrated period can produce meaningful contributions to the taxonomy of useful seaweeds. We look upon these studies as steps along the road of systematics, in which the main progress has to do with getting regional taxonomic information together. In this regard we are especially grateful to our Chinese and Japanese colleagues, who furnished invaluable local literature on taxa; this is as important for this kind of effort as is inventorying species found along a coastline.

Finally, if we may be permitted a "wish list" for the future, it would be for the opportunity to continue to study some of the problems that exist in the taxonomy of the economic algae of the tropics and subtropics. They would include other species of *Sargassum* subgenus *Sargassum*, for we have just made a start on the western Pacific species. Many species of *Gracilaria* and *Polycavernosa* in the Philippines and Indonesia are in need of study before names can be applied. If other *Laurencia* species turn out to have high quality agar, additional studies should be conducted on the numerous taxa. (The advantage of working on *Laurencia* is that at least some species [see the paper by Zablackis and McDermid] can be successfully cultured in the laboratory, and it may be possible to outplant them to tanks.) The fact that we were able to apply Santelices' taxonomic criteria at two workshops has helped us to straighten out the agar-producing genera *Gelidium* and *Pterocladia*, but the Japanese species (of which there are many reported) have not been critically examined recently with more than a narrow geographic perspective. Other genera—*Chondria, Halymenia*, and *Ahnfeltia* among them—appear to have potential industrial uses; their taxonomy is less difficult than the genera we have studied only because there are fewer species in each of the genera.

Acknowledgments

We acknowledge with deep gratitude the support and continued encouragement of Dr. James Sullivan, director of the California Sea Grant College Program. We also thank Dr. Jack Davidson, director of Hawaii Sea Grant, for travel support and a contribution to the cost of providing the illustrations for this volume. The directors of the Pacific Sea Grant programs of Alaska, Washington, and Oregon and the National Sea Grant College Program provided transportation costs for some of the foreign participants, and we are most appreciative.

We cannot forget the warm hospitality shown by our Chinese colleagues; the wonderful meals that we shared; the good times had with other participants; and the interesting sights of Beijing and Qingdao. We express our special thanks to Dr. C. K. Tseng, Xia Bangmei, Lu Baoren, Zhang Junfu, and all others at the Institute for their many kindnesses.

Finally, I express the thanks of all the workshop participants to Bill Magruder and Karla McDermid for taking most of the pictures used in this volume. The line drawings in the papers by Tseng and Lu, and Zhang and Xia Bangmei, the maps and some of the illustrations in the papers by Abbott, and the pictures in the sections by Cheney and Doty were provided by those authors. For the remainder, however, Dr. Magruder is to be thanked for printing and arranging the photographs.

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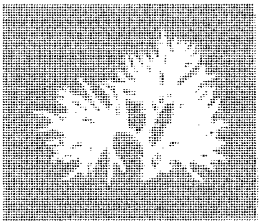
Workshop participants. (Front row, left to right): Zhang Junfu (C. F. Chang), Roy Tsuda, Tseng C. K., I. A. Abbott, J. J. Sullivan, T. Yoshida. (Back row, left to right): Lu Baoren, K. McDermid, W. H. Magruder, Xu Fali, Xia Bangmei, Wang Liming, and Zhou Xiantong.

SECTION I. Western Pacific Asiatic Species of *Sargassum* Subgenus *Sargassum* with Keys to the Species



INTRODUCTION

Tadao Yoshida

Nearly one-half of the approximately 400 species of the brown algal genus *Sargassum* (Fig. 1) are placed in the common tropical and subtropical subgenus *Sargassum*.[1] Members of the genus occupy similar positions on tropical shores that *Laminaria* species do on temperate shores. The subgenus was originally characterized by J. G. Agardh (1889): has axillary fronds that gradually become decompound, usually bearing simple leaves, and with vesicles ("floats") arising within the uppermost part of the leaf; vesicles are spherical to rarely elliptical, terminated by a sharp tip, or without a sharp tip; receptacles, formed on modified axillary branches, are more or less compound, in racemes, panicles, or cymes, sometimes somewhat terete, and tending to be smooth, or sometimes angular and often armed with teeth.

The distinction of the subgenus from other subgenera (*Bactrophycus*, see Abbott and Norris, 1985; *Arthrophycus*,[2] *Phyllotrichia, Schizophycus, Anthophycus*) is not always easily made. Among the features that are used to distinguish subgenus *Sargassum*, the "leaf"[3] is considered to be a distinct appendage on the branch; however, such a leaf is common also in the subgenera *Bactrophycus* and *Arthrophycus*. Expansion of the leaf in the same plane as the branch is vertical or perpendicular to the branch, or in other words, not horizontal, but this is not constant in the subgenus. Some of the species of this subgenus have pinnately divided leaves instead of simple leaves, which characterize the subgenus according to J. G. Agardh. Similar differences are found in some species of the subgenus *Phyllotrichia*. Agardh's description of receptacles as more or less compound for this subgenus also matches the description of receptacles in subgenus *Arthrophycus*.

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[1] Article 21.3 of the International Code of Botanical Nomenclature requires that names of subdivisions of a genus not carry the prefix *Eu-*, such as *Eusargassum*, which is the name J. G. Agardh (1889) gave to this subgenus. We substitute *Sargassum* as a subgeneric name. The type species of the genus *Sargassum* is *S. bacciferum* (Turner) C. A. Agardh, now known as *S. natans* C. A. Agardh, and a member of this subgenus. *Sargassum* C. A. Agardh is a conserved name.

[2] See Abbott, Tseng, and Lu (this volume).

[3] The use of the words "leaf" or "leaves" (without quotes) or stem is not meant to equate the foliar appendages of *Sargassum* with leaves or stems of flowering plants, for of course they are not morphologically homologous. We use these words in a rather loose and neutral way to refer to bladelike appendages and stemlike structures.

J. G. Agardh (1889) subdivided the sugbenus into two groups on the basis of characters shown by the receptacles: Zygocarpicae (receptacles are mixed with vesicles and leaves) and Cladocarpicae. Cladocarpicae are subdivided further into two series, the Acanthocarpicae and Malacocarpicae, on the basis of whether the receptacles are provided with spines. Grunow (1915, 1916), Setchell (1931), and Okamura (1936) followed this scheme as a whole, with minor modifications. Because of lack of time and the unavailability of large suites of specimens, we could not evaluate various features in detail and are unable to provide additional information on the basic taxonomic features that could serve to reorganize the subgenera.

Our initial discussion led to the construction of a list of morphological characters relating to the holdfast, stem, branches, leaves, vesicles, and receptacles. During the discussion and observation of the materials at hand, we noticed that the spinal processes on the branches were developed from the elevation of cryptostomata, at least in *S. polyphyllum.* This is a new observation and must be confirmed in other species in which the branches have small spines or are muricate.

Knowledge of the changes in morphology during development is necessary for the understanding of species limits, but this is lacking for the majority of species. The development of conceptacles is completely unknown for the subgenera *Arthrophycus* and *Phyllotrichia*, which are distributed in the Southern Hemisphere. The changing morphology and evolution of the cauline leaf (leaf arising directly on the stem) are recorded for only a few species. Ecological and phenological features also should be used to supplement the biological characteristics of the species.

Comparison of the specimens brought together in Qingdao showed the uniqueness of the *Sargassum* flora of the Hawaiian Islands. Species of *Sargassum* found in the Hawaiian archipelago, *S. echinocarpum* J. G. Agardh, *S. polyphyllum* J. G. Agardh, *S. obtusifolium* J. G. Agardh, and *S. hawaiiense* Doty et Newhouse, appear to be endemic. The reports of *S. echinocarpum* from other areas of the Pacific (Tonga, by Grunow 1873–1874; Mailiti Island, Solomon Islands, by Setchell 1935; and Taiwan, by Yamada 1950) should be reexamined carefully. It may be that the Hawaiian species are not as isolated as they would appear to be.

On the other hand, from Guam west and south to the mainland of Asia, and southwest and southeast through the many islands of the Pacific, there are several species in common, including *S. polycystum* C. A. Agardh and *S. cristaefolium* C. A. Agardh, both also known from the Indian Ocean.

Finally, a comparison of the *Sargassum* flora between the China mainland, Taiwan, and Japan is difficult to make at present. Until the whole range of variation within a given species can be recognized, it will be impossible to know the geographical range of distribution for each species. Indeed, it is difficult to apply with confidence the name of a known species, even when a study of the type specimen has been made, because these important specimens frequently are lacking crucial features necessary for the final identification of the species. Therefore, we have decided to compile the *Sargassum* species by using arbitrary separate geographical regions; we have agreed, for the most part, on the species names for the taxa that are distributed in common. The regions are divided as follows: (1) Mainland China, Hainan Island, and the Paracel (Xisha) Islands; (2) Japan and Taiwan; (3) Guam and Micronesia; and (4) the Hawaiian Islands. The Chinese material is being investigated by C. K. Tseng and Lu Baoren; the Japanese and Taiwanese, by T. Yoshida; the Guamanian and Micronesian, by Roy Tsuda; and the Hawaiian, by W. H. Magruder.

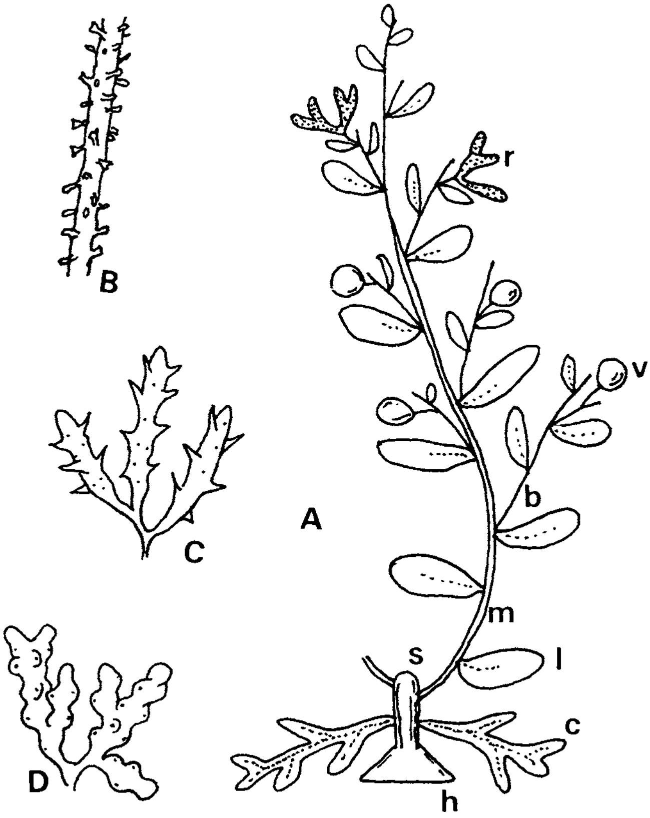

Fig. 1. Diagram of a *Sargassum* plant. *A*, Whole plant. b = secondary branch; c = cauline leaf; h = holdfast; l = leaf; m = main branch; r = receptacle; s = stem; v = vesicle. *B*, Muricate branch. *C*, Receptacle with spines. *D*, Warty receptacle.

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JAPANESE AND TAIWANESE SPECIES OF *SARGASSUM* SUBGENUS *SARGASSUM*

Tadao Yoshida

The Japanese and Taiwanese species have been studied and published on from the beginning of this century by Yendo (1907) and Yamada (1925, 1942, 1944, 1950) and were among the algae that Yamada studied until his death in 1975. Fortunately, the specimens that they studied are kept in the herbaria of the University Museum, University of Tokyo (TI), and the Faculty of Science, Hokkaido University (SAP), and are annotated by Yamada. The survey of *Sargassum* species was not completed by these authors. Several species were represented by only a few specimens. In addition to these, those Taiwanese species treated by Chou and Chiang (1981) were considered and compared with material that Yamada (1925, 1950) and others had obtained from Taiwan. These collections are housed in SAP. Unfortunately, Chiang could not attend the Qingdao meetings and could not help to interpret differences between his identifications and those of Yamada. I tried to follow Yamada's species concept as far as possible.

More than 50 species of *Sargassum* have been reported from the shores of Japan, and I report 20 here in the subgenus *Sargassum*. As more time beomes available for the study of this genus in Japanese waters, it is expected that this number in the subgenus will be increased. In terms of quantity, there are more species from Japan of the subgenus *Bactrophycus*, reported in the papers from the first Workshop on the Taxonomy of Economic Seaweeds (Abbott and Norris 1985). Between 14 and 19 species of *Sargassum* and their relatives (*Hizikia, Coccophora*, and *Myagropsis*) form beds of floating seaweeds in nearshore waters around Japan on both the Japan Sea and Pacific Ocean sides of Kyushu and Honshu. At their peak in May, these beds can attain a density up to 1.6 ton/km^2 or 5.6 ton per square nautical mile (Yoshida 1963). Yoshida also found that the species occurring in floating beds were mainly from nearby shores. These floating seaweeds are intimately related with spawning of several kinds of fishes and a certain period of life history of fishes such as yellowtail.

Key to the Japanese and Taiwanese Species of the Subgenus *Sargassum*

1\. Branches erect, and several main branches transformed into haptera, becoming secondarily attached . . . . (16) *S. polycystum*
1\. All main branches erect, of similar morphology 2

    2. Leaves broad, ovate, elliptical, or spatulate with obtuse apices and coriaceous texture 3
    2. Leaves narrow, lanceolate to linear 9

3\. Leaf margin entire . . . . (15) *S. plagiophyllum*
3\. Leaf margin serrate or double serrate (duplicated) 4

    4. Holdfast scutellate (platter-shaped) 5
    4. Holdfast discoid with smooth surface 7

5\. Leaf often with dentation arranged in two rows 6
5\. Leaf often duplicated (doubled or folded), forming a slightly concave, circular lobe standing perpendicular to blade . . . . (13) *S. ilicifolium*

    6. Main branches compressed, vesicles often provided with wings . . . . (6) *S. coriifolium*
    6. Main branches very slightly compressed, vesicles with two or more sharp points at apices . . . . (18) *S. sandei*

7\. Leaves with symmetrical base, horizontal in expansion, curving upwards . . . . (9) *S. cristaefolium*

7. Leaves with asymmetrical base, vertical in expansion 8
    8. Leaves longer and lanceolate .... (10) *S. echinocarpum*
    8. Leaves elliptical to narrow elliptical .... (7) *S. crassifolium*

9. Leaves furcated 10
9. Leaves simple 11
    10. Leaf margin serrate, receptacles with spines .... (1) *S. alternato-pinnatum*
    10. Leaf margin entire or irregularly serrulate, receptacles warty .... (17) *S. salicifolioides*

11. Main branches flat, leaves and laterals issued alternately in one plane 12
11. Main branches terete or slightly compressed 14
    12. Vesicle stalk longer than vesicle itself 13
    12. Vesicle stalk shorter than vesicle itself .... (20) *S. swartzii*

13. Vesicles with round apices, leaf midrib conspicuous .... (11) *S. henslowianum*
13. Vesicles with sharp tips or with small crown of leaves, leaf midrib immersed .... (5) *S. binderi*
    14. Leaf margin strongly crispate .... (8) *S. crispifolium*
    14. Leaf margin plane, not undulate 15

15. Main branches with short, hard excrescences (muricate) 16
15. Main branches with smooth surface 17
    16. Receptacles filamentous and very slender .... (14) *S. kasyotense*
    16. Receptacles terete and tapering towards apices .... (12) *S. hyugaense*

17. Receptacles spinous .... (2) *S. amabile*
17. Receptacles with warty surface, without spines 18
    18. Leaves narrow linear, 2–3 mm wide .... (3) *S. angustifolium*
    18. Leaves lanceolate, up to 1 cm wide 19

19. Receptacles racemose to paniculate .... (19) *S. siliquosum*
19. Receptacles several times furcate, cymose to paniculate .... (4) *S. assimile*

List of Species and Their Distribution

(1) *Sargassum alternato-pinnatum* Yamada (Fig. 1)
Yamada 1942, p. 599, figs. 28, 29.
Distribution: Honshu, Kyushu; not known elsewhere.

(2) *S. amabile* Yamada (Fig. 2)
Yamada 1942, p. 515, figs. 18, 19.
Distribution: Taiwan; not known since its first collection.

(3) *S. angustifolium* C. Agardh (Fig. 3)
Yamada 1942, p. 507, figs. 12, 13.
Distribution: Shikoku; also reported from Indian Ocean (Srinivasan 1967).

(4) *S. assimile* Harvey (Fig. 4)
Okamura 1936. p. 347.
Distribution: Honshu, Shikoku, Kyushu, Okinawa (type locality: Hong Kong).

(5) *S. binderi* Sonder (in J. G. Agardh)
Yamada 1925, p. 245, fig. 2; Chou and Chiang 1981, p. 143.
Distribution: Taiwan; also reported from Pakistan (Hindustan), the type locality; India (Srinivasan 1967); Sri Lanka (Misra 1966, p. 178); Malaysia and Indonesia (Reinbold 1913).

(6) *S. coriifolium* J. Agardh (Fig 5.)
Yamada 1950, p. 192, fig. 9
Distribution: Taiwan; also reported from the Solomon Islands (Womersley and Bailey 1970), Western Australia (Gazelle), and Pakistan (Hindustan, possibly the type locality).

(7) *S. crassifolium* J. Agardh (Fig. 6)
Yamada 1942, p. 511, figs. 14, 15; Chou and Chiang 1981, p. 135., pl. 1, figs. 1, 2, pl. 2, fig. 4.
Distribution: Taiwan; also reported from vicinity of New Zealand and East Africa, Sri Lanka (Durairatnam 1961), India (Srinivasan 1967), and Malaysia (Reinbold 1913).

(8) *S. crispifolium* Yamada (Fig. 7)
Yamada 1931, p. 72, pl. 20.
Distribution: Honshu, Shikoku, and Kyushu; not known elsewhere.
(9) *S. cristaefolium* C. Agardh (Fig. 8)
Okamura 1936, p. 349; Chou and Chiang 1981, p. 136, pl. 1, figs. 3, 4.
Distribution: Kyushu, Okinawa, and Taiwan; widely distributed through the islands of Indonesia; Sri Lanka (Durairatnam 1961); India (Misra 1966); Kermadec Island (Nelson and Adams 1984).
(10) *S. echinocarpum* J. Agardh (Fig. 9)
Yamada 1950, p. 190, fig. 9.
Distribution: Taiwan, Hawaiian Islands (type locality); also reported from Tonga, Timor, Sumatra, and Solomon Islands (Reinbold 1913).
(11) *S. henslowianum* var. *condensatum* Yamada (Fig. 10)
Yamada 1942, p. 372, fig. 2.
Distribution: Kyushu; not reported since its first collection.
(12) *S. hyugaense* Yamada (Fig. 11)
Yamada 1942, p. 379, figs. 7, 8.
Distribution: Kyushu; not known elsewhere.
(13) *S. ilicifolium* (Turner) C. Agardh (Fig. 12)
Yamada 1942, p. 556, fig. 27; Chou and Chiang 1981, p. 137.
Distribution: Shikoku and Taiwan; also reported from India (Srinivasan 1967).
(14) *S. kasyotense* Yamada
Yamada 1942, p. 553, figs. 22, 23.
Distribution: Taiwan; not known elsewhere.
(15) *S. plagiophyllum* C. Agardh (Fig. 13)
Yamada 1942, p. 516, figs. 20, 21.
Distribution: Taiwan; known elsewhere from India (Misra 1966), Indonesia (Reinbold 1913), and Australia.
(16) *S. polycystum* C. Agardh (Fig. 14)
Yamada 1942, p. 376, figs. 5, 6; Chou and Chiang 1981, p. 137, pl. 1, fig. 6, pl. 2, fig. 5.
Distribution: Okinawa and Taiwan; also widely distributed from Guam west and south (Durairatnam 1961; Misra 1966; Reinbold 1913).
(17) *S. salicifolioides* Yamada (Fig. 15)
Yamada 1942, p. 555, figs. 24–26.
Distribution: Shikoku, the only known locality.
(18) *S. sandei* Reinbold (in Weber-van Bosse) (Fig. 16)
Yamada 1950, p. 191, fig. 8; Chou and Chiang 1981, p. 139, pl. 2, fig. 5.
Distribution: Kyushu, Taiwan, and Flores Island (type locality).
(19) *S. siliquosum* J. Agardh (Fig. 17)
Yamada 1942, p. 503, fig. 9; Chou and Chiang 1981, p. 139, pl. 1, fig. 7, pl. 3, fig. 1.
Distribution: Okinawa and Taiwan; also reported from New Guinea through islands of Indonesia (Reinbold 1913) and Singapore.
(20) *S. swartzii* (Turner) C. Agardh (Fig. 18)
Yamada 1942, p. 371, fig. 1.
Distribution: Taiwan; widely distributed in the Indian and Pacific Oceans (Durairatnam 1961; Misra 1966; Reinbold 1913).

Description of the Species

(1) *Sargassum alternato-pinnatum* Yamada (Fig. 1)

Yamada 1942, pp. 559–561, figs. 28–29; Yamada 1944, p. 2.

Holdfast small, discoid, about 1 cm in diameter; stem very short, terete, scarcely reaching 5 mm in height; main branches up to 50 cm long, angulate, often quadrangular in cross section, about 2 mm in diameter, with short spines on the surface, giving off spirally arranged secondary branches at intervals of about 1–2 cm (appearing pinnate in dried specimens), the laterals up to 25 cm long, more densely muriculate (with short, hard, tubercular excrescences) than the main branches; leaves linear to linear–lanceolate,

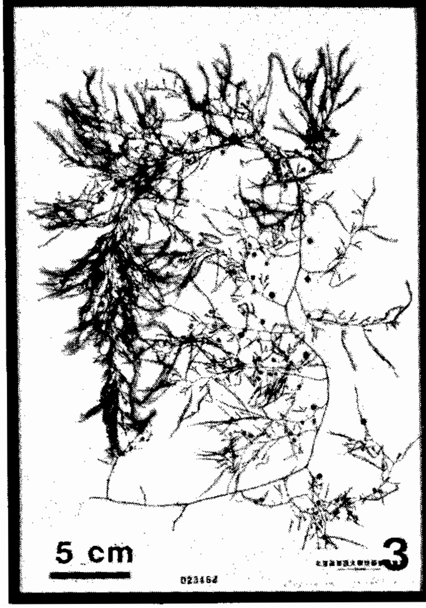


Fig. 1. *Sargassum alternato-pinnatum* **Yamada..**

Fig. 2. *Sargassum amabile* **Yamada.**

Fig. 3. *Sargassum angustifolium* **C. Agardh.**

Fig. 4. *Sargassum assimile* **Harvey.**

alternate-pinnately furcated or simple; base asymmetrical, 1–3 cm long and 1.5–3 mm wide, margins dentate with sharp teeth, midrib reaching the apex; cryptostomata small, disposed incompletely in one row on both sides of the midrib; vesicles subspherical or ovate, up to 6 mm long, usually smooth at apices, rarely with a sharp tip, without cryptostomata; stalks slightly compressed or rarely flattened, slightly longer than the vesicle when young, but short in larger ones, often provided with short spines near the base of the stalk.

Androgynous receptacles terete, 2–2.5 mm long, often forked, warty, provided with sharp spines here and there, cymosely to racemosely arranged.

Remarks: *S. asymmetricum* Yamada is difficult to distinguish from *S. alternato-pinnatum*.

(2) *Sargassum amabile* Yamada (Fig. 2)

Yamada 1942, p. 515, figs. 16, 17; Yamada 1944, p. 1.

Thallus up to 50 cm high; holdfast a small conical disc; stem short, less than 1 cm long, terete, 1–2 mm in diameter, with smooth or somewhat warty surface; main branch terete, about 1 mm in diameter, smooth surface usually without cryptostomata; secondary branches issued at about 3-cm intervals spirally, up to 15 cm long, rarely with cryptostomata; leaves on the lower part of main branch linear-lanceolate, 4–7 cm long and 6–8 mm wide, cuneate at the base, acute at apices, margins toothed with teeth pointing upward from a broadened base (serrato-dentata), or the teeth with narrow base, broadening slightly upward (obsolate-dentate), cryptostomata few in number, scattered over the surface; midrib percurrent; leaves on the upper part of the thallus becoming smaller and narrower; vesicles spherical in larger ones, becoming obovate or elliptical in those of the upper part of the plant, and fusiform in the distal ones, obtuse or apiculate at apices, 3–5 mm long with few cryptostomata; vesicle stalk terete, usually shorter than vesicles.

Androgynous receptacles 5–10 mm long, simple or furcate, two-edged to flattened, or triquetrous, spiny to dentate at margin, racemosely or nearly cymosely arranged on the ultimate branchlets.

Remarks: This species is known only from the type collection.

(3) *Sargassum angustifolium* C. A. Agardh (Fig. 3)

C. A. Agardh 1820, p. 32.

Application of this name: Yamada 1942, p. 507, figs. 12, 13.

Synonyms: *Fucus angustifolius* Turner (Turner 1819, p. 34, pl. 212); *S. vulgare* var. *linearifolium* Yendo (Yendo 1907, p. 145, pl. 17, fig. 5).

Basal part unknown in Japanese specimens; branches filiform with smooth surfaces, cryptostomata not recognizable; leaves thin membranaceous, linear to linear-lanceolate, up to 4 cm long, 2 mm wide, with obtuse apices, margins partially dentate, midrib indistinct and nearly absent in smaller leaves, cryptostomata on leaves small, scattered; vesicles spherical, up to 5 mm long, with round apices; vesicle stalk slender, terete, shorter than vesicle, cryptostomata very few on vesicles.

Androgynous receptacles terete, 5–10 mm long, warty surface without spines, simple or dichotomously branched, often mixed with leaves or vesicles (zygocarpic).

Remarks: This name must be attributed to C. A. Agardh because the name *Fucus angustifolius* Turner (Turner 1819) is a later homonym of that of Gmelin (1768).

(4) *Sargassum assimile* Harvey (Fig. 4)

Harvey 1859, p. 328.

Application of this name: Okamura 1936, p. 347.

Holdfast discoid, 1 cm in diameter, stem short, 0.5–1 cm high, terete, 1.5–2 mm in diameter; main branches terete to compressed, a few cryptostomata scattered as elevated spots, with secondary branches alternately placed at intervals of 2–4 cm; leaves on main branch thin and membranous, lanceolate to linear-lanceolate, base asymmetrical, apex blunt, midrib immersed, reaching close to the apex or disappearing near the apex; margin sparingly and shallowly dentate, cryptostomata scattered; vesicles spherical, round at apex, up to 5 mm long, vesicle stalk dilated above, shorter than vesicles in larger ones, nearly equal in length to smaller ones, cryptostomata rare on vesicles.

Female receptacles terete, 2–3 mm long, furcated several times, without spines, cymosely or paniculately disposed.

Remarks: The type locality was originally described as "Loo Choo." Dawson (1959) pointed out that this was an error and that the correct locality was Lemma Island, near Hong Kong. According to Grunow (1916), this species was androgynous and receptacles were spinulose, both features different from the Japanese specimens.

(5) *Sargassum binderi* Sonder *in* J. G. Agardh

J. G. Agardh 1848, p. 328 (pro parte).

Applications of this name: Yamada 1925, p. 245; Chou and Chiang 1981, p. 143.

Holdfast small, discoid; stem terete, very short, about 5 mm high; main branches flat, 3–4 mm wide, usually up to 30 cm long, with smooth surface; leaves alternate with a phyllotaxis of ½ at intervals of 1–1.5 cm; leaves linear-lanceolate to linear, sessile, with cuneate base, with apices obtuse or acute, midrib immersed, percurrent, and distinct, sometimes vanishing just below the apex, margin serrate, cryptostomata in two rows, each on either side of the midrib; vesicles elliptical, slightly compressed, 9 mm long, 5 mm wide, with a sharp point at apices or with small coronal leaf continuous to wings, cryptostomata present on vesicles; stalk flat and leafy with serrate margin, longer than vesicle itself.

Receptacles terete, 3–5 mm long, warty, dichotomously branched, arranged in three to five racemose clusters.

Remarks: *S. kushimotense*, reported from Taiwan by Chou and Chiang (1981), seems to be similar to this species. As reported from Vietnam (Pham-hoang 1969), *S. binderi* is thought by Chou and Chiang to be a different species.

(6) *Sargassum coriifolium* J. G. Agardh (Fig. 5)

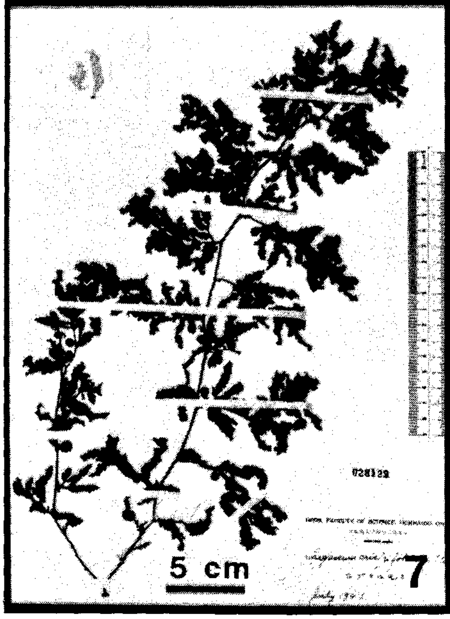
J. G. Agardh 1889, p. 96.

Application of this name: Yamada 1950, p. 192; Womersley and Bailey 1970, p. 295.

Holdfast a platelike disc, 1.5–2 cm in diameter; stem terete with smooth surface, less than 1 cm high and 1–2 mm in diameter; main branch 60+ cm long, 1–2 mm wide, compressed, with smooth surface, with secondary branches alternate at intervals of 2–3 cm, secondary branches less than 10 cm long; leaves on the main branches elliptical to long-elliptical, with round apex and cuneate base, 2.5–3 cm long and 1 cm wide, coriaceous, midrib evanescent, margin serrate, cryptostomata in two rows each on either side of midrib; leaves on secondary branches slenderer, often oblanceolate and with acute apex, margin often provided with double rows of sharp teeth; vesicles elliptical when young, becoming obovoid in more mature ones, up to 5 mm long, apex with a sharp tip, or with small teeth extending to clear wings, cryptostomata present on vesicle; vesicle stalk flat, not longer than vesicle.

Receptacles compressed, 3 mm long, with acute spines; vesicles once or twice branched, cymosely arranged.

Remarks; Yamada (1950) distinguished two forms in this species: f. *duplicatum*



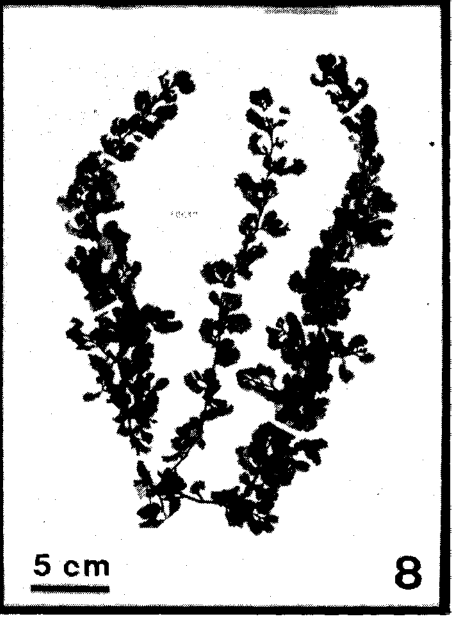


Fig. 5. *Sargassum coriifolium* J. Agardh.

Fig. 6. *Sargassum crassifolium* J. Agardh.

Fig. 7. *Sargassum crispifolium* Yamada.

Fig. 8. *Sargassum cristaefolium* C. Agardh.

Yamada and f. *prolongatum* (Okamura) Yamada. *S. berberifolium* as recognized by Yendo (1907) and Okamura (1936) is probably the same as this species, *S. coriifolium*.

(7) *Sargassum crassifolium* J. G. Agardh (Fig. 6)

J. G. Agardh 1848, p. 326.

Applications of this name: Yamada 1942, p. 511; figs. 14, 15; Chou and Chiang 1981, p. 135, pl. 1, figs. 1, 2, pl. 2, fig. 4.

Holdfast small, discoid, 1 cm in diameter; stem terete with smooth surface, rarely attaining 1 cm high, 2.5 mm in diameter; main branches 30–50 cm long, compressed with smooth surface, secondary laterals 5–8 cm long, alternate at intervals of 1–1.5 cm; leaves elliptical to narrow-elliptical, up to 3.5 cm long and 2 cm wide, with blunt apex and slightly asymmetrical cuneate base, shortly stipitiate or sessile, thick coriaceous, midribs disappear midway to the apex, margin frequently dentate, cryptostomata scattered; vesicles elliptical up to 10 mm long with pointed apices or rarely with small coronal leaves extending to form a spiny fringe, stalk flat, often leafy, as long as or shorter than the vesicle, cryptostomata present on vesicles.

Androgynous receptacles compressed, 2–3 mm long, forked several times, spiny on the margin, forming a condensed cyme.

Remarks: According to Chou and Chiang (1981), the specimens they examined were all female. Grunow (1916) and Yamada (1942) stated that the species was androgynous.

(8) *Sargassum crispifolium* Yamada (Fig. 7)

Yamada 1931, p. 72, pl. 20.

Holdfast a small round disc, about 5 mm in diameter; stem terete, up to 1 cm high; main branches terete, filiform, smooth on surface; leaves shortly petiolate or nearly sessile, linear spatulate, 3–5 cm long and 5–10 mm wide, membranous, obtuse or somewhat acute at the apex, finely and sharply dentate at the margin, usually strongly crispate, midrib clear except near the apex, cryptostomata clear, scattered sparingly all over the surface; vesicles spherical, rarely elliptical, 5–8 mm in diameter, shortly petiolate, smooth with few cryptostomata.

Receptacles terete, one to four times forked, warty, rarely spinous.

(9) *Sargassum cristaefolium* C. A. Agardh (Fig. 8)

C. A. Agardh 1820, p. 13; C. A. Agardh 1824, p. 297.

Applications of this name: J. G. Agardh 1848, p. 325; Sonder 1871, p. 42 (as var. *condensatum*); Grunow 1915, p. 398; J. G. Agardh 1889, p. 91; Reinbold 1913, p. 157; Setchell 1935, p. 265; Børgesen 1936, p. 79; Levring 1960, p. 122; Durairatnam 1961, p. 45, pl. 10, figs. 3–5; Misra 1966, p. 179; Womersley and Bailey 1970, p. 196, fig. 7; Chou and Chiang 1981, p. 136, pl. 1, figs. 3, 4.

Synonyms: *S. duplicatum* Bory (Bory 1828, p. 127; J. G. Agardh 1889, p. 90; Grunow 1915, p. 392; Okamura 1923, p. 10, pl. 205; Pham-hoang, 1969, p. 302, fig. 18; Reinbold 1915, p. 157) and *S. ilicifolium* (Turner) C. Agardh var. *duplicatum* (Bory) (J. G. Agardh 1848, p. 319).

Holdfast discoidal, 1–2 cm in diameter; stem terete, less than 1 cm long, 2–4 mm in diameter, usually without branching; main branches slightly flattened to compressed, with or without ridges at the basal parts, with smooth surface, 10–40 cm long and 2–4 mm wide; leaves spatulate, oblong to lanceolate, 1–2 cm long and 0.5–1.2 cm wide, shortly stipitate with symmetrical base and obtuse to acute apices, midrib vanishing midway to apex; margins irregularly serrate or simple-bifid dentate; cryptostomata raised from the surface, scattered; vesicles elliptical, with or without small appendages, 3–10 mm in

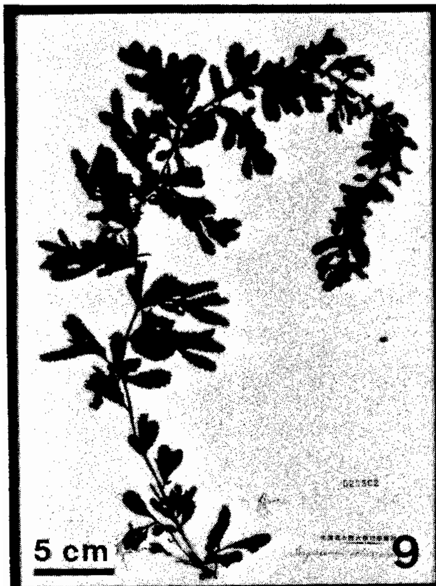


Fig. 9. ***Sargassum echinocarpum*** **J. Agardh.**

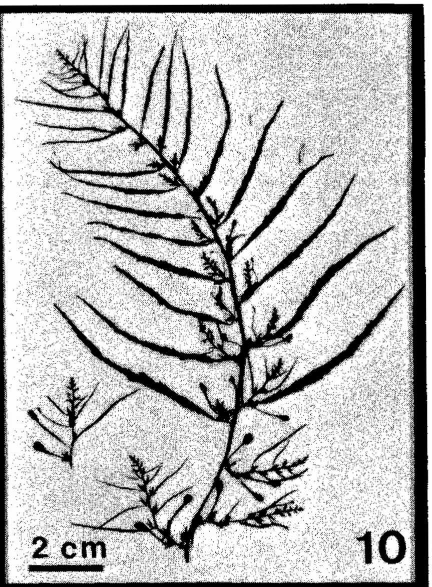


Fig. 10. ***Sargassum henslowianum*** **var.** ***condensatum*** **Yamada.**

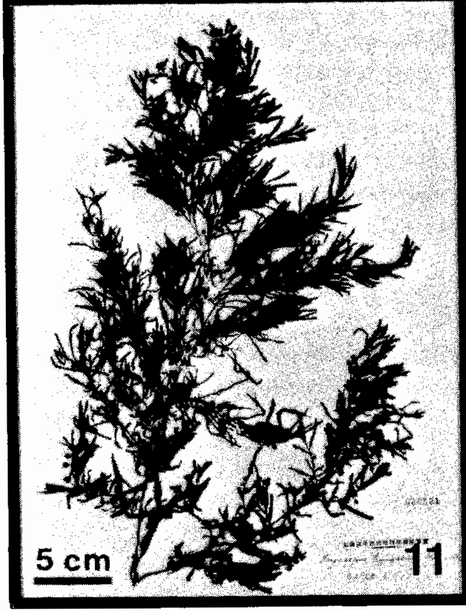


Fig. 11. ***Sargassum hyugaense*** **Yamada.**

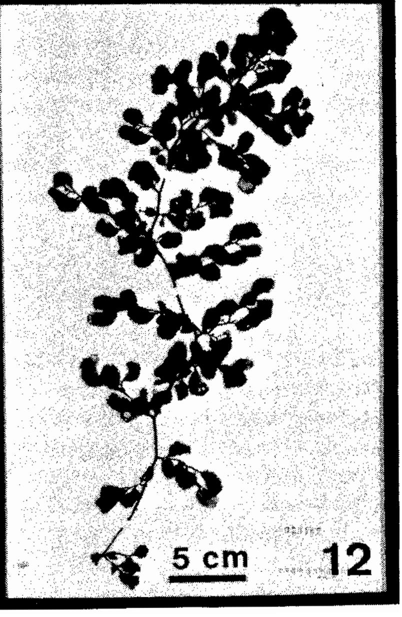


Fig. 12. ***Sargassum ilicifolium*** **(Turner) C. Agardh.**

diameter, with slightly rounded to sharp tips; vesicle stalk terete to flattened, one-half to one-third the length of the vesicles.

Androgynous receptacles compressed with small spines, irregularly forked, 5–10 mm long and 0.5–1 mm wide, with a short sterile stipe, cymosely arranged.

Remarks: U. Soe-Htun and Yoshida (1986) reported the range of variation in branch, leaf, and vesicle morphology. In the opinion of Womersley and Bailey (1970), many taxa such as *S. crassifolium* J. G. Agardh, as interpreted by Reinbold in Weber-van Bosse (1913), Grunow (1915), Dawson (1954), Durairatnam (1961), and Pham-hoang (1969), and *S. coriifolium* f. *duplicatum* Yamada (1950) are possible synonyms of *S. cristaefolium.*

(10) *Sargassum echinocarpum* J. G. Agardh (Fig. 9)

J. G. Agardh 1848, p. 327.

Application of this name: Yamada 1950, p. 190, fig. 9.

Holdfast an elevated disc, 1.5–2 cm in diameter; stem terete, surface nearly smooth, very short, scarcely reaching 1 cm; main branches up to 1 m long, compressed, about 3 mm wide, with smooth surface; secondary branches up to 13 cm long, alternate; leaves distichous in ½ phyllotaxis, oblong or elliptical, 3–4 cm long, 1.2 cm wide, with obtuse apex and cuneate base, shortly stipitate, midrib evanescent but conspicuous when present, margin serrate, sometimes serrate in two series, especially in lower parts of main branch, cryptostomata irregularly scattered, leaves on secondary branch or upper part of main branch becoming slender to lanceolate or broadly linear with acute apex; vesicles ovate or elliptical in shape, up to 1.5 cm long, slightly compressed, with minute spine-like protuberances at margin, coming to a short and sharp point, or a small crown of small leaflike appendages; cryptostomata few on vesicles; stalk shorter than vesicles.

Androgynous receptacles forming dense cluster, 5–8 mm long, branching several times, with a few spines.

Remarks: Yamada (1950) attributed Taiwanese specimens to this species. Careful comparison is needed with specimens from "Sandwich Islands" or Hawaii (type locality).

(11) *Sargassum henslowianum* var. *condensatum* Yamada (Fig. 10)

Yamada 1942, p. 372, fig. 2; Yamada 1944, p. 4.

Basal part unknown. Main branch complanate, 2 mm wide, with smooth surface, secondary branches alternate at intervals of 1.5–2 cm; leaves linear to linear-lanceolate, up to 8 cm long, 8 mm wide, with cuneate base and acute apex, midrib percurrent, margin with sharp and shallow dentation, cryptostomata arranged in rows on both sides of the midrib; vesicles obovoid to spherical, up to 8 mm long, with round apex, stalk flat, often three times longer than vesicle itslf, cryptostomata present on the vesicle.

Female receptacle terete, often conical, 3–4 mm long, with a warty surface, simple or once branched at apices, racemosely arranged, or often paniculately so, especially in lower parts of the receptacular branches.

Remarks: The plant body of this variety is much stouter than the typical *S. henslowianum* from the southern coasts of China. As known in China (Setchell 1931, fig. 6), the species shows exceptionally elongate receptacles among the other taxa in the western Pacific.

(12) *Sargassum hyugaense* Yamada (Fig. 11)

Yamada 1942, p. 379, fig. 7; Yamada 1944, p. 5.

Plant about 50 cm high; holdfast a small disc, 1.5 cm in diameter; stem very short, scarcely reaching 1 cm long, terete, about 3 mm in diameter, surface somewhat warty; main branches compressed, longitudinally angular, about 3 mm wide, spinulose, secondary branches alternate at intervals of about 1.5–2.5 cm; leaves on lower part of main branch arranged in phyllotaxis of ½, long elliptical, 2–2.5 cm long, 7–8 mm wide, with obtuse apex, midrib distinct, reaching apex, leaves of middle part of the main branches linear-lanceolate, 3–8 cm long, 2–2.5 mm wide, rarely furcate, small cryptostomata in two rows along the midrib; vesicles subobovoid or spherical, up to 6 mm long, with round apex, stalk slightly shorter than vesicle, compressed with dentate margin, cryptostomata present on the vesicle.

Androgynous receptacles terete, tapering to the apex, often furcate dichotomously, about 6 mm long, with warty surface and no spines, arranged in a condensed raceme.

(13) *Sargassum ilicifolium* (Turner) C. A. Agardh (Fig. 12)

C. A. Agardh 1820, p. 11.

Basionym: *Fucus ilicifolius* Turner (Turner 1808, p. 113, pl. 51.)

Application of this name: Yamada 1942, p. 556, fig. 27.

Holdfast a platelike disc; stem terete, up to 5 mm high, with smooth surface; main branches more than 1 m long, compressed with smooth surface, secondary branches up to 20 cm long, alternate at intervals of 3–4 cm; leaves cuneate to long-elliptical, up to 3 cm long and 1.2 cm wide, with round apex and asymmetrical base, thick papyraceous, midrib evanescent in the middle part, margin with small, acute teeth, some leaves duplicated, forming a slightly concave, circular lobe perpendicular to the blade, cryptostomata irregularly scattered; vesicles spherical or nearly so, 7 mm in diameter in large ones, smaller ones often obovoid with round apex, often provided with wings, stalk short and compressed.

Male receptacles compressed to flattened, with small spines, cymosely or paniculately arranged.

Remarks: Yamada (1942) recognized a variety *conduplicatum* Grunow for the Japanese flora. Womersley and Bailey (1970) suggested that this variety might be a synonym of *S. cristaefolium*. The specimens identified as *S. duplicatum* J. Agardh (non-Bory) or *S. brevifolium* Kuetzing by Japanese authors are very similar to those identified here as *S. ilicifolium*.

(14) *Sargassum kasyotense* Yamada

Yamada 1942, p. 553, figs. 22, 23; Yamada 1944, p. 6.

Holdfast an elevated conical disc about 1 cm in diameter; stem terete, 2 cm high and 3 mm in diameter, with warty surface; main branches about 40 cm long, terete, angulate, remotely spinulose; secondary branches up to 10 cm long, spirally arranged; leaves linear or linear-lanceolate, nearly sessile, up to 4 cm long and 6 mm wide, obtuse at apices, finely serrate at margin, provided with a percurrent midrib and very small inconspicuous cryptostomata; vesicles obovoid or pyriform, blunt at apex or with small, sharp point; stalk flat, with a marginal wing often dentate. Female receptacles very thin, linear, slightly compressed, repeatedly furcate, bluntly and distantly spined in the upper parts, the surface warty because of elevated conceptacles.

Remarks: This species differs from *S. hyugaense*, which also has stems with warts (verrucose) or hard excrescences (muricate) on their branch surfaces, by being a more slender plant with limited, short laterals. The laterals of *S. hyugaense* are numerous and conspicuously elongate, densely divided again into branches of the third and fourth orders.

(15) *Sargassum plagiophyllum* C. A. Agardh (Fig. 13)

C. A. Agardh 1824, p. 304.

Application of this name: Yamada 1942, p. 516, figs. 20, 21.

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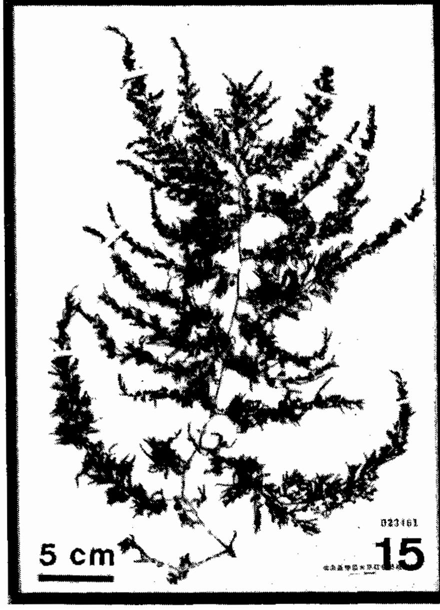

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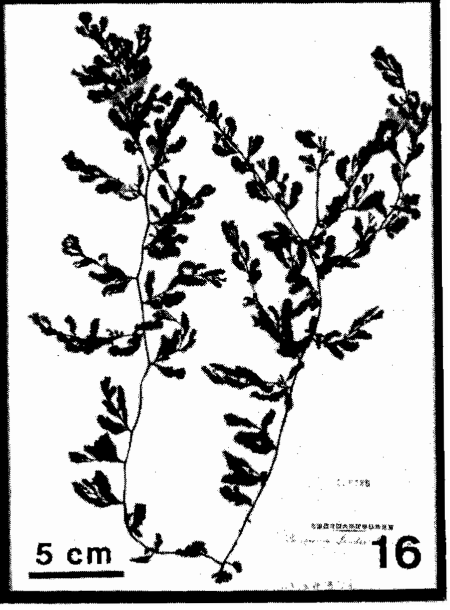

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Fig. 13. ***Sargassum plagiophyllum*** **C. Agardh.**

Fig. 14. ***Sargassum polycystum*** **C. Agardh.**

Fig. 15. ***Sargassum salicifolioides*** **Yamada.**

Fig. 16. ***Sargassum sandei*** **Reinbold**

Basal part unknown in our specimens; main branch terete without spines; secondary branches in a loose spiral at intervals of 1.5–2 cm; leaves up to 3 cm long and 0.5 cm wide, linear, long-elliptical to oblanceolate, apex obtuse or pointed, the base stipitate to wedge-shaped, margin entire and wavy, slightly serrulate near the apex, midrib discernible only near the base, cryptostomata arranged in two rows; vesicles elliptical to obovoid, up to 7 mm long, with apex rounded or coming to a point; stalk flat, longer than the vesicle, cryptostomata present on the vesicle.

Male receptacles terete, 1 cm long, without spines, rarely once branched, disposed racemosely or paniculately; female plant unknown.

Remarks: Yamada (1942) identified the Taiwanese specimens as this species with hesitation. It was not listed again by Chou and Chiang (1981) from Taiwan.

(16) *Sargassum polycystum* C. A. Agardh (Fig. 14)

C. A. Agardh 1824, p. 304.

Synonym: *S. microphyllum* (Yendo 1907, p. 137; Okamura 1931, p. 108; Yamada 1925, p. 247).

Applications of this name: Yamada 1942, p. 376, fig. 5, 6; Chou and Chiang 1981, p. 137, pl. 1, fig. 6, pl. 2, fig. 5.

Thallus up to 60 cm tall; holdfast a conical disc, 7–15 mm in diameter; stem terete, 7–11 mm long, 2 mm in diameter; main branches arranged spirally on the terminal part of the stem, nearly terete, with many cryptostomata that are elevated to form spines; several main branches formed late in season are transformed into stolons with alternately pinnately arranged branches, terminal part of stolons forming secondary attachment discs; leaves on the main branch simple, up to 2.5 cm long and 3–5 mm wide, base asymmetrical, apex obtuse or somewhat acute, midrib reaching the apex, margin irregularly dentate, cryptostomata arranged in two rows along the midrib, slightly raised from the surface; vesicles spherical, small, 2–3 mm in diameter, formed on secondary and tertiary branches; stalk shorter than vesicle, terete; cryptostomata present on the vesicles, raised from the surface.

Dioecious; male receptacle terete, up to 1 cm long, less than 1 mm in diameter, surface smooth, usually unbranched, formed on ultimate branchlet, paniculate or racemose; female receptacle compressed, 2–3 mm long, 1 mm wide, spiny on the margin, usually unbranched, racemose; receptacles carpophyllous (mixed receptacles, leaves, and vesicles).

Remarks: Specimens identified by Yendo (1907, p. 135) as *S. heterocystum* seem to be identical with this species.

(17) *Sargassum salicifolioides* Yamada (Fig. 15)

Yamada 1942, p. 555, figs. 24–26; Yamada 1944, p. 8.

Holdfast a small conical disc; stem terete, up to 5 mm long and 2.5 mm in diameter, with a warty surface; main branches reaching 45 cm, compressed, 2–3 mm wide, very sparingly muriculate (with short, hard excrescences); secondary branches distichously arranged at intervals of about 1–2 cm, the branches 15 cm or less in length, more strongly muriculate than the main branches; leaves on the main axes alternate, with a phyllotaxis of ½, alternate pinnately forked, subdichotomously divided, or simple, up to 6 cm long and 6 mm wide, margins nearly entire or with teeth pointed at the base, becoming broader at their tops; leaf apices obtuse or nearly acute, provided with a percurrent midrib and one incomplete row of cryptostomata on each side of the midrib; vesicles spherical or very slightly elongated up to 6 mm long, pointed at apices, without cryptostomata; stalk terete, shorter than the vesicles themselves.

Androgynous receptacles terete, forked several times, with warty surface, cymosely or subracemosely arranged.

Remarks: Both *S. salicifolioides* and *S. alternato-pinnatum*, from central Japan, have irregularly shaped or divided leaves. They are the only species in the flora that show this character, even though leaf shape, their margins, and the tendency for duplication of margins vary greatly in the genus. On detailed features, the two may be separated on the degree of irregularities of the surface of receptacles: the surface of *S. salicifolioides* is warty, the surface of *S. alternato-pinnatum* has a few spines as well. When the plants are compared, however, the branches of *S. salicifolioides* are leading branches, the secondarily produced ones becoming as long as the first-formed (the main branch), whereas the main branch of *S. alternato-pinnatum* remains dominant, and secondary branches are much shorter than the main branch. The latter species appears to be a much larger, more freely growing plant. Although changes in vegetative form through the life history, or at different ecological conditions, are not known for these taxa, as presently understood from available material, these are observations that can be made.

(18) *Sargassum sandei* Reinbold (Fig. 16)

Reinbold 1913, p. 158, fig. 47.

Application of this name: Yamada 1950, p. 191, fig. 8; Chou and Chiang 1981, p. 139, pl. 1, fig. 7, pl. 3, fig. 1.

Holdfast discoid, about 2 cm in diameter; stem terete, scarcely exceeding 1 cm high, 2–3 mm in diameter; main branches terete or slightly compressed, without spines, secondary branches alternate; leaves cuneate-oblong to linear oblong or broadly linear in shape, up to 4 cm long, very shortly stipitate, asymmetrical cuneate at the base, obtuse and sometimes duplicated at apices, midrib soon disappearing, margin crisply dentate, cryptostomata irregularly arranged; vesicles obovate, up to 8 mm long, sharply pointed or toothed at apices, cryptostomata present on vesicle; vesicle stalk compressed or flattened, shorter than the vesicle itself.

Dioecious; male receptacle terete or compressed or three-sided, less than 5 mm long, once or twice furcated, with few spines or teeth; female receptacles three-sided, dentate to winged with large teeth at the margin, cymosely to racemosely arranged.

Remarks: Specimens in SAP identified by Yamada have larger leaves when compared with the type specimen in the Leiden herbarium (L).

(19) *Sargassum siliquosum* J. G. Agardh (Fig. 17)

J. G. Agardh 1848, p. 316.

Applications of this name: Yamada 1942, p. 503, fig. 9; Chou and Chiang 1981, p. 139, pl. 1, fig. 7, pl. 3, fig. 1.

Holdfast platelike; stem 1.5 cm high, terete, nearly smooth on surface; main branch slightly compressed, about 2 mm wide, with a smooth surface; secondary branches alternate at intervals of 2–3 cm; leaves long-elliptical, coarse dentation on the margin, apex obtuse, base asymmetrical, midrib becoming inconspicuous and not reaching the apex, cryptostomata scattered irregularly, leaves on basal part of branch measuring 4.5 cm long and 1 cm wide, smaller leaves on the secondary laterals 1.5–3 cm long and 0.5–1.2 cm wide; vesicles obovoid to nearly spherical, up to 7 mm long, with round apex, cryptostomata rarely present on the vesicle; vesicle stalk flattened, shorter than the vesicle.

Dioecious; male receptacles terete, filamentous, up to 1.6 cm long, without spines, racemosely or paniculately branched, often with vesicles.

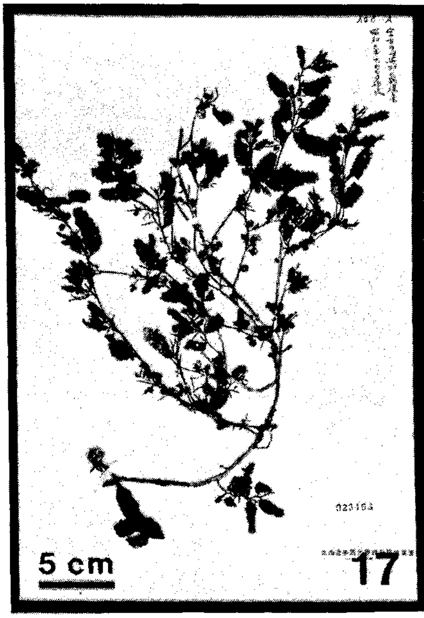
Remarks: *S. siliquosum* is included in one of the "subtribes" of J. G. Agardh that includes *S. henslowianum*. Both taxa are characterized by elongate receptacles; those of *S. siliquosum*, however, are shorter than those of *S. henslowianum*.

(20) *Sargassum swartzii* (Turner) C. A. Agardh (Fig. 18)
C. A. Agardh 1820, p. 11.
Basionym: *Fucus swartzii* Turner (Turner 1819, p. 110, pl. 248.)
Application of this name: Yamada 1942, p. 371, fig. 1.

Basal part not known in Taiwanese specimen, reported elsewhere to have a disc-shaped holdfast; main branch flat, 3 mm wide, without spines, secondary laterals alternate at intervals of 2–3 cm; leaves thick, lanceolate to linear-lanceolate, apex acute, base broad cuneate, up to 4 cm long and 6 mm wide, phyllotaxis ½, midrib inconspicuous, reaching the apex, margin with acute teeth or irregular small teeth, cryptostomata forming two rows on both sides of midrib; vesicles spherical, about 9 mm long in larger ones and obovoid or ellipsoid in smaller ones, apex round or with a sharp point; stalk flat and leafy, similar in length to the vesicle, cryptostomata few on the vesicles.

Androgynous receptacles terete or compressed, about 5 mm long, with small spines on apical part, often forked, cymosely arranged.

Remarks: This species is known from the Persian Gulf through the Indian Ocean and in various locations in the western Pacific. The variations shown by the geographical populations are not known.



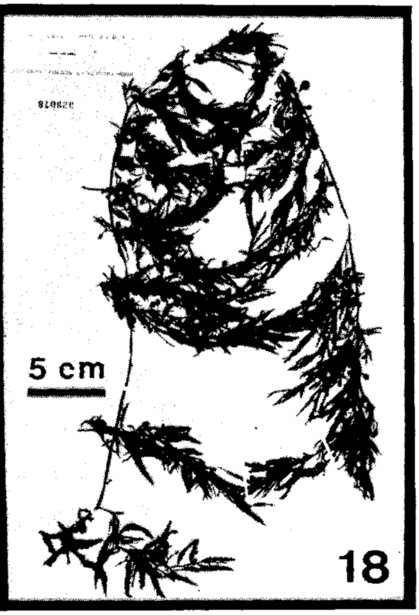


Fig. 17. ***Sargassum siliquosum*** **J. Agardh.**

Fig. 18. ***Sargassum swartzii*** **(Turner) C. Agardh.**

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STUDIES ON CHINESE SPECIES OF ZYGOCARPIC *SARGASSUM*

Tseng C. K. and Lu Baoren

Abstract

The Chinese species of *Sargassum* subgenus *Sargassum* that bear fertile older branchlets having receptacles intermixed with leaves or with vesicles (section *Zygocarpicae*) are reviewed. Of a total of 16 known species in that group, Setchell earlier accepted 11 in his treatment of the Hong Kong seaweeds. Since then, *S. polycystum* has been transferred to the *Zygocarpicae*, and five new species have been described. Altogether, this group recorded from China now has 17 species. This paper presents a systematic arrangement that includes a new series, *Cinerea*, and a new species group, "*Longifructa*" that contains two new species, *S. nozhouense* Tseng et Lu and *S. longifructum* Tseng et Lu.

Introduction

The genus *Sargassum* was established by C. A. Agardh in 1820 (C. A. Agardh, 1820), when he began to lay the foundation of a new system of classification of the algae. J. G. Agardh revised the system of C. A. Agardh on the classification of *Sargassum* and published a new arrangement of the species in 1848 (J. G. Agardh 1848), and again in 1889 (J. G. Agardh 1889), according to his particular idea of evolution within the genus. This was followed by systems by Grunow (1915, 1916) and Setchell (1931, 1935a, 1936). J. G. Agardh's system is in need of revision, but as Setchell mentioned, to date there is "no more satisfactory arrangement of the species of *Sargassum* than that of J. G. Agardh and it seems best to follow that at least, as somewhat changed and adopted by Grunow in his 'Additamenta'." We shall, therefore, follow the J. Agardhian system of 1889, as modified by Grunow (1915) and Setchell (1935a). In this system five subgenera are recognized; the last one is *Eusargassum*, which, according to the present International Botanical Code, (Article 21.3, ICBN), should be subgenus *Sargassum*. This subgenus is divided again into two or more sections. This chapter is devoted to a discussion of the Chinese species of zygocarpic *Sargassum* (section *Zygocarpicae*).

The zygocarpic *Sargassum* are characterized by plants typically slender, with the fructiferous branches forming what J. G. Agardh called a "heteroclite cyme," in which the receptacles of the inflorescences are intimately joined with the leaf and vesicle structures, in typical forms at least, so that the vesicles seem to spring directly from the leaves. In the treatment of the *Zygocarpicae* by J. G. Agardh (1889), 10 species were mentioned; whereas Grunow (1915) listed 16, including three species belonging to "*Carpophylleae dubiae*." Setchell (1935a) divided the *Zygocarpicae* into two sections that are now the subsections *Holozygocarpicae* with five species in two species groups, and *Pseudozygocarpicae* with six species in three species groups. The *Pseudozygocarpicae* take the place of Grunow's "*Carpophylleae dubiae*." They are apparently closely related to such typical holozygocarpic species as *S. angustifolium* and have inflorescences with a slightly greater differentiation of the axes, not showing leaf and vesicle structures immediately arising from the receptacles. Altogether, 11 species of zygocarpic *Sargassum* have been accepted for China by Setchell (1935a).

Some Remarks on Setchell's Treatment of Zygocarpic *Sargassum*

In his study of Chinese *Sargassum*, W. A. Setchell had access to many authentic specimens, including some type specimens, and his points of view have been quite authoritative. He expressed doubts on four determinations, namely, *S. angustifolium*

(Turner) C. A. Agardh, *S. carpophyllum* J. G. Agardh, *S. aemulum* Sonder, and *S. tenue* J. G. Agardh. All of these require clarification from our point of view.

The first species group of the subsection *Holozygocarpicae* are the *Carpophylleae* J. G. Agardh, lim. mut., characterized by the possession of *malacocarpic androgynous fusiform receptacles,*[1] and *S. carpophyllum* J. G. Agardh, both of which are followed by a question mark. Setchell studied the type specimen of *Fucus angustifolius* Turner, gave an elaborate discussion of its complexities, and was inclined to agree with J. G. Agardh's interpretation of the Turnerian *F. angustifolius*: "After carefully considering all phases of the situation, it seems best to regard the later (?) conception of J. G. Agardh as to the nature of *S. angustifolium* as the more plausible and to refer certain Hong Kong plants to it" (Setchell 1935a). We agree with and are following Setchell's interpretation and are referring to this species some slender plants with narrow percurrent leaves having small distinct cryptostomata scattered in a single line along each side of the midrib and with androgynous receptacles rounded in section, forked one to three times with surfaces irregularly tumid, acute at their summits, and usually, at least the upper ones, bearing both leaflets and minute, stalked vesicles.

The *S. carpophyllum* J. G. Agardh also carries a question mark. This species was credited to the Hong Kong region by its author on the basis of a specimen in Areschoug's Herbarium, which was identified as *S. carpophyllum* var. *compressa* by Grunow (1915). According to the original description of *S. carpophyllum* by J. G. Agardh (1848), the receptacles are supraaxillary, lanceolate-cylindrical, forked with the outer fork prolonged into a leaflet, the interior into a receptacular branch. This is Setchell's interpretation of J. G. Agardh's species of 1848 and probably also that of 1889. The technical type is from Ceylon, and the next specimen comes from Hong Kong. We have compared drawings of the receptacles of this species by Durairatnam (1961) from Ceylon and those by Setchell (1935a) from Hong Kong with our specimens and found that they agree with each other quite well. We therefore are removing the question mark from the species.

Another zygocarpic *Sargassum* with a question mark is *S. aemulum* Sonder, which is placed in the species group *Tenerrima* with flattened, two-edged, dentate receptacles. This species appears in J. G. Agardh's monograph as a synonymn under *S. flavicans* (Mert.) C. A. Agardh, but Grunow (1915) separated it on account of its flattened, androgynous receptacles, and listed *S. cristatum* J. G. Agardh as a synonym of it. Setchell (1935a) found a scrap of a specimen, which he identified with *S. aemulum* Sonder var. *carpophylloides* Grunow, characterized by the *receptaculis androgynis subclavitis subfastigiata-paniculatis, spinulosis, androgynis.*[2] This variety does appear to be quite different from the species, characterized by "receptaculis solitaris, ramis subfurcatis." Because we have not found this variety ourselves, we have followed Grunow's and Setchell's interpretations of the species.

The fourth species in this group with a question mark is *S. tenue* J. G. Agardh, for which Setchell established a species group *Tenuia.* Both J. G. Agardh (1889) and Grunow (1915) listed *S. gracile* Greville (Greville 1849) as a synonym for this species, whereas they put *S. flexile* Greville (Greville 1849) as a synonym under *S. angustifolium.*

[1] *Malacocarpic androgynous fusiform receptacles* means that these species have receptacles that are smooth to a little rough on the surface, forming a compoundly branched fertile structure, the fertile branches thick, bearing sperms and eggs on the same receptacles that taper at both ends. In general, malacocarpic means with smooth receptacles. (Editor)

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[2] *Receptaculis androgynis subclavatis subfastigiata-paniculatis, spinulosis, androgynis* means hermaphroditic receptacle nearly club-shaped, the branches bearing the receptacles fan-shaped or having branchlets in a tufted, loose cluster, with many small spines. (Editor)

Setchell (1935a), however, was of the opinion that both *S. gracile* Greville and *S. flexile* Greville are synonyms of *S. tenue* J. G. Agardh. We have studied a specimen under the collecting number Herklots 192 (studied and distributed by Setchell and now deposited at the Herbarium, British Museum [BM]) and have found both the male and the female elements in the same specimen. The latter have supraaxillary compressed female forked receptacles, dentate at the apices with leaf and vesicle structures, typically holozygocarpic, and the former have cylindrical, forked male receptacles with a few spines and pseudozygocarpic. Apparently J. G. Agardh and Grunow were correct in placing only *S. gracile* in synonymy with *S. tenue* J. G. Agardh. *S. flexile* with sharply dentate leaves appears to be more related to *S. angustifolium.* Setchell has only found the pseudozygocarpic male receptacles, which are not provided with spines, however, and on which basis he has placed the species group in the *Pseudozygocarpicae.* Having found typically holozygocarpic female receptacles, we have transferred the species group *Tenuia* back to the *Holozygocarpicae.*

Thus, 11 species of zygocarpic *Sargassum* have been accepted by Setchell. Although they are old species, clarification of their nature is difficult. Setchell has gone through the history of these species and classified their nature. We have been able to remove question marks from these species, namely *S. angustifolium* (Turner) C. A. Agardh, *S. carpophyllum* J. G. Agardh, and *S. tenue* J. G. Agardh. However, we must keep the question mark for *S. aemulum* Sonder because we are unable, so far, to see adequate collections of the species.

Studies on Chinese Zygocarpic *Sargassum* Since Setchell

Tseng and Lu (1978) published a zygocarpic *Sargassum* from Lingyangjiao of the Xisha Islands, namely, *S. tenerrimum* J. G. Agardh but with smaller leaves with conspicuous cryptostomata and distinct midrib, smaller vesicles and smaller receptacles toothed at the edges and apices. They also reported on the carpophyllous[3] nature of the receptacles of *S. polycystum*, which consequently is transferred to the *Zygocarpicae.* Later, Tseng and Lu (1979) published another carpophyllous *Sargassum*, namely *S. parvivesiculosum*, characterized by small vesicles with variously shaped earlike wings, by the prominently raised dark brown cryptostomata, and by the presence of carpophyllous toothed receptacles. In *Common Seaweeds of China* (Tseng 1983), Lu and Tseng (1983) illustrated 8 of the 11 zygocarpic species accepted by Setchell from Hong Kong and the three aforementioned species. Recently, Tseng and Lu (1987) have published three more new species of *Sargassum* namely *S. laxifolium, S. longifructum*, and *S. nozhouense*, all belonging to the *Zygocarpicae.* Thus, there are, at present, 17 species of *Sargassum* in China belonging to *Zygocarpicae.*

Key to Chinese Species of Zygocarpic *Sargassum*

1. Basal parts of main axes with elongated branched stolons . . . . *S. polycystum*
1. Basal parts of main axes without stolons 2
    2. Carpophyllous,[3] some receptacles giving rise to leaf or vesicle structures 3
    2. Pseudocarpophyllous,[4] receptacles intimately intermingled with leaf or vesicle structures 13

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[3] *Carpophylleae*, a series defined (as a tribe) by J. G. Agardh as meaning receptacles finally compound cymes, the cyme heteromorphic (of mixed branchlets), the receptacles often intermixed with leaves or with vesicles; single branches either rather terete, verrucose (lumpy) and with often without spines, or two-edged to angular, and dentate-serrate at the apex. (A cyme is formed by a broad cluster of branchlets, flattened across the top.) (Editor)

3. Receptacles malacocarpic[1] 4
3. Receptacles acanthocarpic[5] 6

4. Receptacles of two kinds, male and female separate . . . . *S. nozhouense*
4. Receptacles of one kind, androgynous 5

5. Leaves linear-lanceolate, to 5 cm long, 2 mm broad . . . . *S. angustifolium*
5. Leaves lanceolate, to 5 cm long, 6 mm broad . . . . *S. carpophyllum*

6. Receptacles one of a kind, androgynous 7
6. Receptacles of two kinds, male and female separate 11

7. Receptacles cylindrical, toothed . . . . *S. parvivesiculosum*
7. Receptacles compressed, two-edged or three-sided 8

8. Leaves smaller to 1 cm long and 2 mm broad . . . . *S. subtilissimum*
8. Leaves larger, more than 1.5 cm long 9

9. Leaves acute at the apices . . . . *S. aemulum*
9. Leaves obtuse to rounded at the apices 10

10. Leaves coarser, partially or completely lacking midribs . . . . *S. assimile*
10. Leaves thinner, with midrib disappearing below apices . . . . *S. tenerrimum*

11. Male receptacles very long, to 3–4 cm . . . . *S. longifructum*
11. Male receptacles much shorter 12

12. Leaves narrowly linear to lanceolate, to 5 cm long . . . . *S. tenue*
12. Leaves elliptic or obovate, to 2–3 cm long . . . . *S. laxifolium*

13. Receptacles malacocarpic[1] 14
13. Female receptacles acanthocarpic[5] 16

14. Mature receptacles in short cymose or racemose inflorescence . . . . *S. incanum*
14. Mature receptacles in long paniculate inflorescence 15

15. Leaves thicker, with cryptostomata . . . . *S. vachellianum*
15. Leaves thinner without cryptostomata . . . . *S. graminifolium*

16. Upper leaves almost without vein, lower leaves with vein vanishing below the middle . . . . *C. cinereum*
16. Leaves with vein midway to well above the middle . . . . *S. glaucescens*

Description of the Species

Sargassum aemulum Sonder (Fig. 1)

Sonder 1852, p. 672; Grunow 1915, p. 376; Setchell 1935a, p. 10, pl. 9, figs. 1–3; Pham-Hoang 1967, p. 287, fig. 10.

Synonym: *Sargassum cristatum* J. G. Agardh (J. G. Agardh 1889, p. 84, table 25).

This species was described by Sonder (1852) and was collected from Holdfast Bay, Australia, presumably by Ferdinand von Mueller. According to Sonder's description, the frond is 30 cm or more long, main axis short, cylindrical, about 2.5 cm long, and 2 mm thick. Primary branches compressed or flattened below, about 2 mm broad, slender and subangular above with cylindrical branches, branchlets 5–10 cm long. Leaves greenish-yellow, membranous, lanceolate, 3 cm long, 4 mm broad, acute at the apex, narrow at the base, slightly spiny, serrated on the margins, and with a double series of cryptostomata on

[4] *Pseudozygocarpicae*, a subsection of the section *Zygocarpicae* in which pedicels of receptacles are usually constant (present), whereas they may be absent in the subsection *Holozygocarpicae*; and in which receptacles are paired with leaves, or receptacles paired with vesicles, whereas in subsection *Holozygocarpicae*, compound receptacles may be paired with leaves only, or with both leaves and vesicles.

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[5] Acanthocarpic (after section *Acanthocarpicae*) in which (usually) branched receptacles are borne in the axils of vesicles or leaves and receptacles are usually spiny or dentate.

Fig. 1. ***Sargassum aemulum*** **Sonder.**

Fig. 2. ***Sargassum angustifolium*** **(Turner) C. Agardh.**

Fig. 3. ***Sargassum assimile*** **Harvey.**

Fig. 4. ***Sargassum carpophyllum*** **J. Agardh.**

each side of the midrib. Vesicles spherical, to about 4 mm in diameter, shortly pointed at the apex, and with a flattened pedicel about equal to its diameter in length.

Receptacles elliptical or oblong, pedicellate, flattened or rarely three-sided above, solitary or nearly forked, 4–5 mm long, 2 mm broad or more, with winged margins, the wings mostly duplicate dentate with the teeth acuminate, slightly spiny (After Setchell 1935a).

Although no plant of the Hong Kong assemblage seems to agree very closely with *S. aemulum* Sonder (in strictly typical form), one scrappy specimen, intermingled with other zygocarpic forms, collected at West Point, Victoria, Hong Kong Island, by G. A. C. Herklots in March 1930, seems to stand apart and to answer fairly well to the description of the "var.? *carpophylloides* Grun." of his *S. aemulum* (see Grunow 1915, p. 376). The axis, however, is smooth, but not always "zygocarpic" (Setchell 1935).

Distribution: Holdfast Bay, Australia (type locality), and China (Hong Kong).

Remarks: As we have stated before, we have not found this species ourselves, and we follow Grunow and Setchell in interpretation of this species.

Sargassum angustifolium (Turner) C. A. Agardh (Figs. 2, 18)

C. A. Agardh 1820, p. 32, 1824, p. 305; J. G. Agardh 1848, p. 309, 1889, p. 81, pl. 25, fig. 1; Kützing 1861, pl. 17, fig. 1; Grunow 1915, p. 365; Setchell 1935a, p. 3, pl. 1, figs. 1–4; Yamada 1942b, p. 19, pls. 12–13; Lu and Tseng 1983, p. 22, pl. 112, fig. 3.

Basionym: *Fucus angustifolius* Turner (Turner 1819, p. 35, pl. 212);

Synonyms: *Sargassum flexile* Greville (Greville 1849, p. 29, pl. 11, fig. 3); *Sargassum vulgare* var. *linearifolium non* J. Agardh (Yendo 1907, p. 145, pl. 17, fig. 5).

Fronds yellow-brown, about 50–80 cm high, slender with irregular branches. Main axes cylindrical, about 3–5 mm high, arising from discoid holdfasts and stout, giving rise to several primary branches. Primary branches cylindrical, smooth, slender, about 1 mm in diameter, giving off much more slender secondary branches, beset with branchlets. Basal leaves thickened, 3 cm long, 3–4 mm broad, with conspicuous percurrent midribs. Leaves of the branches linear-lanceolate, 4–5 cm long, 1.5–2 mm broad, shallowly dentate at the margins, midribs percurrent, cryptostomata very small, scattered on both sides of the midrib (vein). Leaves of the branchlets somewhat shorter and narrower, 3–4 cm long, 1–1.5 mm broad, or much narrower, with irregular short teeth at the margins. Vesicles nearly spherical, 2–3 mm in diameter, rounded at apices, pedicellate.

Plant androgynous. Receptacles cylindrical to fusiform, malacocarpic, usually forked two to three times, characteristically carpophyllous, the upper portion of the receptacles bearing leaflets or minute vesicles, solitary or two to three arranged in a short zigzag raceme.

Habitat: Drifted ashore, Hong Kong in January to March (Tseng 2613, McClure 21, 71a); on the lower intertidal and subtidal rocks, Hainan Island in June (Tseng 396); Nanao Island, Guangdong (AST 59-4234); Weizhou Island, Guangxi, in April (AST 55-1893).

Distribution: India (probable type locality; China (Hong Kong), and Japan.

Remarks: The type of *F. angustifolius* Turner has been examined by Setchell (1935a). We agree with his opinion (1935a, p. 5) that *S. angustifolium* is androgynous. As J. G. Agardh (1889) and Grunow (1915) have done, *S. flexile* is accepted as a synonym of the present species. We also agree with the monograph of Yendo (1907, p. 145, pl. 17, figs. 5a and 5b) that it may be identical with *S. angustifolium* (Turner) J. Agardh. The species may be readily recognized by its linear leaves and carpophyllous malacocarpic receptacles.

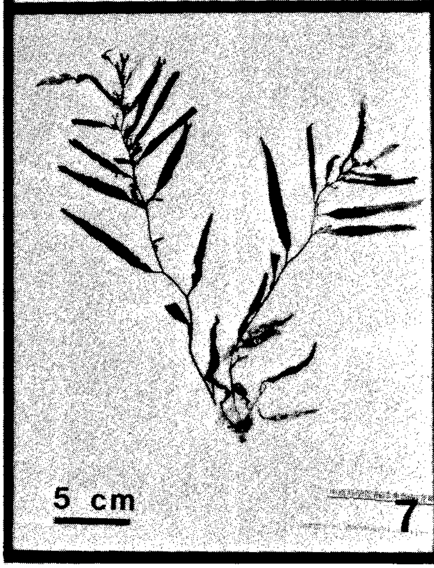

Fig. 5. *Sargassum cinereum* J. Agardh.
Fig. 6. *Sargassum glaucescens* J. Agardh.
Fig. 7. *Sargassum graminifolium* (Turner) J. Agardh.
Fig. 8. *Sargassum incanum* Grunow.

Sargassum assimile Harvey (Figs. 3, 21)

Harvey 1859, p. 328; De Toni 1895a, p. 39; Yendo 1905, p. 159, 1907, p. 141, pl. 17, figs 2 and 3; Grunow 1915, p. 371; Setchell 1935a, p. 9, pl. 7; Okamura 1936, p. 347; Pham-Hoang 1967, p. 290; Lu and Tseng 1983, p. 224, pl. 13, fig. 1.

Synonym: *Sargassum linifolium (non* Turner) (Cotton 1915, p. 110 [fide Setchell])

Fronds yellow-brown, about 70–80 cm in height, arising from small discs. Main axes terete, very short, bearing several primary branches, cylindrical, smooth, giving rise to several secondary branches in the leaf axils. Leaves on the primary branches oblong with strongly oblique cuneate bases, obtuse at the apices, sharply dentate at the margins, about 2–3 cm long, 4–5 mm broad, midrib delicate, vanishing below apices; leaves on the secondary branches oblong to slightly lanceolate, 1–2 cm long, 3–4 mm broad, midrib obscure, with short teeth at the margins, obtuse or rounded at the apices; cryptostomata small, scattered all over the leaves. Vesicles spherical, mucronate at apices, about 2–3 mm in diameter, on petioles compressed above.

Plants androgynous, receptacles foliiferous, two-sided to irregularly three-sided, 7–9 mm long, 0.8–1 mm broad, often several times furcate, dentate at margins, giving rise to small leaf or vesicle structures.

Habitat: Drifted ashore, Hong Kong in April to May (Tseng 2710, Tseng 2774, Tseng H-153).

Distribution: Japan (Ryukyus, type locality), China (Hong Kong), and Viet Nam.

Remarks: *S. assimile* is an Indo-west Pacific species so far distributed between perhaps Nagasaki, Japan, through the Ryukyu Islands and extending to the Hong Kong region and finally to Ceylon in the west. It is characterized by oblong leaves from a strongly cuneate base, partially without midrib above, and very obscure midrib vanishing below the apex on the lower leaves, and receptacles elongated and foliiferous, often forked, remotely dentate. Grunow divided it into seven varieties, all with a question mark. With the scanty amount of materials on hand, we are unable to set the limits of the so-called varieties.

Sargassum carpophyllum J. Agardh (Figs. 4, 19, 20)

J. G. Agardh 1848, p. 304, 1889, p. 82, pl. 25, fig. 2; Grunow 1888, p. 24, pl. 6, fig. 1, 1915, p. 366; Setchell 1935a, p. 7, pls. 3, 4, and 9, figs. 5–8; Durairatnam 1961, p. 41, pl. 8, figs. 4–7; Misra 1966, p. 173, fig. 91; Lu and Tseng 1983, p. 224, pl. 112, fig. 2.

Fronds yellow-brown, reaching a height of 80 cm and arising from discoid holdfasts. Main axis cylindrical, very short, 2–3 mm in height, and about 1 mm in diameter, bearing several smooth cylindrical, erect primary branches. Secondary branches beset with branchlets, cryptostomata on the branches and branchlets conspicuous but not projecting. Leaves of the primary and secondary branches lanceolate, acuminate, 2–5 cm long, 4–6 mm broad, shallowly toothed at the margins, midrib vanishing below the apices, and cryptostomata scattered on both sides of the midrib. Leaves of the branchlets with unequal bases and short stipes, narrowly linear-lanceolate, 1–2 cm long, 1–2 mm broad, irregularly dentate at the margins and with midribs. Vesicles spherical, 3–4 mm in diameter, rounded at the apices, on short cylindrical pedicels.

Receptacles subcylindrical or fusiform, malacocarpic, acute at the apices, usually forked two to three times, carpophyllous, solitary or two to three arranged in a short raceme. Androgynous with both oogonia and antheridia in the same conceptacle of the receptacle.

Habitat: Growing on subtidal rocks, Nozhou Island, Guangdong Province in May (AST 55-1753).

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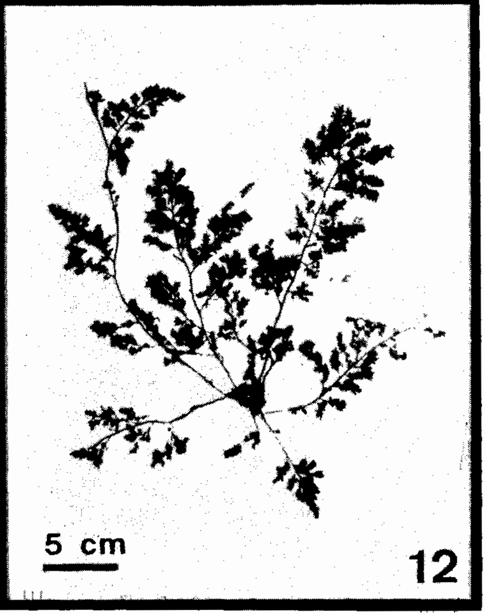

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Fig. 9. *Sargassum laxifolium* Tseng et Lu.
Fig. 10. *Sargassum longifructum* Tseng et Lu.
Fig. 11. *Sargassum nozhouense* Tseng et Lu.
Fig. 12. *Sargassum parvivesiculosum* Tseng et Lu.

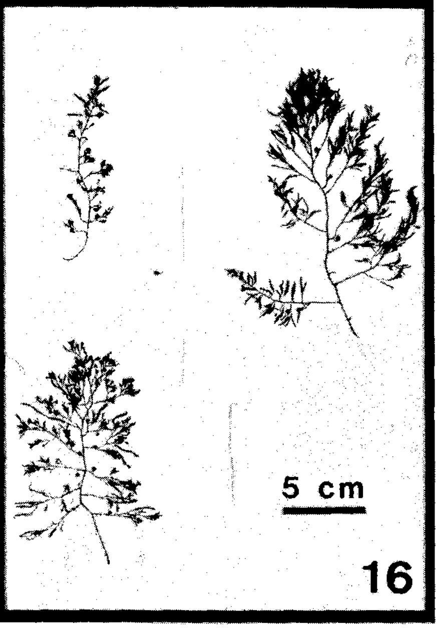


Fig. 13. *Sargassum polycystum* **C. Agardh.**
Fig. 14. *Sargassum subtilissimum* **Tseng et Lu.**
Fig. 15. *Sargassum tenerrimum* **J. Agardh.**
Fig. 16. *Sargassum tenue* **J. Agardh.**

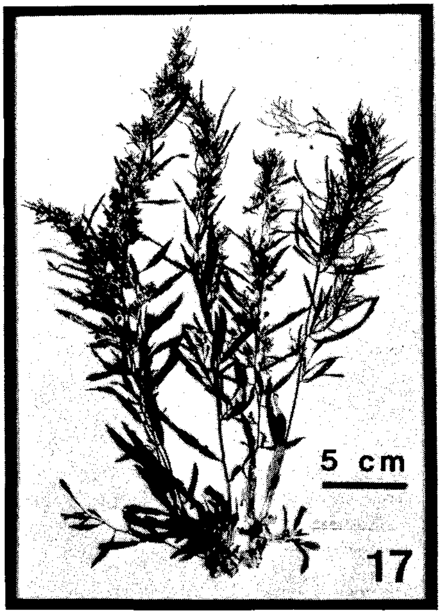


Fig. 17. ***Sargassum vachellianum*** **Greville.**

Distribution: Ceylon (type locality), China (Hong Kong, Nozhou Island), Taiwan, and India.

Remarks: Our specimen is coarser than those referred to as *S. angustifolium* (Turner) C. A. Agardh, with broader leaves, 2–5 cm long, 4–6 mm broad. This species can be recognized by its lanceolate leaves with carpophyllous malacocarpic receptacles. The plant assigned to it by Pham-Hoang (1967) definitely is not *S. carpophyllum* and is most probably *S. parvivesiculosum* Tseng et Lu (Tseng and Lu 1979) on the basis of the small vesicles with variously shaped earlike wings, without midrib or faintly veined leaves and the toothed receptacles (cf. fig. 9 of Pham-Hoang with fig. 4 of Tseng and Lu). Chou and Chiang (1981) reported *S. carpophyllum* J. G. Agardh from Taiwan; however, they mentioned that the plant is dioecious and the female plant has complanate receptacle with spines, which is not the case with *S. carpophyllum.* We are not sure, however, as to the identity of their plant.

Sargassum cinereum J. G. Agardh (Figs. 5, 33)

J. G. Agardh 1848, p. 305, 1889, p. 84; Grunow 1915, p. 378; Setchell 1935a, p. 14, pls. 10, 11; Durairatnam 1961, p. 141, pl. 8, figs. 1–3; Lu and Tseng 1983, p. 226, pl. 114, fig. 1.

Fronds slender, covered by an ashy-grey tinge. Main axes very short, bearing terete, smooth, primary branches at their upper parts. Secondary branches and branchlets similar to primary branches in habit. Basal leaves membranous, oblong, about 2.5–3 cm long, 7–8 mm broad, rounded at the apices, with midribs vanishing above the middle of the leaves, dentate at the margins. Leaves of the branchlets lanceolate, 2–2.5 cm long, 3–4 mm broad, cuneate at the base, somewhat truncate at the tips, midrib vanishing below apices of the leaves, margins wavy or entire, sometimes with a few coarse teeth,

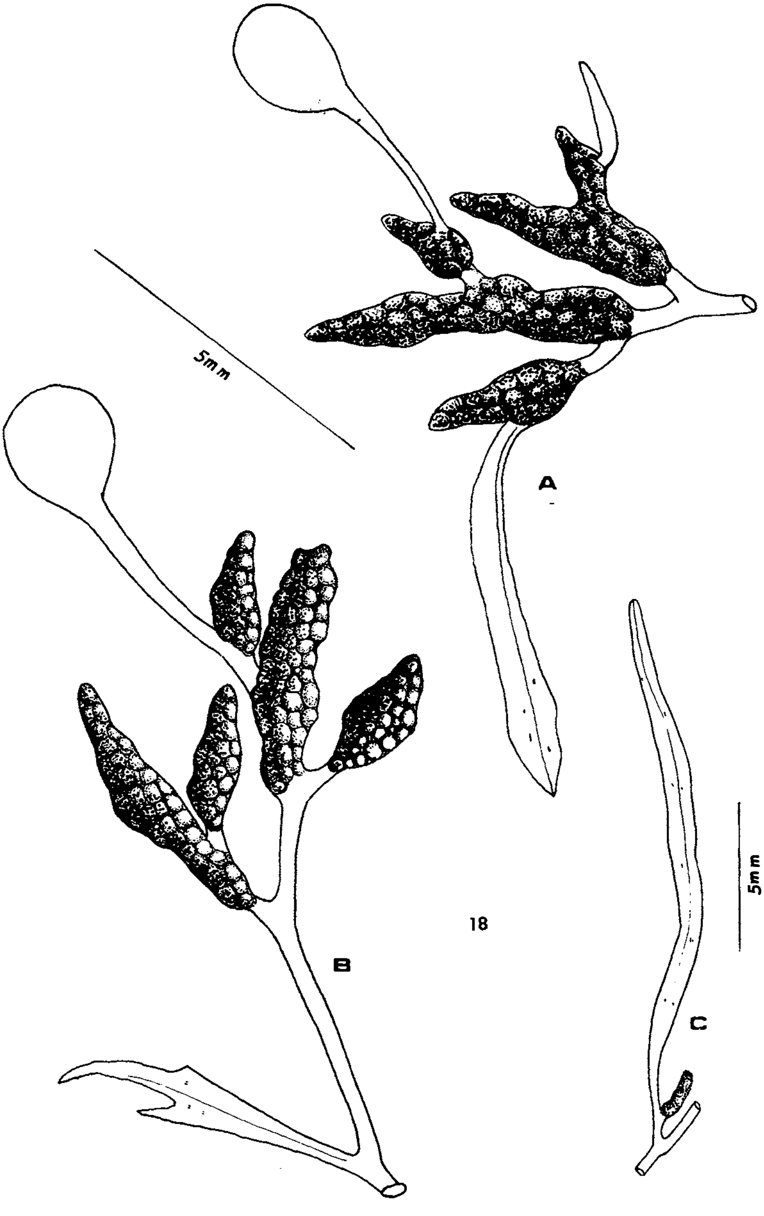


Fig. 18. ***Sargassum angustifolium*** **(Turner) C. Agardh.** ***A, B,*** **Upper portion of branch with leaf bearing androgynous receptacles with a leaf.** ***C,*** **Upper leaves.**

cryptostomata scattered along both sides of the vein. Vesicles spherical, about 4 mm in diameter, obovate, rounded, usually with a sharp tip, with pedicels foliaceous above, subcylindrical below.

Male receptacles cylindrical, with a few minute teeth, 8–10 mm long, 1 mm in diameter, single or two to three together in short, leafy, and vesiculiferous racemes.

Female receptacles are short, three-sided, coarsely dentate, single or two to three together in a short, leafy, and vesiculiferous raceme.

Habitat: Drifted ashore, Hong Kong in January (McClure 84, sterile), in March (Herklots 5, female young), in April (Tseng HK 154a, male); on rocks in lower intertidal region, Nozhou Island, Guangdong (AST 82-65 female).

Distribution: China (Hong Kong, type locality), Ceylon, and Australia.

Remarks: *S. cinereum* is a characteristically ashy-grey (cinerascent) plant and dioecious, with both male and female plants. Its oblong cuneate leaves have veins vanishing below the middle and upper leaves. It is principally a Chinese plant but is now also found in Ceylon and Australia.

Sargassum glaucescens J. G. Agardh (Figs. 6, 34)

J. G. Agardh 1848, p. 306, 1889, p. 84; Cotton 1915, p. 110; Grunow 1915, p. 379; Setchell 1935a, p. 16, pls. 13–15; Pham-Hoang 1967, p. 291, fig. 12; Tseng and Lu 1979, p. 3, pl. 2, fig. 2; Chou and Chiang 1981, p. 145; Lu and Tseng 1983, p. 228, pl. 115, fig. 2.

Synonyms: *Sargassum debile* Greville (Greville 1849, p. 276, pl. 5); and *Sargassum ornatum* Greville (Greville 1848, p. 205, pl. 4).

Fronds glaucescent, reaching a height of 50 cm or more, arising from discoid holdfasts. Main axes very short, cylindrical, smooth, about 4 mm long, 2.5 mm in diameter, giving rise to several primary branches, subcylindrical or compressed, about 2 mm in diameter. Secondary branches beset with short and slender branchlets. Leaves elongated-ellipsoid or elongated-lanceolate, to 18 mm long, 7 mm broad, apices blunt, bases cuneate with short stalks, conspicuously dentate at the margins, midrib vanishing below the apices, cryptostomata prominent on both sides of the midrib. Vesicles spherical, apices often with a sharp tip, 2–2.5 mm in diameter with cylindrical pedicels about 1 mm long.

Dioecious. Male receptacles cylindrical, smooth, unequally forked, apices acute. Female receptacles single or aggregated, about 3–5 mm long, flattened to three-sided, with sharp teeth at the margins and apices, both male and female receptacles often arranged in racemes, strictly pseudozygocarpic, receptacles often with leaf or vesicle structures intermingled below.

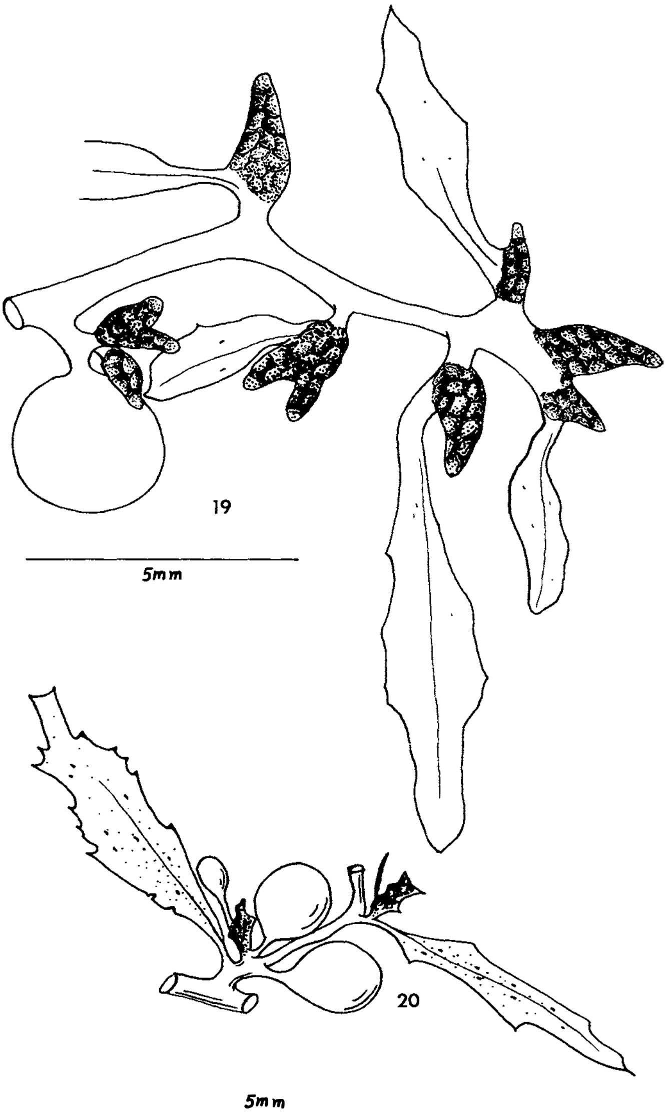
Habitat: Growing on subtidal rocks, Hainan Island in February to April (AST 73-505, AST 73-531, AST 76-156) and drifted ashore, Hong Kong in May (Tseng H 0636), and Xisha Islands in June (AST 75-1282).

Distribution: China (Macao, type locality; Hainan, Hong Kong, Xisha Islands), Taiwan, Viet Nam, and Singapore.

Remarks: In the discussion of the present species, four different names are to be considered: *S. glaucescens* J. G. Agardh (J. G. Agardh 1848), *S. debile* Greville and *S. ornatum* Greville (Greville 1849), and *Sargassum ivanii* Montagne (Kützing 1849). All the specimens come from Macao, and *S. glaucescens* has the priority. Grunow (1915) has differentiated three varieties. How different the varieties are from one another remains to be determined. For instance, the variety *ivanii* (Montagne) Grunow has typically elongated-lanceolate leaves, but the female plants have leaves of the typical form (var. *glaucescens*), whereas the male plants of the variety *ivanii* do not. *S. glaucescens* is distributed between Taiwan on the east to Viet Nam and Singapore on the west. Evidently sex and age may play an important role in the variation.

Sargassum graminifolium (Turner) J. G. Agardh (Figs. 7, 31)

J. G. Agardh 1848, p. 303, 1889, p. 81; Kützing 1849, p. 615, 1860, pl. 28, fig. 1; De



Figs. 19, 20. Fig. 19, *Sargassum carpophyllum* J. Agardh. A fertile branchlet bearing leaf, vesicles, and androgynous receptacles with a vesicle. Fig. 20, *Sargassum tenerrimum* J. Agardh. A fertile branchlet bearing leaf, vesicles, and androgynous receptacles with a vesicle.

Toni 1895a, p. 38; Grunow 1915, p. 365; Tseng 1933, p. 59; Setchell 1935a, p. 17, pl. 12, fig. 2, pl. 17; Okamura 1936, p. 346; Lu and Tseng 1983, p. 230, pl. 236, fig. 1.

Basionym: *Fucus graminifolius* Turner (Turner 1819, p. 32, pl. 210).

Fronds greenish or brown, 50 cm or more in height, attached to discoid holdfast. Main axes very short, terete, bearing several flattened, primary branches, about 40–50 cm high, 1–1.5 mm broad. Secondary branches irregularly and alternately arranged, bearing

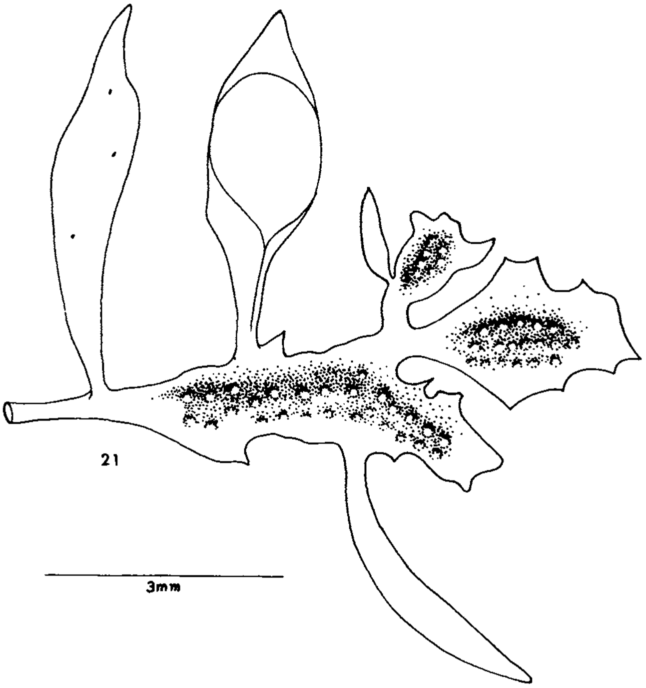


Fig. 21. *Sargassum assimile* Harvey. A two-sided androgynous receptacle with the vesicle and leaves.

short branchlets with membranous leaves without cryptostomata. Lower leaves lanceolate, 7–8 cm long or more, 8–11 mm broad with narrower cuneate bases and short pedicels, shallowly coarsely dentate at the margin, apices blunt, midrib distinct, upper leaves about similar length but much narrower, only 4–5 mm broad. Vesicles elliptical or obovate, 3–4 mm in diameter, on pedicels compressed above and subcylindrical below, sometimes arranged in pairs and with forked pedicels.

Plants dioecious, but of similar kind, all malacocarpic, terete, 8–10 mm long, 0.5–1 mm broad, variously branched, wartlike, fairly closely arranged in panicles, frequently intermingled with leaf or vesicle. Generally speaking, the male receptacles are very much elongated, whereas the female ones are much shorter.

Habitat: Growing on lower intertidal and subtidal rocks, Zhoushan Island in May to June (Tseng 1443, AST 56-1634, AST 63-4115), Xiangshan in June (AST 63-4312), Nanjidao in July (AST 63-4498), and Zhejiang and Taishan (Guangdong Province) in spring (AST 54-4402).

Distribution: Endemic in China (Zhejiang, Fujian, Guangdong, and Macao).

Remarks: The source of the type of *F. graminifolius* is unknown. It was, however, quite striking, with a color and substance like dried tea leaves that led Turner to describe it as a new species in spite of the fact that only a sterile fragment was available. The second specimen of this plant was that collected by G. von Martens in 1861; a photograph of that specimen was made by Setchell (Setchell 1935a, pl. 17) and for the first time an enlarged part of the receptacles was given (Setchell 1935a, pl. 12, fig. 2). That is all the information we have had on this plant. In fact, Yendo (1907) listed this plant in his

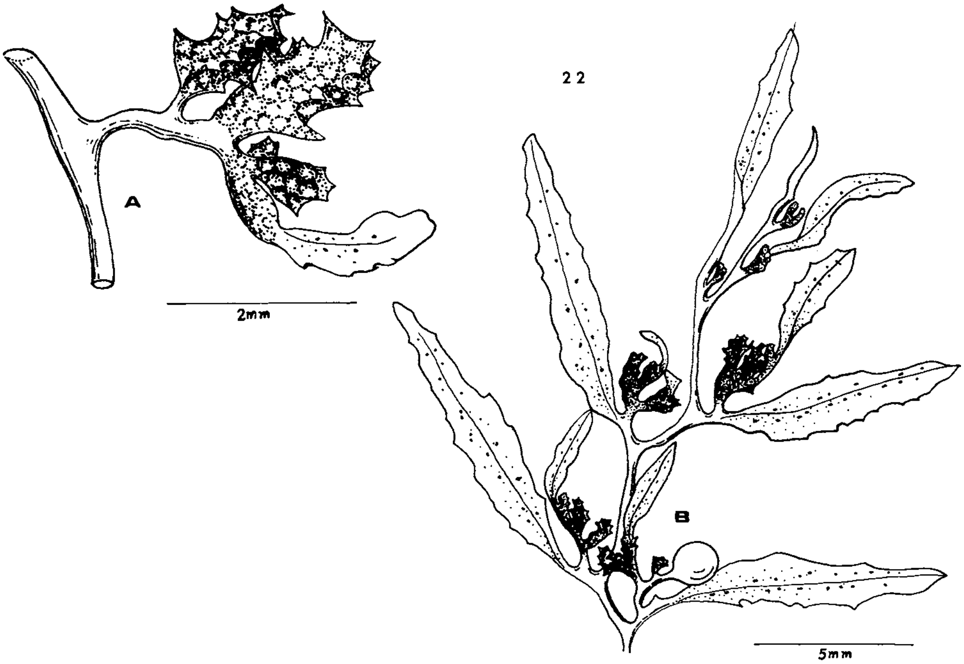


Fig. 22. *Sargassum subtilissimum* Tseng et Lu. *A,* Three-sided androgynous receptacles with a leaf. *B,* Fertile branchlet bearing leaves, vesicle, and androgynous receptacles with leaf. (After Tseng and Lu 1978)

monograph, and said he had several specimens in accord with the descriptions and figures of the aforenamed species but that he had not seen any reproductive organs. He did illustrate a fragment showing the receptacles, leaves, and vesicles. The illustration does not belong, however, to *S. graminifolium*, which is pseudozygocarpic instead of holozygocarpic as was shown. The inflorescence is definitely not that of *S. graminifolium.* The specimen of Martens, with only portions of branches, "has the compressed axes, the distant short branchlets of few leaves each, the occasional twin vesicles with forked pedicels, the leaves of proper shape, margins, petiole and costa, and devoid of cryptostomata" (Setchell 1935a, p. 18). Because of the scarcity of this species, the more common *S. vachellianum* has been taken by many authors to be synonymous with *S. graminifolium.* It was Setchell who visualized the difference between the two closely related but different species. He emphasized two factors: the twin vesicles and the leaves devoid of cryptostomata. We do have specimens with twin vesicles; these, however, are found also in *S. vachellianum.* The leaf characteristics are, however, quite constant (i.e., membranous, tea-leaf-colored leaves, devoid of cryptostomata) and may be relied upon for differentiating these two closely related species.

Sargassum incanum Grunow (Figs. 8, 30)

Grunow 1915, p. 379; Setchell 1935a, p. 15, pl. 1, figs. 5–9, pl. 2.

Fronds yellow-brown, cinereous (ashy), to about 20 cm long, main axes very short, cylindrical, about 3 mm long, arising from a discoid holdfast, and giving rise to several primary branches from its distal part. Primary branches compressed below, cylindrical above, smooth, 16–19 cm long, 1.5–2 mm in diameter; secondary branches shorter,

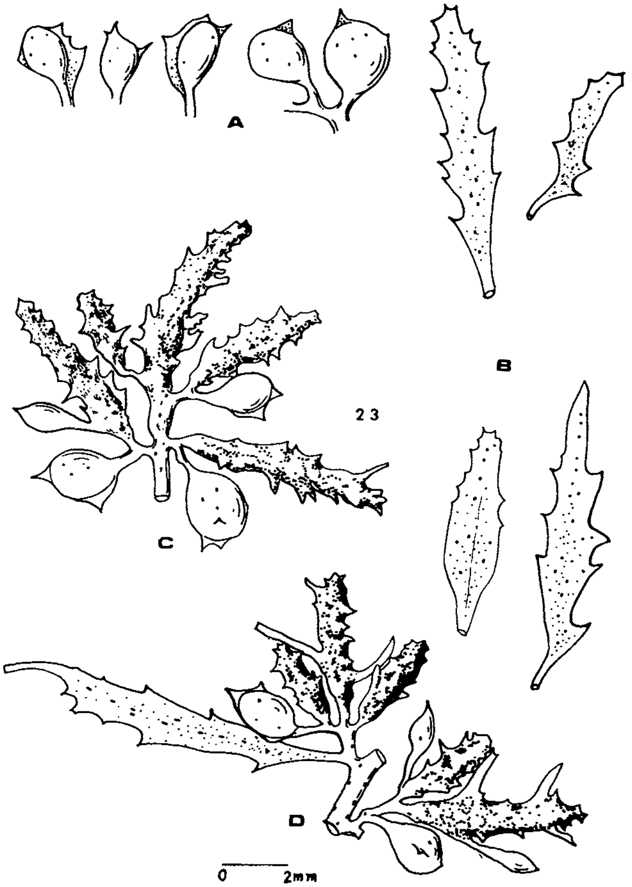


Fig. 23. ***Sargassum parvivesiculosum*** **Tseng et Lu.** ***A*, Vesicles. *B*, Leaves. *C, D*, Fertile branchlets bearing leaves, vesicles, and androgynous receptacles. (After Tseng and Lu 1979)**

cylindrical, smooth, beset with branchlets with dense leaves, vesicles, and receptacles. Lower leaves oblong-lanceolate 3–4.5 cm long, 8–10 mm broad, obtuse or acuminate at apex, wavy at the margin, midrib conspicuous; cryptostomata scattered in both sides of the midrib, base cuneate with subsessile or very short stipe. Upper leaves linear, 2.5–3 cm long, 1.5–2 mm broad, with coarse teeth at margin, obtuse or acute at apex, midrib conspicuous, percurrent, cryptostomata irregularly scattered in both sides of the vein. Vesicle spherical, 3–4 mm in diameter, smooth, rounded at apex, with a filiform stipe, 4–5 mm long.

Plants androgynous, receptacle fusiform, smooth, 2–3 mm long, 0.6–1 mm in diameter, usually branched in its upper part, solitary or two to three receptacles arranged in short raceme, the whole inflorescence often intermingled with leaf or vesicle below.

Habitat: Drifted ashore, Hong Kong in February (McClure 73, 83c) and June (Tseng 2639); on rocks in the lower intertidal region, Xuwen, Guangdong in March (AST 55-143, AST 55-1433a); Weizhou Island, Guangxi in November (AST 54-4412); Fungcheng, Guangxi in May (AST 55-2181).

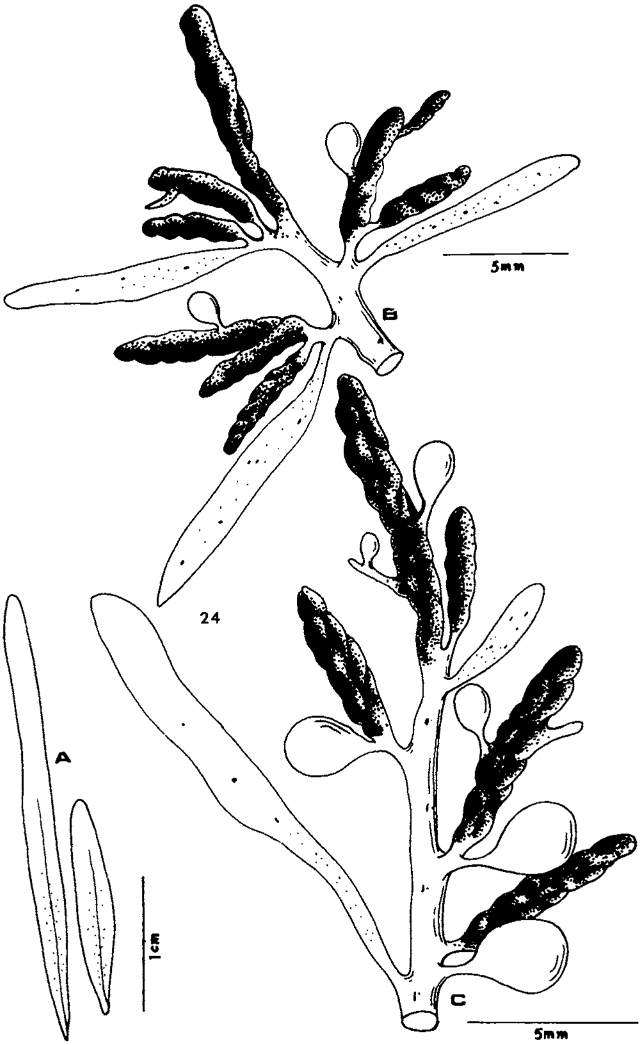


Fig. 24. ***Sargassum nozhouense*** **Tseng et Lu.** ***A*****, Basal leaves.** ***B*****, Fertile branchlet bearing female receptacles with vesicles.** ***C*****, Fertile branchlet bearing male receptacles with vesicle. (After Tseng and Lu 1987)**

Distribution: Endemic in China (Shanhai, Guangzhou, Hong Kong (type locality), Guangdong Province, and Guangxi Province).

Grunow (1915) separated this species from J. G. Agardh's *S. cinereum* because the upper leaves are less evidently cuneate, less oblique, and not larger toothed at the apex. Besides, the leaves are dentate with percurrent midrib. There seems to be no difficulty in separating these two species. Grunow (1915, p. 379) separated this from *S. cinereum* J. Agardh, apparently in the belief that the sexes were separate, since the ones seen were male. He concurrently reported a "var.? *ketelsii* Grun.," also from China, with small spiny female receptacles and slightly longer, spineless male receptacles. Although Setchell

Figs. 25, 26. Fig. 25, *Sargassum longifructum* Tseng et Lu. A fertile branchlet bearing leaf and forked male receptacles with vesicles. (After Tseng and Lu 1987). Fig. 26, *Sargassum polycystum*, male receptacles.

(1935a) correctly interpreted the nature of *S. incanum*, he stated, "The receptacles of *S. incanum*, however, are usually simple, less flattened, and are dioecious." As illustrated, (Setchell, 1935, pl. 1, figs. 5–9) the receptacles of Setchell's plant are malacocarpic, fusiform, sometimes forked, and arranged in short racemes. Undoubtedly Setchell also was influenced by Grunow's statement that it is dioecious. We have sectioned many receptacles of the various aforementioned members and found only one kind of receptacle, which is androgynous. If *S. incanum* Grunow is androgynous, how can we explain the variety *ketelsii* with spiny receptacles? The only explanation is that *ketelsii* is not *S. incanum* but perhaps a form of *S. cinereum* or an undescribed species.

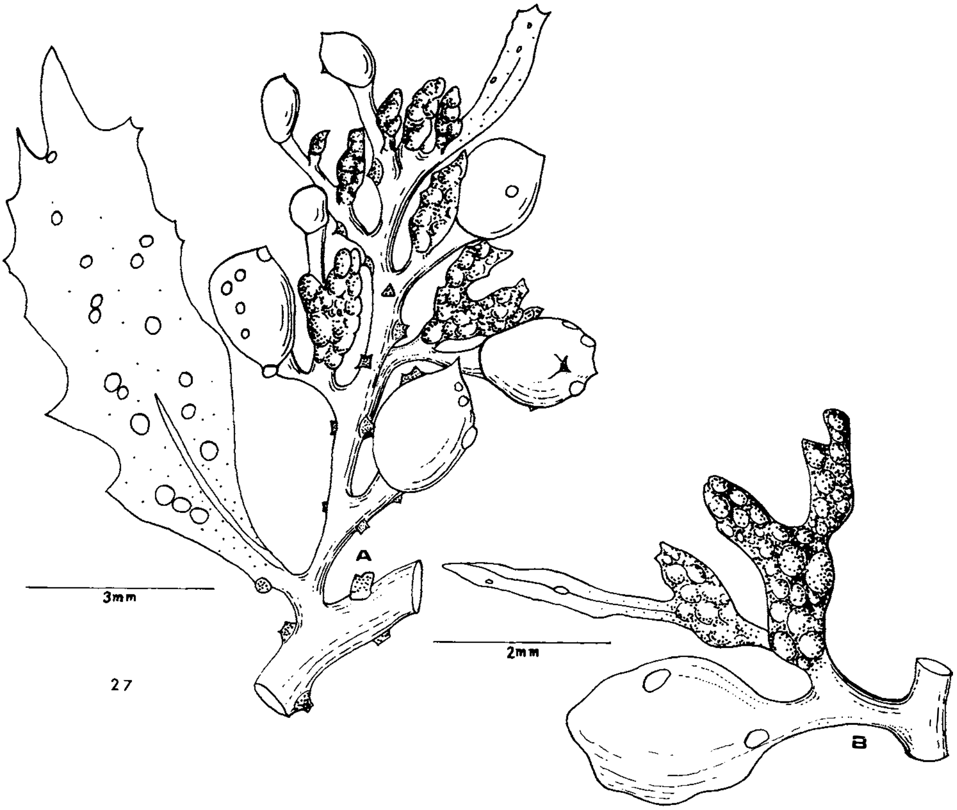


Fig. 27. *Sargassum polycystum* C. Agardh. *A*, Fertile branchlet with leaf, vesicles, and female receptacle. *B*, Vesicle and female receptacle with leaf. (After Tseng and Lu 1978) (See Fig. 8 for male receptacles.)

Sargassum laxifolium Tseng et Lu (Figs. 9, 29)
Tseng and Lu 1987 (in press).

Fronds slender, yellowish brown. Primary branches smooth, cylindrical, to about 70–75 cm high, 1 mm in diameter. Secondary branches similar to the primary branches in habit, to about 15–25 cm high, less than 1 mm in diameter, with fructiferous glanduliferous branchlets. Leaves on primary and secondary branches elliptic or obovate, to about 2–3 cm long, 10–15 mm broad, obtuse at the apex and oblique and asymmetrical at the base, dentate at the margin, with short stipe, indistinct midrib, usually vanishing below the middle parts or one-third of the leaves, and conspicuous cryptostomata scattered on the leaves. Leaves on the branchlets very similar to the ones on the primary branches in habit, elliptic, about 1.5–2 cm long, 5–10 mm broad, rounded at apex, dentate at margin, with a very oblique, asymmetrical base, without a midrib or faintly veined and with conspicuous cryptostomata scattered on the leaves. Vesicles spherical or ovate, 4–5 mm in diameter, with sharp tip, some with wings at margin on short stipes.

Plant dioecious. Female receptacles two- to three-sided, 2–3 mm long, 1–1.5 mm broad, usually branched once or twice with sharp teeth at the margin and apices, two or three arranged in short racemes on the basal part of foliar stipe or vesicle. Typically

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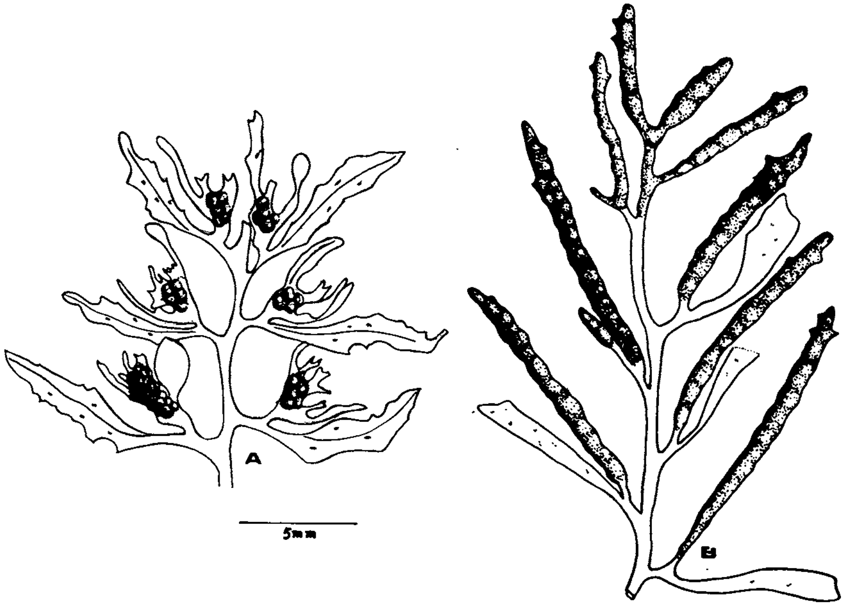

Fig. 28. ***Sargassum tenue*** **J. Agardh.** ***A*****, Fertile branch with leaves and flattened female receptacle.** ***B*****, Male receptacles.**

holozygocarpic, and with small leaves or vesicles immeditely arising from the female receptacles. Male receptacles not seen.

Habitat: Drifted ashore, Saiwan, Hong Kong in May (Tseng 2782).

Distribution: Endemic in China (Hong Kong, type locality).

Remarks: The present species is closely related to *S. assimile* Harvey, differing in its elliptic or obovate leaves, its midrib vanishing below the middle part, and its vesicle with cylindrical stipe.

Sargassum longifructum Tseng et Lu (Figs. 10, 25)

Tseng and Lu 1987 (in press).

Fronds of medium size, yellow-brown. Main axis short, cylindrical, smooth, to about 6 mm high, 1.5 mm in diameter. Primary branches arising from the distal part of the axis, cylindrical, smooth, to 39 cm high, about 1 mm in diameter. Secondary branches slender and short, to about 10 cm high, beset with small filiform fructiferous branchlets with dense leaves, vesicles, and receptacles. Basal leaves membranous, lanceolate, with entire or somewhat undulate margin, to 6 cm long, 7 mm broad, acuminate at the apex, with oblique asymmetric base, percurrent vein, and obscure cryptostomata. Leaves on branches and branchlets thinner, narrow lanceolate, with denticulate margin 2–3 cm long, 1–2 mm broad, acuminate at the apex, oblique cuneate at the base, with a filiform short stipe, midrib percurrent vanishing below the apex, cryptostomata scattered on both sides of the costa. Vesicle spherical or ovate, 1–2 mm in diameter, rounded or apiculate at the apex, with cryptostomata and a filiform stipe, 3–4 mm long, a few vesicles with flat foliaceous stipes.

Plant dioecious. Male receptacles slender, malacocarpic, giving rise to leaf or vesicle structures, usually branching once or twice, about 3–4 cm long, 1 mm in diameter, solitary

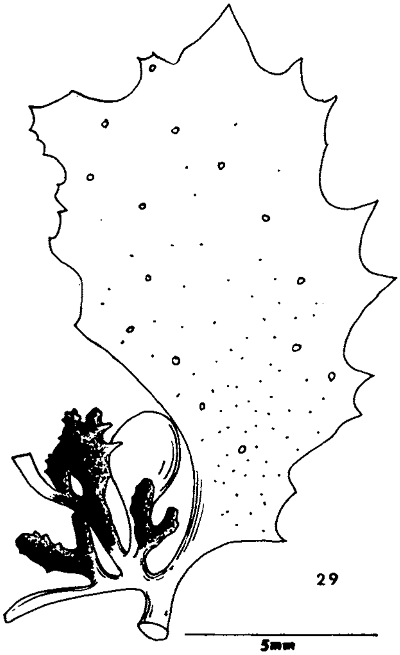

Fig. 29. *Sargassum laxifolium* Tseng et Lu. A fertile branchlet bearing leaf, vesicle, and female receptacle with a leaf. (After Tseng and Lu 1987)

or in short racemes of two or three in axil of the leaflets. Female plant not found. Holdfast lacking.

Habitat: Drifted ashore, Nozhou Island, Guangdong in April (AST 55-1767, male).

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

Remarks: The present species is characterized by its slender, branched, and elongated male receptacle, 3–4 cm long and 1 mm in diameter. Such an elongated receptacle is rather unique in the section *Zygocarpicae*. The female plant has yet to be discovered; it may be malacocarpic like *Sargassum nozhouense* or acanthocarpic like *Sargassum tenue*.

Sargassum nozhouense Tseng et Lu (Figs. 11, 24)

Tseng and Lu 1987 (in press).

Fronds slender, medium size, to about 60 cm high, arising from a discoid holdfast. Main axis short, cylindrical, smooth, about 5 mm high, 2 mm in diameter. Primary branches cylindrical, smooth, about 60 cm high, 1–1.5 mm in diameter. Secondary branches with dense leaves, vesicles, and receptacles. Some dark glandular dots on branches and branchlets, easily visible in fresh specimens. Basal leaves membranous, narrow-lanceolate, margin entire, obtuse at apices, to 2–3 cm long, 2–3 mm broad, base of the leaf cuneate with a cylindrical stipe and obscure midrib vanishing below the middle of the leaf. Cryptostomata rare, irregularly scattered on surface of the leaves. Leaves on both branches and branchlets linear, margin entire, without midrib, to 10–15 mm long, to 1–2 mm broad, with a filiform short stipe, and a few scattered cryptostomata, with a cylindrical stipe to about 1 mm long.

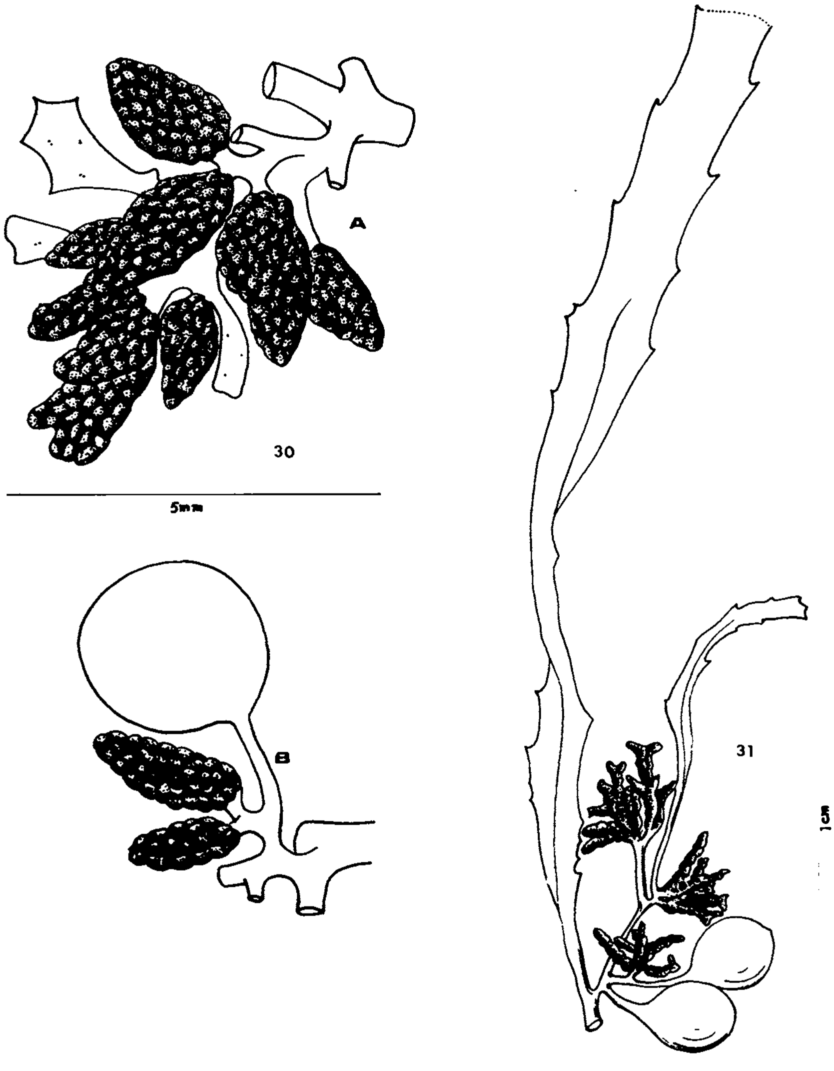

Fig. 30, 31. Fig. 30, *Sargassum incanum* Grunow (upper and lower figures to the right). *A, B*, Fertile branchlets with leaf, vesicle and androgynous receptacles. Fig. 31, *Sargassum graminifolium* (Turner) J. Agardh (figure on left). A fertile branchlet with leaf, vesicle, and androgynous receptacles.

Plants dioecious. Female and male receptacles terete, with short stipes tapering towards the apices, single or branched once or twice, solitary or in short racemes of two or three in axils of leaves, male receptacles 4–5 mm long, 0.2–0.4 mm in diameter, female ones 3–4 mm long, 0.3–0.5 mm in diameter. Carpophyllous, the leaflets or vesicle immediately arising from the receptacles (this characteristic is more common in the female plant than in the male plant).

Habitat: Growing on the lower intertidal and subtidal rocks, Nozhou Island, Guangdong in May (AST 73-536).

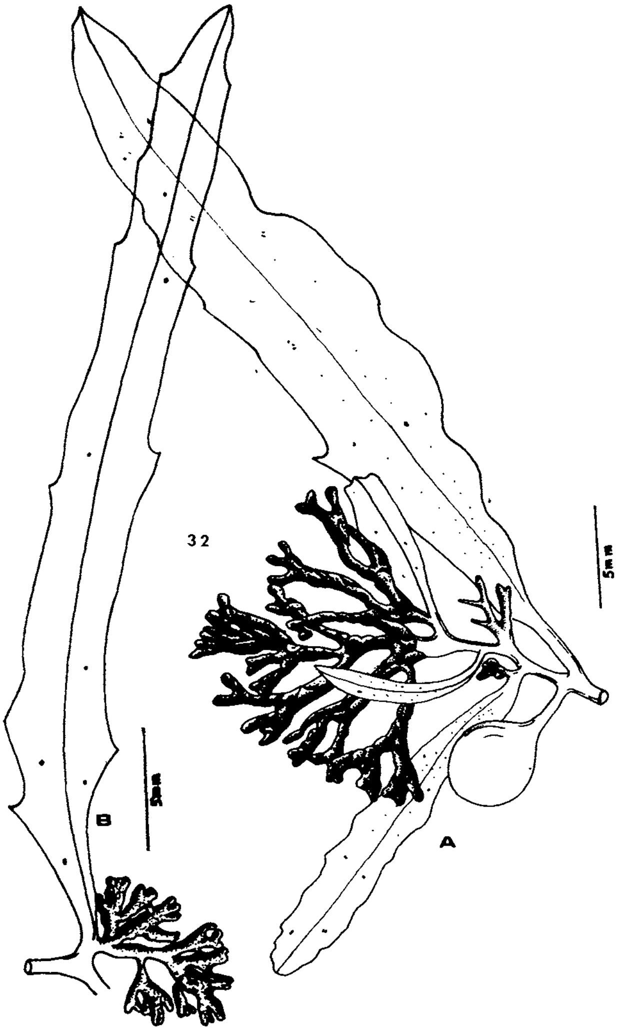

Fig. 32. ***Sargassum vachellianum*** **Greville.** ***A*****, A fertile branchlet with leaves, vesicle, and male receptacle.** ***B*****, Female receptacles.**

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

Remarks: This species is related to *S. carpophyllum* J. Agardh, which is androgynous, differing, besides its separated sexes, also in its thicker, smaller narrow-lanceolate leaves with entire margin, without midribs except for some of the basal leaves, obtuse at the apices and in its vesicles rounded at apices. It is, so far, the only malacocarpic *Sargassum* within the *Holozygocarpicae*.

Sargassum parvivesiculosum Tseng et Lu (Figs. 12, 23)

Tseng and Lu 1979, p. 5, pl. 5, fig. 4.

Synonym: *Sargassum carpophyllum (non* J. Agardh) (Pham-Hoang 1967, p. 284, fig. 9).

Fronds yellow-brown, holdfasts scutate, discoid, attaining a height of 30–50 cm or more. Main axes terete, smooth, very short, about 2–4 mm long, 1.5–2 mm in diameter, several primary branches arising alternately from their upper parts. Primary branches cylindrical to slightly compressed with prominent, dark cryptostomata, irregularly scattered on the surface. Secondary branches alternately arranged, beset with branchlets with dense leaves, vesicles, and receptacles. Basal leaves usually elongated, elliptic, 1–1.5 cm long, 2–3 mm broad, with toothed margins and cuneated bases, obtuse at the apices, midrib very inconspicuous. Middle and upper leaves asymmetrical, 6–10 mm long, 0.5–1.5 mm broad, usually eight to 10 times as broad as long, with irregular sharp serate margins, unequal base, without midribs. Cryptostomata conspicuously raised, dark, scattered all over the surface of the leaves. Vesicles very small, ovate, with a sharp tip when young, but obovate, rounded at the apices, with earlike wings on both sides of the vesicles and short pedicels when older.

Monoecious, with compressed, wartlike structures, about 1–2 mm long, 0.2–0.3 mm broad, with very short pedicels. Receptacles androgynous, with antheridia aggregated in the upper parts and oogonia in the lower ones.

Habitat: Drifted ashore, Zhongjiandao in May (AST 75-1300) and Guangjindao in May (AST 75-1305c), Xisha Islands, China.

Distribution: Endemic in China (Xisha Islands).

Remarks: In the Agardhian system, this species is a member of *Tenerrima* group of the series *Carpophylleae*, characterized by its small vesicles with variously shaped earlike wings, by its prominently raised, dark-brown cryptostomata, and by the receptacles compressed with teeth or spine usually immediately growing out to form a small leaf or vesicle. This is quite unique in the *Tenerrima* group.

Sargassum polycystum C. Agardh (Figs. 13, 26, 27)

C. A. Agardh 1824, p. 304; J. G. Agardh 1848, p. 310, 1889, p. 119; Grunow 1915, p. 444; Reinbold 1913, p. 169; Setchell 1935b, p. 266; Yamada 1942a, p. 376, figs. 5, 6, 1950, p. 193; Tseng et al. 1962, p. 92, pl. 5, fig. 36; Pham-Hoang 1967, p. 306, fig. 21; Tseng and Lu 1978, p. 6, pl. 4, fig. 6; Chou and Chiang 1981, p. 134, pl. 2, figs. 1–2; Lu and Tseng 1983, p. 236, pl. 119, fig. 1.

Synonyms: *Sargassum brevifolium* Greville (Greville 1849, p. 108, pl. 4; *Sargassum pygmaeum* (Kützing) 1861, pl. 15; *Sargassum microphyllum (non* C. Agardh) (Yendo 1907, p. 137; Okamura 1931, p. 108; Yamada 1925, p. 247); *Sargassum ambiguum* Sonder (Sonder 1871, p. 41).

Fronds yellow-brown, about 60–100 cm high. Main axes cylindrical 5–11 mm high, 2 mm in diameter, with wartlike processes, giving rise to several erect primary branches and descending to several elongated branched stolons. Primary branches terete, 1.5–2 mm in diameter, 40–60 cm long. Secondary branches beset with small fructiferous branchlets. Both primary and secondary branches and branchlets conspicuously provided with many dark short processes. Leaves on primary branches ovate, oblong, midribs often percurrent, 2–4 cm long, 8–12 mm broad, dentate at the margins. Leaves of branchlets smaller, narrow-lanceolate, 10–12 mm long, 2–3 mm wide, dentate at margins, midrib usually vanishing below the apices of leaves, which are rounded at the tips. Cryptostomata prominently raised, irregularly scattered on both sides of the veins. Vesicles small, ovate, 1.5–2 mm in diameter, usually crowned with a leaflet or a sharp tip, with raised processes scattered on the surface of the vesicles.

Dioecious; male receptacle cylindrical, malacocarpic, branched one or two times, 3–5 mm long, 0.5–0.6 mm in diameter. Female receptacle fusiform, compressed, often forked, toothed at apex, 1–2.5 mm long, 0.2–0.4 mm in diameter, sometimes bearing small leaflets or vesicles, solitary or arranged in racemes.

Habitat: Growing on the lower intertidal and subtidal rocks. Hainan Island in February to June (AST 55-668, AST 55-726, AST 58-5020, AST 73-368, AST 76-301, AST 80-2032, AST 82-73) and Xisha Islands in January to June (AST 57-5001, AST 57-5482, AST 58-4063, AST 76-422, AST 76-118, AST 80-699).

Distribution: Indonesia (Sunda Island, type locality), Micronesia, Philippines, Singapore, Australia, Japan, China, Sri Lanka, and India.

Remarks: The present species is easily recognized by the presence of stolons from the lower parts of the main axis, which is quite unique among the *Sargassum*. This is the first time that the carpophyllous nature of the female receptacles of this plant has been noted. It is placed within the *Holozygocarpicae* with smooth receptacles.

Sargassum subtilissimum Tseng et Lu (Figs. 14, 22)

Tseng and Lu 1978, p. 2, pl. 1, figs. 1–2.

Fronds yellow-brown, slender about 70–80 cm high. Main axes very short and small, cylindrical, about 4–5 mm long, 1–2 mm in diameter, giving rise to several smooth primary branches, more or less compressed below, about 1 mm broad, cylindrical upwards, with alternately arranged secondary branches. Branchlets short, copiously provided with leaves, vesicles, and receptacles. Leaves membranous, thin, lanceolate, 2 mm broad, 10–15 mm long, slightly acute or blunt at the apices, midrib conspicuous, often percurrent, cryptostomata conspicuous, in series arranged on both sides of the vein, their margins shallowly dentate. Vesicles spherical, subspherical, or ovate, 1–2 mm or more in diameter, usually rounded at the apices, but sometimes with wings on both sides, petioles cylindrical, somewhat flattened above.

Receptacles androgynous, bearing small leaflets or vesicles, compressed, or three-sided, toothed at the edges, teeth sometimes becoming broadly winglike, simple or forked, 1–1.5 mm long with short stipe, solitary or arranged in racemes.

Habitat: Drifted ashore, Lingyangjiao, Xisha Islands in May (AST 75-1189).

Distribution: Endemic in China (Xisha Islands).

Remarks: *Sargassum subtilissimum* Tseng et Lu is a very slender species, apparently closely related to *S. tenerrimum* J. G. Agardh originally described from Bombay, India, and later reported from Hong Kong on the South China coast. This species is characterized by the slender frond with thin leaves and by the frequent occurrence of the carpophyllous receptacles, as in the case of the Bombay plant. It differs from the Bombay plant, *S. tenerrimum* J. G. Agardh, by having (1) smaller leaves, generally about 1 cm long and 2 mm broad, with conspicuous cryptostomata, and distinct midrib, some even percurrent; (2) smaller vesicles, generally 1–2 mm in diameter, with cryptostomata and blunt at the apices; and (3) smaller receptacles, 1–2.5 mm long, more often three-sided, sometimes compressed, and toothed at the edges and the apices, the teeth sometimes becoming broadly winglike.

Sargassum tenerrimum J. G. Agardh (Figs. 15, 20)

J. G. Agardh 1848, p. 305, 1889, p. 83; Kützing 1849, p. 626; Grunow 1915, p. 370; Børgesen 1933, p. 10, pl. 2, fig. 6, 1935, p. 40; Setchell 1935a, p. 8, figs. 5–6; Durairatnam 1961, p. 42, figs. 8–10; Misra 1966, p. 174, fig. 92; Pham-Hoang 1967, p. 288, fig. 11; Lu and Tseng 1983, p. 238, pl. 120, fig. 2.

Synonym: *Sargassum campbellianum* Greville (Greville 1848, p. 274, pl. 5).

Fronds greenish-brown, slender and soft, about 30–50 cm high, arising from small conical discs. Main axes terete, very short, 5 mm high, about 1 mm in diameter, with irregularly and alternately branched primary branches. Primary branches cylindrical, very smooth, beset with similar branches and branchlets. Lower leaves oblong-lanceolate, about 6–7 cm long, 12–15 mm broad, upper ones gradually smaller upwards, linear-lanceolate, each with narrow rounded apex, elongated cuneate base, and short stipe, irregularly sinuate-dentate at the margins, very thin, translucent, midrib very delicate, disappearing below apex, cryptostomata scattered about, 3–4 mm in diameter, on short pedicels, often possessing a sharp point, or crowned with a leaf.

Plants androgynous, receptacles verrucose, two-edged to three-sided, 2–3 mm long, usually bearing small leaflets or vesicles, with teeth at the apices, repeatedly forked and becoming racemes.

Habitat: Growing on subtidal rocks, Hainan Island in March (AST 76-171, 79-189), Weizhou Island, Guangxi, in May (AST 78-018), and Hong Kong in May (Tseng H-063c).

Distribution: India (Bombay, type locality), Ceylon, China (Hong Kong, Hainan Island, and Guangxi), and Viet Nam.

Remarks: We have carefully compared our plants with a specimen of *S. tenerrimum* J. G. Agardh collected from its type locality—Bombay, India—by the late F. Børgesen; the plants agree with each other fairly well, except that our specimens are younger with smaller receptacles. This seaweed may be recognized by its slender, soft leaves with two- to three-sided receptacles with teeth at the apices.

Sargassum tenue J. G. Agardh (Figs. 16, 28)

J. G. Agardh 1848, p. 303, 1889, p. 84; Grunow 1915, p. 372; Setchell 1935a, p. 12, pl. 9, figs. 4, 6, 7.

Synonym: *Sargassum gracile* Greville (Greville 1849, p. 504, pl. 11).

Fronds yellow-brown, 30–40 cm high. Primary branches filiform, cylindrical, and slender, about 30 cm or more long, alternately branched throughout their entire length, giving a pyramidal outline. Upper leaves narrowly linear to lanceolate, entire or distinctly dentate, 2–3.5 cm long, about 1 mm broad, sharply attenuate at both ends, midrib not very distinct, vanishing below the apices, cryptostomata uniseriate on both sides of the indistinct vein. Stipe slender. Vesicle spherical with cryptostomata, 2–2.5 mm in diameter, apiculate, sometimes with a leaf at apices.

Plant dioecious. Male receptacle cylindrical, 9–10 mm long, 0.4–0.5 mm in diameter, branched once or twice, with a few spinnules above. Female receptacle two-sided when mature, dentate at the apices, branched once or twice, often forked at the tip, 5–7 mm long, 1–2 mm wide, solitary or two to five arranged in short racemes, giving rise directly to leaf or vesicle structures. Main axes and holdfast lacking.

Habitat: Drifted ashore, Hong Kong in May (Herklots 192).

Distribution: India (type locality) and China (Hong Kong).

Remarks: *Sargassum tenue* J. G. Agardh is a species credited with seven varieties by Grunow (1915). With the small amount of materials available, it is difficult to make any comment, but we do doubt very much whether all these varieties belong to the same species. For instance, we cannot see the reason for recognizing *S. tenue* var. *gobonensis* Grunow (*S. tenue* Kützing, as illustrated in Tab. Phyc. vol. X, pl. 7, fig. 2), and *S. tenue* var.? *capillaris* (Kützing) Grunow (*S. capillaris* Kützing in Tab. Phyc. vol. xvi, pl. 2). *S. gracile* Greville is characterized by very narrow linear leaves with female receptacles shortly cuneate with apices conspicuously dentate. The difficulty in interpreting this species is that the only illustration of the female by Greville (1849) is definitely too exaggerated, and the only illustration of the male receptacle by Setchell (1935a) is too young. We have made a careful study of "Herklots 192," which was determined by

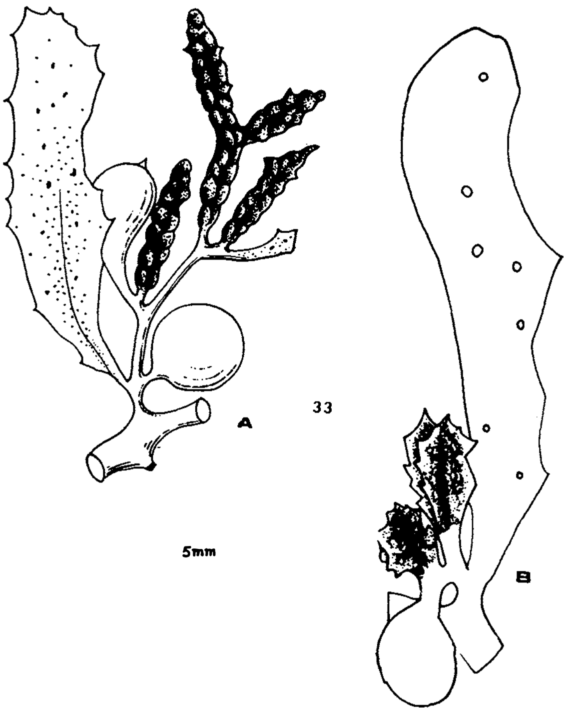

Fig. 33. ***Sargassum cinereum*** **J. Agardh.** ***A*****, Fertile branchlet with leaf, vesicle, and male receptacle.** ***B*****, Female receptacles.**

Setchell to be *S. tenue* J. Agardh. We agree with Setchell's interpretation of the species, but Setchell dealt only with a very young specimen of the male plant and had no female ones. We are fortunate to have found both male and female plants in the same specimen and have illustrated the characteristic of the species. *S. tenue* J. G. Agardh is easily recognized by its leaves, which are generally very narrow, similar to those of *S. angustifolium*; by its female receptacles, which are typically holozygocarpic and dentate at the apices; and by its rather elongated and cylindrical male receptacle with a few spines.

Sargassum flexile Greville has been considered a synonym of the present species by Setchell (1935a), whereas J. G. Agardh and others prefer to treat it as a synonym of *S. angustifolium* (Turner) C. Agardh. We agree with the latter opinion because the leaves in *S. flexile* are too closely dentate, and the receptacles are somewhat different in shape.

Sargassum vachellianum Greville (Figs. 16, 32)

Greville 1848, p. 204, pl. 4; Setchell 1935a, p. 19, pl. 16; Tseng et al. 1962, p. 91, pl. 5; Lu and Tseng 1983, p. 240, pl. 121, fig. 1.

Fronds dark-brown, coarse, attaining a height of 80 cm or more. Main axes arising from the scutate, conical discoid holdfast. Main axes very short, about 1.5–2 cm long, cylindrical, with many scars, giving rise to several primary branches from their upper portions. Primary branches flattened, 50–80 cm or more long, 1.5–2 mm wide. Secondary branches from both sides of the primary branches and beset with many branchlets. Lower leaves elongatedly lanceolate, 6–8 cm long, about 6–8 mm broad, entire or with a few shallow teeth at the margins. Leaves on secondary branches

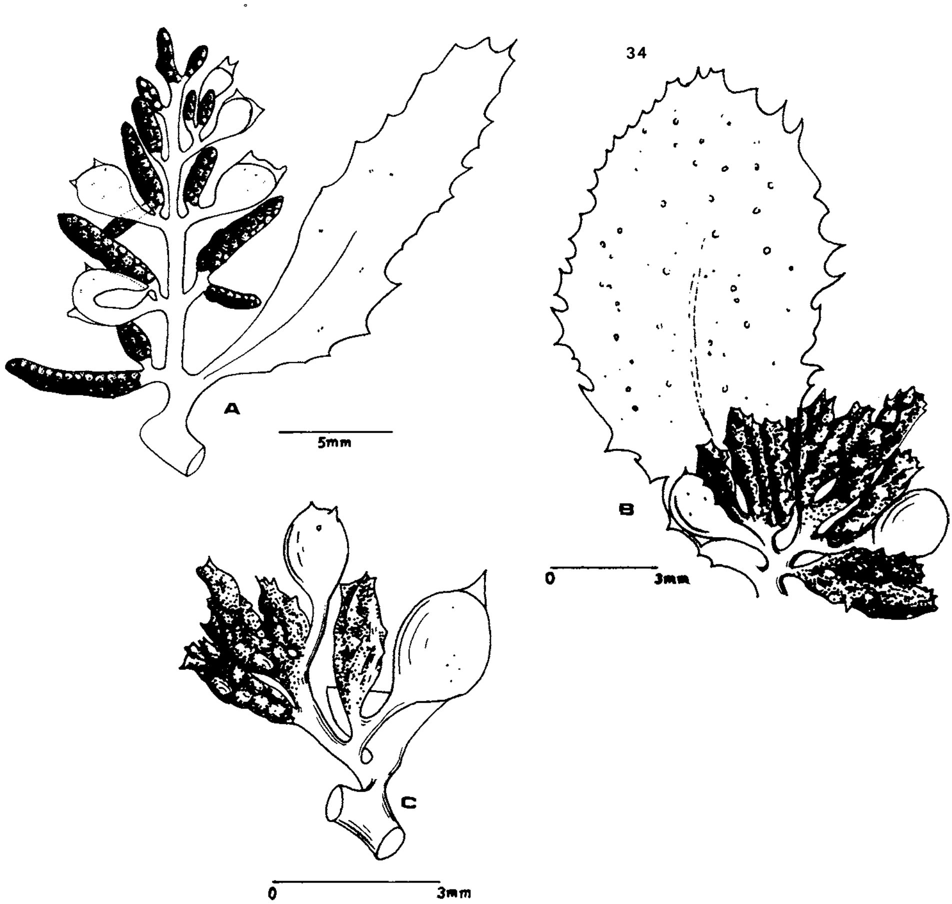

Fig. 34. ***Sargassum glaucescens*** **J. Agardh.** ***A*****, A fertile branchlet with leaves, vesicles, and male receptacles.** ***B, C*****, Three-sided female receptacles, vesicle, and leaf. (B and C after Tseng and Lu 1987)**

acuminate with oblique bases, about 4–6 cm long, 3–6 mm wide, with teeth at the margins, midrib distinct, percurrent, cryptostomata very abundant, scattered in several series over two sides of the midrib. Vesicles usually spherical, about 5 mm in diameter, on cylindrical, sometimes foliaceous pedicels.

Plants dioecious. There is no morphological difference between male and female plants. The inflorescences are typically paniculate, but the male receptacles are larger and longer, and the female receptacles smaller and shorter and also much darker in color. They are all cylindrical, bifurcate, 0.5–1 mm in diameter, often with short leaves and vesicles intermingled below.

Habitat: Growing on lower intertidal and subtidal regions, Nanjidao and Beijidao, Zhejiang, in July (AST 63-4325, AST 59-3374), Pingtan and Huian, Fujian, in June (AST 82-490, AST 64-410), Nozhou, Guangdong in May (AST 73-590, AST 82-87, AST 86-1235), and Shangchuandao, Guangdong in January to February (AST 55-1027, AST 60-3592); drifted ashore, Hong Kong in November (McClure A 626, Tseng 2794).

Distribution: Endemic to China (Macao, type locality, Zhejiang, Fujian, Guangdong, and Hong Kong).

Remarks: *Sargassum vachellianum* Greville is a common plant on the China coast between Zhejiang in the north and Guangxi in the west, and to date, its distribution has been confined to China. It has been many years since *S. vachellianum* Greville was made synonym of the earlier published *S. graminifolium* (Turner) J. Agardh. It was not until Setchell (1935a) pointed out the differences between the two species that *S. vachellianum* finally came out of its fate as a synonym, and it is now enjoying an independent status. *Sargassum vachellianum* is, in general, a more ample plant with thicker leaves and abundant cryptostomata on the leaves and more ample receptacular structures.

Systematic Arrangement for the Chinese Species of *Zygocarpicae*

Altogether 17 species of zygocarpic *Sargassum* have been reported so far from China. For the systematic arrangement of the section *Zygocarpicae*, Setchell (1936) divided it into two subsections: *Holozygocarpicae* and *Pseudozygocarpicae*. Although Setchell has differentiated two subsections, he still kept a single tribe for both subsections, namely *Carpophylleae* J. Agardh, which is divided into five species groups. We are making a small modification of Setchell's system for the arrangement of the species with the following changes:

1. Establish a species group *Longifructa* to take care of *S. nozhouense* and *S. longifructum*, which are dioecious with malacocarpic male receptacles and probably also malacocarpic female receptacles.
2. Move the *Tenuia* to *Holozygocarpicae.*
3. Move *S. incanum* Grunow from *Cinerea* to *Vachelliana*, which is placed at the beginning of the *Pseudozygocarpicae* instead of at the end.
4. Establish a new series *Cinerea* to receive the members of the *Pseudozygocarpicae.*

With the aforementioned changes, the systematic arrangement of Chinese species of section *Zygocarpicae* is as follows:

1. Subsection *Holozygocarpicae* Setchell
    Series 1. *Carpophylleae* J. G. Agardh
        Species group 1. *Carpophylleae* J. G. Agardh
            1. *Sargassum angustifolium* (Turner) C. A. Agardh
            2. *S. carpophyllum* J. G. Agardh
        Species group 2. *Tenerrima* Setchell
            3. *S. tenerrimum* J. G. Agardh
            4. *S. assimile* Harvey
            5. *S. subtilissimum* Tseng et Lu
            6. *S. aemulum* Sonder
            7. *S. parvivesiculosum* Tseng et Lu
        Species group 3. *Longifructa* Tseng et Lu
            8. *S. nozhouense* Tseng et Lu
            9. *S. longifructum* Tseng et Lu
        Species group 4. *Tenuia* Setchell
            10. *S. polycystum* C. A. Agardh
            11. *S. tenue* J. G. Agardh
            12. *S. laxifolium* Tseng et Lu

2. Subsection *Pseudozygocarpicae* Setchell
   - Series 2. *Cinerea* Tseng et Lu
     - Species group 5. *Vachelliana* Setchell
       - 13. *S. incanum* Grunow
       - 14. *S. graminifolium* (Turner) J. G. Agardh
       - 15. *S. vachellianum* Greville
     - Species group 6. *Cinerea* Setchell
       - 16. *S. cinereum* J. G. Agardh
       - 17. *S. glaucescens* J. G. Agardh

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CLARIFICATION OF SOME SUBGENERIC NOMENCLATURE IN *SARGASSUM* SUBGENUS *SARGASSUM*

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Abstract

A few of the subgeneric ranks for *Sargassum* subgenus *Sargassum* are recognized for species that occur in China and neighboring areas. Several subgeneric ranks are brought into line with the recommendations of the International Code of Botanical Nomenclature. Owing to information from new species assigned to the *Sargassum* subsection *Pseudozygocarpicae*, the *Sargassum* series *Carpophylleae* is recognized, and a new series is established for the taxa included by Grunow in his "Tribe I-b *Carpophylleae dubiae*": *Sargassum* series *Cinerea* Tseng et Lu under the subsection *Pseudozygocarpicae*, section *Zygocarpicae* of the subgenus *Sargassum*.

Introduction

Although many algal genera are subdivided into subgenera, few contain enough species to make further division useful for the sake of taxonomy. In the genus *Sargassum* C. Agardh, J. G. Agardh (1848, 1889) recognized taxonomic categories or groups below the subgeneric level as useful to the taxonomist dealing with tens to hundreds of species within a subgenus. Although it may be possible to include species of *Sargassum* within a flora without referring to subgeneric classification of the numerous species, changes in taxonomy can be achieved only by making clear the options of either strengthening the classification or abandoning it and starting over. No one, or no group of scholars, is presently in a position to do the latter. Upon examining literature on the *Sargassum* subgenera *Bactrophycus* (Tseng et al. 1985) and *Sargassum*, the first author of this paper noted that there were conflicts in the nomenclatural status of ranks that are used in these subgenera. This paper clarifies the status of the categories that apply to the Chinese and some other Asiatic species included in the subgenus *Sargassum* (=*Eusargassum* of J. G. Agardh 1898; Grunow 1915, 1916a, 1916b; and Setchell 1931, 1935, 1936).

The groups or taxa used by J. G. Agardh (1889), Grunow (1915, 1916a, 1916b), and Setchell (1931, 1935, 1936) are presented in Table 1. In the case of Setchell, the taxon name in the last paper was used when there was a question.

Table 1. *Sargassum* subgenus *Sargassum*

Taxon Name	Ranks		
	J. G. Agardh (1889)	Grunow (1915, 1916a, 1916b)	Setchell (1931, 1935, 1936)
Zygocarpicae	Series	Series	Section
Carpophylleae	Tribe	Tribe Ia	Species group
Carpophylleae dubiae	—	Tribe Ib	Subsection
Holozygocarpicae	—	—	Subsection
Pseudozygocarpicae	—	—	Subsection
Cladocarpicae	Series	Series	Section
Acanthocarpicae	Series	Series	Series
Malacococarpicae	Series	Series	Series

According to Article 4.1 of the *International Code of Botanical Nomenclature* (Voss et al. 1983), the following categories are permitted for ranks within a genus: genus, subgenus, sectio (section), subsectio (subsection), series, subseries, and species. Because the category *tribe* cannot be used for this subgeneric level (being restricted to the level of family) according to the Code (Article 34.4), replacing it with another term is required, and similar ordering of the ranks within a portion of the subgenus *Sargassum* is called for.

Sargassum C. A. Agardh (C. A. Agardh 1820, p. 1) *nomen conservandum*
- *Sargassum* subgenus *Sargassum*
  - Synonym: Section III, *Eusargassum* J. G. Agardh (J. G. Agardh 1848, p. 303) (Article 22.1 and Tseng et al. 1985, p. 2).
  - Synonym: Subgenus *Eusargassum* J. G. Agardh (J. G. Agardh 1889, p. 36).
- *Sargassum* section *Zygocarpicae* (J. G. Agardh) Setchell (Setchell 1935, p. 2).
  - Basionym: Series I: *Zygocarpicae* J. G. Agardh (J. G. Agardh 1889, p. 36).
  - Subsection *Holozygocarpicae* Setchell (Setchell 1935, p. 3).
    - Series *Carpophylleae* (J. Agardh ex Setchell) Abbott, Tseng et Lu, *stat. nov.*
      - Basionym: *Sargassum* species group *Carpophylla* Setchell (Setchell 1935, p. 3).
      - *Sargassum* tribe *Carpophylleae* J. G. Agardh (J. G. Agardh 1848, p. 303, *nom. invalid*). [misplaced rank, see Art. 33.4].
        - Type: *Sargassum carpophyllum* J. G. Agardh (J. G. Agardh 1848, p. 304). (Art. 22.4).
  - *Sargassum* subsection *Pseudozygocarpicae* Setchell (Setchell 1935, p. 12).
    - *Sargassum* series *Cinerea* Tseng et Lu, *series nov.* (Fig. 5 in Tseng and Lu, this volume).
      - Capiens species quae sunt dioeciae et plerumque cinereae.
        - Type: *Sargassum cinereum* J. G. Agardh, 1848: 305.
      - Containing species that are dioecious and frequently cinerescent (ashy-grey in color).

Other ranks that are referred to in Tseng and Lu (this volume, "Studies on Chinese Species of Zygocarpic *Sargassum*") include the following:

Sargassum section *Cladocarpicae* (J. G. Agardh) Setchell (Setchell 1936) was published validly by J. G. Agardh (1889, p. 34) as *Sargassum* series *Cladocarpicae*, although it was not earlier used by J. G. Agardh (1848), or by Grunow (1915, 1916a, 1916b). It seems best to omit it from further consideration as its taxonomic status is uncertain (i.e., its species appear to contain a mixture of receptacle types [Setchell 1936]). Nomenclaturally, its name must be lectotypified, which will clarify its taxonomic status.

Sargassum section ***Acanthocarpicae*** (J. G. Agardh) Abbott, Tseng, et Lu, *stat. nov.*
- Basionym: *Sargassum* tribe IX, *Acanthocarpicae* J. G. Agardh (J. G. Agardh 1848, p. 321), *nom. invalid.* [misplaced rank, Art. 33.4]
- Synonym: *Sargassum* series II. *Acanthocarpicae* J. G. Agardh (J. G. Agardh 1889, p. 85).
- Synonym: *Sargassum* series II. *Acanthocarpicae* Grunow (Grunow 1915, p. 381).
- Synonym: *Sargassum* series *Acanthocarpicae* Setchell (Setchell 1936, p. 2).

Sargassum section ***Malacocarpicae*** (J. G. Agardh) Abbott, Tseng et Lu, *stat. nov.*
- Basionym: *Sargassum* series II. *Malacocarpicae* J. G. Agardh, (J. G. Agardh 1889, p. 101).
- Synonym: *Sargassum* series *Malacocarpicae* Grunow (Grunow 1916a, p. 19).

Synonym: *Sargassum* series III. *Malacocarpicae* Setchell (Setchell 1931, p. 249; 1936, p. 10).

Note: *Sargassum* tribe V *Carpophylleae* J. Agardh (J. G. Agardh 1848, p. 303), although given a prominent place in Agardh's classification (i.e., the first category under his *Sargassum* subgenus *Eusargassum*), was used (by implication of suffix) under Setchell's (section) *Zygocarpicae* as (subsection) *Carpophylleae* (Setchell 1931, p. 248). However, in his later study of Hong Kong Sargassaceae, Setchell (1935) used this name for "species group," a category without recognized standing at this time. In following Art. 4.2, however, it can be interpreted as a supplementary rank. In 1935, also, Setchell used Grunow's earlier proposed tribe I-b *Carpophylleae dubiae* in the same rank as *Carpophylleae*, here interpreted as a series. Grunow's tribe (an invalid rank for a genus) is reconstituted here as *Sargassum* series *Cinerea* Tseng et Lu.

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SARGASSUM FROM MICRONESIA

Roy T. Tsuda

Abstract

The description and distribution of the four species of *Sargassum* recognized in Micronesia are presented. The species are *S. crassifolium* J. Agardh, *S. cristaefolium* C. Agardh, *S. obtusifolium* J. Agardh, and *S. polycystum* C. Agardh.

Introduction

The genus *Sargassum* (Phaeophyta, Fucales) is, by far, the largest and most conspicuous benthic alga, when present, on the reef flats of Micronesian islands. This genus can be found growing profusely in selected tidal pools on wave-washed benches; only at one site off the windward side of Guam has *Sargassum* been found beyond the reef margin on the deeper reef terrace in water 7 m deep.

Few papers (Tsuda 1972a, 1972b; De Wreede 1973; Soe-Htun and Yoshida 1986) have addressed the taxonomy of *Sargassum* in Micronesian waters. Most have listed species of *Sargassum* in reference to floristic studies (Okamura 1916; Glassman 1952; Taylor 1966; Tsuda 1972c, 1981) or floristic compilations (Reinbold 1901, Schmidt 1928, Tsuda and Wray 1977). The remaining papers have mentioned species of *Sargassum* in terms of ecological studies, (i.e., algal zonation [Kanda 1944, Tsuda 1977]), algal seasonality (Tsuda 1974), algal productivity (March 1974), herbivorous fish (Bryan 1975), algal phytogeography (Tsuda 1976), and geological studies (Cloud 1954).

The aforementioned studies have attributed nine species of *Sargassum* to Micronesian waters: *S. crassifolium* J. Agardh, *S. cristaefolium* C. Agardh, *S. duplicatum* J. Agardh, *S. granuliferum* C. Agardh, *S. ilicifolium* (Turner) J. Agardh, *S. microphyllum* C. Agardh, *S. oligocystum* Montagne, *S. polycystum* C. Agardh, and *S. tenerrimum* J. Agardh. On the basis of personal collections and examination of specimens, as well as studies by other workers in the Pacific (Pham-Hoang 1967, Chou and Chiang 1981, Tseng 1983), it appears that only four species can be recognized from Micronesian waters: *S. crassifolium, S. cristaefolium* (= *S. duplicatum* and *S. ilicifolium*), *S. obtusifolium* (= *S. tenerrimum* as reported by Tsuda 1972b) and *S. polycystum* (= *S. microphyllum*, and *S. granuliferum* as reported by De Wreede 1973). The fifth species, reported by De Wreede (1973) as *S. oligocystum* (= *S. echinocarpum* J. Agardh), from Palau, has not appeared in any of my collections made in this island group within the past 18 years.

Vegetative Key to the Micronesian Species

1. Branches with short spines; lower branches forming rhizoidal system . . . . *S. polycystum*
1. Branches smooth; lower branches not forming rhizoidal system 2
    2. Leaves lanceolate forming dense whorls around secondary branches; leaves never turbinarioid . . . . *S. obtusifolium*
    2. Leaves turbinarioid or flattened; never forming dense whorls around secondary branches 3
3. Secondary branches clearly compressed . . . . *S. cristaefolium*
3. Secondary branches terete . . . . *S. crassifolium*

Description and Micronesian Distribution

Sargassum crassifolium J. G. Agardh (Fig. 1)

J. G. Agardh 1848, p. 326.

Thallus up to 20 cm high, attached to substratum by a single discoid holdfast. Secondary branches terete and smooth. Leaves ovate, about 2 cm long, and weakly or strongly turbinarioid. Vesicles spherical and smooth, occasionally with "leaflet," up to 4 mm in diameter.

Receptacles slightly moniliform, with few spines, forming loose or compact clusters about 6 mm long.

Specimens Examined: RT 2148 (fertile), reef margin, Eoet Islet, Ulithi Atoll, 19 June 1968; RDW 46b (fertile), reef margin, Eoet Islet, Ulithi Atoll, 13 July 1968; RT 4773 (sterile), outer reef flat near reef margin, between Ngajangel and Ngariungs Islets, Kayangel Atoll, 17 January 1976.

Distribution: Mariana Islands: Guam (Taylor 1966, p. 357; not found on Guam since report of 1918 collection). Caroline Islands: Kayangel Atoll, Palau (Tsuda 1976, p. 279, 1981, p. 46); Ulithi Atoll, Yap (De Wreede 1973, p. 79, as *S. cristaefolium*; Tsuda 1976, p. 279).

Remarks: *S. crassifolium* is very similar to the turbinarioid-leaf form of *S. cristaefolium.* The secondary branches, however, are conspicupously terete as opposed to the distinct compressed branches of *S. cristaefolium.*

Sargassum cristaefolium C. A. Agardh (Fig. 2)

C. A. Agardh 1823, p. 13.

Synonyms: *Sargassum duplicatum* J. G. Agardh (J. G. Agardh 1889, p. 90; *Sargassum ilicifolium* (Turn.) J. G. Agardh (J. G. Agardh 1848, p. 318).

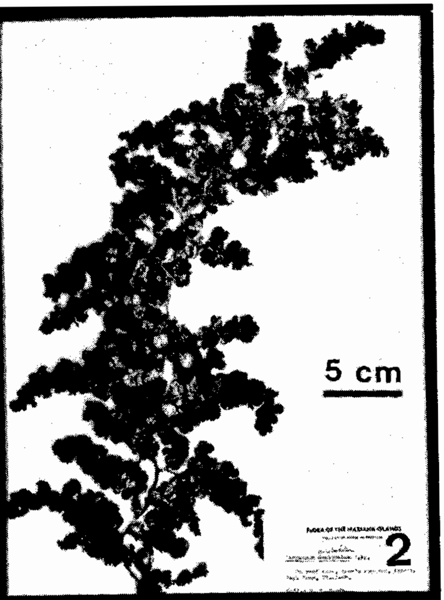
Thallus up to 30 cm high, attached to substratum by a single discoid holdfast. Secondary branches compressed and smooth. Leaves narrow and straplike, about 4–5 cm long in younger plants; successive leaves during maturation becoming shorter, about 1–3 cm long, and thickened to form the characteristic turbinarioid feature. Vesicles spherical and smooth, up to 15 mm in diameter.

Receptacles slightly moniliform, with few spines, forming loose or compact clusters about 5 mm long.

Specimens Examined: RT2221a, reef margin, Asanite Bay, Guam, 13 July 1968; RT3048, outer reef flat, Tanguisson, Guam, 7 May 1970; RT5352, reef terrace, at 4 m, Hawaiian Rock, Guam, 17 May 1977; RT3302b, wave-washed bench, Bird Island, Saipan, 20 May 1970; RT2640, tide pool, Songsong, Rota, 3 March 1969; WJT128, Degusa Beach, Pagan, 14 January 1975; RT5016, tide pool, East Island, Maug, 9 July 1975; WJT291, Uracas, 20 January 1975; PL61, Rock Island, Palau, 13 July 1968; RHR368c, outer reef flat, Herit Island, Truk, 18 July 1969; RT2361, outer reef flat, Madolenihm, Pohnpei, 22 August 1968.

Distribution: Mariana Islands: Guam (Taylor 1966, p. 357 and Tsuda 1972a, p. 41, both as *S. duplicatum*; Tsuda 1972b, p. 102); Saipan (Okamura 1916, p. 7); Rota; Anatahan, Pagan, Maug, and Uracas (Tsuda and Tobias 1977, p. 71). Caroline Islands: Palau (Okamura 1916, p. 7); Yap; Truk (Tsuda 1972c, p. 8, as *S. duplicatum*); Pohnpei (Okamura 1916, p. 7).

Remarks: I had reported previously (Tsuda 1972b) that two morphologically distinct thalli were evident on the reef margins of Guam and attributed them to represent the male and female thalli. During the past years, the morphological differences within the same population first observed during 1967 to 1969 do not seem as conspicuous now.



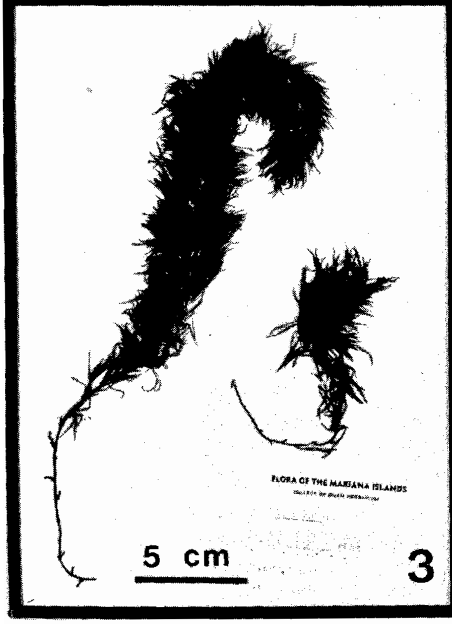


Fig. 1. ***Sargassum crassifolium*** **J. Agardh.**
Fig. 2. ***Sargassum cristaefolium*** **C. Agardh.**
Fig. 3. ***Sargassum obtusifolium*** **J. Agardh.**
Fig. 4. ***Sargassum polycystum*** **C. Agardh.**

Sargassum obtusifolium J. G. Agardh (Fig. 3)

J. G. Agardh 1848, p. 339.

Thallus golden-brown, up to 40 cm high, and attached to substratum by a single discoid holdfast. Secondary branches primarily arise from the base, smooth, and mostly terete but occasionally slightly flattened. Leaves narrow-lanceolate, serrated on edges, 1–2 mm wide and up to 6 cm long, forming dense whorls around the secondary branches. Vesicles spherical, rare, or absent.

Receptacles branched forming small clusters.

Specimens Examined: RT2267a, tide pool on wave-washed benches, Janum Point, Guam, 15 August 1968; RT2296, tide pool on *Porolithon* reef margin, Pati Point, Guam, 16 August 1968; RT3658, wave-washed bench, Aguijan, 13 August 1970; RT3702, tide pool, Laderan Cliffs, Tinian, 18 August 1970.

Distribution: Mariana Islands; Guam (Tsuda 1972b, p. 103, as *S. tenerrimum*), Tinian, Aguijan.

Remarks: The Mariana specimens seem to resemble closely the bushy whorled forms of this species found in Hawaii. The Hawaiian specimens, however, have distinctly compressed secondary branches. *S. obtusifolium* seems restricted to wave-washed benches on the windward coast of the islands.

Sargassum polycystum C. A. Agardh (Fig. 4)

C. A. Agardh 1824, p. 303.

Synonym: *Sargassum microphyllum* C. A. Agardh (C. A. Agardh 1823, p. 33).

Thallus up to 2 m long, attached to substratum by a discoid holdfast as well as a dense rhizoidal basal system, which gives rise to several erect branches. Secondary branches terete, with numerous Y-shaped spines. Leaves thin, with frilled serrated margins, up to 5 cm long and 1 cm wide on immature thalli, decreasing in size to about 1 cm long and 4 mm wide on more mature terminal branches. In some cases, the terminal portion of mature thalli consists of leafless secondary branches bearing numerous receptacles and minute spherical vesicles about 2 mm in diameter.

Specimens Examined: RT2097, inner reef flat, Tumon Bay, Guam, 10 February 1968; RT2265, inner reef flat, Pago Bay, Guam, 11 August 1968; RT1967, inner reef flat, Laulau Beach, Saipan, 24 February 1968; RT2709, inner reef, Tatachog Point, Rota, 13 March 1969; P-67-A1-46-20, causeway to Arakaosen Island, Palau, 2 August 1967; RT2368, lagoon, Sokehs, Pohnpei, 4 September 1968; RT5371, reef flat, south of Mil Entrance, Yap, 20 July 1977.

Distribution: Mariana Islands: Guam (Taylor 1966, p. 357; Tsuda 1972a, p. 41, 1972b, p. 103), Saipan, Rota, Pagan (Tsuda and Tobias 1977, p. 71). Caroline islands: Palau (Kanda 1944, p. 741, as *S. microphyllum*); Yap, Pohnpei. Micronesia: (De Wreede 1973, p. 40, as *S. granuliferum*).

Remarks: This species, a perennial, is abundant on the inner reef flats.

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SARGASSUM (PHAEOPHYTA, FUCALES, SARGASSACEAE) IN THE HAWAIIAN ISLANDS

William H. Magruder

Abstract

Although 14 or more species names have been applied to specimens of *Sargassum* from Hawaii, only five species are recognized as occurring there: *S. echinocarpum* J. G. Agardh, *S. hawaiiensis* Doty et Newhouse, *S. obtusifolium* J. G. Agardh, *S. polyphyllum* J. G. Agardh, and an unidentified species. A key for identification is provided, and a description with the range of character variation in Hawaiian populations is given for each species.

Introduction

As elsewhere in many subtropical and tropical areas, species of *Sargassum* in Hawaii are the largest and among the most common and conspicuous seaweeds. They are usually encountered in midintertidal to shallow subtidal areas of rocky coasts that have at least moderate wave action and on reef flats, but they can be found from supratidal pools to depths of more than 200 m. Dense stands of one or more species are often present on low intertidal benches and on reef flats, and dense stands are also known from deeper water (Doty et al. 1974, Fig. 2), although they are not commonly encountered.

At least 14 different species names and a number of varieties and forms have been applied to specimens of *Sargassum* from Hawaii; however, in this paper, only five species are recognized as occurring there. This opinion is based on my own extensive observations of herbarium specimens and populations in nature and the observations of several others, notably Maxwell Doty, Robert De Wreede, and Jan Newhouse. Of the five, one cannot be identified to species because of the limited amount of material, and the other four were originally described from the Hawaiian Islands. Only three species are commonly encountered: *S. echinocarpum* J. G. Agardh, *S. obtusifolium* J. G. Agardh, and *S. polyphyllum* J. G. Agardh. *Sargassum hawaiiensis* Doty et Newhouse is known only from deep water, and the unidentified species is known only from Pearl and Hermes Atoll in the northwest Hawaiian Islands. All previous subspecific names applied to Hawaiian specimens are not recognized in this paper because the characters used to distinguish them are insignificant when compared with the range of characters found in populations in nature.

Sargassum has many systematic problems. Most of them are related to its widespread distribution in the tropics and subtropics, the presence of many highly variable characters, the lack of assessment of these characters, and the large amount of work done in the 1800s and early 1900s by taxonomists who had little or no experience with *Sargassum* in nature. This led to a great many species names, many of which will likely prove to be synonyms. Indeed, if the criteria for establishing and distinguishing species used by most earlier workers were followed, it would be possible to recognize many more species of *Sargassum* in Hawaii.

The purpose of this paper is not only to allow for the identification of *Sargassum* species in Hawaii but also to document the range of variation in character found in Hawaiian populations. It is hoped that this will be useful in establishing the range of variation for species in other areas and, ultimately, in reducing the number of species names around the world. Some of the names based on Hawaiian specimens may eventually prove to be synonyms of species described earlier from other areas. Reports of the species originally described from Hawaii in other areas of the Pacific and Indian

Oceans certainly indicate fewer species with a much wider range than the currently accepted names and ranges do.

Key to Hawaiian Species of *Sargassum*

1. Primary branch axes without spines above fourth leaf 2
1. Primary branch axes with few to many spines above fourth leaf (Figs. 21, 49, 58) 3
    2. Primary branch axes usually flattened or compressed above fourth leaf; primary branch leaves length to width ratio usually less than 6 to 1; receptacles with spines (Fig. 14); most vesicles with apical appendage or widely ovate in outline . . . . *S. echinocarpum*
    2. Primary branch axes terete or slightly compressed above fourth leaf; primary branch leaves length to width ratio usually greater than 6 to 1; receptacles without spines (Fig. 41); most vesicles without apical appendage and not widely ovate in outline . . . . *S. obtusifolium*
3. Primary branch leaves usually more than 5 cm long and more than 0.6 cm wide; primary branch axes usually with a few simple or slightly branched spines . . . . *S. hawaiiensis*
3. Primary branch leaves usually less than 5 cm long and less than 0.6 cm wide; primary branch axes uaually with highly branched spines 4
    4. Primary branch leaves usually more than 2 mm wide; receptacles in tight clusters; vesicle petioles usually flattened, with wings and/or spines (Fig. 53) . . . . *S. polyphyllum*
    4. Primary branch leaves usually less than 2 mm wide; receptacles in loose clusters; vesicle petioles terete, without wings or spines (Fig. 60) . . . . *Sargassum* sp.

Description of the Species

Sargassum echinocarpum J. G. Agardh (Figs. 1–14)

J. G. Agardh 1848, p 327.

NonSargassum echinocarpum (Greville 1848, p. 87).

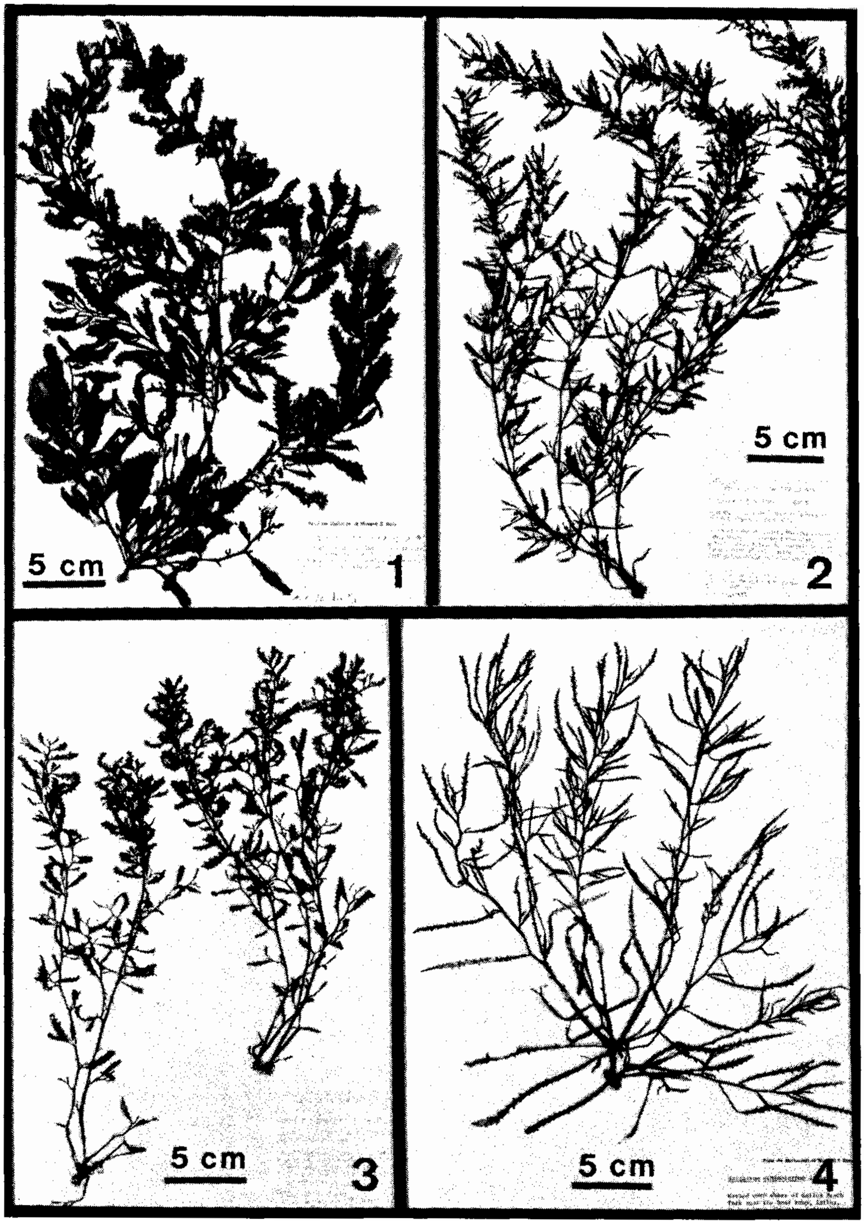
Type Locality: Hawaiian Islands (as Sandwich Islands).

Type Specimen: Lund. A lectotype needs to be selected from J. G. Agardh's specimens (Yoshida 1986, pers. comm.).

Representative Hawaiian Specimens: BISH 507095, 508767, 508855, 509001, 509002, 509013.

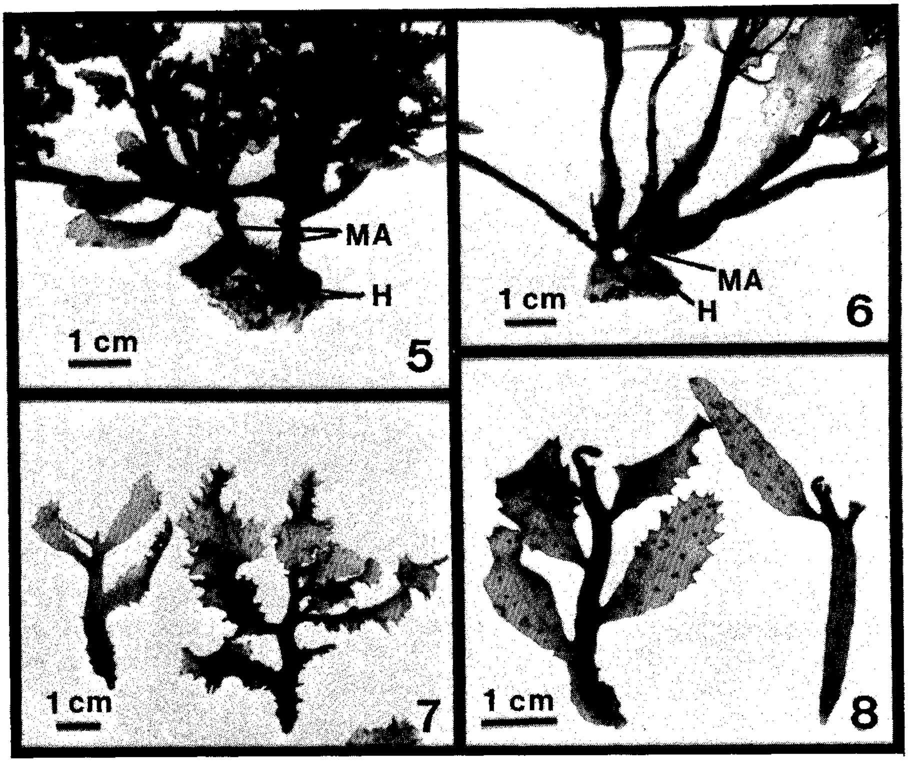
Hawaiian References: Gaudichaud 1826–1830, pp. 90, 150 [as *S. aquifolium* (Turner) C. A. Agardh]; Martens 1868, p. 78 (as *Carpacanthus turneri* Kützing and *Carpacanthus echinocarpus* J. G. Agardh); Chamberlain 1880, p. 33; Kuntze 1881, p. 222; J. G. Agardh 1889, p. 87; De Toni 1895, p. 46; Tilden 1901, p. 108; Lemmermann 1905, p. 659; Setchell 1905, p. 101; Reed 1907, p. 88; Grunow 1915, p. 383; MacCaughey 1918, p. 141; Neal 1930, p. 58, fig. 15c; Howe 1934, p. 33; Tsuda 1965, p. 14, 1966, p. 6; Doty 1971, p. 104; De Wreede 1973, p. 45, figs. 43–47, 50, 60, and 63 (as *S. oligocystum* Montagne), 1976, p. 178, 1978, p. 23; Abbott and Williamson 1974, p. 14, fig. 7; Littler and Doty 1975, p. 125; Fortner 1978, p. 22; Magruder and Hunt 1979, p. 51, fig. on p. 50; St. John and Titcomb 1983, p. 4; Abbott 1984, p. 23, fig. 7.

References from Other Areas: *S. echinocarpum* var. *vitiensis* from Ovalau Island, Fiji, Grunow 1874, p. 6; from New Caledonia, Grunow 1915, p. 383. *S. echinocarpum* from Samoa, Reinbold 1897, p. 270. *S. echinocarpum* from Atapupu, Timor Island, and Padang, Sumatra Island, Indonesia, Reinbold 1913, p. 155. *S. echinocarpum* var. *phyllocysta* from Tonga, Grunow 1915, p. 383. *S. echinocarpum* var. *ambigua* from Jiddah, Saudi Arabia; Mitsiwa, Ethiopia; and Mombasa, Kenya, Grunow 1915, p. 383. *S. echinocarpum* from Fiji, MacCaughey 1918, p. 141. *S. echinocarpum* var. *phyllocysta* from Malita Island, Solomon Islands, Setchell 1935, p. 265; Womersley and Bailey (1970,



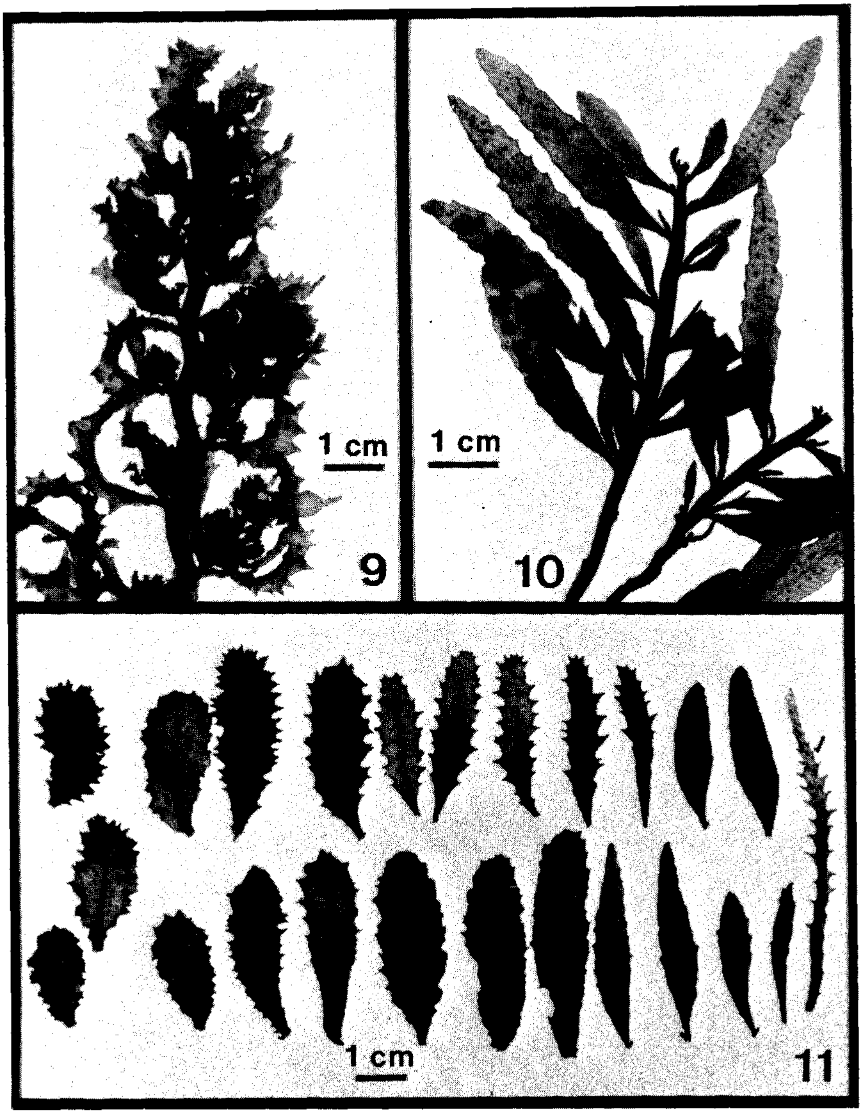
Figs. 1–4. *Sargassum echinocarpum*, dried specimens. Fig. 1, BISH 509001. Fig. 2, BISH 508767. Fig. 3, BISH 507095. Fig. 4, BISH 509002.

p. 300) comment that the two fragmentary specimens are inadequate for determination. *S. echinocarpum* from Taiwan, Yamada 1950, p. 190, fig. 7. *S. echinocarpum* from Taiwan, Yoshida 1987, this volume.



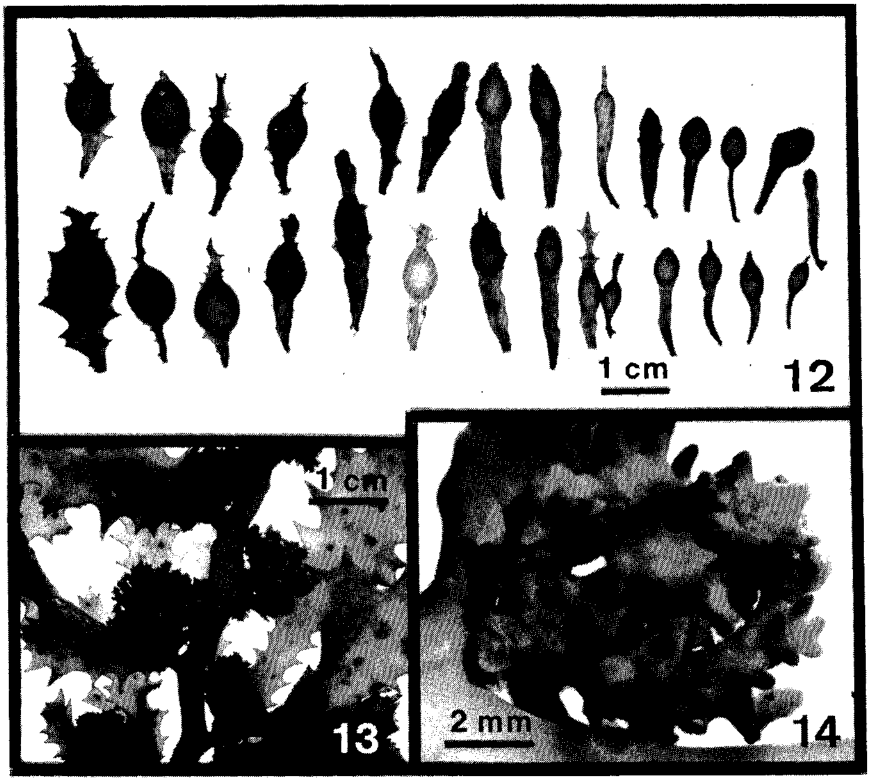
Figs. 5–8. *Sargassum echinocarpum*, liquid-preserved specimens. Figs. 5 and 6, Holdfasts (H), main axes (MA), and lower parts of primary branches. Figs. 7 and 8, Young primary branches.

Thalli (Figs. 1–4) 0.5–1.75 m tall when reproductive; light golden-brown to dark olive-brown. Holdfasts (Figs. 5, 6) conical to discoid; smooth or rarely slightly furrowed; 0.5–3.5 cm in diameter, 0.5–2 cm high. Main axes (Figs. 5, 6) terete, 2–6 mm in diameter, to 20 mm high; one to four per holdfast; rarely branched. Cauline leaves narrowly oblong or narrowly elliptic, branched zero to six times; to 7 cm long, 0.5–1.5 cm wide; margin entire, serrate, or dentate. Primary branch axes (Figs. 7–10) erect; nearly always flattened, compressed, or leaflike (Figs. 7, 8) below first to fourth leaf; usually flattened or compressed above, but occasionally terete; 2–4 mm in diameter or to 8 mm wide. Without spines, except when axes are flattened, small wings or a few lateral spines may be present below first to fourth leaf; with or without cryptostomata. Primary branch leaves (Figs. 9–11) sessile or with short petiole. Usually obovate, elliptic, or narrowly elliptic, but sometimes oblanceolate, lanceolate, narrowly oblong, or otherwise; vertically or horizontally oriented; flat or curved towards axis; 2–8 (12) cm long, 0.3–2 cm wide, 0.03–0.3 cm thick; length to width ratio usually 1.5:1 to 6:1, but up to 17:1. Branched leaves on primary and higher order branches have not been observed in more than 500 specimens examined, except that damaged leaves may proliferate. Margins often aculeate, but also dentate, serrate, double serrate, slightly incised, or nearly entire; straight or wavy in lateral view; occasionally duplicated. Midrib slightly or not raised above leaf surface; 0.5–1 mm wide; usually running to near apex. Cryptostomata prominent, slightly raised above leaf surface; opening circular to narrowly elliptic; 0.4–1.5 mm in



Figs. 9–11. ***Sargassum echinocarpum*, liquid-preserved specimens. Figs. 9 and 10, Upper parts of primary branches. Fig. 11, Primary branch leaves from six thalli showing morphological variations.**

diameter or length; in one to two regular or three to four irregular rows on each side of midrib. Phyllotaxis often 1/2, but also 1/3, 1/4, 2/5, or otherwise. Secondary branches usually remaining short compared with primary branch, occasionally one to three nearly as long as primary branch. Vesicles (Fig. 12) often present on subtidal thalli, often lacking on intertidal thalli, usually replacing leaves on secondary and higher order branches. Morphology variable on individual thalli and highly variable on different thalli. Vesicle shape from elliptic in outline on otherwise little modified leaf to widely ovate in outline



Figs. 12–14. *Sargassum echinocarpum*, liquid-preserved specimens. Fig. 12, Vesicles from five thalli showing morphological variations. Figs. 13 and 14, Receptacle clusters showing characteristic spines.

(rarely circular) without apical appendages; however, most usually with apical appendage; 2–12 mm in largest dimension; most with cryptostomata. Vesicle petiole 0.5–3 cm long, 0.1–1 to 1 cm wide; flattened and leaflike with serrulate or aculeate margin to terete and smooth; with cryptostomata.

Receptacles (Figs. 13, 14) usually in tight, highly branched clusters; with few to many spines; terete to compressed; 0.5–2.0 mm in diameter or wide, 3–15 mm long. Receptacle clusters initially replacing secondary or higher order branches, or leaves on these branches, eventually terminating primary and higher order branches. Leaves on older fertile primary and higher order branches deciduous, leaving only receptacle clusters and vesicles (if present).

Habitat: Common in almost all midintertidal and low rocky intertidal and shallow subtidal areas with at least moderate wave action and on reef flats. Rarely encountered below 5 m, but one specimen (BISH 508341) dredged from 225 m off Molokai. Dense populations of large thalli often found in areas where fresh water mixes with ocean water. Populations frequently winter seasonal, especially on north- and west-facing shores exposed to large winter storm waves from the north Pacific Ocean. In these areas, dense winter populations often present only as holdfasts during summer months.

Distribution: Hawaiian collections from Laysan, Necker, Nihoa, Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii.

Remarks: *Sargassum echinocarpum* J. Agardh is the most commonly encountered and most variable *Sargassum* in Hawaii. Intertidal thalli are usually less than 30 cm tall, often with flattened primary branch axes and wide, thick spiny leaves. Reef flat populations are usually larger, often similar in morphology to intertidal thalli or with slightly compressed or terete primary branch axes and long, narrow, thin leaves without spines, especially when growing in sandy areas. *Sargassum echinocarpum* is often found growing with *S. obtusifolium* and, in general, has shorter, wider leaves with more spiny margins. However, unless foliose vesicles or the characteristic spiny receptacles are present, the long, narrow leaf forms can be extremely difficult to distinguish from *S. obtusifolium*.

Sargassum hawaiiensis Doty et Newhouse (Figs. 15–27)

Doty and Newhouse 1966, p. 144, fig. 4.

Type Locality: Off Kaneohe Bay, Oahu, Hawaii.

Type Specimen: BISH 499798 (Doty No. 19134).

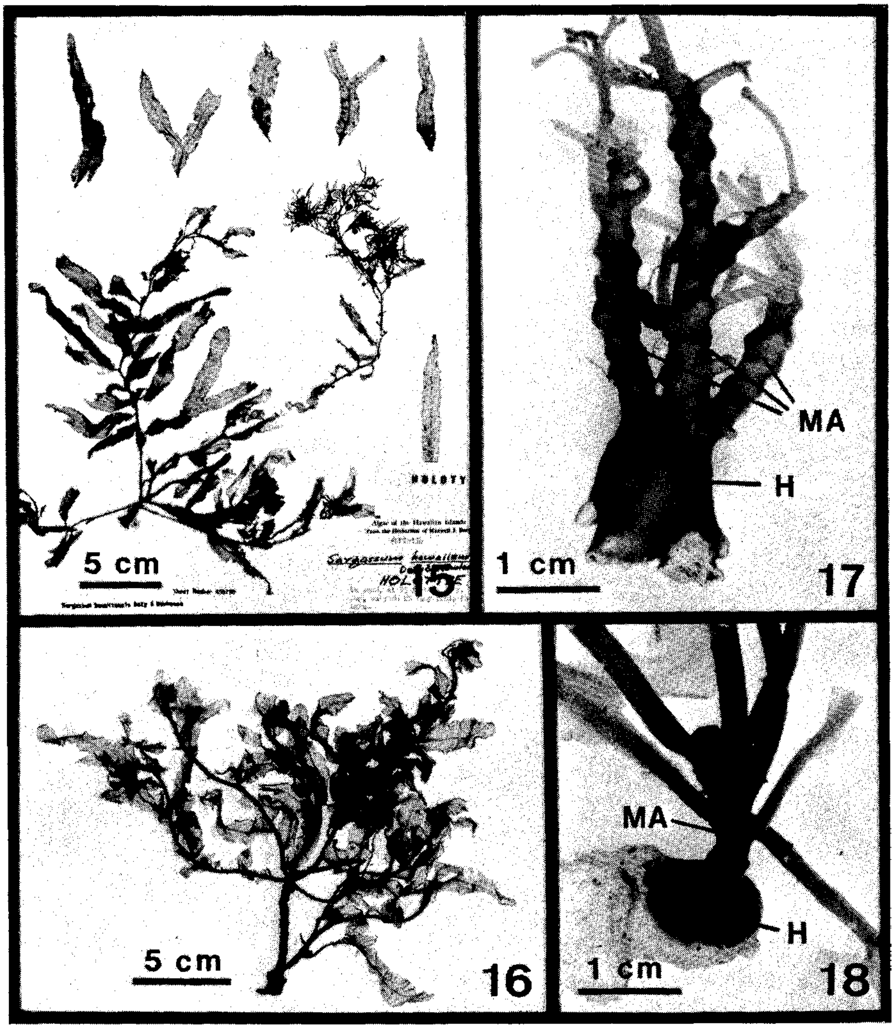
Representative Specimens: BISH 508765, 508846, 508847.

Hawaiian References: De Wreede 1973, p. 49, figs. 78, 79; De Wreede and Jones 1973, p. 60, figs. 1, 2; Doty et al. 1974, p. 352; Balazs 1979, p. 110.

Thalli (Figs. 15, 16) 6–65 cm tall when reproductive; golden-brown to brown. Holdfasts (Figs. 17, 18) discoid to conical; smooth to occasionally slightly furrowed; 0.5–3 cm in diameter, 0.3–2 cm high. Main axes (Figs. 17, 18) terete; 3–8 mm in diameter, to 60 mm long; one to five per holdfast; with obvious large scars from cauline leaves and primary branches; one specimen with branched main axis. Cauline leaves narrowly elliptic; branched zero to two times; to 9 cm long and 1.5 cm wide; margins entire to dentate. Primary branch axes (Figs. 18–21) erect; terete or slightly compressed below first leaf (Figs. 18, 19), rarely with wings (Fig. 20) or leaflike; terete or slightly compressed above (Fig. 21); 2.5–4 mm in diameter. Usually with at least a few simple or slightly branched spines (Fig. 21), rarely without; usually with a few cryptostomata. Primary branch leaves (Figs. 22–24) sessile or with terete pedicel to 1 cm long. Narrowly elliptic, narrowly oblong, or linear; flat; usually simple, occasionally branched once; 4–15 cm long, 0.7–2 cm wide, 0.01–0.04 cm thick; length to width ratio 4 to 1 or greater; leaf margin entire, crenulate, dentate, or serrate; straight or slightly wavy in lateral view. Midrib conspicuous; 0.3–1.0 mm wide; slightly raised above leaf surface; extending to near apex of leaf. Many irregularly arranged small cryptostomata on each side of midrib; very slightly or not raised above leaf surface; opening circular, 0.1–0.2 mm in diameter. Phyllotaxis 2/5 on the three thalli examined. Secondary branches usually short compared with primary branch. Vesicles (Fig. 25) present only on fertile secondary branches on the two specimens with vesicles examined. Circular in outline; smooth; without appendages; 3–7 mm in diameter. Petiole terete, delicate; 5–15 mm long, 0.3–1.0 mm in diameter.

Receptacles (Figs. 26, 27) usually in loose, open clusters; terete; smooth but with conspicuous lumps from conceptacles; unbranched or branched several times; occasionally with short nonfertile sections; 0.5–1.5 mm in diameter, to 2.5 cm long. Receptacle clusters initially replacing secondary or higher order branches or leaves on these branches, eventually terminating primary and secondary branches, rarely just terminating primary branch. Leaves deciduous on older fertile branches, leaving only receptacles and vesicles. What appeared to be leaves growing directly from several receptacles proved to be young plants attached to the receptacle.

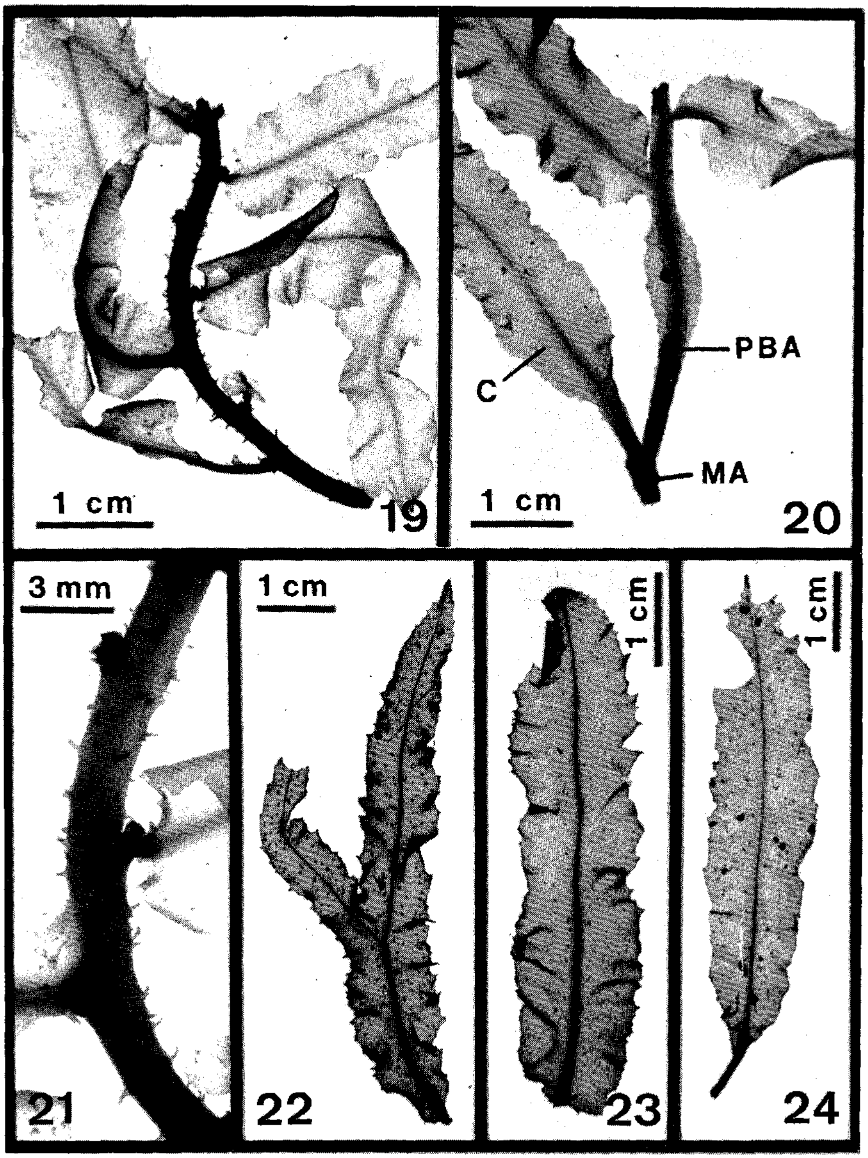
Habitat: Known only from dredged and SCUBA collections in deep water (14–200 m). Growing on a variety of substrata, including mollusk shells, coralline algae, and coral rubble.



Figs. 15–18. *Sargassum hawaiiensis*. Fig. 15, Holotype, BISH 499798, dried specimen. Fig. 16, Liquid-preserved isotype, BISH 509291. Figs. 17 and 18, Holdfasts (H), main axes (MA), and lower parts of primary branches and cauline leaves, liquid-preserved specimens.

Distribution: Known only from the Hawaiian Islands; collections from Oahu, Molokai, and Maui. A record from Kure Atoll (Balazs 1979) is not documented by a specimen.

Remarks: Species that are known only from deep water should always be examined closely as they may be only thalli of shallow-water species with morphological variations induced by deep-water conditions. With regard to the two other Hawaiian *Sargassum* species with spines on the primary branch axes, *S. hawaiiensis* appears distinct from deep-water (75 m) *S. polyphyllum*, which, in turn, is very similar to shallow-water specimens. It is possible that *S. hawaiiensis* and the *Sargassum* sp. from Pearl and Hermes Atoll are the same species, but this is not possible to determine without obtaining more specimens of both for comparison.

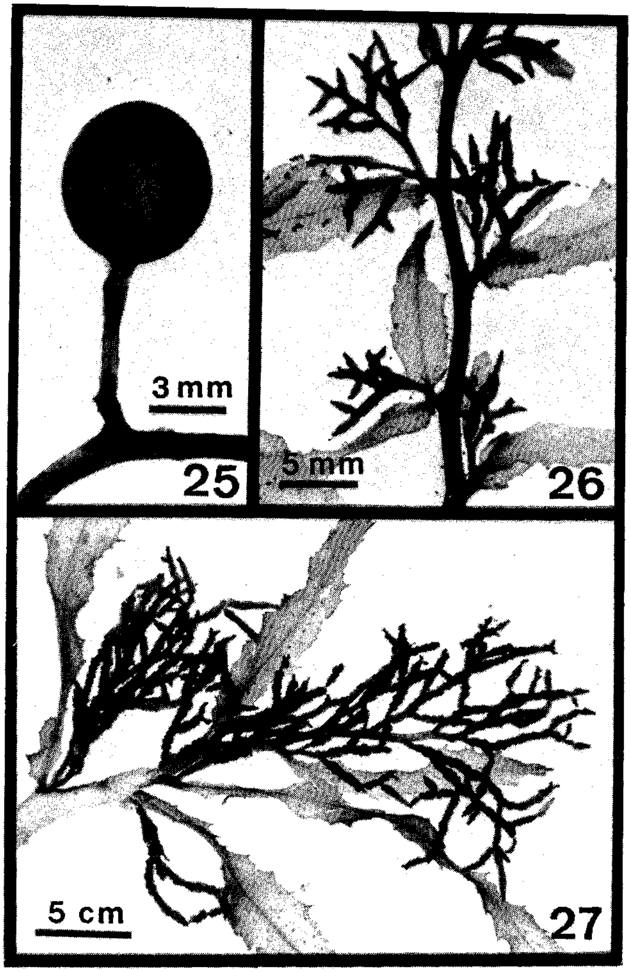


Figs. 19–24. *Sargassum hawaiiensis*, liquid-preserved specimens. Fig. 19, Young primary branch. Fig. 20, Young primary branch (PBA), cauline leaf (C), and main axis (MA). Fig. 21, Enlargement of Fig. 19, showing simple or slightly branched spines on primary branch axis. This axis had the most branched spines of any observed. Figs. 22–24, Primary branch leaves.

Sargassum obtusifolium J. G. Agardh (Figs. 28–41)

J. G. Agardh 1848, p. 339.

Synonyms: *S. obtusifolium* forma *chamberlainii* (Grunow 1916, p. 29); *S. obtusifolium* forma *lendigersides* (Grunow 1916, p. 29).



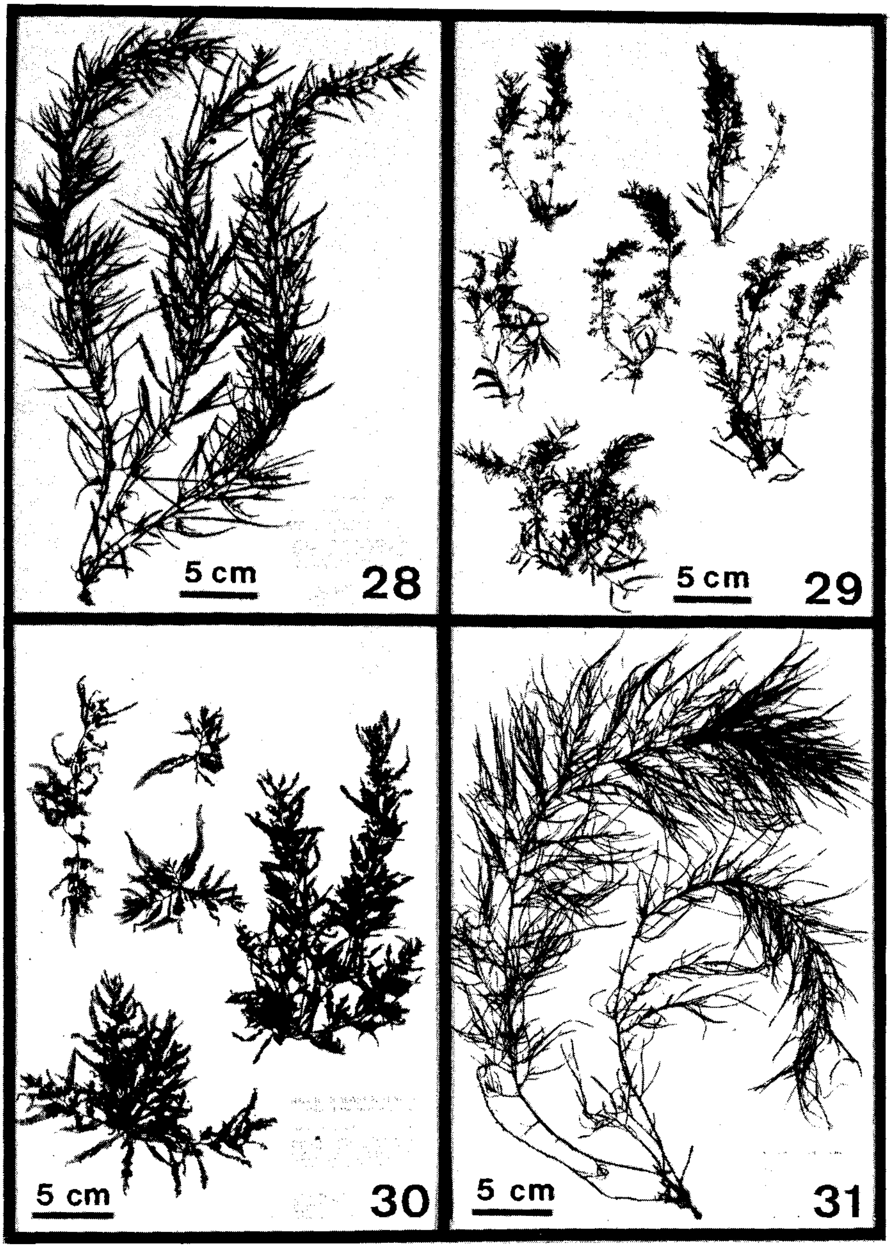
Figs. 25–27. *Sargassum hawaiiensis*, liquid-preserved specimens. Fig. 25, Vesicle. Figs. 26 and 27, Receptacle clusters.

Type Locality: Hawaiian Islands (as Sandwich Islands).

Type Specimen: Lund. A lectotype needs to be selected from J. G. Agardh's specimens (Yoshida 1986, pers. comm.).

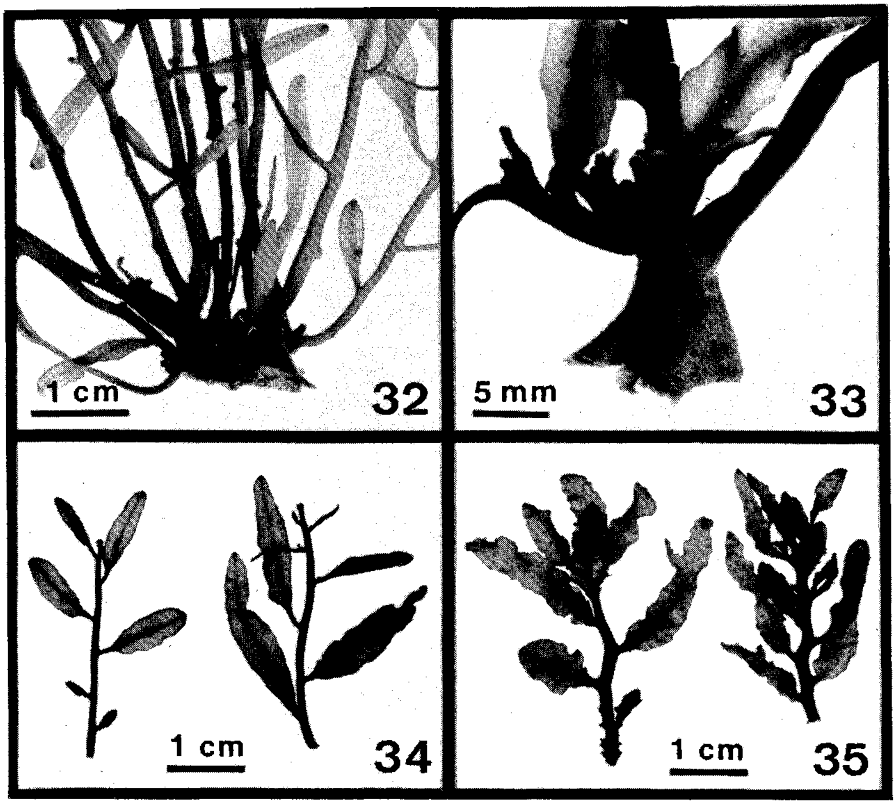
Representative Hawaiian Specimens: BISH 508766, 509003, 509016, 509290.

Hawaiian References: Gaudichaud 1826–1830, pp. 90, 150 (as *S. cuneifolium* J. G. Agardh); Martens 1868, p. 74; Dickie 1877, p. 453; Chamberlain 1880, p. 33 (as *S. cymosum* J. G. Agardh); Kuntze 1881, p. 225; De Toni 1895, p. 79; J. G. Agardh 1889, p. 103; Tilden 1901, p. 108 (as *S. cymosum*); Lemmermann 1905, p. 659; Reed 1907, p. 88 (as *S. cymosum*); Grunow 1916, p. 29; MacCaughey 1918, p. 140 (as *S. cymosum*); Neal 1930, p. 60, fig. 15b (as *S. echinocarpum* variety?); Howe 1934, p. 39 (as *S. vulgare* var. *linearifolium* J. Agardh); Tsuda 1965, p. 15 (as *S. obtusifolia*), 1966, p. 6; De Wreede 1973, p. 177, figs. 64–77, 1976, p. 178, 1978, p. 23; Littler and Doty 1975, p. 125; Magruder and Hunt 1979, p. 51, fig. on p. 50; St. John and Titcomb, 1983, p. 4.



Figs. 28–31. *Sargassum obtusifolium*, dried specimens. Fig. 28, BISH 508766. Fig. 29, BISH 509016. Fig. 30, BISH 509290. Fig. 31, BISH 509003.

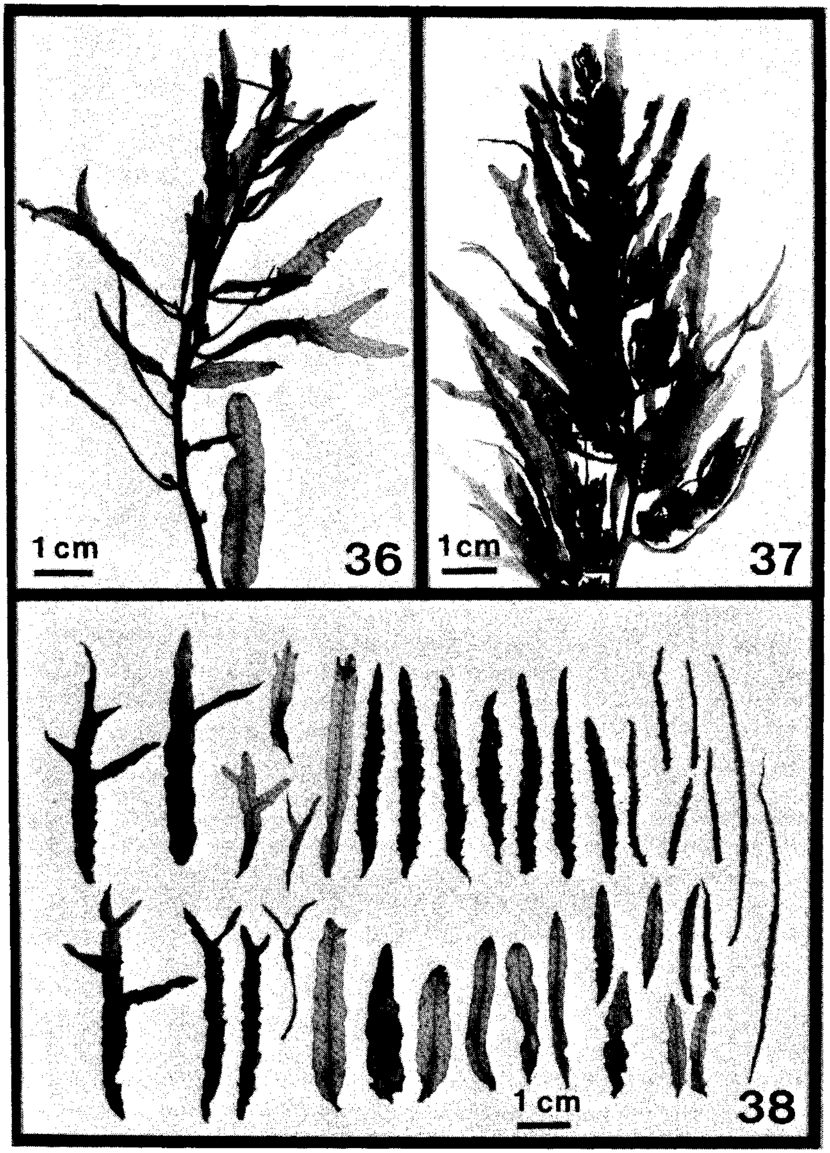
References from Other Areas: *S. obtusifolium* from Tahiti, Society Islands, Grunow 1867, p. 57; considered doubtful by Setchell (1926, p. 97). *S. obtusifolium* var. *reichelii* from Singapore, Grunow 1916, p. 29. *S. obtusifolium* var. *boraborense* from Bora Bora,



Figs. 32–35. *Sargassum obtusifolium*, liquid-preserved specimens. Figs. 32 and 33, Holdfasts, main axes, and lower parts of primary branches. Figs. 34 and 35, Young primary branches.

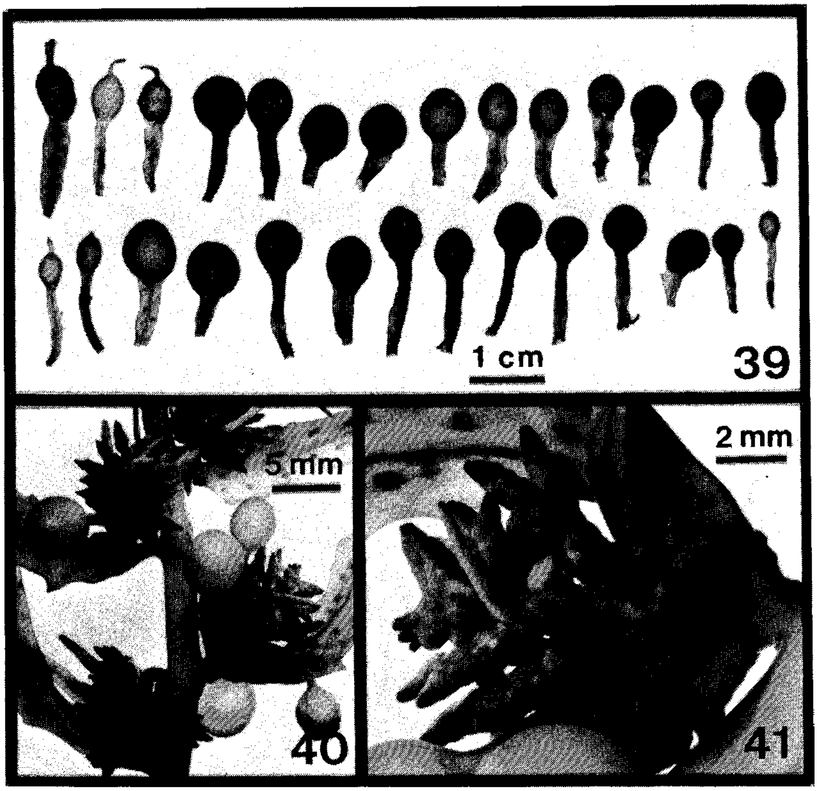
Society Islands, Grunow 1916, p. 30; elevated to *S. boraborense* (Grunow) by Setchell (1926, p. 94). *S. obtusifolium* from Guam, Tsuda 1987, this volume.

Thalli (Figs. 28–31) 4–100 cm tall when reproductive; light golden-brown to dark olive-brown. Holdfasts (Figs. 32, 33) conical to discoid; usually smooth, rarely slightly furrowed; 0.5–2.5 cm wide, to 1.5 cm high. Main axes (Figs. 32, 33) terete, 2–4 mm in diameter, to 40 mm tall; one to 12 per holdfast; rarely branched. Cauline leaves narrowly oblong or narrowly elliptic; flat; branched zero to six times; 3–12 cm long, 0.3–1 cm. wide; margin entire, slightly dentate, or serrate. Primary branch axes (Figs. 34–37) erect; terete or slightly compressed (Figs. 34, 35) below first or second leaf, rarely leaflike; nearly always terete above, rarely slightly compressed; 1–4 mm in diameter; without spines except small wings or a few spines may occur below first or second leaf, and one or two simple spines may be present on each side of leaf attachment. With or without a few cryptostomata. Primary branch leaves (Figs. 36–38) sessile or with petiole to 1 cm, lanceolate, narrowly elliptic, linear, or filiform; usually flat; 2–12 cm long, 0.1–1 cm wide, 0.02–0.1 cm thick; length to width ratio usually 6:1 to 20:1, but up to 60:1; many but not all thalli with at least one branched leaf (one to six times). Leaves vertically or horizontally oriented. Margin usually dentate, serrate, entire, or aculeate; usually straight or slightly wavy in lateral view. Midrib slightly raised above leaf surface; 0.2–0.8 mm wide; running



Figs. 36–38. *Sargassum obtusifolium*, liquid-preserved specimens. Figs. 36 and 37, Upper parts of primary branches. Fig. 38, Primary branch leaves from six thalli showing morphological variations.

to near apex, rarely absent. Cryptostomata mostly in one regular row on each side of midrib, occasionally in two to three irregular rows; opening circular to elliptic; 0.2–0.5 mm in diameter or length; slightly or not raised above leaf surface. Phyllotaxis often 1/3 or 2/5, but also 1/2, 1/4, 1/5, or otherwise. Secondary branches usually remaining short compared with primary branch, occasionally one to three nearly as long as primary branch. Vesicles (Figs. 39, 40) often present on subtidal thalli, often lacking on intertidal

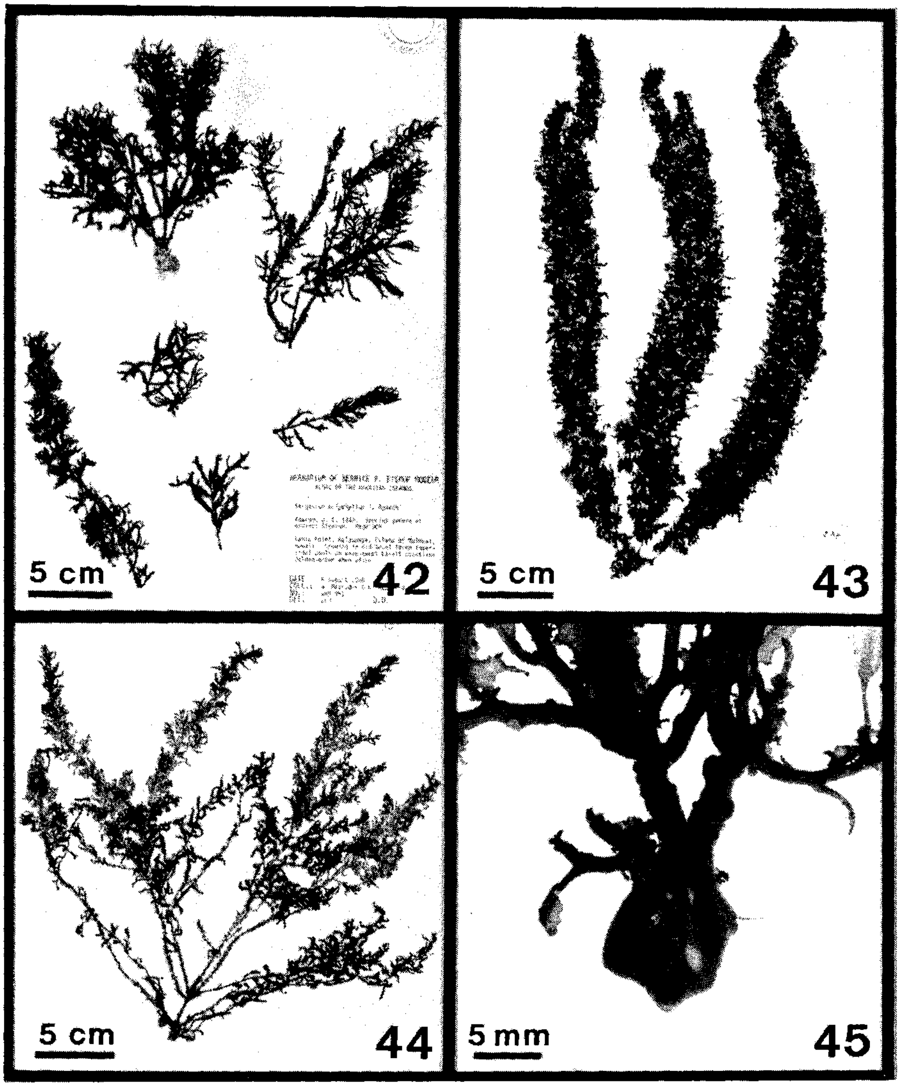


Figs. 39–41. ***Sargassum obtusifolium*, liquid-preserved specimens. Fig. 39, Vesicles from six thalli showing morphological variations. Figs. 40 and 41, Receptacle clusters.**

thalli; usually replacing leaves on secondary and higher order branches. Vesicles circular, widely obovate, or elliptic in outline, rarely widely ovate; 2–8 mm in largest dimension; wings never on distal half; most without, but occasionally a few with, a simple apical appendage; sometimes with a few cryptostomata. Petiole 4–15 (30) mm long, 1–3 mm wide; usually flattened, occasionally terete; rarely with one or two spines or small wings.

Receptacles (Figs. 40, 41) usually in tight clusters; most terete, rarely slightly compressed; nearly always without spines, very rarely with one or two spines, and young branches on highly branched receptacles can resemble spines; conceptacles producing noticeable bumps on surface; unbranched or more commonly with one to four (many) branches; 3–12 mm long, 0.5–1.5 mm in diameter. Receptacle clusters initially replacing secondary and higher order branches or leaves on these branches, eventually terminating primary and higher order branches. Leaves deciduous on older fertile primary and higher order branches, leaving only receptacle clusters and vesicles (if present).

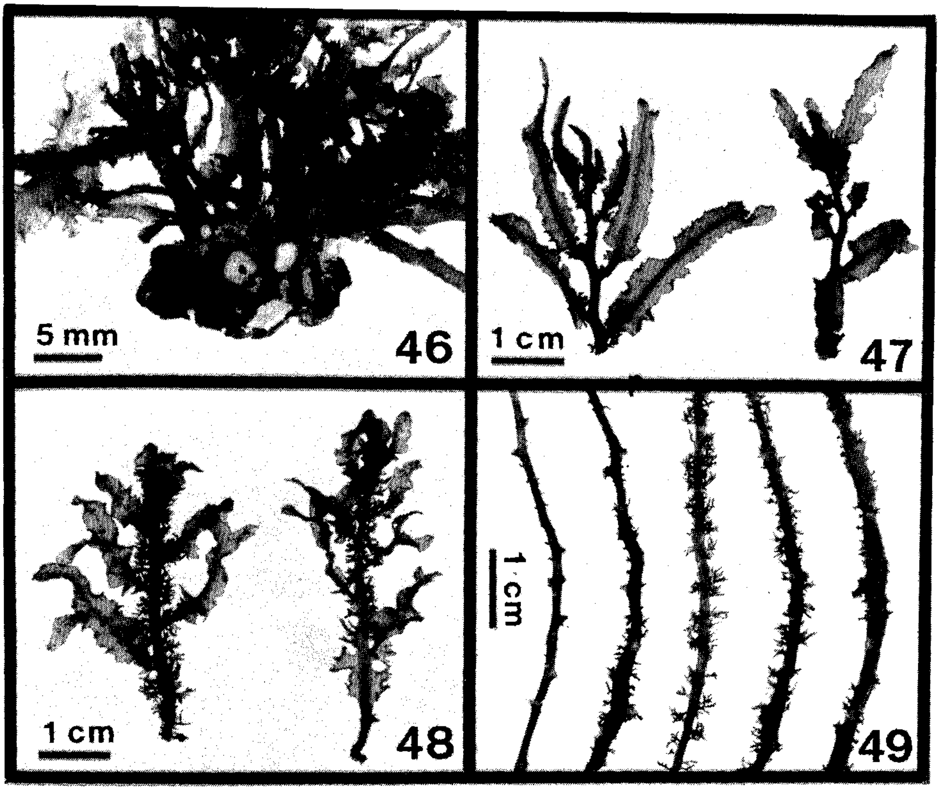
Habitat: Common in most rocky midintertidal and low intertidal (including tide pools) and shallow subtidal areas with at least moderate wave action and on reef flats. Rarely encountered below 3 m, deepest known specimen from 10 m. Populations frequently winter seasonal, especially on north- and west-facing shores exposed to large winter storm waves. In these areas, dense winter populations present only as holdfasts in summer months.



Figs. 42–45. *Sargassum polyphyllum*. Fig. 42, BISH 507155, dried specimen. Fig. 43, BISH 504510, dried specimen. Fig. 44, BISH 504511, dried specimen. Fig. 45, Holdfast, main axes, and lower parts of primary branches, liquid-preserved specimen.

Distribution: Hawaiian collections from Pearl and Hermes Atoll, Laysan, Necker, Nihoa, Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii.

Remarks: *Sargassum obtusifolium* is the second most common *Sargassum* in Hawaii. Intertidal thalli are usually less than 30 cm tall; reef flat thalli are usually larger. It is often found growing with *S. echinocarpum*. In general, *S. obtusifolium* has longer, narrower leaves with smoother margins than *S. echinocarpum*. However, it can be difficult to distinguish from *S. echinocarpum* thalli with long, narrow leaves unless its characteristic smooth, spineless receptacles are present.



Figs. 46–49. *Sargassum polyphyllum*, liquid-preserved specimens. Fig. 46, Holdfast, main axes, and lower parts of primary branches. Two main axes and most primary branches have been cut away for viewing. Figs. 47 and 48, Young primary branches. Fig. 49, Primary branch axes with spines. Leaves and secondary branches have been cut away for viewing.

Sargassum polyphyllum J. G. Agardh (Figs. 42–55)

J. G. Agardh 1848, p. 308.

Synonyms: *Sargassum polyphyllum* var. *fissifolium* (Grunow 1886, p. 44); *Sargassum densum* (Dickie 1877, p. 453); *Sargassum incisum* (Dickie 1877, p. 453); *Sargassum polyphyllum* var. *densa* (Dickie) (Grunow 1916, p. 39).

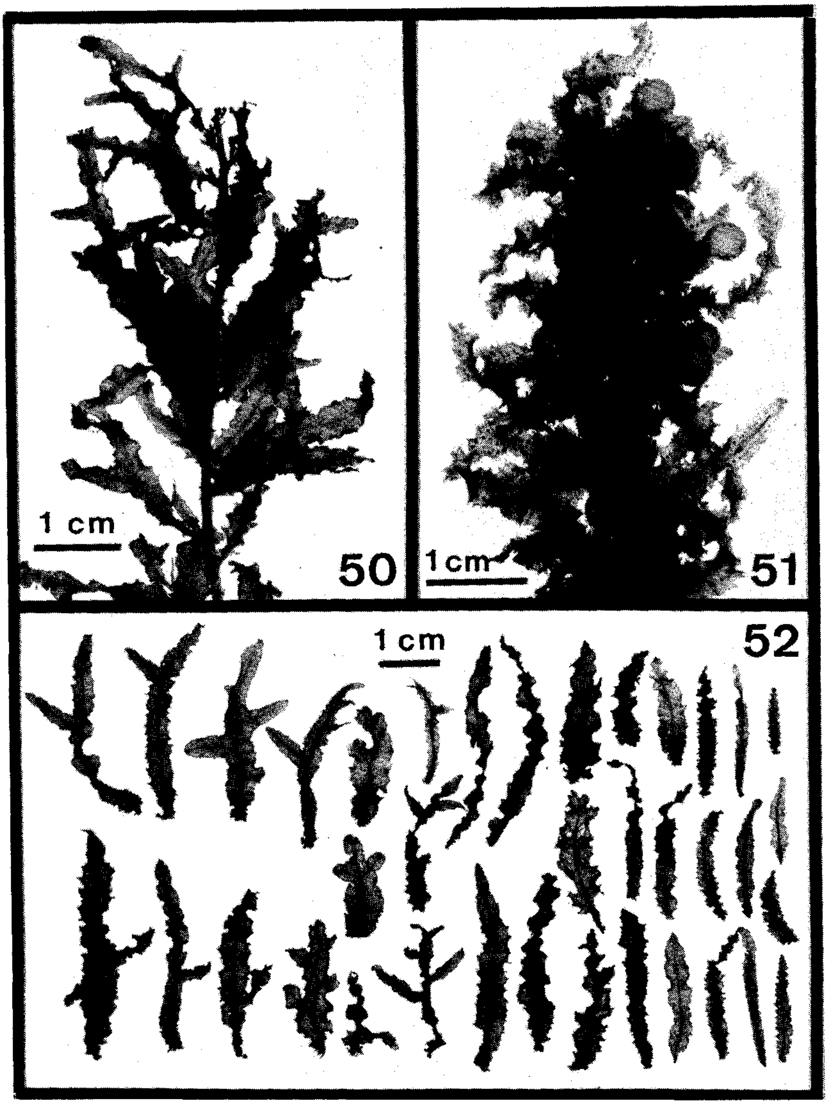
NonSargassum polyphyllum (Mertens 1849, p. 609).

Type Locality: Hawaiian Islands (as Sandwich Islands).

Type Specimen: Lund. A lectotype needs to be selected from J. G. Agardh's specimens (Yoshida 1986, pers. comm.).

Representative Hawaiian Specimens: BISH 504507, 504510, 504511, 507155.

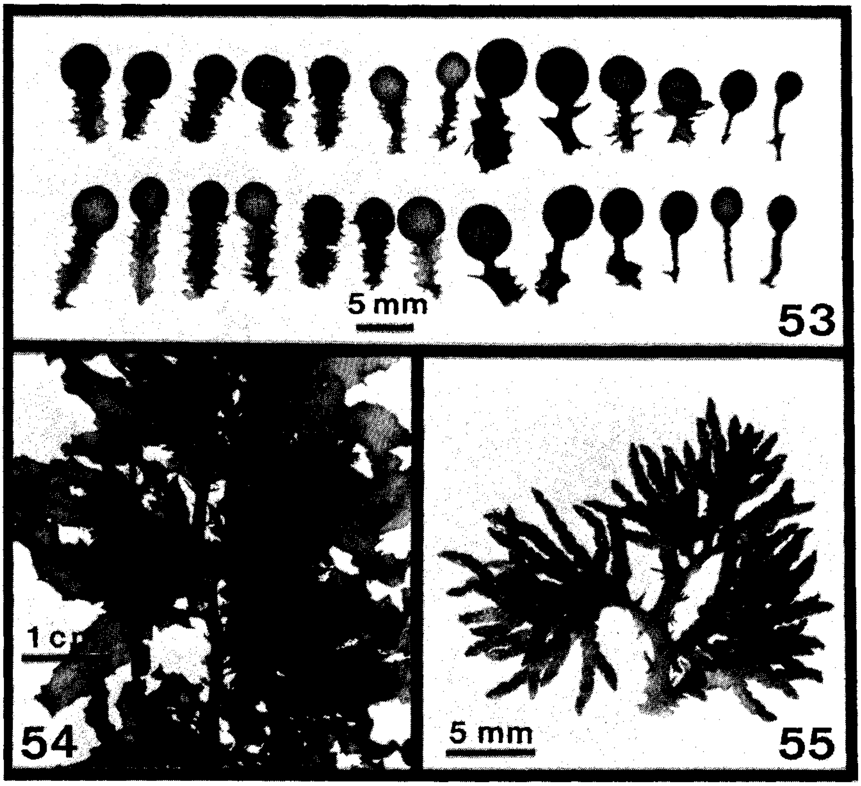
Hawaiian References: Martens 1868, p. 72 (as *S. polyphyllum* Mertens); Dickie 1877, p. 453 (as *S. densum* and *S. incisum*); Chamberlain 1880, p. 33; Kuntze 1881, p. 222 (as *S. densum*), p. 224 (as *S. incisum*), p. 227; De Toni 1895, p. 85; J. G. Agardh 1889, p. 108; Reinbold 1899, p. 290; Tilden 1901, p. 108; Lemmermann 1905, p. 659; Reed 1907, p. 88; Grunow 1916, p. 38; MacCaughey 1918, p. 140; Neal 1930, p. 57, fig. 15a; Howe 1934, p. 33 (as *S. polyphyllum* var. *fissifolium*); Tsuda 1965, p. 15; De Wreede 1973, p. 40, figs. 17–28, 1976, p. 179, 1978, p. 23; Doty et al. 1974, p. 356; Balazs 1979, p. 111; Magruder and Hunt 1979, p. 53, fig. on p. 52.



Figs. 50–52. *Sargassum polyphyllum*, liquid-preserved specimens. Figs. 50 and 51, Upper parts of primary branches. Fig. 52, Primary branch leaves from six thalli showing morphological variations.

References from Other Areas: *S. polyphyllum* var. *horridula* (Grunow) from Ovalau Island, Fiji, and New Caledonia, Grunow 1916, p. 38. *S. polyphyllum* var. *gaertneri* from South China, Grunow 1916, p. 39.

Thalli (Figs. 42–44) 4–70 cm tall when reproductive, light golden-brown to dark-brown. Holdfasts (Figs. 45, 46) conical to discoid; smooth or slightly furrowed; to 2.5 cm in diameter and 1.5 cm tall. Main axes (Figs. 45, 46) terete; 2–5 mm in diameter, to 90 mm long; one to 12 main axes per holdfast; with obvious large scars from cauline leaves and primary branches; rarely branched. Cauline leaves narrowly elliptic or narrowly oblong;



Figs. 53–55. *Sargassum polyphyllum*, liquid-preserved specimens. Fig. 53, Vesicles from six thalli showing morphological variations. Figs. 54 and 55, Receptacle clusters.

usually branched one to two times; 1–5 cm long, 0.2–0.8 cm wide; margin entire to serrulate. Primary branch axes (Figs. 47–51) erect; terete or slightly compressed below first or second leaf, occasionally with wings or leaflike (Figs. 47, 48); terete or slightly compressed above; 0.5–4 mm in diameter; always with spines, usually with many highly branched or peltate spines (Fig. 49), rarely with only a few simple spines. Branched or peltate spines usually formed by growth of the area around cryptostomata, elevating it up to 4 mm above the axis surface. Primary branch leaves (Figs. 50–52) sessile or with short, flattened petiole, petiole usually with spines. Narrowly oblong, narrowly elliptic, lanceolate, or linear; flat to spirally twisted; horizontally oriented; 1–6 cm long, 0.1–0.8 cm wide, 0.02–0.05 cm thick; length to width ratio 2.5:1 to 30:1. Most, but not all, thalli with at least one branched leaf (one to six times). Margin aculeate, slightly incised, denticulate, serrate, serrulate, or nearly entire; wavy or straight in lateral view. Midribs slightly raised above leaf surface, usually running to near apex. Wings and/or spines sometimes developing on upper and/or lower surface or midrib. Cryptostomata in one or two rows on each side of midrib; opening circular; 0.1–0.25 mm in diameter; often noticeably raised above leaf surface. Phyllotaxis 1/3, 1/4, 2/5, or otherwise. Secondary branches variable, remaining short compared with primary branch on some thalli, several nearly as long as primary branch on others; inconspicuous on some thalli, but others with very closely spaced leaves and higher order branching that completely obscure the main axes (Fig.

43). Vesicles (Figs. 51, 53) common on subtidal thalli, rare on intertidal thalli; usually replacing leaves on secondary or higher order branches. Circular, widely elliptic, widely ovate or widely obovate in outline without apical appendages; occasionally with a few lateral spines or wings on lower half; with a few cryptostomata, occasionally elevated above vesicle surface. Vesicle petiole usually flattened or compressed, with spines or wings with dentate, aculeate, or incised margins, occasionally smooth and terete; 4–15 mm long, 1–5 mm in diameter or wide.

Receptacles (Figs. 54, 55) in tight to open clusters; terete; mostly smooth, but occasionally with a few spines on lower parts; simple to branched several times; conceptacles forming noticeable lumps on surface; 4–10 mm long, 0.8–1.5 mm in diameter. Receptacle clusters initially replacing secondary or higher order branches or leaves on these branches, eventually terminating primary and higher order branches. Leaves deciduous on older fertile branches, leaving only receptacle clusters and vesicles (if present) on axes.

Habitat: From high intertidal pools and water-filled cracks to a depth of 75 m, often forming dense stands in large tide pools and on reef flats.

Distribution: Hawaiian collections from Midway Atoll, Laysan, Maro Reef, Necker, Kauai, Oahu, Molokai, Maui, Lanai, and Hawaii.

Remarks: When growing in intertidal areas, thalli are usually in pools and not exposed to air at low tide. Thalli from high intertidal and midintertidal areas are usually less than 20 cm tall, with lanceolate leaves and entire to dentate margins; thalli from deeper water and reef flats are usually larger, often with narrowly elliptic or narrowly oblong leaves with aculeate to slightly incised margins. It is sometimes found growing with *S. echinocarpum* and/or *S. obtusifolium.* The spiny primary branch axes of *S. polyphyllum* usually allow it to be distinguished easily from either of these species.

Sargassum sp. (Figs. 56–61)

Representative Hawaiian Specimens: BISH 489264, 508764.

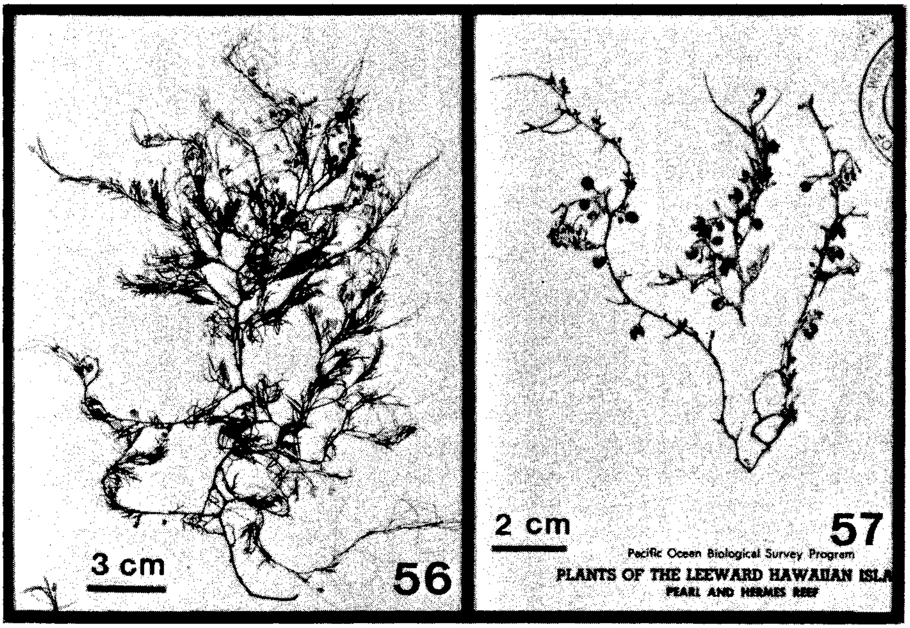
Hawaiian references: Howe 1934, p. 39 (as *S. piluliferum* (Turner) C. Agardh); Tsuda 1966, p. 6 (as *S. piluliferum*); De Wreede 1973, p. 50.

Thalli (Figs. 56, 57) 20–40 cm tall; golden-brown. Holdfasts unknown. Main axes unknown. Cauline leaves unknown. Primary branch axes terete; 1–3 mm in diameter; with simple to highly branched or peltate spines (Fig. 58), branched or peltate spines with elevated cryptostomata at apex. Primary branch leaves sessile, lanceolate or linear on vegetative areas of thallus, filiform on reproductive areas (Fig. 59); flat; simple or with one to four branches; 2–6 cm long, 0.05–0.2 cm wide, 0.02–0.1 cm thick; length to width ratio 12 to 1 or greater. Leaf margin entire or serrate. Leaves in vegetative areas with midrib, slightly raised above leaf surface; in reproductive areas without midrib (or only consisting of the midrib?) with cryptostomata. Phyllotaxis unknown. Secondary branches up to one-half the length of primary branches. Vesicles (Fig. 60) present on the two specimens examined, replacing leaves on primary and higher order branches. Spherical to widely obovate; without wings or appendages; 3–6 mm in diameter; with cryptostomata. Vesicle petiole terete, delicate; 4–12 mm long, 0.3–0.5 mm in diameter.

Receptacles (Figs. 58, 61) forming loose, open clusters; terete; smooth; branched zero to five times; 5–30 mm long, 0.4–1 mm in diameter. Clusters replacing secondary and higher order branches or leaves on these branches, not terminating primary branches on the two specimens examined.

Habitat: Reef lagoon.

Distribution: Partial thalli collected only three times from Pearl and Hermes Atoll in the northwest Hawaiian Islands.



Figs. 56 and 57. *Sargassum* sp., dried specimens. Fig. 56, BISH 489264. Fig. 57, BISH 508764.

Remarks: Although identified as *S. piluliferum* by Howe (1934) and Tsuda (1966), the specimens are fragmentary and without the distinguishing holdfasts. Until specimens with holdfasts are obtained, it is not possible to determine this species. At present, all that can be said is that the narrow leaves, loose receptacle clusters, and long, thin, terete vesicle petioles of these specimens appear to distinguish it from the other Hawaiian species with highly branched spines on the branch axes, *S. polyphyllum*. (See also discussion of *S. hawaiiensis*.)

Acknowledgements

I thank the University of Hawaii Sea Grant College Program for financial support and the Department of Botany, Bernice P. Bishop Museum, for allowing me time for this work.

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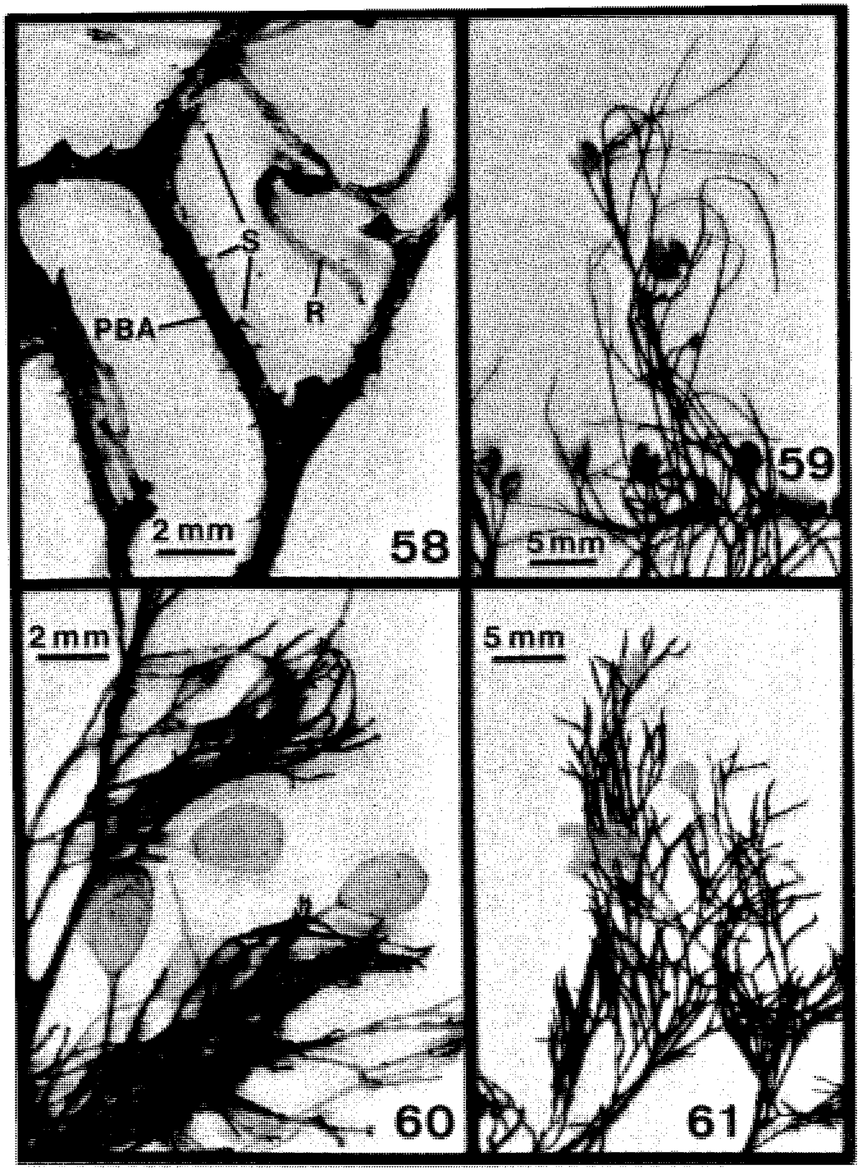

Figs. 58–61. *Sargassum* sp., dried specimens. Fig. 58, Primary branch axis (PBA) with branched spines (S) and receptacle (R). Fig. 59, Filiform and mostly branched primary branch leaves and vesicles at apex of primary branch. Fig. 60, Vesicles. Fig. 61, Receptacle clusters and vesicles.

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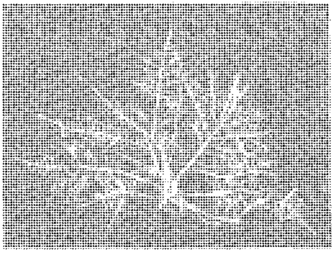
SECTION II. Gelidiales



INTRODUCTION

Isabella A. Abbott

Unfortunately, illness prevented Dr. Santelices from joining the workshop in Qingdao to study the Chinese Gelidiales, and work in the south of China prevented Xia Enzhan from being present. So the two contributions that follow were done independently, without benefit of discussions with one another. The keys provided by the two groups of workers give two ways of arriving at species; in the cases of *Gelidium divaricatum* and *G. pusillum*, they are "key pairs," which would indicate that to these workers they have some features in common.

About 150 specimens of Chinese Gelidiales were brought for Dr. Santelices to study when he came to Honolulu 3 months after the workshop. Comparisons were made with a certain number of Japanese specimens of Gelidiales previously given to him by Professor T. Yoshida at the first workshop.

The contribution of Zhang and Xia Enzhan is valuable because it refers to Chinese literature, much of which is unavailable in the West or written in Chinese, and for which it is difficult to obtain a translator with a technical vocabulary.

TAXONOMIC STUDIES ON CHINESE GELIDIALES (RHODOPHYTA)

Bernabé Santelices

Abstract

The taxonomic status of eight species of Gelidiales from China and two other species reported for Taiwan is reviewed. The genus *Gelidiella* is represented here by *G. acerosa* (Forsskål) Feldmann et Hamel, whereas the genus *Pterocladia* includes *P. capillacea* (Gmelin) Bornet et Thuret. The genus *Gelidium* is represented by *G. amansii* (Lamouroux) Lamouroux, *G. crinale* (Turner) Lamouroux, *G. divaricatum* Martens, *G. japonicum* (Harvey) Okamura, *Gelidium planiusculum* Okamura, *G. pusillum* (Stackhouse) Le Jolis, and *G. vagum* Okamura. The validity of *G. pacificum* Okamura is discussed, and the need for a new genus for *G. japonicum* Okamura is questioned. Discrepancies among the type illustrations of *G. amansii* and the materials now included in that species are reported. Bispores and zonate tetrasporangia were found in *G. divaricatum*.

Introduction

Eight species of *Gelidium* have been reported for the coast of China (Tseng 1983), and five additional species have been described for the coast of Taiwan (Fan 1951). As is common in temperate and warm waters, several of these species are conspicuous members of intertidal and subtidal communities, and in many areas they are said to be locally preponderant in density, cover, and biomass. In such areas, these species are ecologically and economically important. Several are food for invertebrates and fishes, some are consumed directly by indigenous people as food suplements, and many are gathered from wild beds to be used as raw materials for industrially or domestically produced agar. About 150 metric tons of dry *Gelidium* and *Pterocladia* are known to be gathered in China, and an additional 50–60 tons are collected in Taiwan (Yamada 1976, Santelices 1988). Moreover, many of these species are also productive in geographically related areas, such as Japan and Korea, where the combined annual crop is said to be close to 6000 metric tons of dry matter (Yamada 1976). All together, therefore, several of these species form the basis for close to 30% of the world production of *Gelidium* and *Pterocladia*, which is estimated to range annually from 16,000 to 19,000 metric tons of dry matter (Santelices 1988).

As is common in the taxonomic studies of *Gelidium* and *Pterocladia*, many descriptions of the species have been based on external morphology only, which is extremely variable. Some of the names have been based on only a few herbarium specimens, barely representing the range of variation expressed in field populations of each species. Therefore, it is often difficult to outline sharp specific limits for these species unless patterns of external morphological variation can be established, and these must be evaluated as to their stability if they are to be used as taxonomic characters. Furthermore, the morphological variation must be compared with the one or, at most, several specimens that represent the nomenclatural types. In all the areas in which these studies have been undertaken, they have resulted in a reduction in the number of names for the species distinguished in a given area (Dixon 1966; Stewart 1968, 1974, 1976; Santelices 1976a, 1977; Stewart and Norris 1981; Santelices and Montalva 1983). Often a sharper boundary between species has revealed the existence of common, economically and ecologically important, yet undescribed, species (e.g., Santelices and Abbott 1985). Studies on morphological variation of some Japanese species of *Gelidium* have been pursued (Akatsuka 1982), but most of the species of the Sino-Japanese subregion of the Indo-West Pacific Floristic Region remain to be critically examined. This review is a first step towards testing the species concepts and the specific limits of the

Chinese entities now included in the genera *Gelidium, Gelidiella*, and *Pterocladia*.

The present study reviews the taxonomic status of eight species of Gelidiales common in China (*Gelidiella acerosa, Gelidium amansii, G. crinale, G. divaricatum, G. pacificum, G. pusillum, G. vagum*, and *Pterocladia capillacea*) and two of the five other species reported for Taiwan (*G. japonicum* and *G. planiusculum*). Although three other species have been reported for Taiwan (*G. kintaroi, G. latiusculum* and *G. yamadae*), no representative specimens of them were available for this study.

Materials and Methods

Herbarium specimens used in this study were brought from the Institute of Oceanology (AST) by Dr. Abbott for my use in Honolulu. I understand that these specimens were chosen as representative of the species and that many more are available in China. Sections were cut from the specimens by hand, hydrated, stained with 1% aqueous aniline blue, acidified, and mounted in glucose syrup. I have retained this set of slides (Santiago).

Key to the Common Chinese Species of Gelidiales

1. Internal rhizoidal filaments (hyphae) absent . . . . *Gelidiella* (*G. acerosa*)
1. Internal rhizoidal filaments (hyphae) present 2

   2. Cystocarps unilocular, with one or more ostioles on only one surface. Carposporangia usually in short chains . . . .*Pterocladia* (*P. capillacea*)
   2. Cystocarps bilocular, with one or more ostioles on each surface. Carposporangia not in short chains . . . . .3 (*Gelidium*)

3. Thallus less than 5 cm high 4
3. Thallus more than 5 cm high 6

   4. Axes filiform, cylindrical, or slightly compressed, sparsely branched . . . . *G. crinale*
   4. Axes cylindrical at the base, compressed above, irregularly branched, frequently less than 3 cm high 5

5. Erect branches arising at regular intervals from creeping axes, invested with bipinnate, divaricate branches . . . . *G. divaricatum*
5. Erect branches cylindrical at the base, lanceolate or compressed above, single or with small proliferations, some branches incurved downwardly becoming creeping axes . . . . *G. pusillum*

   6. Erect axes very compressed, to 4 mm broad, sparsely branched, with a midrib . . . . *G. japonicum*
   6. Erect axes cylindrical at the base, compressed above, less than 3 mm broad, variously branched, without a midrib 7

7. Erect axes and primary branches lanceolate, branches many, of various lengths, often regularly arranged, terminal pinnae with acute apices . . . . *G. amansii*
7. Erect axes and primary branches invested with or ending in filiform branchlets 8

   8. Erect axes and primary branches often forming broad, blunt apices continuing into narrow, filiform projections. Filiform branchlets often abundant, investing margins and tips of erect axes and branchlets . . . . *G. planiusculum*
   8. Axes strap-shaped, widened and compressed at the branching points, and invested with two types of branches: one type narrow and elongate, with acute apex and invested with higher order, spinous branches; second type strap-shaped, similar to the percurrent axes. Branches incurved at the base . . . . *G. vagum*

Descriptions of Chinese and Taiwanese Species of Gelidiales

GELIDIELLA

Gelidiella acerosa (Forsskål) Feldmann et Hamel (Fig. 1)

Feldmann and Hamel 1934, p. 533.

Synonym: *Fucus acerosus* Forsskål (Forsskål 1775, p. 190).

The Chinese materials studied (Fig. 1) fit fairly well with the general description of this species. Thalli are up to 5 cm high, with several tufted, entangled, cylindrical, erect axes rising from creeping axes that are decumbent and arcuate, attached to the substratum by stoloniferous rhizoids. Erect axes are cylindrical or very slightly compressed, normally opposite or subopposite pinnae, up to 15 mm long, generally shorter apically and frequently incurved abaxially.

As is commonly found in this species, the tetrasporangia are oblong, cruciately divided, and sparsely and irregularly disposed on the apical portion of vegetative pinnae, which have been modified into swollen branches of conical shape.

Distribution and Remarks: According to Tseng (1983), in China this is an economically important seaweed used as raw material for agar production. It occurs mainly in Guangdong Province, especially around Hainan and the Xisha Islands. The materials examined for this study included 10 specimens collected between 1957 and 1960 around Hainan. The species was originally described from the Red Sea, and later reports have confirmed a basically tropical distribution (see Santelices 1977 for a review).

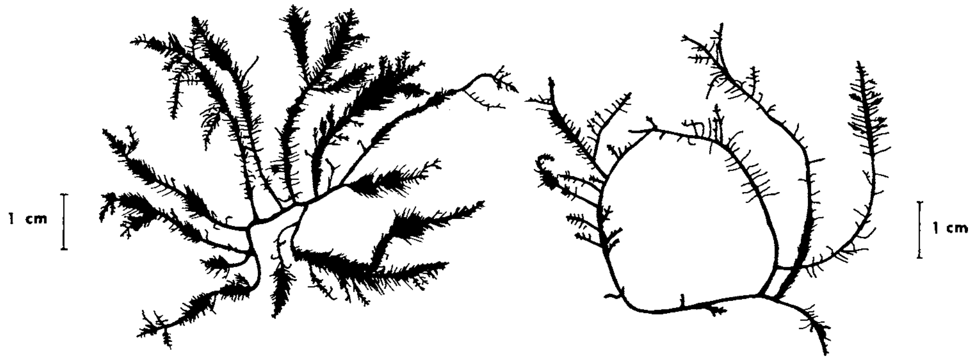


Fig. 1. Morphological variation in *Gelidiella acerosa* from Hainan, China. The well-branched specimen on the left (No. 594268) was collected June 7, 1959; the specimen on the right (No. 594291) was collected August 21, 1960.

GELIDIUM

Gelidium amansii (Lamouroux) Lamouroux (Figs. 2–4)

Lamouroux 1813, p. 129.

Synonym: *Fucus amansii* Lamouroux (Lamouroux 1805, p. 48, pl. 26, figs. 2–5).

This species is abundantly represented among the Chinese materials examined (36 specimens). Plants are attached by a rhizomatous holdfast that produces many upright axes of up to 16 cm long and up to 15 mm broad (Fig. 2). Erect axes are invested with few or many, oppositely or alternately arranged, lateral branches similar in shape and appearance to the erect axes. Primary branches are of three orders with regularly or irregularly disposed, alternate or opposite branches. Terminal pinnae characteristically have acute apices (Fig. 3). In transection the cortical cells are rounded, up to 7.5 µm in diameter, increasing in size inwardly. Medullary cells are rounded, with thick walls, up to 30 µm in diameter.

Tetrasporangial sori are on elongate-ovate or oblong branchlets. Seemingly apical growth continues after spore production; therefore, in these materials, tetrasporangial sori frequently are found beneath the branch apices (Fig. 3). Tetrasporangia are arranged without order in the sori. They are rounded, cruciately divided, and up to 25 µm in diameter. In surface view, cystocarps are spherical or slightly elongated, up to 0.4–0.6 mm, often subterminal beneath a simple (infrequently branched) lanceolate apex. Cystocarps often have a 50–55 µm broad sterile margin.

Distribution: The species is said to be abundant on the Yellow Sea coast and along the western East China Sea. It is also abundant in Japan, Korea, and the Pacific coast of the Soviet Union (Tseng 1983).

Remarks: The range of morphological variations found in *G. amansii* among the Chinese specimens, as well as among specimens from elsewhere (Okamura 1934, Fan 1951, Akatsuka 1982), includes the morphologies in the description of *G. pacificum* Okamura. Okamura (1914) distinguished *G. pacificum* as having larger fronds, broader branches, more expanded and rounded tetrasporangial branchlets, and more aggregated tetrasporic and cystocarpic pinnae than *G. amansii*. These are morphologically variable characters shared by specimens included in the populations of *G. amansii*. According to Akatsuka (1982), in 1954 Suto questioned the separation of *G. pacificum* from *G. amansii*. Akatsuka (1982) statistically tested morphological differences between the two species and found no interspecific differences in cell sizes or shapes. He concluded that width and thickness of main axes and branches were the only characters possible to use in distinguishing the two species, but he did not provide variability ranges nor statistical treatments for these morphological characters. Additional studies seem necessary to evaluate the taxonomic status of these two species and to characterize the field variation of the populations of *G. amansii*. When Okamura first described *G. pacificum* (Okamura

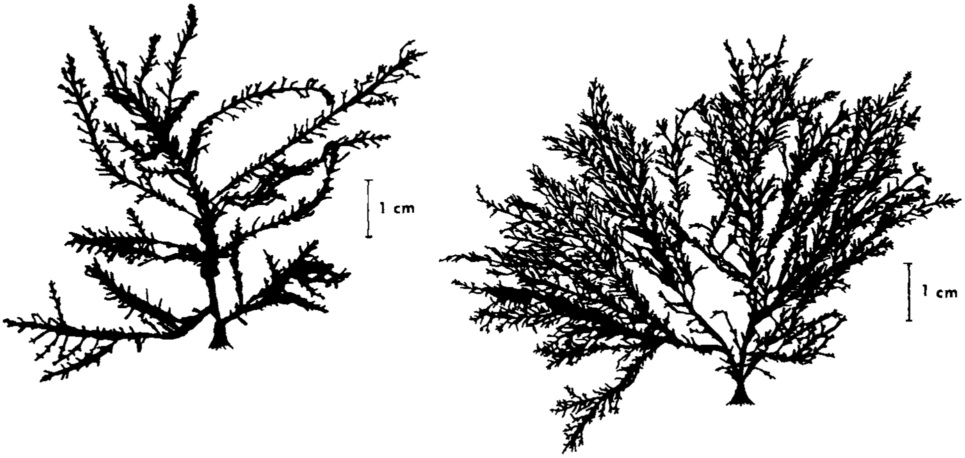


Fig. 2. Morphological variation in the Chinese specimens examined of *Gelidium amansii*. The uppermost plant (No. 541893) was collected in Fujian, May 1, 1954. The other plant corresponds to herbarium sheet No. 58695 collected in Qingdao, July 28, 1958.

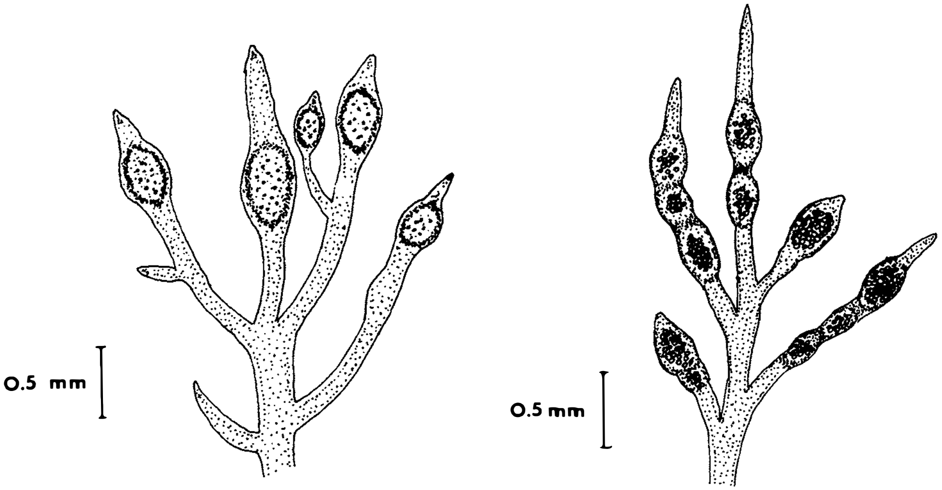


Fig. 3. Terminal portions of cystocarpic and tetrasporangial branchlets in *Gelidium amansii*.

1914, p. 99), he recognized that the species was so closely related to *G. amansii* that the two were often confused with each other. He indicated, however, that the more robust *G. pacificum* preferred habitats with strong waves and fast tidal currents, whereas the more delicate *G. amansii* preferred rather calm places. Therefore, it might be possible to look for habitats with intermediate levels of wave impact and tidal flows and thus determine whether there are two species or two ecotypes of the same species.

Gelidium amansii was originally described by Lamouroux (1805) from materials collected "sur les côtes de l'île de France et de Madagascar." As explained previously, in later studies, the species has been found repeatedly in areas (such as Japan, China, Taiwan) far removed and climatically different from the type locality. The description provided by Lamouroux (1805) is too general to characterize and define the species. The illustration provided by Lamouroux (1805, pl. 26, figs. 2–5) illustrates a well-branched and a poorly branched plant (Fig. 4). Branching in the well-branched plant is not as pinnate as shown by many of the Chinese specimens examined, or as commonly described for the Japanese populations (Okamura 1934, Akatsuka 1982). Furthermore, the terminal pinnae illustrated by Lamouroux are much longer than the terminal branches shown by the specimens attributed to this species. The unbranched plant illustrated (Lamouroux 1805, pl. 26, fig. 5) has almost naked primary branches, an exceptional condition observed in Japanese and Chinese *G. amansii* materials. As Okamura (1934) noticed, even small, young fronds of the so-called *G. amansii* in Japan are regularly pinnate, having almost a pyramidal outline. As the plant becomes older, branching becomes more complex. Thalli from deep water, which are larger and more devoid of branches than shallower plants, have close alternate branching (Okamura 1934). Therefore, a significant morphological difference apparently exists between the type materials described and illustrated by Lamouroux (1805) and the individuals commonly associated with this species. The problems are likely to be solved only after extensive studies of the field variation of the species now recognized as *G. amansii* and after reevaluation of the type materials. Segi (1959) examined the plants described by Lamouroux, but he probably was unaware of the morphological differences described here and did not comment on this matter. The photographic reproduction published by Segi (1959) confirms the morphological differences described here.

Frequently the name of the species has been used as *G. amansii* Lamouroux. However, Lamouroux (1805, p. 48) first placed it in *Fucus* as *F. amansii*. Later he transferred the species to his newly created genus *Gelidium* (Lamouroux 1813, p. 129). Therefore, the correct authors for the species should be *G. amansii* (Lamouroux) Lamouroux.

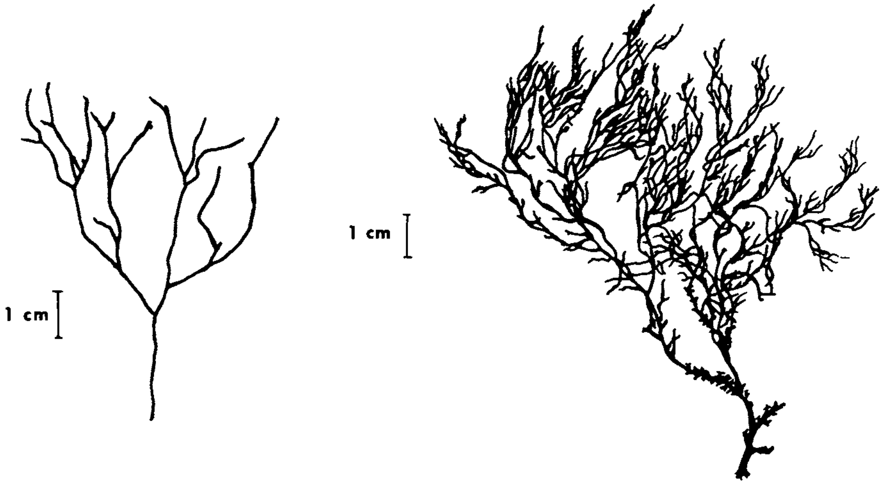


Fig. 4. Reproduction of the original illustrations of *Fucus amansii* (= *Gelidium amansii*) provided by Lamouroux (Lamouroux 1805).

Gelidium crinale (Turner) Lamouroux (Fig. 5)

Lamouroux, in Bory 1825, p. 191.

Synonym: *Fucus crinalis* Turner (Turner 1819, pl. 198).

The materials studied contain several tuft-forming thalli composed of cylindrical prostrate axes (150 μm in diameter) attached by stoloniferous rhizoids formed at regular or irregular intervals opposite cylindrical, upright branches of up to 5 cm high (Fig. 5). Erect axes are cylindrical at the base, up to 200 μm in diameter, and cylindrical or flattened apically. When flat, the apical parts are up to 150 μm thick, up to 200 μm broad at apices, and up to 500 μm broad at the origin of branches. Although normally restricted to the apical half of erect axes, branching is highly variable among the plants studied. In some specimens, branching is sparse, irregular, appearing as dichotomies rather than as pinnules. In others, branching is abundant, irregularly pinnate up to three orders, opposite or irregular along the axes. Sometimes several branches arise from a single point on the axes. The filiform axis often becomes wider at these branching points. External cortical cells are rounded or slightly ovoid in surface view, 5–7 by 6–10 μm and slightly elongated in transection (up to 7 μm). Inner cortical cells increase in size inwardly, grading into a medulla of elongated cells, rounded in transection, of 10–18 μm in diameter. Abundance of rhizoids varies greatly among individual axes and among parts of the same plant. They

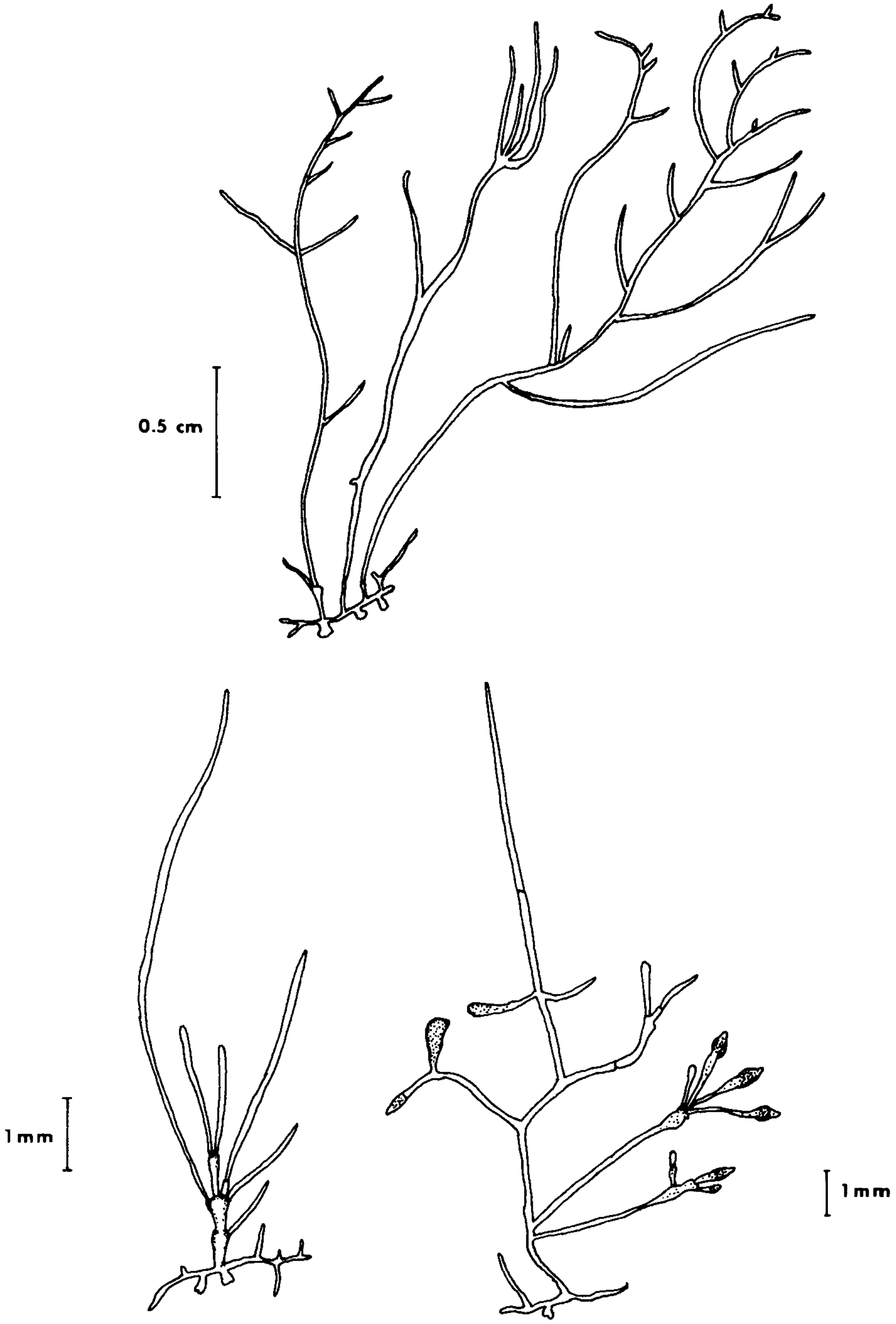


Fig. 5. Specimens of *Gelidium crinale* collected in Fujian showing branching variation and sporophylls.

can range from being almost absent or inconspicuous to being very abundant in the cortex or the medulla or both.

Tetrasporangia are borne on spatulate, lanceolate, or irregularly shaped sori at the upper and somewhat compressed ends of branches and axes. As the sorus empties, vegetative growth is resumed. The occurrence of subapical sori or even old, empty sori beneath new, more apical sori is common. Tetrasporangia are spherical in surface view, cruciately divided, up to 30 µm in diameter. Cystocarps are not seen.

Distribution: The materials studied include three specimens collected in Qindgao and six plants from Fujian. According to Tseng (1983), in China this species is also used as raw material for agar production. In Guangdong Province, it is known by the vernacular name of *Goumaocai.*

The species was originally described from England. Later authors have reported this taxon from several places in the Atlantic Ocean, both Europe and North America; the Red Sea; the Indian Ocean; the Mediterranean Sea; and the Pacific Ocean (see Santelices 1977 for a review). Often it occurs in intertidal habitats on sandy rocks. Throughout this wide range, several other entities have been confused with this species, and further research is likely to narrow the specific limits and restrict the geographical distribution.

Remarks: Some significant advance has been achieved in recent years through the gathering of fertile gametophyte plants. Thus, the finding of unilocular cystocarps on herbarium specimens of *G. crinale* var. *luxurians* Collins from California allowed Stewart (1974) to merge that variety with *Pterocladia media* Dawson. More recently, Umameshwara Rao and Kalieperumal (1980) transferred *G. heteroplastos* Børgesen to the genus *Pterocladia* upon finding unilocular cystocarps in materials from India. *Gelidium heteroplastos* had been described as a separate entity by Børgesen (1934), but the morphological similarity with *G. crinale* has made even Børgesen (1939, 1943) and other authors (Santelices 1977) doubt the distinction of the two species. The limits between *P. media* and *P. heteroplastos* and the limits between the present concept of *G. crinale* and morphologically similar species such as *G. arenarium* (Kylin 1938) and *G. sinicola* Gardner (Gardner 1927) are in need of critical evaluation.

Gelidium divaricatum Martens (Figs. 6, 7)

Martens 1868, p. 30, pl. 8, fig. 4.

Thalli are small, brownish to reddish purple, somewhat cartilaginous, densely caespitose, up to 2 cm high, consisting of linear, cylindrical, or slightly compressed creeping axes, 150–250 µm wide, attached to the substratum by irregularly disposed peglike holdfasts (Fig. 6). Erect branches arise from the creeping axes either at more or less regular intervals or, more infrequently, originate radially in numbers of two to five. Branches are up to 300 µm in diameter, cylindrical, often filiform, bipinnately branched with opposite or alternately disposed pinnulae, which often are unequal and commonly divaricate with acute or blunt apices. Cortical cells are rounded, about 5–6.5 µm in diameter, gradually increasing in size inwardly. Medullary cells are colorless, distinguished clearly in the thicker portions of the thallus only, nearly isodiametric in transection, up to 18 µm in diameter and with frequent lateral cytoplasmic connections.

Bisporangia and zonately and cruciately divided tetrasporangia are arranged without order in rounded or expanded sori on terminal or subterminal portions of obtuse ramuli with somewhat rounded to slightly claviform apices. Cruciately divided tetrasporangia are the most frequently found, outnumbering bisporangia and zonate tetrasporangia in the proportion of 50:10:1, respectively. Spores are elongated, slightly pyriform in outline, 35 by 60 µm. Cystocarps are terminal or subterminal in rounded, obtuse branches. In

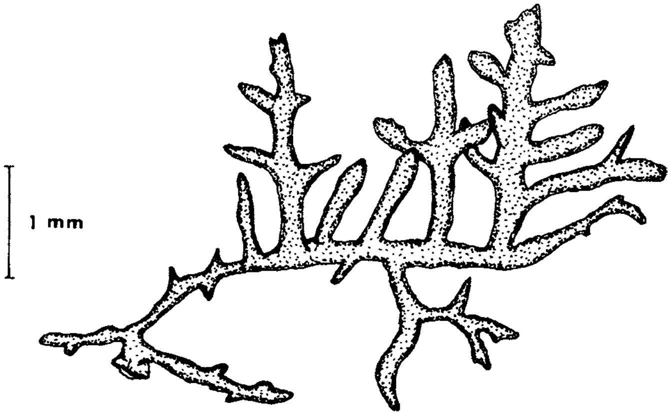


Fig. 6. External habit of a *Gelidium divaricatum* plant from Qingdao.

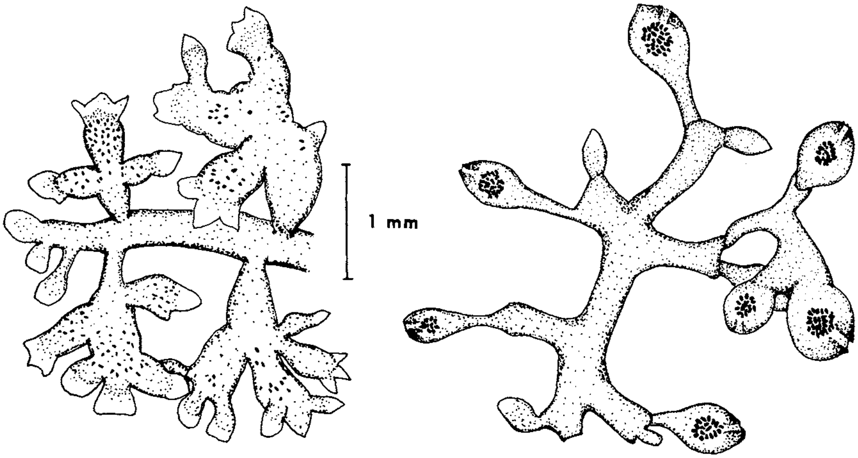


Fig. 7. Tetrasporangial and cystocarpic branchlets of *Gelidium divaricatum*.

surface view, cystocarps are globose, 300 by 400 µm and up to 0.5 mm thick, with one excentric ostiole on each surface of the frond, without a prominent peristome, but frequently with a clear apical notch (Fig. 7).

Distribution: This species was first described and illustrated by Martens (1868, pp. 30, 31, table 8, figs. 4, 4b) from materials collected in Hong Kong. Later studies (Okamura 1900, 1934; Tseng 1983) have reported the species distributed along the entire coast of China, including Hong Kong and Taiwan; along the coast of Japan from Hinga and Tosa to Rikuzan Prefecture; and in Vietnam and Korea. In Japan, the species is known by the vernacular name of *Hime tengusa*; in China, it is called *Shihua* and *Tanmae*. Everywhere it is said to occur on rocks, barnacles, mollusks, and other types of consolidated solid substratum near the high tide level, forming densely matted clumps, expanding in wide patches, and reaching larger sizes and more branched morphologies under shaded conditions. In spite of its small size, the species is reportedly used as raw material in agar production in China.

Remarks: Since their first descriptions, several authors (Okamura 1900; De Toni 1897, 1924) have called attention to the morphological similarity between *G. divaricatum* and *G. pusillum.* Indeed, *G. divaricatum* approaches *G. pusillum* var. *conchicola* Piccone et Grunow in some aspects of external morphology and *G. pusillum* var. *pulvinatum* (C. Agardh) Feldmann in the type of habitats where it occurs (see Santelices 1977 for a review of the several varieties recognized under *G. pusillum*). In sterile thalli, the filiform, cylindrical axes with opposite or alternate divaricate pinnules and the abundance and distribution of rhizoidal filaments segregate *G. divaricatum* from the aforementioned two forms of *G. pusillum.* The presence of bisporangia and zonate tetrasporangia and the dimensions of the cruciate tetrasporangia can be used as additional characters in fertile thalli.

Gelidium divaricatum seems to be the first species of *Gelidium* in which zonate tetrasporangia have been found. Bisporangia were previously observed by Fan (1961) in *G. pristoides.*

Gelidium japonicum (Harvey) Okamura

Okamura 1901, p. 57, pl. 21.

Synonym: *Suhria japonica* Harvey (Harvey 1859, No. 26).

In this species, the fronds are compressed, up to 5 cm high and 0.5 cm broad, often with a slight thickening similar to a midrib along the median portion of the fronds. Branching is absent or very irregular, with branches appearing as expanded proliferations from the margins and the surface of the thallus.

Cystocarps and tetrasporangial sori are said to be produced at the apical parts of proliferations. However, reproductive structures were not observed in the only specimen studied here.

The external cortical cells of *G. japonicum* are arranged in tetrads along most of the thallus, and in surface view of middle regions of the thallus, they are shorter and narrower than in other species of *Gelidium.*

Distribution: *Gelidium japonicum* also occurs in northern Taiwan and along the central and southern Pacific coast of Japan (Okamura 1934; Fan 1951; Akatsuka 1983, 1986).

Remarks: On the basis of the characters of the external cortical cells, also shown by *G. pristoides*, Akatsuka (1983) first segregated these two species from all other common *Gelidium* species and then erected a new genus, *Onisuka*, to receive them (Akatsuka 1986). However, Akatsuka (1986) also recognized that the most basal parts of the thallus had similar cell lengths, for example, in *G. japonicum* and *G. amansii* and between *G. pristoides* and *G. pusillum.* Furthermore, as discussed in a separate contribution in this volume (Rodríguez and Santelices 1987), the presence of tetrads is a common feature of all species of *Gelidium* and *Pterocladia* in the parts of the thallus close to the apex. Different species, depending on the patterns of cell division and elongation, might have tetrads along the axes at variable distances from the tips, as tetrads indicate areas where cell division is still common and where the distances between cells and the cell shapes have not been modified by cell growth. It is not surprising then that none of the 19 species of *Gelidium* and none of the five species of *Pterocladia* studied by Rodríguez and Santelices (1987) had tetrads near the basal parts of the thallus. This is in agreement with the observation of Akatsuka (1986) that no significant differences exist in cell sizes in the most basal parts of the fronds of *G. japonicum* and *G. pristoides* as compared with other species of *Gelidium.* Therefore, the creation of a new genus based on this clearly variable character is not justified.

Gelidium planiusculum Okamura (Fig. 8)
Okamura 1935, p. 442.

The plants studied are purple-red, compressed, up to 13 cm high, consisting of several distichously, pinnately branched, percurrent axes rising from a massive, rhizomatous holdfast. Erect axes are clearly compressed, 1–1.5 mm broad at the base, 1.5–2 mm at the uppermost parts of the thallus (Fig. 8). Branching of erect axes varies from one to three orders, occurring throughout the length of the axis, or restricted to the apical two-thirds of erect axes, disposed alternately or opposite along the axis, slightly narrowed and incurved at the base. Erect axes and branches often produce broad, blunt apices that continue into narrow, filiform projections. Second and higher order branchlets also become filiforms apically. In surface view, the cortical cells are rounded, up to 7 μm in diameter. In transection, they are isodiametric, up to 6 μm in diameter, gradually increasing in size inwardly. Medullary cells are ovoid, running parallel or oblique to the main axis, up to 25 μm in diameter, and with numerous medullary cells of smaller diameter intermixed in the central parts of the medulla. Rhizoidal filaments are abundant in the inner cortex, although a few are dispersed among the medullary cells.

Tetrasporangial sori are on lanceolate, spatulate sporophylls arising on the filiform branchlets. Tetrasporangia are arranged without order in irregularly shaped sori, spherical, cruciately divided and up to 35 μm in diameter. Cystocarps are not seen.

Distribution: This species is endemic to Taiwan, in the coastal area between Shuiwei and Peikuan (Fan 1951).

Remarks: The most characteristic morphological feature of this species is the nearly continuous fringe of filiform branchlets along the margins and tips of erect axes and branchlets. Somehow this morphology recalls the morphology adopted by some species of *Gelidium* and *Pterocladia* when cultivated under free-floating conditions (Santelices 1976a) or when living under conditions of intense sunlight and reduced water movement (Santelices 1976b). From that perspective, *G. planiusculum* perhaps could be interpreted

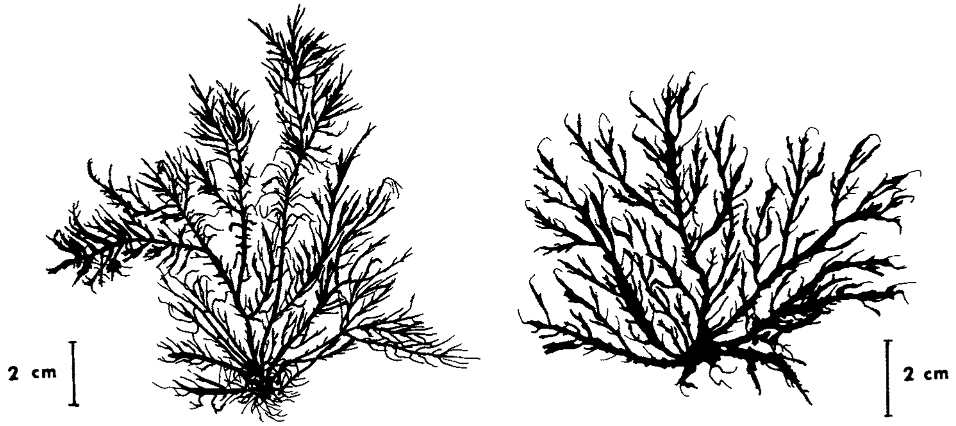


Fig. 8. Morphological variation in *Gelidium planiusculum* collected in Taipei, Hsien, Taiwan.

as an ecotype of different species. However, the presence of tetrasporangial sporophylls on these filiform projections and the peculiar medullary structure of the frond, with large and small medullary cells, are characters not yet found in other species in the same area.

Gelidium pusillum (Stackhouse) Le Jolis (Fig. 9)
Le Jolis 1863, p. 139.
Synonym: *Fucus pusillus* Stackhouse (Stackhouse 1801, pl. 6).

Two forms of *G. pusillum* are represented in the Chinese materials studied: *G. pusillum* var. *cylindricum* Taylor and *G. pusillum* var. *pacificum* Taylor. The plants identified within the variety *cylindricum* (Taylor 1945) are dark red, up to 1.2 cm high, attached to the substratum by cylindrical creeping axes (240 µm in diameter) with small holdfasts at irregular intervals. Erect axes are cylindrical, sometimes slightly lanceolate apically, up to 500 µm wide, normally finishing in truncate apices with several proliferations. In all the specimens examined, the erect axes are made up of imbricated segments (Fig. 9). They seemingly result from apical destruction followed by resumption of growth until a new event causes apical destruction. In fact, less than 10% of the 50 erect axes here studied had apical cells. All of them had truncated apices. Grazing could be assumed to be one of the factors producing this growth pattern; however, the imbrications produced by apical destruction and new growth are too short along a given axis and too common among all axes for grazing to be a likely cause. In a few individual plants, apical die-back from what seems to be an empty apical tetrasporangial sorus was observed and perhaps accounts for the imbricated construction of the axis. Apical die-back after spore release also occurs in *Pterocladia caerulescens* (Santelices 1976, 1978) and has profound morphological effects. This condition has not been observed in other varieties of *G. pusillum*; therefore, if this interpretation is correct, the variety *cylindricum* of *G. pusillum* might correspond to a different species.

The variety *pacificum* (Taylor 1945, Loomis 1960, Santelices 1977) is represented in the Chinese materials by a handful of plants, attached by cylindrical creeping axes, up to

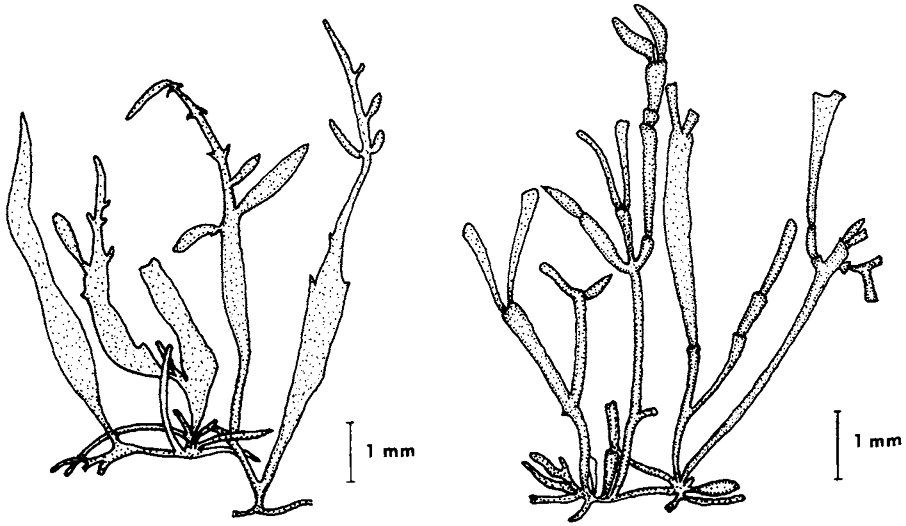


Fig. 9. General habit of plants of *Gelidium pusillum* collected in Hainan, February 1976. They represent the variety *pacificum* (left) and the variety *cylindricum* (right).

100 µm in diameter, with holdfasts at regular intervals (Fig. 9). Erect axes are cylindrical below, up to 200 µm in diameter, and flat, spatulate, or lanceolate distally, appearing as blades with short stalks. Blades have lanceolate or spatulate marginal branchlets or proliferations from the truncate upper end of blades. Frequently, several erect axes or branches curve downwardly and become new creeping axes. Plants are purplish-red, up to 2 cm high.

Distribution: According to Tseng (1983), the species occurs along the entire coast of China. Elsewhere the species is widespread in most temperate and warm seas. Several different varieties normally are assigned to the species, and some have been revised recently (Santelices 1977). However, critical experimental studies on the specific limits of these small-sized taxa are missing, and perhaps several different species of *Gelidium* are included in our present concept of *G. pusillum.*

Gelidium vagum Okamura (Fig. 10)

Okamura 1934, p. 58, pls. 25, 32, figs 8–10.

The plants are purple-red, compressed, up to 6 cm high, composed of one to several distichously, pinnately branched percurrent axes rising from a stoloniferous holdfast (Fig. 10). Percurrent axes are cylindrical, becoming abruptly narrowed into one to several very acute and sometimes incurved apices. Both margins of the percurrent axes are invested with two types of branches (Fig. 10). Some are narrowed and elongated, or filiform, with acute apex, and in turn invested with a higher order, spinous branches. Others are strap-shaped, widened, and compressed as the main percurrent axis, supporting higher order branches that might be either filiform or compressed. Some of these strap-shaped, widened branches have a narrowed, almost cylindrical, base. Others have a widened base that contributes further to provide the strap-shaped appearance to the thallus. Branches have a basal deflection angle, and frequently they are curved upwardly, with very acute tips. The number of filiform vs. strap-shaped branches changes from one plant to another and probably is significantly modified by local ecological conditions.

In surface view, the uppermost and middle parts of the axes have external cortical cells elongated and arranged in rows parallel to the main axes, up to 5 by 12 µm. In the basal-most parts of the axes, they are subcuboidal, rectangular, with acute angles, and up to 10 by 12 µm. In transection, they are nearly isodiametric, up to 8 µm, slightly increasing in size inwardly. Medullary cells are rounded, up to 25 µm in diameter, with thick walls. Hyphae are restricted mainly to the medullary tissue, often in bundles of up to 10 to 12. In thicker parts of the thallus, they can also be found in the inner cortex.

Tetrasporangia and cystocarps are not seen.

Distribution: In China, this species is used as raw material for agar production. It occurs along the Yellow Sea coast. In addition, it has been reported from Japan and Taiwan (Okamura 1934, Fan 1951). All the specimens studied came from Qingdao, collected at various dates between 1960 and 1982.

Pterocladia capillacea (Gmelin) Bornet et Thuret (Fig. 11)

Bornet and Thuret 1876, p. 57, pl. 20, figs. 1–7.

Synonym: *Fucus capillaceus* Gmelin (Gmelin 1768, p. 146, pl. 15, fig. 1).

All the Chinese materials examined had been identified previously as *P. tenuis* Okamura. Additional materials of this species identified under the name of *P. nana* Okamura might be expected to be found in additional collections, as these are the specific epithets most commonly provided to the species in the Sino-Japanese subregion of the Pacific Ocean. Field studies in several areas of the world (Moore 1945, Dawson 1952, Stewart 1968, Santelices 1977) have shown that the morphological variability of natural

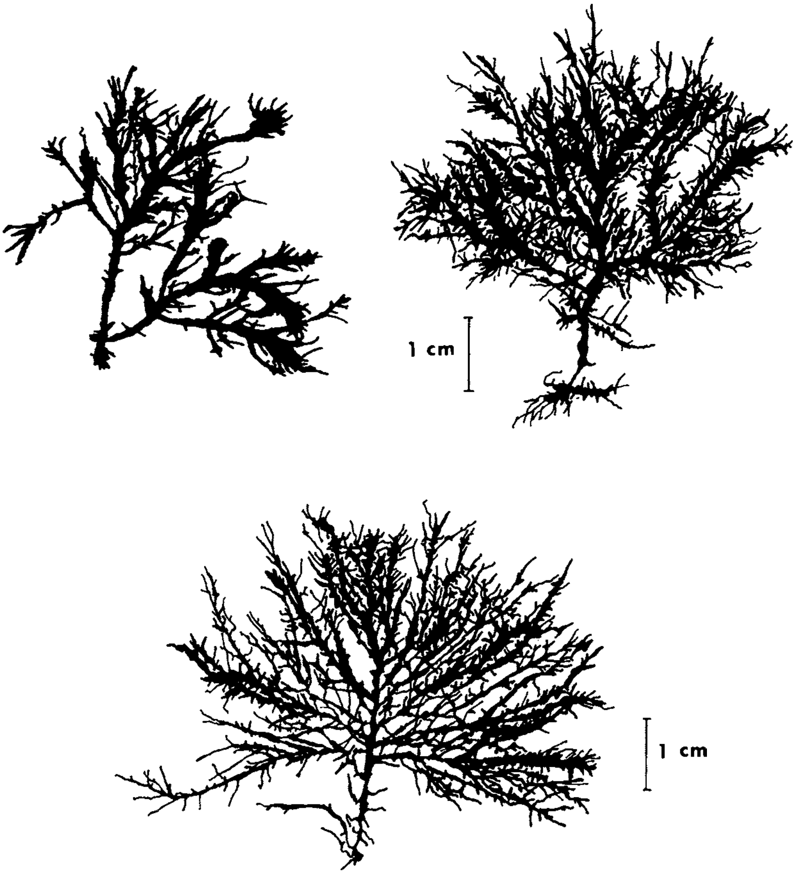


Fig. 10. External morphological variation in *Gelidium vagum* collected in Qingdao, May 12, 1964.

populations of *P. capillacea* includes the taxonomic concepts of the aforementioned two *Pterocladia* species as well as those of several other species (*P. densa* Okamura, *P. pyramidale* (Gardner) Dawson, *P. okamurai* (Setchell et Gardner) Taylor, *P. robusta* Taylor, *P. mexicana* Taylor, and *P. complanata* Loomis).

The plants studied are purple-red, compressed, up to 8 cm high, consisting of one to several distichously, pinnately branched percurrent axes rising from a holdfast of entangled stolons (Fig. 11). The erect axes are slightly flattened below, strongly flattened above, with spatuliform or attenuated apices, up to 0.5 mm in diameter at their bases and up to 1.8 mm broad in the flat parts. Branching of up to 3–4 orders generally is restricted to the upper two-thirds of the frond. In the materials examined, branching is two to three times pinnate in the pyramidal outline, with opposite or alternate pinnules, 1–2 mm broad, abruptly constricted at the base and with obtuse apices.

Tetrasporangia are disposed without order, covering areas of small or large branches. Tetrasporangia are cruciately divided, rounded, and up to 30 µm in diameter. Cystocarps are not seen.

Fig. 11. Some morphological variants of *Pterocladia capillacea* from China. Both specimens were collected in Fujian, June 1954.

Distribution: In China, the species is known under the vernacular name of *Yimaocai* (Tseng 1983) and is reportedly common on the entire coast. The specimens studied had been collected in Qingdao, Fujian, and Guangdong at different dates between 1953 and 1973. *Pterocladia capillacea* is used for food and as raw material for agar production. Elsewhere the species has a widespread distribution in temperate and warmer waters (see Stewart 1968 and Santelices 1977).

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CHINESE SPECIES OF *GELIDIUM* LAMOUROUX AND OTHER GELIDIALES (RHODOPHYTA), WITH KEY, LIST, AND DISTRIBUTION OF THE COMMON SPECIES

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

Key to Common Chinese Species of Gelidiales

1. Internal rhizoidal filaments absent . . . . *Gelidiella acerosa*
1. Internal rhizoidal filaments present at least in the older parts of the plants 2

    2. Cystocarps unilocular . . . . *Pterocladia capillacea*
    2. Cystocarps bilocular . . . . 3. *Gelidium* spp.

3. Thallus small, less than 2 cm tall 4
3. Thallus large, more than 2 cm tall 5

    4. Erect branches terete or slightly compressed, branch axil nearly right-angled, branches with numerous short opposito-alternate ultimate branchlets . . . . *G. divaricatum*
    4. Erect flat branches ovato-lanceolate, axil not as above, branches simple or sparingly pinnate . . . . *G. pusillum*

5. Median line of main branches thickened like a midrib . . . . *G. japonicum*
5. Thallus not as above 6

    6. Thallus rather wiry, branches with loosely somewhat tri-tetrastichous ultimate branchlets . . . . *G. crinale*
    6. Thallus not wiry, ultimate branchlets simply divided 7

7. Thallus less than 10 cm tall 8
7. Thallus more than 10 cm tall 10

    8. Branches contiguous, repeatedly pinnate . . . . *G. yamadae*
    8. Branches not as above 9

9. Basal branches the longest . . . . *G. tsengii*
9. Basal branches nearly equal in length . . . . *G. vagum*

    10. Thallus flattened throughout, branches blunt at apex 11
    10. Thallus flattened to compressed, at least in the lower portion, branches acute at apex 12

11. Ultimate branchlets dense; cortex composed of two to four layers . . . . *G. johnstonii*
11. Ultimate branchlets few, on clavate branchlets; cortex composed of one layer . . . . *G. kintaroi*

    12. Plants regularly branched; proximal branches decompound pinnate branchlets . . . . *G. pacificum*
    12. Plants irregularly branched, branches very regularly and elegantly pinnated with equally long branchlets . . . . *G. amansii*

List and Distribution of Gelidiales in China

Gelidiella acerosa (Forsskål) Feldmann et Hamel (Fig. 1)

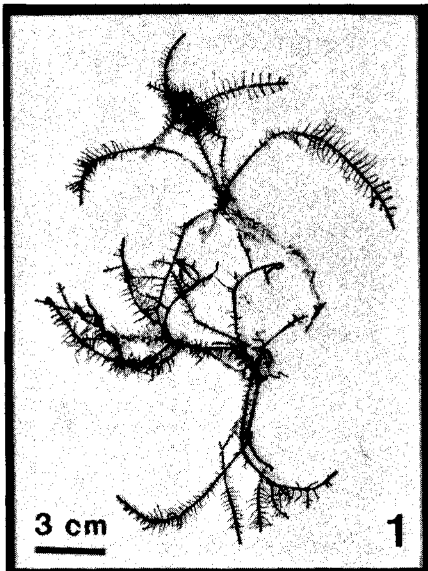
Zhang Junfu and Xia Bangmei 1979, p. 21, fig. 1; pl. I, fig. 9.

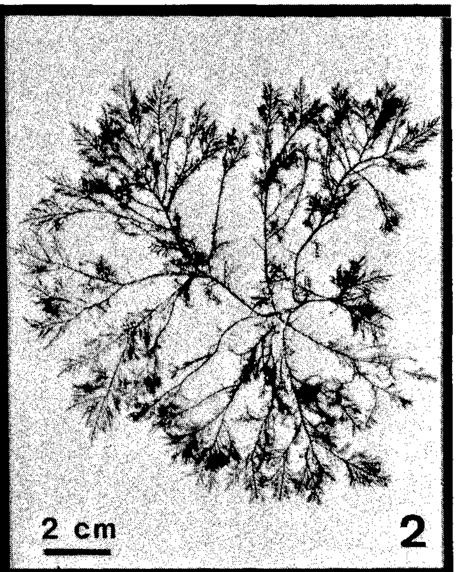
Distribution: Hainan Island and Xisha Island, Guangdong Province (Zhang and Xia B. 1979; Zhang et al. 1983).

Gelidium amansii (Lamouroux) Lamouroux (Fig. 2)

Tseng et al. 1962, p. 116, fig. 27, 1; fig. 28, 1, 2; pl. 7, fig. 51.

Distribution: Beidaihe, Hebei Province (Grubb 1932); Qingdao (Tseng and Li 1935); abundant on the Huanghai coast (Tseng and Chang 1952); western Donghai coast (Tseng et al. 1962; Zhang et al. 1983); Xiamen, Fujian Province (Tseng 1936); northern Taiwan (Fan 1951; Chiang 1962a, under *G. amansii* f. *latioris* and *G. amansii* f. *elegans*).





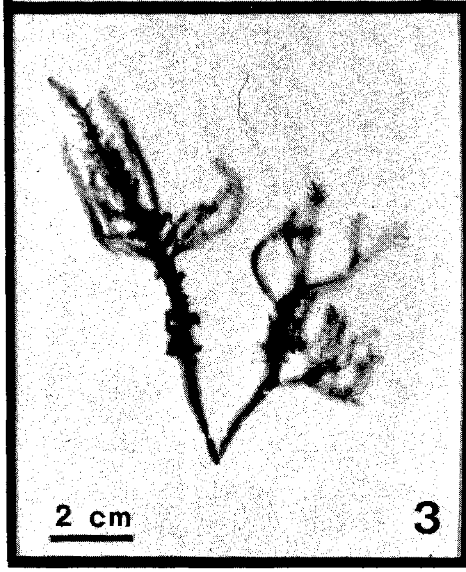


Fig. 1. ***Gelidiella acerosa*** **(AST 80-2223).**

Fig. 2. ***Gelidium amansii*** **(AST 56-300).**

Fig. 3. ***Gelidium crinale*** **(AST 82-216).**

Fig. 4. ***Gelidium divaricatum*** **(AST 82-591).**

Gelidium crinale (Turner) Lamouroux (Fig. 3)

Tseng et al. 1962, p. 121, pl. 7, fig. 55.

Distribution: Xiamen, Fujian Province (Tseng 1936); common on entire coast (Tseng 1938; Tseng et al. 1962; Tseng and Chang 1963; Zhang et al. 1983).

Gelidium divaricatum Martens (Fig. 4)

Tseng et al. 1962, p. 118, fig. 29, pl. 7, fig. 52.

Distribution: Hong Kong (Martens 1866; the type locality); Xiamen, Fujian Province (Tseng 1936); Yentai, Weihai, Qingdao, Shandong Province (Tseng 1938); Huanghai and Donghai coasts (Tseng and Chang 1959); common on entire coast (Tseng et al. 1962, Zhang et al. 1983).

Gelidium japonicum (Harvey) Okamura (Fig. 5)

Tseng et al. 1962, p. 120, fig. 31; pl. 7, fig. 54.

Distribution: Xiamen, Fujian Province (Tseng et al. 1962, Zhang et al. 1983); in Taiwan at Shuiwei, Yeliu, Pachymen, Tali, Patoutsu, Chiuaoti, Santiaochiao, Hehsing, Peikuan, Kuishan (Fan 1951, Chiang 1962a, Tseng et al. 1962, Zhang et al. 1983).

Gelidium johnstonii Setchell et Gardner

Tseng et al. 1980, p. 59, figs. 1, 2, pl. 1D.

Distribution: Hong Kong (Tseng et al. 1980); Penghu Island, Taiwan (Fan 1951, as *G. kintaroi*; Segi 1955).

Gelidium kintaroi (Okamura) Yamada

Fan 1951, p. 12, fig. 7, pl. 4, fig. 1.

Distribution: Xiamen, Fujian Province (Segi 1955) in Taiwan at Hsinghuatien, Tapientou, Chientsuchiao, Laomei, Shimen, Shuiwei, Yeliu, and Pachymen (Fan 1951).

Gelidium latiusculum Okamura

Fan 1951, p. 5, fig. 3; pl. 1, fig. 3.

Distribution: In Taiwan at Shuiwei, Yeliu, Chiuaoti, Santiaochiao, Hehsing, Kuishan, and Banjiashiuh (Fan 1951, Chiang 1962a).

Gelidium pacificum Okamura (Fig. 6)

Tseng et al. 1962, p. 119, fig. 30; pl. 7, fig. 53.

Distribution: Zheijiang and Fujian Province (Tseng et al. 1962, Zhang et al. 1983); Donghai coast (Tseng and Chang 1963).

Gelidium planiusculum Okamura

Fan 1951, p. 7, fig. 4; pl. 3, figs. 1, 2.

Distribution: In Taiwan at Pachymen, Shuiwei, Yeliu, and Peikuan (Fan 1951; Chiang 1962a).

Gelidium pusillum (Stackhouse) Le Jolis (Fig. 7)

Tseng et al. 1980, p. 59.

Distribution: Beidaihe, Hebei Province (Grubb 1932); Qingdao, Shandong Province; Hong Kong (Tseng et al. 1980); rare on Huanghai coast and common on Nanhai coast, (Tseng and Chang 1963); in Taiwan at Pachymen and Patoutsu (Fan 1951, Chiang 1962a).

Gelidium tsengii Fan

Fan 1961, p. 248, fig. 1.

Distribution: Hong Kong (Fan 1961). Not collected again.

Gelidium vagum Okamura (Fig. 8)

Zhang and Xia, E. 1986, p. 521, figs. 1, 2; pl. 1, figs. 1–9.

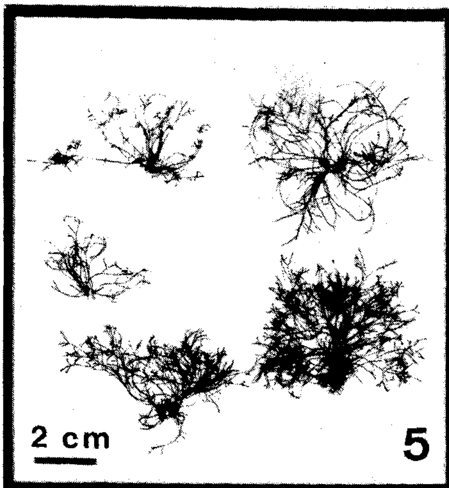
Synonyms: *Gelidium grubbae* (Fan 1961, p. 247); *Gelidium chungii* Setchell et Gardner (*nomen nudum*).

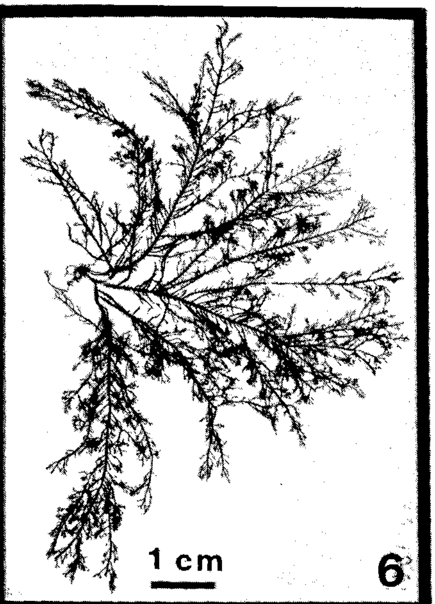
Distribution: Beidaihe, Hebei Province; Weihai, Shandong Province (Fan 1961 as *G. grubbae* Fan); Huanghai coast (Zhang et al. 1983, Zhang and Xia E. 1986).

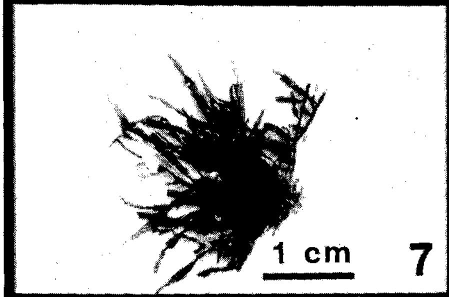
Gelidium yamadae Fan

Fan 1951, p. 10, fig. 6; pl. 5.

Distribution: In Taiwan at Hsinghuatien, Tapientou, Chientsuchiao, Laomei, Shimen, and Peikuan (Fan 1951, as a new name for *Gelidium densum* Okamura, a later homonym of *G. densum* Gardner (Gardner 1927)). Not reported again.







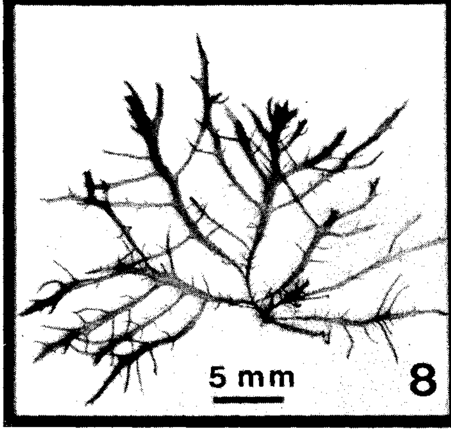


Fig. 5. ***Gelidium japonicum*** **(AST 53-1604).**

Fig. 6. ***Gelidium pacificum*** **(AST 54-1859).**

Fig. 7. ***Gelidium pusillum*** **(AST 80-2495).**

Fig. 8. ***Gelidium vagum*** **(AST 65-31).**

Fig. 9. ***Pterocladia capillacea*** **(AST 82-215).**

Pterocladia capillacea (Gmelin) Bornet et Thuret (Fig. 9)

Tseng et al. 1962, p. 122, figs. 27:2, 28:3, 4; pl. 7, fig. 56.

Synonyms: *Pterocladia tenuis* Okamura (Fan 1951, Tseng et al. 1962, Zhang et al. 1983); *Pterocaldia nana* Okamura (Fan 1951, Chiang 1962).

Distribution: Common on entire coast (Tseng et al. 1962, Zhang et al. 1983); in Taiwan at Hsinghuatien, Tapientou, Chientsuchiao, Laomei, Shimen, Shuiwei, Yeliu, Pachymen, Patoutsu, Chiuaoti, Santiaochiao, Tali, Hehsing, Peikuan, Kuishan (Fan 1951), and Penghu Island (Chiang 1962b).

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SEPARATION OF *GELIDIUM* AND *PTEROCLADIA* ON VEGETATIVE CHARACTERS

Deni Rodríguiz and Bernabé Santelices

Abstract

Cystocarpic structure is the only presently accepted morphological character segregating the red algal genera *Gelidium* and *Pterocladia* (Gelidiales). However, because of the common scarcity of sexual thalli, this character is of limited application for routine taxonomic purposes. Two proposed vegetative differences, shape of medullary cells and distribution of rhizoidal filaments, have not gathered general recognition. Three others are tested here with 19 species of *Gelidium* and five species of *Pterocladia*. The presence of basally incurved branches seems of limited use for generic segregation. The significant variation in shape and size of cortical cells along the axis limits their taxonomic use except when comparisons are restricted to basal parts of erect axes. The position of the apical cell in relation to cortical cells and lateral initials allows generic segregation in all but one of the 24 species studied.

Introduction

Cystocarpic structure is the only presently accepted morphological character segregating *Gelidium* from *Pterocladia* (see Santelices 1974 and Santelices and Stewart 1985 for a review). However, because of the common scarcity of sexual thalli, this character is of limited application for routine taxonomic purposes.

Several vegetative characters have been proposed for segregation of the two genera (Fig. 1), but none has been generally accepted yet. Form and disposition of medullary cells were proposed by Okamura (1934), who distinguished the rounded and loosely packed medullary cells of *Gelidium* from the more angular and closely packed medullary cells of *Pterocladia*. The great variability shown by this character on a larger number of species (Loomis 1949; Dixon 1958; Stewart 1968) has rendered it useless for generic segregation.

Okamura (1934) also suggested rhizoidal localization as a segregative character. Thus, the rhizoids (also called hyphae) were in the cortical or in the external medullary cells of *Gelidium*, contrasting with their disposition among the inner medullary cells in the species of *Pterocladia*. Later authors evaluated the taxonomic validity of this character and concluded that it is too variable to be taxonomically reliable (see Santelices 1974 for a review).

Stressing external rather than internal morphological differences, Stewart (1968) suggested that the lateral branches of unlimited growth of *Gelidium* had a basal bending at the point of branching that was absent in the species of *Pterocladia*. She observed that basally incurved branches were common among the Californian species of *Gelidium* but were lacking in the species of *Pterocladia*. The taxonomic validity of this character has not been tested further.

Recently, Akatsuka (1981) suggested that the form, shape, and disposition of cortical cells might allow segregation of *Gelidium* from *Pterocladia*. Working with Japanese species, Akatsuka (1981) found that the surface cortical cells of *Gelidium* were ovoid, elliptical, and polygonal, with round corners and irregularly arranged. In *Pterocladia*, the cells were ovoid, pyriform, or elliptical, with their longer axis nearly parallel to thallus axis. In later studies, Akatsuka (1986a) suggested that this feature could be applied to non-Japanese species of *Gelidium* and *Pterocladia*. The usefulness of this character has not been evaluated by other authors.

Recent studies of apical morphology in a variety of species of *Gelidium* and *Pterocladia* (Rodríguez and Santelices 1987) revealed that the apical morphology is a rather conservative character for most species. When the spatial relationships between the apical cell of the main axis (axial apical initial) and the initial of lateral branches (lateral initials) were studied, intergeneric differences in the pattern of morphological organization were observed. In *Pterocladia* the axial apical initial as well as the morphologically similar lateral initials were found strictly only in depressions between the lobes formed by the marginal projection of the outer cortical cells. In *Gelidium*, lateral initials have the shape of an inverted cone and are smaller than the globose, dome-shaped axial apical initials. Axial apical initials occur at the tip of axes, remaining exposed beyond the cortical cells, or in depressions between cortical lobes. Initials of lateral branches of unlimited growth occur both at depressions and at the summit of the lobes. The differences in the locations of these initials were based on a limited number of species in the earlier study (Rodríguez and Santelices 1987). The present study intends to evaluate the taxonomic importance of apical morphology in a larger number of species, and to reexamine some of the taxonomic characters proposed previously by Stewart (1968) and Akatsuka (1981).

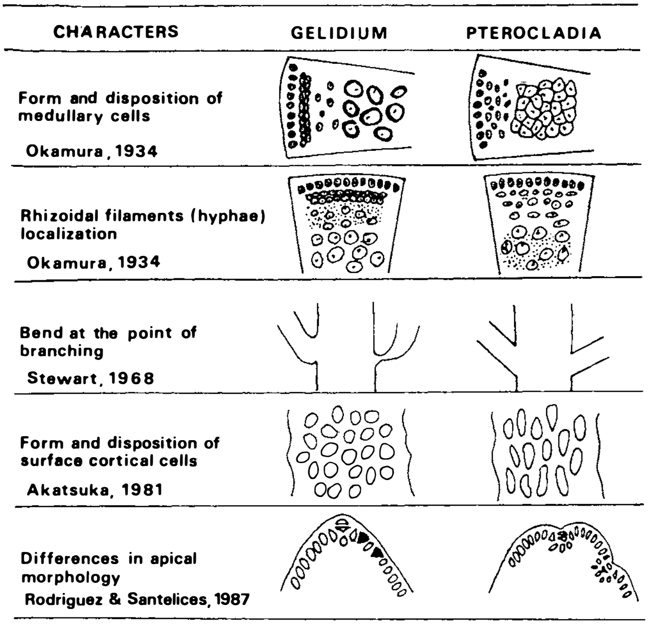

Fig. 1. Morphological vegetative features proposed in the literature to segregate *Gelidium* from *Pterocladia*.

Material and Methods

Data were obtained from herbarium specimens and freshly collected plants of five species of *Pterocladia* and 19 species of *Gelidium* (Table 1). In general, the study was restricted to the larger-sized species in both genera, as the taxonomy of small-sized species is less well understood.

Basally incurved branches were defined as those showing a deflection angle generated by the change in direction of the branch (see Fig. 2). In branches without basally incurved bases, the original ramification angle remains constant without deflection. Measurements of the deflection angle were made by using camera lucida drawings or photographic copies taken under a stereomicroscope.

Table 1. List of Species Studied

Species	Date and Place of Collection	Identified by
P. bulbosa Loomis	April 21, 1974 Black Point, Oahu, Hawaii	B. Santelices
P. caerulescens (Kützing) Santelices	Sept. 26, 1971 Kuhio Beach, Oahu, Hawaii	B. Santelices
	Jan. 19, 1972 Maalaea Bay, Maui, Hawaii	
P. capillacea (Gmelin) Bornet et Thuret	Jan. 19, 1971 Maalaea Bay, Maui, Hawaii	B. Santelices
	Sept. 4, 1971 Pupukea, Oahu, Hawaii	
P. lucida (Turner) J. Agardh	April 8, 1962 Houghton Bay, New Zealand	M. J. Parsons
	Feb. 15, 1970 Waitangi Beach, New Zealand	
P. tenuis Okamura (= *P. capillacea* cf. Santelices, this volume)	June 1933 Kanagawa Prefecture, Japan	ex. herb. Okamura
G. amansii (Lamouroux) Lamouroux	April 7, 1977 Falun, Taipei, Taiwan	Y. M. Chiang
G. amansii f. *elegans* (Kützing) Okamura	Aug. 3, 1933 Ehime Prefecture, Japan	ex. herb. Okamura
G. arborescens Gardner	June 20, 1974 Pebble Beach, California	I. A. Abbott
G. chilense (Montagne) Santelices et Montalva	May–Sept. 1982 Central Chile	B. Santelices
G. coulteri Harvey	July 4, 1974 Mussel Point, California	I. A. Abbott
	June 3, 1984 La Jolla, California	J. Stewart
G. crinale (Turner) Lamouroux	Aug. 11, 1913 Onno-Machi, Japan	ex. herb. Okamura
G. decumbens Okamura	June 13, 1933 Kanagawa Prefecture, Japan	ex. herb. Okamura
G. howei Acleto	Feb. 8, 1974 Piura, Perú	J. Acosta
G. japonicum (Harvey) Okamura	May 20, 1959 Patoutsu, Keelung, Taiwan	Y. M. Chiang
	Sept. 1, 1968 Wakayama Prefecture, Japan	T. Yamamoto
G. lingulatum Kützing	May 16, 1976 Valdivia, Chile	B. Santelices
	July 10, 1976 San Antonio, Chile	
G. linoides Kützing	Sept. 8, 1933 Shizouka Prefecture, Japan	ex. herb. Okamura

Table 1. List of Species Studied (cont'd.)

Species	Date and Place of Collection	Identified by
G. nudifrons Gardner	June 2, 1984 La Jolla, California	J. Stewart
G. planiusculum Okamura	Jan. 28, 1980 Pi-tou-Chiao, Taipei, Taiwan	Y. M. Chiang
G. pluma Loomis	April–June 1974 Pupukea, Oahu, Hawaii	B. Santelices
G. pristoides (Turner) Kützing	Sept. 29, 1968 Jeffreys Bay, South Africa	B. Santelices
G. purpurascens Gardner	June 1, 1974 Mission Point, California	I. A. Abbott
	July 4, 1974 Mussel Point, California	
G. pusillum (Stackhouse) Le Jolis	Sept. 1971 Pupukea, Oahu, Hawaii	B. Santelices
	Jan. 1972 Maalaea Bay, Maui, Hawaii	
	Feb. 1972 Pupukea, Oahu, Hawaii	
	June 1974 Pebble Beach, California	
	May 1985 Horcón, Quintero, Chile	
G. rex Santelices et Abbott	Jan.–Oct. 1984 San Antonio, Chile	B. Santelices
G. robustum (Gardner) Hollenberg et Abbott	June 2, 1984 La Jolla, California	J. Stewart
G. tenue Okamura	May 14, 1933 Kanagawa Prefecture, Japan	ex. herb. Okamura

Patterns of size and arrangement of cortical cells were studied in 20 microscopic fields for each species at four levels along the thallus, namely in the apical, subapical, middle, and basal-most parts. Basal parts were defined as those occurring between 1 and 2 cm from the prostrate axis. Apical parts were defined as the first 500 µm immediately below the apical cell. Subapical parts included the next 500 µm. In addition to surface-view observations, longitudinal and transverse sections of the basal-most parts were studied to understand tridimensional shape and disposition of cortical cells. In this case, the material was cut off at various thicknesses, from 5 to 20 µm, by means of freezing and paraffin microtomes, and the sections were stained with alcian blue and light green. Cells in these sections were photographed. Tridimensional reconstructions of cell sizes, cell volumes, and cortical tissues were prepared by using the photographs.

The apical structure of vegetative axes and branches was studied by using entire apices or longitudinal sections of tips obtained with a freezing microtome, cut at various thicknesses, from 5 to 20 µm, and stained with methyl blue. Drawings were prepared by using a camera lucida.

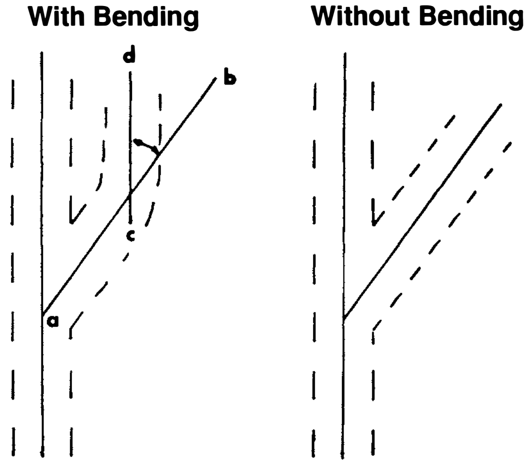

Fig. 2. Bending angle produced by the change of direction of basally incurved branches.

Observations and Discussion

Basally Incurved Branches: Basally incurved branches (in earlier literature, geniculate branches) were shown (Table 2) by most *Gelidium* species included in this study. In *G. pusillum* (Stackhouse) Le Jolis, however, some populations showed and others lacked the basally incurved branches. In addition, in given plants of *G. japonicum* (Harvey) Okamura, some branches were incurved, and others lacked the character. Two species of *Pterocladia, P. bulbosa* Loomis and *P. caerulescens* (Kützing) Santelices, had basally incurved branches, whereas only some branches of *P. lucida* (Turner) J. Agardh showed them. It was concluded, therefore, that this character is unreliable for generic segregation.

Shape and Disposition of Cortical Cells: Detailed study of shape and disposition of cortical cells indicated differences in cell size, cell shape, size of intercellular spaces, and spatial disposition along the axes (Fig. 3). In general, four types of arrangement were observed: Cells may be isolated one from the other or may be aggregated, forming pairs or tetrads. In addition, they may be regularly (forming rows) or irregularly arranged.

Examination of cell arrangement in the apical and subapical parts of the thallus indicated that most species of *Gelidium* and *Pterocladia* have irregularly disposed cells that might or might not be arranged in pairs. A few species of *Gelidium* and one species of *Pterocladia* had regularly arranged tetrads. Cells disposed in pairs and tetrads represent cases in which the original pattern resulting from cell division has not been modified by later elongation. Such modification was observed in middle parts of all species of *Gelidium* and *Pterocladia* included in this study except for *G. pristoides* (Turner) Kützing and *G. japonicum.* Tetrads in these last two species were observed throughout the axes. However, cells forming pairs also were found at these levels, indicating that cell arrangement is due to growth.

When the basal-most parts of the axes are considered, an almost complete generic segregation occurs. In all the species of *Gelidium,* cortical cells close to the base were rounded, irregularly disposed, and without forming pairs or tetrads. With the exception of *P. bulbosa,* all species of *Pterocladia* had cortical cells elongated, pyriform, or elliptical

Table 2. Species Showing Presence or Absence of Basally Incurved Branches

	With Bending	Without Bending	With and Without Bending
Gelidium			
	G. amansii	*G. pusillum*	*G. japonicum*
	G. arborescens		*G. pusillum*
	G. coulteri		
	G. crinale		
	G. decumbens		
	G. howei		
	G. lingulatum		
	G. linoides		
	G. nudifrons		
	G. planiusculum		
	G. pluma		
	G. pristoides		
	G. purpurascens		
	G. rex		
	G. robustum		
	G. tenue		
Pterocladia			
	P. bulbosa	*P. capillacea*	*P. lucida*
	P. caerulescens	*P. tenuis*	

and with their longer axis nearly parallel to the thallus. In the case of *P. bulbosa*, 50% of the observations found cells similar to the *Gelidium* species; the other 50% found cells similar to the *Pterocladia* species.

Tridimensional reconstructions of the basal-most cells in *Gelidium* (Fig. 4) suggested cubic or spherical shapes with two or more parallel opposing faces tending to form right angles between the faces. The tissue appearance obtained with a study of cell volumes indicated a tendency toward a radial disposition, with many contacting points but few contacting surfaces and therefore an abundance of intercellular spaces. By contrast, volumetric reconstructions of the basal-most cells of *Pterocladia* indicated elongated, elliptical, pyriform cells with many parallel faces and always with the larger axis parallel to the main axis of the thallus. The tissue reconstruction showed a lineal disposition of cells, with fewer contacting points and more contacting surfaces with neighboring cells than in the case of *Gelidium*.

These results support only partially the suggestions proposed by Akatsuka (1981) for segregating *Gelidium* from *Pterocladia*. Shape and disposition of cortical cells often are too variable along most axes to be considered a reliable taxonomic character. Variability derives from the combined process of cell division and cell elongation, which, in most species, occurs at least along the uppermost half of the erect axis. Therefore, the usefulness of the character is restricted to comparisons of the basal-most parts of erect thalli where cell division and cell elongation have ceased.

It is particularly interesting that the arrangement of external cortical cells forming pairs or tetrads indicates proportionally high rates of cell division and reduced spatial modification by cell enlargement. Several species of *Gelidium* and *Pterocladia* show this type of cellular arrangement in subapical parts, including *G. decumbens* Okamura, *G.*

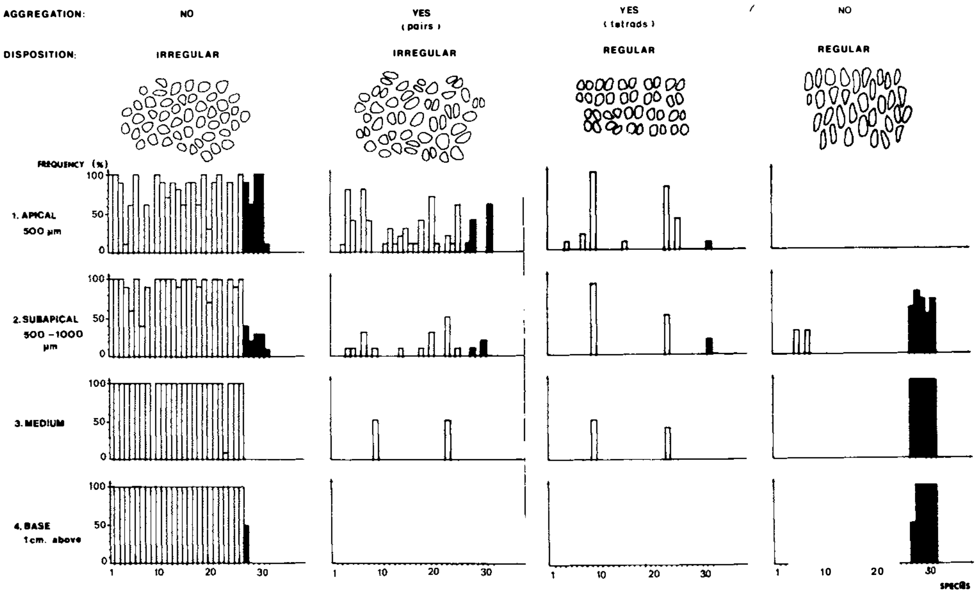

Fig. 3. Types of arrangement and aggregation of surface cortical cells found at several heights along the axes of the species of *Gelidium* and *Pterocladia* included in this study. Cells can be isolated or close together forming pairs or tetrads and regularly (forming rows) or irregularly arranged. Numbers refer to the following species: 1. *G. amansii*; 2. *G. amansii* f. *elegans*; 3. *G. arborescens*; 4. *G. chilense*; 5. *G. coulteri*; 6. *G. crinale*; 7. *G. decumbens*; 8. *G. howei*; 9. *G. japonicum*; 10. *G. lingulatum*; 11. *G. linoides*; 12. *G. nudifrons*; 13. *G. planiusculum*; 14. *G. pluma*; 15. *G. purpurascens*; 16. *G. pusillum* (Horcón); 17. *G. pusillum* (Pebble Beach, a); 18. *G. pusillum* (Pebble Beach, b); 19. *G. pusillum* (Pupukea, a); 20. *G. pusillum* (Pupukea, b); 21. *G. pusillum* (Maalaea Bay); 22. *G. pusillum* (Pupukea, c); 23. *G. pristoides*; 24. *G. rex*; 25. *G. robustum*; 26. *G. tenue*; 27. *P. bulbosa*; 28. *P. caerulescens*; 29. *P. capillacea*; 30. *P. lucida*; 31. *P. tenuis.*

chilense (Montagne) Santelices et Montalva, *G. purpurascens* Gardner, *G. robustum* (Gardner) Hollenberg et Abbott, and *P. tenuis* Okamura. The presence of cells arranged forming tetrads or pairs is more persistent along the axis of *G. pristoides* and *G. japonicum*, suggesting that cell division persists longer and occupies a larger proportion of the lower parts of the axes in these species. However, the feature is lost in the basal-most parts of the thallus where cell growth has disrupted the orderly cell pattern observed distally. It is not surprising, then, that all the genera of the Gelidiaceae with cortical cells arranged in tetrads along large portions of erect axes (*Suhria, Porphyroglossum*, and some species of *Gelidium*) also have abundant proliferous pinnules, which probably represent increased activity of lateral initials along the erect axes. The use of surface cells forming pairs or tetrads for the segregation of the new genera *Onisuka* and *Pterocladiastrum* (Akatsuka 1986a, 1986b) is of doubtful taxonomic value. *Onisuka* was segregated from *Gelidium* to receive *G. pristoides* and *G. japonicum*, and *Pterocladiastrum* was segragated from *Pterocladia* to include the forms "robust" and "poor knights" of *P. lucida*. A more profound understanding of the effects that cell division and growth might have on shape and disposition of cortical cells, as well as much more data on individual and population variations of these and other characters, seems required before validating these two new genera.

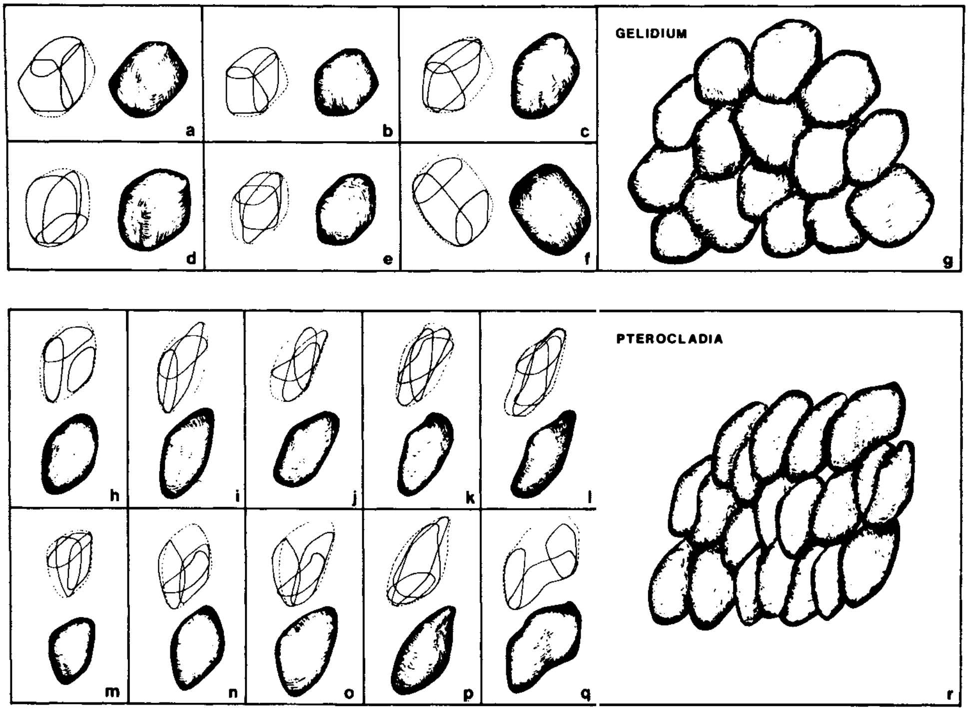

Fig. 4. Volumetric reconstruction of cortical cells in *Gelidium* and *Pterocladia*. Figs. 4a to 4q represent volumetric composition for different cortical cells in species of each genus. Figs. 4g and 4r represent tridimensional reconstructions of the layer of external cortical cells.

Apical Morphology: Examination of the apices of the 19 species of *Gelidium* and the five species of *Pterocladia* (Table 1) indicated that, with the exception of *P. bulbosa*, apical morphology might be used as a taxonomic character segregating both genera. In *P. capillacea* (Gmelin) Bornet et Thuret, *P. caerulescens*, and *P. tenuis*, the apical initial was found (Fig. 5A) lying in a depression between the two apical lobes formed by the projection of the outer cortical cells beyond the outer limits of the apical initial. In *P. lucida* (Fig. 5B), apical and lateral initials occurred at close distance along the apical margins, and both types of initials were found strictly only in depressions between the marginal lobes. In *Gelidium*, the lateral initials also might occur at close or at long distances from the apical initial. When they are at great distance, the apical initial can project itself beyond the cortical cells, forming a very acute margin, as in most species of *Gelidium* (Fig. 5C), or it can remain at the same level of the cortical cells, as in *G. arborescens* Gardner, *G. decumbens*, and *G. howei* Acleto. In both cases, the apical initial was never found in a depression between cortical lobes as in the case of *Pterocladia*.

When the apical initials and the lateral initials occur closely along the apical margins, the tips can be attenuated slightly, as in *G. lingulatum* Kützing and *G. planiusculum* Okamura (see Fig. 5E); rounded, as in *G. purpurascens* and *G. robustum* (see Fig. 5F); or flattened, as in *G. rex* Santelices et Abbott (see Fig. 5I). Only in *G. amansii* (see Fig. 5G), *G. pluma* (see Fig. 5H), and *G. chilense* (see Fig. 5J), are the tips broad and bilobed or multilobed. In these cases, the apical initials could occur at depressions between cortical

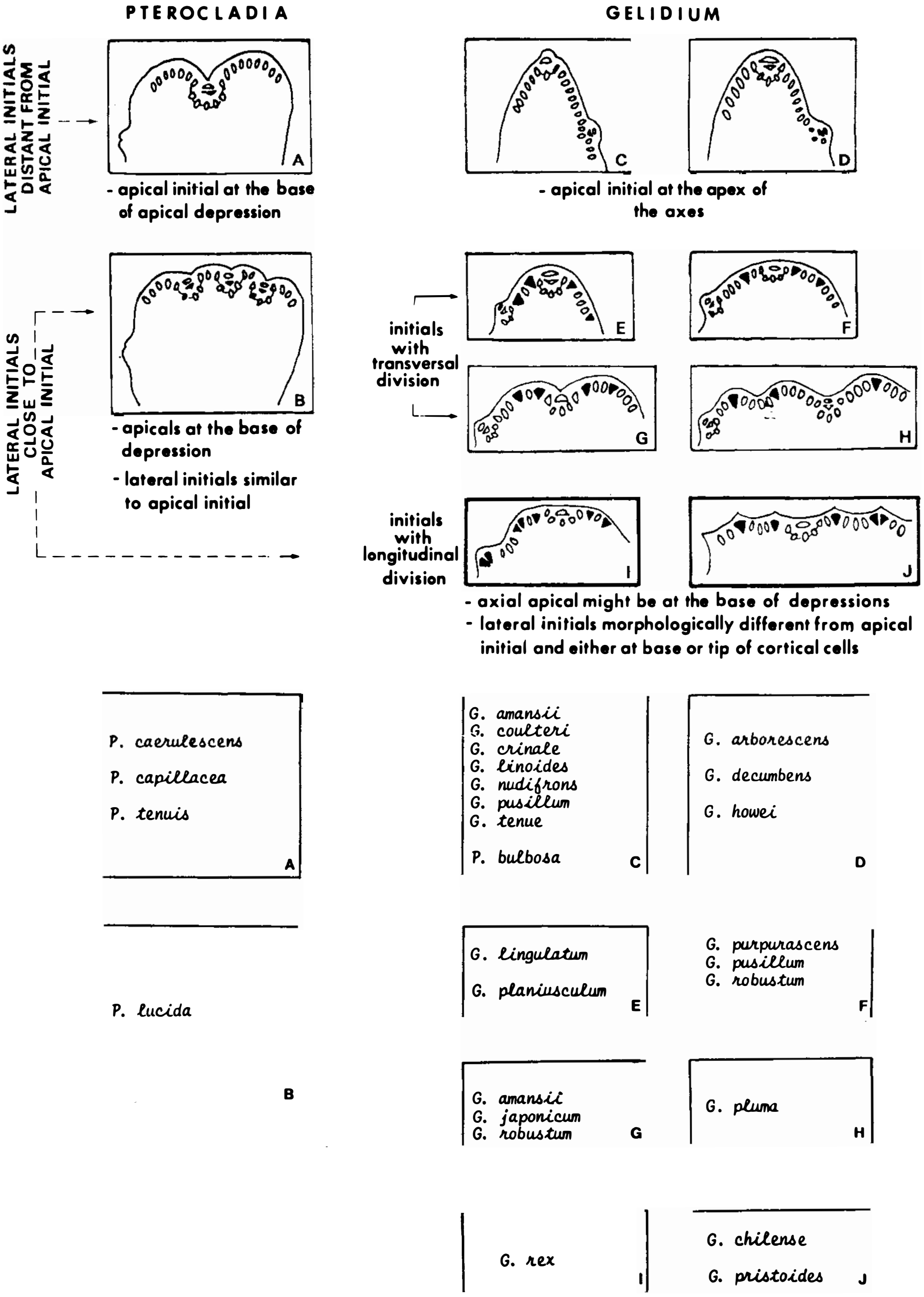

Fig. 5. Patterns of apical structure in species of *Gelidium* and *Pterocladia*.

lobes. However, the lateral initials are indistinct in a depression or at the summit of lobes. As anticipated (Rodríguez and Santelices 1987), in all the species of *Gelidium* examined, the lateral initials were morphologicaly different (smaller and with the shape of an inverted cone) from the globose, dome-shaped apical initial.

These results suggest that apical morphology is a promising character segregating the two genera, although some care should be taken. The character does not apply to *P. bulbosa* in which the erect axes are very acute, terminating in a projecting apical cell. Other, small-sized species of *Pterocladia* such as *P. caloglossoides* (Howe) Dawson might show this apical structure as well. The whole complex of small-sized *Pterocladia* and *Gelidium* is still taxonomically confused, and other generic and specific limits should be established for them before this character is applied.

Most species of *Gelidium* included in this study showed a transverse division of the lateral initials. However, in three species (*G. chilense, G. pristoides*, and *G. rex*), the first division of the lateral initial was longitudinal, contrasting with the transverse division of the corresponding axial apical cell. Whether these observed differences are constant and species-specific is not known.

Conclusion

In conclusion, three morphological characters appear so far to be adequate for segregating *Gelidium* from *Pterocladia*, namely cystocarpic structure, shape and orientation of cortical cells in the basal-most parts of erect axes, and apical architecture of erect axes. None of the three characters individually allows complete generic segregation. *Pterocladia lindauerii* Fan has two unequally developed locules in the cystocarps, and *P. bulbosa* has the apical structure as well as shape and disposition of cortical cells of the basal-most parts of the axes; both taxa resemble *Gelidium* in these features.

Acknowledgements

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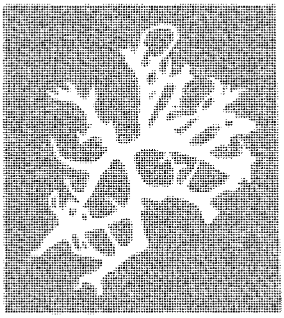
SECTION III. The Red Algal Genera *Gracilaria* and *Polycavernosa*: Additional Species from the Western Pacific



INTRODUCTION

Isabella A. Abbott

Since the publication of the conclusions of the previous workshop (Abbott and Norris 1985), which contained papers by Xia, Yamamoto, Chiang, Abbott, Tsuda, and Norris on *Gracilaria* and papers by Fredericq et Norris, and Xia et Abbott on *Polycavernosa*, a number of changes have been made on Pacific species of these two genera. Some of the more recent studies clearly have been inspired by the results of the workshop, such as the removal by Zhang and Xia (1985) of *Gracilaria verrucosa* from the Chinese flora (to *G. asiatica* Zhang et Xia) and the recognition of several species as synonyms of *G. salicornia* (C. Agardh) Dawson by Xia (1986). This last paper was published in China, and distribution of it is slow, so the results are summarized here.

The basionym for this combination is *Sphaerococcus salicornia* C. Agardh (C. A. Agardh 1820, pl. 8; 1822, p. 302). The synonyms include *Corallopsis salicornia* (C. Agardh) Greville (Greville 1830, p. 43); *C. dichotoma* Ruprecht (Ruprecht 1851, p. 318); *C. cacalia* J. Agardh (J. G. Agardh 1852, p. 583); *Gracilaria cacalia* (J. Agardh) Dawson (Dawson 1954, p. 2); *C. opuntia* J. Agardh (J. G. Agardh 1876, p. 409); *C. salicornia* var. *minor* Sonder (Sonder 1871, p. 56); *C. minor* (Sonder) J. Agardh (J. G. Agardh 1876, p. 409); *Gracilaria minor* (Sonder) Chang et Xia (Chang and Xia 1962, p. 64); *G. crassa* Harvey ex J. Agardh (J. G. Agardh 1876, p. 417); *G. canaliculata* (Kützing) Sonder (Sonder 1871, p. 56); *Sphaerococcus canaliculatus* Kützing (Kützing 1868, p. 82).

Examinations of large populations of *G. salicornia (sensu lat.*) in Guam and Hawaii showed specimens in whole and in part that could be placed in any one or more of these named taxa. Furthermore, a comparison with material from Manila Bay, the Philippines (type locality of *G. salicornia*), showed variations that encompassed the descriptions of these species. These observations also confirm those of Trono et al. (1983, p. 27) on *G. salicornia* in the Philippines.

In other species of *Gracilaria*, among the criteria recently illuminated for recognition of subgenera is the location of spermatangia and the shape of the sorus bearing them (Yamamoto 1978). Arrangements known as the Textorii-type, consisting of shallow saucerlike depressions in which spermatangia are borne, were described by Zhang and Xia (1984) as grading into the Verrucosa-type conceptacles, which are generally oval-shaped pockets; these observations were recently substantiated for a North Carolinian species by Reading and Schneider (1986). Both Chinese and Atlantic materials were identified as *G. blodgettii.* These observations were not meant to cast doubt upon the system of Yamamoto (1978) but rather point up the close attention to detail that must be applied to the species limits of *Gracilaria.* It is becoming clear, for example, that all species with generally oval-shaped conceptacles do not belong to *G. verrucosa* (Abbott 1985, Bird and McLachlan 1982) and that species discrimination within this subgenus must rely also on other features of the reproductive system. Despite the excellent documentation of Zhang and Xia (1984) and Reading and Schneider (1986), it is premature to discard the use of spermatangial location as a subgeneric feature.

Also, in the previous workshop volume, the Micronesian material identified by Tsuda (1985) as *G. arcuata, G. cacalia,* and *G. crassa* has been placed with his *G. salicornia* by Meneses and Abbott (1987) who examined all of the *Gracilaria*-like material in the Guam herbarium. They verified Tsuda's recognition of *G. eucheumoides* but were uncertain about the status of his *G. edulis* and *G. coronopifolia.* Tsuda's records of *G. radicans* and *G. verrucosa* were based on previous literature; they were not recognized as being among the Guam specimens. A new species of *Polycavernosa* from Saipan was named, but two species of *Polycavernosa* and one of *Gracilaria* were left without specific names because the material was lacking the full reproductive complement. Seven taxa for Micronesia are a small number of species for this far-flung island group, and further collections should increase the number of species.

The Taiwanese *G. verrucosa* (Chiang 1985, p. 81) has been examined and is being placed among the material being described in this volume as a new variety of *G. tenuistipitata* by Zhang and Xia. Independently, I had similar material from Thailand and thought that it represented an undescribed species. However, after studying the Chinese material at the second workshop, it became clear that the Thai, Taiwanese, and Chinese materials are the same entity.

Finally, three new species from Malaysia and one from the Philippines of *Polycavernosa* are described (Xia and Abbott 1987), and a new combination in this genus is recognized. Although these, and the Guamanian *Polycavernosa*, have been accepted for publication and are due to be published in 1987, I do not wish this current paper to be cited as the place of their publication, and I am being cautious about using the names of these taxa that are not yet published.

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ON TWO NEW *GRACILARIA* (GIGARTINALES, RHODOPHYTA) FROM SOUTH CHINA

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

Abstract

A new variety of *Gracilaria tenuistipitata* Chang et Xia and a new species, *G. heteroclada* are described from south China. The new variety *liui* possesses slender thalli and abundant branching as contrasted to the broader and less-branched variety *tenuistipitata*. It grows in quiet water and has the capacity of continuing to elongate without appreciably changing its habit. *Gracilaria heteroclada* joins the small number of taxa that show Chorda-type spermatangia, which are disposed in superficial groups. It is distinguished from two western Pacific Chorda-type species, *G. chorda* Holmes and *G. lemaneiformis* (Bory) Weber-van Bosse, on its branching pattern and the structure of the cystocarp.

Introduction

New material of *Gracilaria* has been collected since 1976 when we (Chang and Xia 1976) published information on Chinese species, and this material has provided us with either mature specimens or spermatangial material that we could use to expand our information. We report here a new variety of *G. tenuistipitata* Chang et Xia, originally described from Guangdong Province, and a new species, *G. heteroclada*, from Hainan Island.

Materials and Methods

From dried herbarium specimens, sections were cut by hand, floated out in water, stained with 1% cotton blue, and mounted in glucose syrup.

Description of the Species

Gracilaria tenuistipitata var. *liui* var. nov. (Figs. 1, 3–9)

Differt a var. *tenuistipitata* thallis gracilibus ferentibus numerosos laterales ramulos subtiles breves ad longos flagelliformes, hos saepe tantum 0.25 mm diam. Ramificatio plerumque ex axibus percurrentibus.

Differing from the variety *tenuistipitata* by the slender thalli bearing numerous, delicate, short to long flagelliform lateral branchlets, these frequently only 0.25 mm in diameter. Branching mostly from percurrent axes. Cystocarpic structure (Fig. 4) and shallow Textorii-type spermatangia (Fig. 8) similar to variety *tenuistipitata*.

The name for the variety honors Prof. Liu Sijian, vice-director of Zhanjiang Fisheries College in Zhanjiang, Guangdong Province, China, who has made significant contributions to the farming of this seaweed.

Holotype: Haikou, Hainan Island, Guangdong Province, China, April 1, 1986, tetrasporangial, cultured in a pond, leg. Zhang Junfu and Xia Bangmei, AST 86-652 (AST).

Syntypes: Guangdong Province: Haikang County, April 8, 1986, AST 86-698 (AST, BISH); AST 86-690, AST 86-691, cystocarpic; AST 86-692, spermatangial; AST 86-694, cystocarpic, tetrasporangial. Haikou, Hainan Island, April 1, 1986, cystocarpic, AST 86-650, AST 86-685; same place, Abbott 17969, leg. Zeng Fen, August 1986; Dongfang County, Hainan Island, April 4, 1986, spermatangial, AST 86-666. Guangxi Province: Hepu County, in March; AST 86-715, AST 86-585, spermatangial; AST 86-586, tetrasporangial; AST 86-635, cystocarpic; AST 86-636, AST 86-642; in April: AST 86-708,

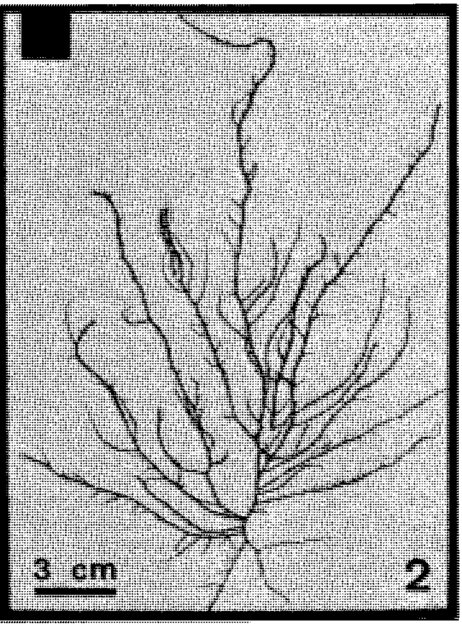


Fig. 1. Habit of *Gracilaria tenuistipitata* var. *liui* Zhang et Xia. Holotype, AST 85-652, from Haikou, Hainan Island, China.

Fig. 2. Habit of *Gracilaria heteroclada* Zhang et Xia. Holotype, AST 80-2338, from Yenggehai, Hainan Island, China.

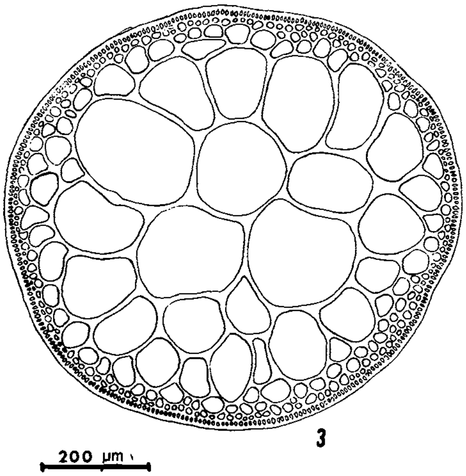
AST 86-709, AST 86-710, AST 86-716, tetrasporangial; Beihai, in March: AST 86-505, AST 86-508, AST 86-515. Taiwan: TungKang, Ping-tung County, cystocarpic, August 20, 1982, leg. Y. M. Chiang (AST 2973, BISH); same place, tetrasporangial, August 11, 1981, leg. Y. M. Chiang (AST 2973, BISH); Anpin (Chiang 3555, tank culture). Thailand: Pattani, HAii 0014, leg. Jack Fisher (AST, BISH); same place, February 26, 1986 (AST, BISH); Da Toh, July 3, 1986 (Abbott 17768, AST, BISH).

Variety *tenuistipitata*, as shown by pl. 1, fig. 3 of Chang and Xia (1976) has few, elongate lateral branches placed about the main axis in a loose spiral, the laterals with no further branches, or (rarely) subdichotomous.

This new variety frequently occurs naturally in fish ponds and shallow intertidal areas on muddy substrate. When cultivated, as in Hepu, Guangxi Province, and in Taiwan (as *G. verrucosa* of Chiang 1981 and Shang 1976), the thalli are usually detached and without holdfasts. They may then tumble about in fairly large masses. Intermediates between *G. tenuistipitata* var. *tenuistipitata* as shown by the type specimen (Chang and Xia 1976, pl. 1, fig. 3) and Fig. 1 in this paper (the type specimen) of variety *liui* exist, but we think it necessary to single out this variety because it could easily be distinguished as another species.

Gracilaria heteroclada Zhang et Xia sp. nov. (Figs. 2, 10–17)

Thallis 10–50 (–70) cm longis, cylindricis, succulentis, fragilis, fractis; ramis primariis 1–2 (–3) mm diam., in seriebus 2–4 irregularibus; ramulis 0.2–0.5 mm diam. numerosis longioribus vel brevibus spinescentibus, gracilibus; tetrasporangiis per corticem vix



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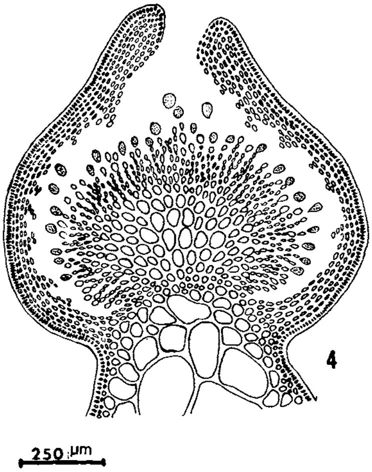

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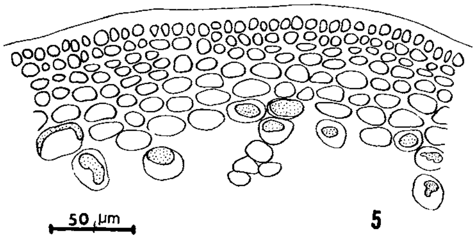

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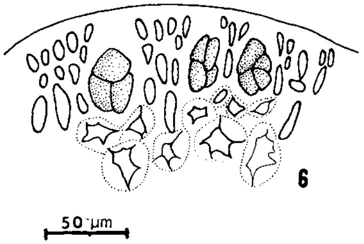

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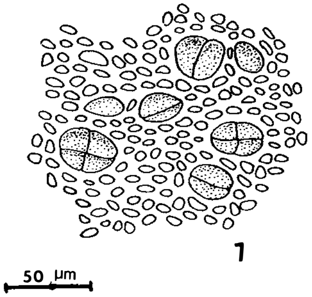

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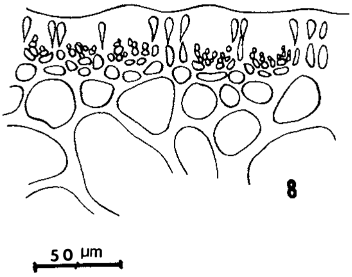

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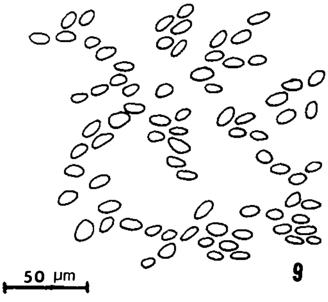

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Figs. 3–9. *Gracilaria tenuistipitata* var. *liui*. Fig. 3, Transection of main axis, showing relationship of cortical to medullary cells. Fig. 4, Longitudinal section of cystocarp. Fig. 5, Longitudinal section of pericarp. Fig. 6, Transection of part of cortex with tetrasporangia. Fig. 7, Surface view of tetrasporangia. Fig. 8, Transection of spermatangial arrangements (textorii-type). Fig. 9, Surface veiw of male frond.

alteratum dispersis; cystocarpiis 800–1000 µm diam., subglobosis vel subconicis, erostratis, basi econstrictis; spermatangiis superficialibus.

Thallus (Fig. 2) erect, solitary or caespitose, arising from a small disc, cylindrical throughout, usually 10–50 (–70) cm long; main axis percurrent or not, 1–2 (–3) mm in diameter, with two to four orders of branches; succulent, brittle, and easily broken; fleshy, light red to kelp (dark) green, dark brown and slightly hardened when dry, adhering to paper on drying; branches irregularly alternate, secund or furcate, with second order long, third order short, sometimes spinose, 0.2–0.5 mm in diameter, gradually tapering towards the apex and nonconstricted at the base; branches and branchlets are distinguished clearly. Thallus in transverse section (Fig. 11) consisting of a medulla of large parenchymatous cells, 200–531 µm in diameter, with walls 8–10 µm in diameter, surrounded by two to three layers (Fig. 10) of small roundish cells, 13–33 µm in diameter, the outermost layer 7–10 by 4–7 µm in diameter, pigmented and with surface jelly 3 µm thick; transition from medulla to cortex abrupt (Figs. 3).

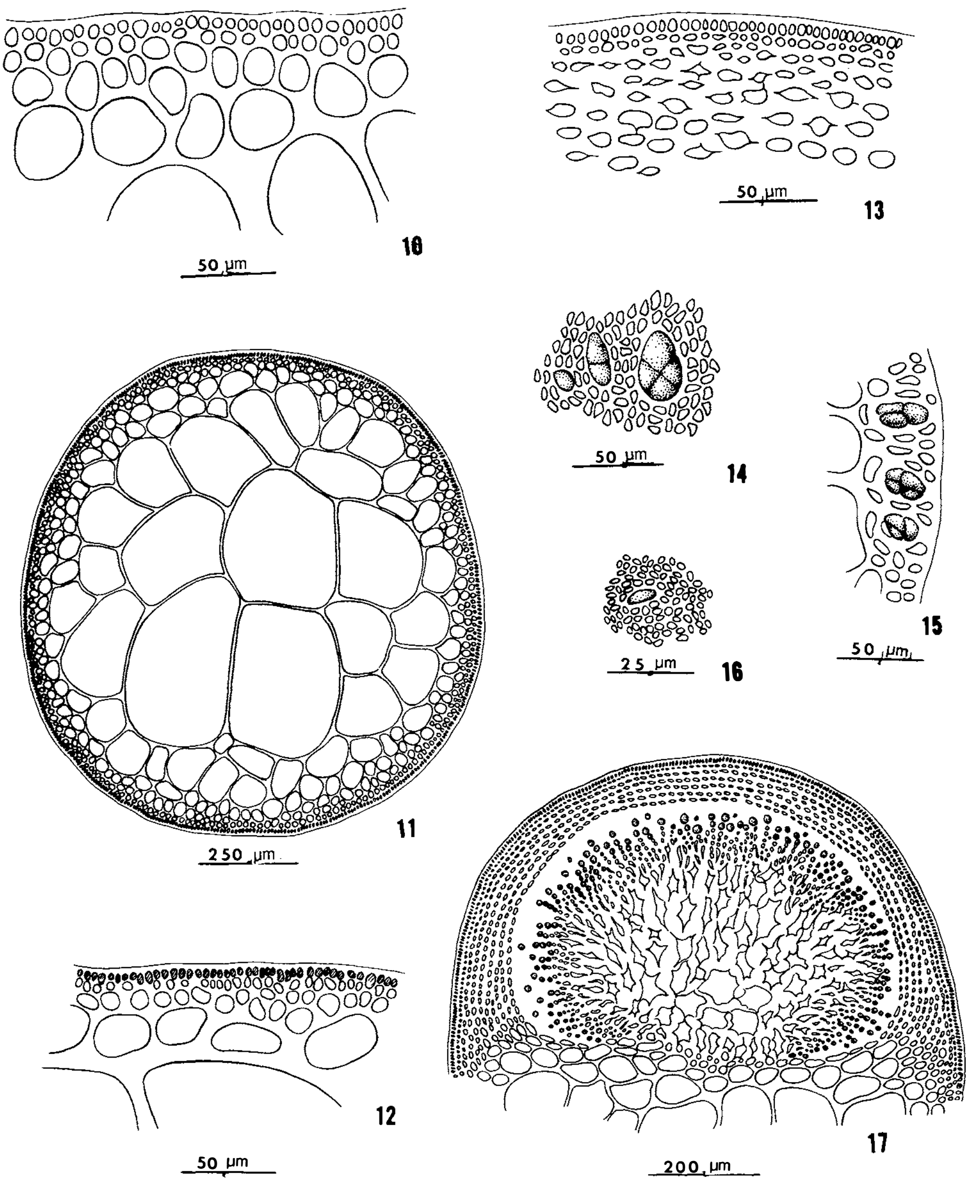
Tetrasporangia scattered among the surface layers of frond, ovoid or oblong (Figs. 14–15) in surface view, 33–36 by 16–26 µm in diameter, ovoid to cylindrical in transverse section 20–30 µm by 13–19 µm in diameter, surrounded by slightly modified cortical cells, cruciately or occasionally irregularly tetrahedrally divided. Cystocarps (Fig. 17) prominently protruding or subconical, 500–780 µm by 830–1000 µm diameter, nonrostrate or slightly rostrate, nonconstricted at base; gonimoblast consisting of parenchymatous cells, the cell walls obscure and cell contents irregularly connected to each other, about 23–82 by 13–20 µm in diameter (Fig. 17); pericarp (Fig. 13) thin, 76–100 µm thick, consisting of seven to eight layers of cells, of which the outermost layer is pigmented and cells roundish-cuboidal to oval, whereas the inner layers have cells that are horizontally oval-elliptical with rounded corners and obscure cell walls (Fig. 11). Spermatangia (Fig. 12, 16) superficial and continuous over the thallus surface.

Known only from Guangdong Province, the species is named for the different sizes of branches of the second and third orders. Those of the second order are elongate laterals; those of the third order are short, delicate, and spinelike.

Holotype: On shells or gravel in mud flats and in tide pool or canal in midtidal to low intertidal region, AST 80–2338, cystocarpic, from Yinggehai, Hainan Island, Guangdong Province, China, April 29, 1980, leg. Zhang Junfu and Xia Bangmei (AST). Isotypes from the same place and date, AST 80-2337, spermatangial; AST 80-2338a, cystocarpic. AST 80-2358, tetrasporangial, from the same place and by the same collectors, April 30, 1980 (AST, BISH). Other material: Xindi, Xuwen County, Guangdong Province, in March: AST 55-1494, tetrasporangial, cystocarpic; AST 55-1506, tetrasporangial, cystocarpic; in April: AST 55-1668, tetrasporangial, cystocarpic; AST 66-543, tetrasporangial, cystocarpic; Dongfang County, Hainan Island, in April: AST 86-659, cystocarpic; AST 86-660, AST 86-661, AST 86-667, all tetrasporangial.

The species takes its name from its long and short-to-spinelike branches.

This species shows a close morphological similarity to *G. bursa-pastoris* (Gmelin) Silva from China, but the latter has spermatangia in shallow depressions as opposed to being borne superficially and shows large gonimoblast cells and numerous absorbing filaments in the cystocarp. According to the spermatangial configuration, *G. heteroclada* resembles *G. chorda* Holmes and *G. lemaneiformis* (Bory) Weber-van Bosse but differs from *G. chorda* on the smaller medullary cells, by thicker cell walls and the structure of the pericarp; from *G. lemaneiformis* by the thin cuticle, thicker cell wall, small cystocarps, smaller size of carpospores, and by the larger cells of the gonimoblast filaments that have numerous secondary pit connections. Gonimoblast cells of *G. lemaneiformis* from the



Figs. 10–17. ***Gracilaria heteroclada.*** **Fig. 10, Transection of part of main axis, showing cortex. Fig. 11, Transection of main axis, showing large medullary cells. Fig. 12, Transection of cortex, showing superficial spermatangia (chorda-type). Fig. 13, Longitudinal section of pericarp. Fig. 14, Surface view of tetrasporangia. Fig. 15, Transection of cortex, showing tetrasporangia. Fig. 16, Surface view of male frond, with a basal cell of a hair (stippled). Fig. 17, Longitudinal section of cystocarp.**

type locality (Paita, Peru) are notably small, and the gonimoblast is stalked (Abbott, 1983).

Some elongate plants were found in a shallow ditch where there was more water motion than in other places.

Acknowledgements

We thank Dr. Isabella A. Abbott and the anonymous reviewers for their help in improving this paper. We acknowledge Karla McDermid for the Latin description of *G. tenuistipitata* var. *liui.* We also thank Dr. Abbott for the specimens of the new variety from Taiwan and Thailand.

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SOME SPECIES OF *GRACILARIA* AND *POLYCAVERNOSA* FROM THAILAND

Isabella A. Abbott

Abstract

Four species of *Gracilaria* and four of *Polycavernosa* are described from Thailand. Of the species of *Gracilaria*, two, *G. tenuistipitata* var. *liui* and *G. firma*, are range extensions from south China; one is a new species, *G. irregularis*; and the fourth is a species common throughout the Pacific, *G. salicornia*. Two of the species of *Polycavernosa, P. fisheri* and *P. changii*, have been described recently from Malaysia. One, *P. fastigiata*, which is the type species of the genus and known previously from south China, the Philippines, and Malaysia, is reported from Phuket and Laem Hin. The second is a new species, *P. percurrens*. *Polycavernosa* has not been reported previously from a definite location in Thailand. Only one of the previously reported species of *Gracilaria, G. cacalia* (=*G. salicornia*), is recorded again.

Introduction

Examination of hundreds of specimens of gracilarioid algae from Guam and Micronesia (GUAM), the Philippines (Doty Herbarium), south China (AST), Indonesia (L), and Malaysia (Doty Herbarium and BISH) has provided a good idea of what taxa might be found in those geographical areas even if names cannot be applied with certainty to all of the specimens. A few of the species have proved to be widespread, such as *Gracilaria salicornia* (C. Agardh) Dawson in the sense of Xia (1986). Examination of specimens previously assigned to *G. verrucosa* (Trono et al. 1983 from the Philippines; Yang and Chiang 1982 and Chiang 1985 from Taiwan) has shown them to be other species, as Zhang and Xia (1985) have also shown for Chinese specimens. Xia and Abbott (1987) identified the bulk of specimens from Malaysia as species of *Polycavernosa*, with three new species and one new combination, and the description of *P. fastigiata*, described previously from Hainan Island, was enlarged upon. A fourth new species, *P. divergens*, was described from the Philippines.

An opportunity to examine gracilarioids from Thailand was taken when it became clear that some of the species represented range extensions from south China and that others were new species. New material from Indonesia to supplement the information from the collections of the Siboga expedition (Weber-van Bosse 1928) and reexamination of the large numbers of specimens from the Philippines will aid in completing knowledge of western Pacific gracilarioids.

Three species and one form of *Gracilaria* from Thailand have been reported by Velasquez and Lewmanomont (1975); additionally, *G. verrucosa* was named as one of several edible species of algae by Lewmanomont (1978). In the former paper, *G. cacalia* was listed as a new combination, without citation of the basionym; as shown in the Introduction to Section III, this species has been merged (Xia 1986) with *G. salicornia* (C. Agardh) Dawson. Citing the earlier identifications by Reinbold (1901), Velasquez and Lewmanomont listed *G. confervoides*, a name that has been replaced by *G. verrucosa* (Hudson) Papenfuss, and *G. dura* and its form *prolificans* Reinbold; the latter was described from Koh Chang (12° 05′ N, 102° 25′ E) by Reinbold (1901).

This paper reports four species of *Gracilaria*, of which one is newly described, and four species of *Polycavernosa*, of which one is new. Assuming that the four taxa previously reported by Velasquez and Lewmanomont (1975) are recognized as individual species, a total of 11 species of gracilarioids is reported for Thailand.

Materials and Methods

The algae were collected in the course of investigating sites that might serve for the mariculture of these agar-producing seaweeds. The sites were near Laem Sok Point (near 12°, 02.53′ N and 102°, 35′ E) near the Cambodian border (Fig. 14) and in the region of Pattani and Songkhla (near 7°, 30′ N and 100°, 30′ E) (Fig. 15) near the Malaysian border. More specific localities are cited in the following sections.

Material was dried in the field or placed in 4% formalin and returned to Honolulu and dried there. Because all material eventually must be compared to other dried material, including type specimens if already named, dried material was preferred. Some of the specimens, when sectioned, responded to rehydration in water very well, but most did not. Sections were cut dry, placed in a weak sugar solution for 5–10 min. or in surfactants such as dilute detergent, washed, stained in 1% aqueous aniline blue or 0.5% toluidine blue O for a short period, intensified with 1% HCl, washed off, and drained, and 50–85% glucose syrup (Karo, a brand name of Corn Products, Inc.) was applied as a mounting medium.

Results

Key to Thai Species of *Gracilaria* and *Polycavernosa*

This key is written on the premise that identification of taxa in the field may be desirable, and thus the species of *Gracilaria* and *Polycavernosa* are mixed in the key. Examination of male plants showing multicavitied spermatangial arrangements (Fig. 1) in isolated groups and of cystocarps with basal absorbing filaments are the only certain criteria for distinguishing species of *Polycavernosa*.

1. Thalli delicate, main axes less than 1 mm thick, branches of second or higher order numerous 2
1. Thalli robust, main axes upwards of 1.5 mm thick, branches rarely more than two orders 5

    2. Second-order branches short and hairlike; cystocarps when present nearly same diameter or larger than bearing branch . . . . *G. tenuistipitata* var. *liui*
    2. Second-order branches nearly same diameter and length as axes 3

3. Branching open, branches elongate, bearing short, hairlike ultimate branches . . . . *P. fisheri*
3. Branching unilateral (to one side) or fastigiate (like a fan) 4

    4. Branches in fastigiate clusters, axes and laterals of nearly same diameter throughout . . . . *P. fastigiata*
    4. Branches unilateral or irregularly unilateral but not fastigiate; main axes percurrent; all orders of branches slender at bases, gradually becoming broader at their apices . . . . *P. percurrens*

5. Branch segments inflated, succulent when fresh, tapering at each end . . . . *P. changii*
5. Branch segments not inflated, but may become constricted at basal end 6

    6. Plants erect, branching pectinate (like a comb), or irregularly dichotomous 7
    6. Plants decumbent or entangled, axes and branches undulate to constricted and beadlike . . . . *G. salicornia*

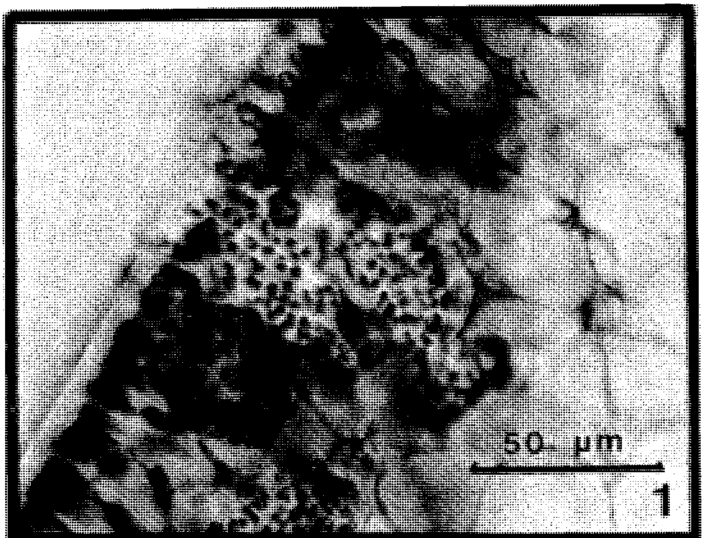
7. Plants less than 7 cm tall, second-order branches short, undivided or pectinate . . . . *G. irregularis*
7. Plants more than 10 cm tall, second-order branches unilateral or irregularly formed, with basal portions stipitate . . . . *G. firma*

Description of the Thai Species

GRACILARIA

Gracilaria firma Zhang et Xia (Figs. 3, 4)

Chang (Zhang Junfu) and Xia Bangmei 1963; 1976, pp. 143–145; 162–163, figs. 38–39.



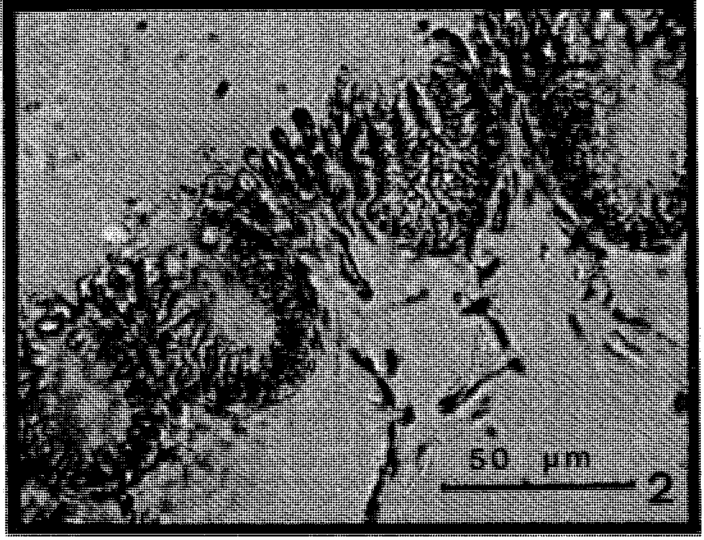
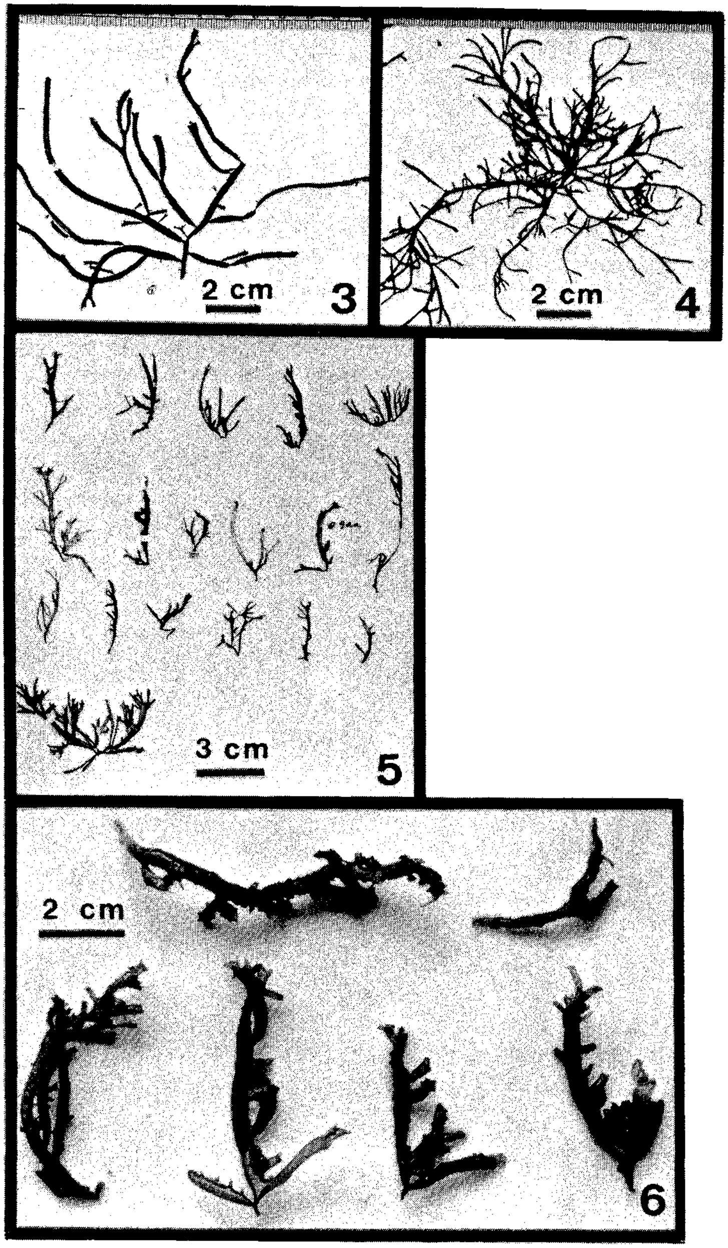


Fig. 1. Spermatangial caves of *Polycavernosa fastigiata* (HAI 0015 from Phuket, Thailand).

Fig. 2. Spermatangial conceptacles (verrucosa-type) of *Gracilaria irregularis* (HAI 0003) from Ao Len, Trat Peninsula, Thailand.

Thai Specimens: Thalli erect, terete, compressed on drying but rehydrating to the the terete condition, 4 to 14 cm long, 1–4 mm thick, axes and branches robust, texture firm to leathery; branching irregular, alternate, at times unilateral, usually only two orders of branching, but when detached or caged, one to three more orders possible, these short and describing a fringe on the second order. Cortex one to two cells thick, followed inwardly by one to three layers of cells 13–15 µm in diameter radially, then upwards of 80 µm in diameter radially through the medulla, being slightly reduced before the subcortex on the other side is reached.



Figs. 3, 4. ***Gracilaria firma*** **Chang et Xia. Fig. 3, A specimen from Ao Len, Trat Peninsula, Thailand (HAI 0001). Fig. 4, A specimen (A 17976 from Khung Kraben) showing proliferating branchlets characteristic of caged material.**

Figs. 5, 6. ***Gracilaria irregularis*** **Abbott. Fig. 5, Holotype sheet showing irregular branching after which this species is named (HAI 0001). Fig. 6, Some thalli before pressing to show fleshy nature of axes and branches (HAI 0003).**

Tetrasporangial plants more numerous than cystocarpic and spermatangial; not significantly different in branching pattern. Tetrasporangia with a mean of 20–40 µm (range, 18–49; *n* = 20). Spermatangial plant more slender than tetrasporangial and cystocarpic; verrucosa-type spermatangial conceptacles.

Cystocarps 1–1.25 mm high, about 1 mm broad, with the gonimoblast less than 0.5 mm high (the clear pericarp wall occupying half or more of the height); rostrate. Gonimoblast in longitudinal section broad, the gonimoblast filaments narrow, with numerous reticulate pit connections; occasional upper absorbing filaments along the lateral and upper sides, each 8–10 µm thick, not reaching the pericarp except at the lower lateral edges; pericarp thick-walled, protoplasts flattened ovals of seven to eight rows, followed by two to three rows of inner netlike rows.

Distribution: The type and other materials are known from gravel and dead coral in tide pools in Guangdong Province, south China, and the specimen chosen for illustrating this species (Chang and Xia 1963, pl. 2, fig. 4) does not resemble the Thai specimens, but examination of type and other specimens at Qingdao identified the two sets of materials as being one.

This species was found on the Trat Peninsula (northeast Thailand, Fig. 14) and near Songkhla (Fig. 16) in the southwest of the Gulf of Thailand. Specimens from the first area are listed first: Ao Len, 12°, 4′ N, 102° 33′ E, from deeper water, A 17972, June 24, 1986, leg. J. R. Fisher; Khung Kraben, a proliferous caged specimen in pond, A 17976, June 25, 1986, leg. J. R. Fisher; Ko Loi, near 12° 7′ N, 102° 34′ E, shallow intertidal in silty sand, A 17799, June 24, 1986, leg. J. R. Fisher; Ko Loi, on rock and gravel, A 17801, June 25, 1986, leg. J. R. Fisher; Ko Loi, A 17975, June 25, 1986, leg. J. R. Fisher; Chantaburi pond, loose stock, A 17992, October 14, 1986, leg. J. R. Fisher; same place, material originally from Ko Loi, A 17997, June 24, 1986, leg. J. R. Fisher; same place, but in a cage, A 17974, June 24, 1986, leg. J. R. Fisher; small stocky plants used for grow-out at Ko Yo, A 17980, July 2, 1986, leg. J. R. Fisher. Songkhla: from polyethylene line, Ko Yo Island, Songkhla, October 13, 1986, leg. J. R. Fisher. Pattani, A 17985, July 1986, leg. J. R. Fisher.

Gracilaria irregularis sp. nov. (Figs. 2, 5, 6)

Thalli erecti, 3–10 cm alti axe cylindrico percurrente 2–2.5 mm diam. Ramificatio irregularis, interdum secunda; rami secundi et tertii ordinis diametro variantes, aliqui in medi-sectionibus inflati; rami tertii ordinis plerumque breves, interdum spiniformes, saepe congesti. Thalli i tetrasporangiferi similes gametophytis ramificatione. Tetrasporangia 28–35 µm diam. Cystocarpia conspicua, tholiformia, non constricta. Massa gonimoblasti demissa, circa 200 µm diam., fila gonimoblasti dense reticulata; fila absorbentia carentia. Pericarpium 10–12 seriebus cellularum protoplasto ovali ad stellatum. Conceptacula spermatangiorum typi "verrucosa," ovalia ad obovata, plurima; contigua conceptacula saepe coalescentia.

Thalli (Figs. 5, 6) erect, 3–10 cm tall with a percurrent cylindrical axis 2–2.5 mm in diameter. Branching irregular, sometimes secund; second- and third-order branches of various diameters, some inflated in midsections; the third order usually short, sometimes spinelike, frequently crowded.

Tetrasporangial thalli similar to gametophytes in branching. Tetrasporangia 28–35 µm in diameter. Cystocarps conspicuous, dome-shaped, not constricted. Gonimoblast mass low, about 200 µm in diameter; gonimoblast filaments densely reticulate; absorbing filaments lacking. Pericarp with 10–12 rows of cells, with protoplast oval to star-shaped. Spermatangial conceptacles verrucosa-type (Fig. 2), oval to obovate, numerous; adjoining ones frequently coalescing.

Holotype: Attached to shell and rock fragments, in sandy mud, 0.5 m depth at Ao Len, Trat Peninsula, Thailand, 12° 4′ N, 102° 33′ E, A 18003 (HAI 0001 and HAI 0003), leg. T. F. Mumford, Jr., February 20, 1986, deposited in B. P. Bishop Museum, Honolulu (BISH); isotypes in BISH, AST, US, and Kasetsart Univ.

Remarks: The relatively short, erect, turgid axes with very irregular branching is not a habit commonly encountered in *Gracilaria*. My only other experience with this habit is with *G. turgida* Dawson from California, which, however, has textorii-type spermatangia (Dawson 1961, p. 213) and ultimately is a taller plant (to 15 cm). No other *Gracilaria* or *Polycavernosa* in the western Pacific that I have examined looks like *G. irregularis*.

Gracilaria salicornia (C. Agardh) Dawson (Fig. 7)

Basionym: *Sphaerococcus salicornia* C. Agardh (C. A. Agardh 1822, p. 302). *G. salicornia* (C. Agardh) Dawson (Dawson 1954, pp. 4–6).

Synonyms may be found in the summary of the publication of Xia (1986) in the "Introduction" to Section III.

Plants less than 1 cm to about 10 cm long, less than 0.1 cm to 0.5 cm wide, completely smooth margins, to undulate, and partly constricted; irregularly branched.

Sterile, cystocarpic, and spermatangial plants found.

Distribution of Thai Specimens: Trat Peninsula: Ao Len, 12° 4′ N, 102° 33′ E, HAI 0002, February 20, 1986, leg. T. Mumford; Ao Len, A 17774, March 22, 1986, leg. J. R. Fisher and T. Mumford; Ko Loi, 12° 7′ N, 102° 35′ E, A 17800, June 24, 1986, leg. J. R. Fisher.

Remarks: *G. salicornia* (as *G. cacalia*) was originally reported for Thailand by Dawson (1954) from Saen Soek, also in the northern Gulf of Thailand near 13° 20′ min. N. Velasquez and Lewmanomont (1975) also listed *G. cacalia*.

Number A 17774 (Fig. 7) from Ao Len has a parasite on it that Dr. Yamamoto is now studying. He has observed similar parsites on *G. salicornia* from southern Japan.

Gracilaria tenuistipitata var. *liui* Zhang et Xia (Figs. 8, 9)

(See Zhang and Xia in this volume where this variety is described as new.)

Differing from variety *tenuistipitata* by slender thalli bearing numerous, delicate, short to long flagelliform lateral branchlets, these frequently only 0.25 mm in diameter. Branching is mostly from percurrent axes.

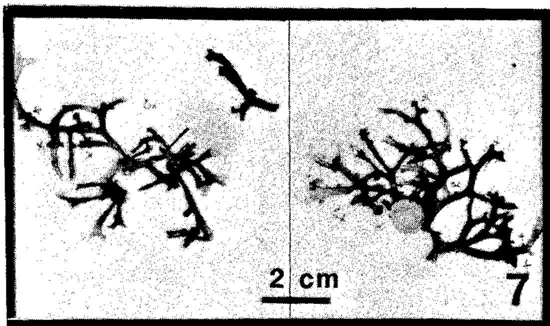
The cystocarpic structure and shallow textorii-type spermatangia are similar to var. *tenuistipitata*.

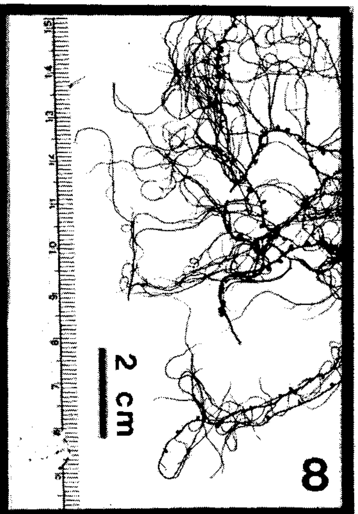
Thai collections (all leg. J. R. Fisher): HAI 0014, Pattani, April 7, 1986 (AST, BISH); Abbott 17768, Pattani, February 26, 1986 (AST, BISH); A 17802, Ban Da Toh, Pattani (Fig. 8), July 3, 1986.

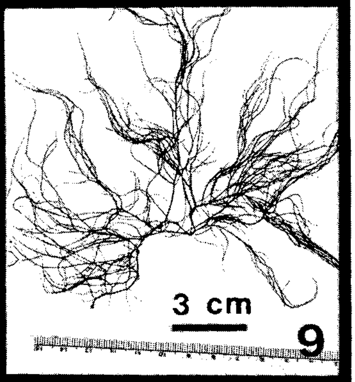
Taiwanese collections (leg. Y. M. Chiang): Ting Kang, Ping-tung Hsien, cystocarpic, February 20, 1982 (AST, Taiwan); same place, tetrasporangial, August 11, 1981 (AST, Taiwan); Chiang 3555, Anpin (tank culture) (BISH).

Remarks: The specimens from Thailand are similar to the following specimens from Hepu, Kwansi Province (cultured in ponds): AST 86-642, March 25, 1986; AST 96-650, April 1, 1986; AST 86-670, April 4, 1986, and AST 86-688, April 8, 1986, all leg. Zhang Junfu and Xia Bangmei, and to those furnished by Zeng Fen from Hainan Island, collected in August 1986.

This new variety frequently occurs naturally in fish ponds and shallow intertidal areas on muddy substrata. When cultivated, as in Hepu and in Taiwan (Fig. 9) (as *G. verrucosa* of Chiang 1981 and Shang 1976), the thalli are usually detached and without holdfasts. They may then tumble about in fairly large masses. Intermediates exist between *G.*







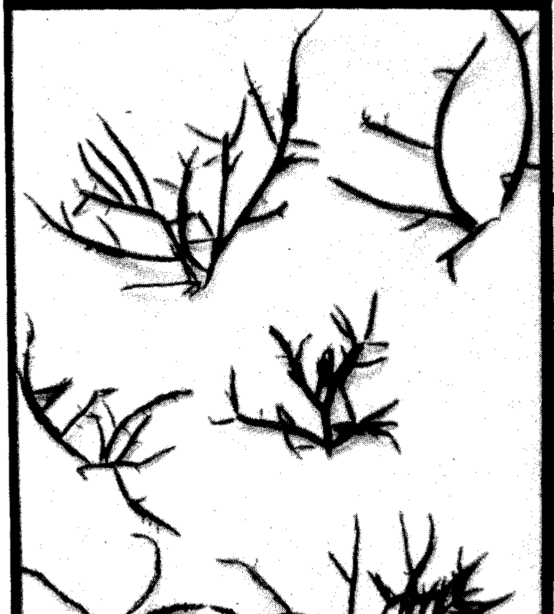


Fig. 7. ***Gracilaria salicornia*** **(C. Agardh) Dawson. Habit of two cystocarpic plants that would have qualified as** ***G. crassa.*** **These two specimens have parasites on them. (A 17774 from Ao Len, Trat Peninsula, Thailand.)**

Figs. 8, 9. ***Gracilaria tenuistipitata*** **var.** ***liui*** **Zhang et Xia. Fig. 8, Part of a cystocarpic plant from Ban Da Toh, Pattani, Thailand (A 17802). Fig. 9. A specimen from Yung Kang, Ping Tung, Taiwan, leg. Y. M. Chiang.**

Fig. 10. ***Polycavernosa changii*** **Xia et Abbott from Ao Len, Trat Peninsula, Thailand (A 17773).**

tenuistipitata var. *tenuistipitata* as shown by the type specimen (Zhang and Xia 1976, pl. 1, fig. 3) and the type specimen of variety *liui* (see Zhang and Xia, this volume), but we think it necessary to single out this variety because it could easily be distinguished as another species. Its habit resembles that of *G. lemaneiformis* as reported from the Hawaiian Islands (Abbott 1985, p. 85).

POLYCAVERNOSA

The species of *Polycavernosa* (Chang and Xia 1963; Xia and Abbott 1985, 1987) are distinguished from *Gracilaria* species principally on the basis of the multicavitied spermatangial arrangements that are isolated from each other in surface and cross-sectional views and by basal absorbing filaments that are large columnar cells with few to many spinelike arms that are found at the lateral bases of, or underneath, the gonimoblast. As in *Gracilaria* (*sensu lat.*), upper absorbing filaments that are more delicate and elongate and without arms may or may not occur between the carposporophyte mass and the pericarp.

Polycavernosa changii Xia et Abbott (Figs. 10–12)
Xia and Abbott 1987.

Thai Specimens: Thalli bushy, with spreading branches rarely more than two orders; axes and leading branches 1.5–3.5 mm wide, generally inflated, the ultimate branches frequently tapering at each end, the basal portion tending to become stipitate; holdfast a small disc, primary axis soon obscured by branches.

Cystocarpic, male, and tetrasporangial specimens similar to those described from Malaysia (Pinang, the type locality), although among the fewer specimens available from Thailand, the tetrasporangial plants are more robust than the gametophytes, and in one number (A 17775a), branching is more dense.

Collections: Ao Len, 12°, 4′ N, 102°, 33′ E, southeast muddy shore of Trat Province, A 17773, 17775a, March 22, 1986, leg. J. R. Fisher and T. F. Mumford, Jr.; same place and collectors, A 17972, June 24, 1986, growing with *Solieria robusta*, which it resembles in color and succulence.

Remarks: The plants from Malaysia tend to be bushier and dry black, whereas the Thai material has few orders of branches and dries a greenish-brown.

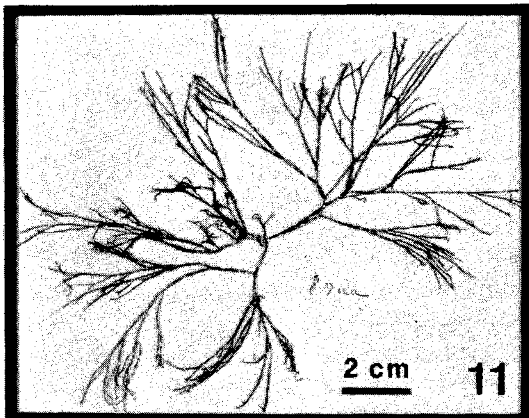
Polycavernosa fastigiata Chang et Xia (Fig. 11)
Chang and Xia 1963, pp. 119–126.

Thai Specimens: The three collections more closely resemble the material from Hainan Island than the majority of materials from Malaysia, which, for the most part, were large plants with very irregular branching. Two sheets of specimens from Laem Hin, near 12° 10′ N, 102° 34′ E, an eroded limestone bench with potholes filled with sandy mud in which the plants were growing, are short and irregularly branched, with few signs of the clustered, fastigiate branches shown by the third sheet, from off Phuket (open ocean rather than sandy mud). The last sheet is "typical" *fastigiata*.

Collections: Laem Hin, north of Ko Loi, Trat Peninsula, leg. T. F. Mumford, Jr., November 15, 1986, HAI 4007; same place and collector, HAI 4001, December 2, 1986; HAI 0015 (Fig. 11), purchased at Sapam Market, Phuket, April 9, 1986, by J. R. Fisher.

Polycavernosa fisheri Xia et Abbott (Fig. 12)
Xia and Abbott 1987, p. 411.

Thai Specimens: Plants frequently between 18 and 24 cm tall, multifariously branched, axes 0.5–1.5 mm wide, the second-order branches 0.5–1.0 mm in diameter,



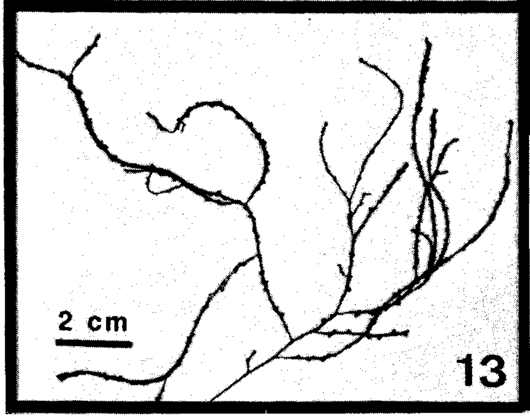


Fig. 11. ***Polycavernosa fastigiata*** **Chang et Xia, spermatangial thallus, from Phuket, Thailand (HAI 0015).**

Fig. 12. ***Polycavernosa fisheri*** **Xia et Abbott, from Phe Fisheries Station; transplanted from Ko Yo, Songkhla, Thailand (A 17989).**

Fig. 13. ***Polycavernosa percurrens*** **Abbott, holotype, from Ko Yo, Songkhla, Thailand (A 17986).**

elongate, frequently becoming leading branches; branches mostly confined to upper half of plant, mostly subdichotomous but occasionally unilateral; when in pond culture with reduced water motion, axes and laterals are not distinct from each other, the plants becoming thin and as much as 30 cm long.

Tetrasporangial specimens tend to have more open and more numerous branches than cystocarpic plants. Third-order branchlets (more common on tetrasporangial plants than gametophytes) fine, short, and hairlike.

Collections: Phe Fisheries Station, (northwest of Trat Peninsula), caged material originally from Ko Yo, Songkhla, A 17988, A 17989, October 7, 1986, leg. J. R. Fisher; Ban Da To, Pattani, A 17798, July 3, 1986, leg. J. Fisher; same place, HAI 0013, April 7, 1986, leg. T. F. Mumford, Jr. From the region of Songkhla: Fisheries Research Station, Ko Yo, Songkhla, A 17767 and HAI 006, February 26, 1986, leg. J. R. Fisher; Ao Si, Ko Yo, Songkhla, HAI 004, February 26, 1986, leg. J. R. Fisher; same place and date, HAI

005, leg. Payao Intasuwan; same place, A 17795, August 2, 1986, leg. J. R. Fisher; on stones and shell fragments in 0.5 m depth west of spoil bank near Bo Keng, Songkhla, HAI 009, March 11, 1986, leg. J. R. Fisher.

Remarks: *Polycavernosa fisheri* is the commonest species in the vicinity of Pattani and Songkhla (especially the latter, where natural ponds or lakes open into the ocean). The type material was purchased in a market in Malaysia [near Kota Bahru, Kelantan, (Fig. 15), on the eastern side of the Malay Peninsula] and is said to have come from Pattani. Jack Fisher (pers. comm. 1987) has found that the exporter of seaweed comes from Pattani, but it is likely that the original material of *P. fisheri* came from Songkhla where the bulk of the species is to be found.

Polycavernosa percurrens sp. nov. (Fig. 13)

Thalli erecti ad partim decumbentes; axis inferior tenuis, latiorescens distaliter, gradatim ab 0.5 ad 2 mm diam.; ramificatio irregularis ad alternam; numerus ramorum et ordinum ramificationum minor in plantis tetrasporangiferis et spermatagiferis quam in plantis cystocarpiis. Plantae tetrasporangiferae ramis primariis diametro fere eodem atque in axe principali; in sectione transversa, cellulis basalibus capillorum conspicuis. Dispositiones spermatangiorum 3–4 cavernis. Cystocarpia latiora quam alta, non constricta; fila gonimoblasti gracilia, reticulata; basalia fila absorbentia lateralia et centralia sub gonimoblasto. Pericarpium 11–12 seriebus cellularum parietibus tenuibus et contentis rotundatis.

Thalli erect to partially decumbent, 12–18 cm long; lower axis slender, becoming broader distally, gradually from 0.5 to 2 mm in diameter, percurrent, branching irregular to alternate; number of branches and branching orders fewer in tetrasporangial and spermatangial plants than in cystocarpic plants, but cystocarpic plants more slender. Tetrasporangial plants with primary branches nearly same diameter as main axis; in cross section, with basal cells of hairs conspicuous. Spermatangial arrangements with three to four caves. Cystocarps broader than high, not constricted; gonimoblast filaments slender, reticulate; basal absorbing filaments lateral and central beneath gonimoblast. Pericarp with 11–12 rows of thin-walled cells with rounded contents.

Cortex of two layers, the cells about 8 µm in diameter, followed inward by three to four layers of outer small medullary cells, 10–18 µm in diameter, then abruptly by large cells of the medulla, the largest 120–250 µm in diameter.

Tetrasporangial plants with cruciate tetrasporangia, 13 x 28 µm in unmodified cortex, basal hair cells numerous. Spermatangial plants with spermatangial arrangements of three to four caves, 24 x 31 µm ($n = 8$) in surface view, the total arrangements 3 µm deep by 71 µm broad (range, 39–62 by 52–78 µm; $n = 8$) in cross section of thallus. Cystocarps about twice as broad as high when mature; gonimoblast filaments elongate, 6 x 20 µm, with many secondary pit connections; carpospores appearing one at a time (chains of spores tardy in forming; basal absorbing filaments conspicuous, branched at lower lateral edges of gonimoblast; simple, unbranched ones along base of gonimoblast; a few upper absorbing filaments also present. Pericarp with 11–12 rows of cells with rounded protoplasts and thin walls.

Holotype: Abbott 17986 (Fig. 13), a sheet of cystocarpic plants (BISH), from Ko Yo, Songkhla, Thailand, growing on polyethylene line, October 13, 1986, leg. J. R. Fisher; isotypes under this number (sporophytes and gametophytes) deposited BISH, AST, US.

Other specimens from Ko Yo, Songkhla, A 17987, by the same collector on the same date, and caged material at Phe Fisheries Station, Ro Yang Province, A 17989, October 13, 1986, leg. J. R. Fisher.

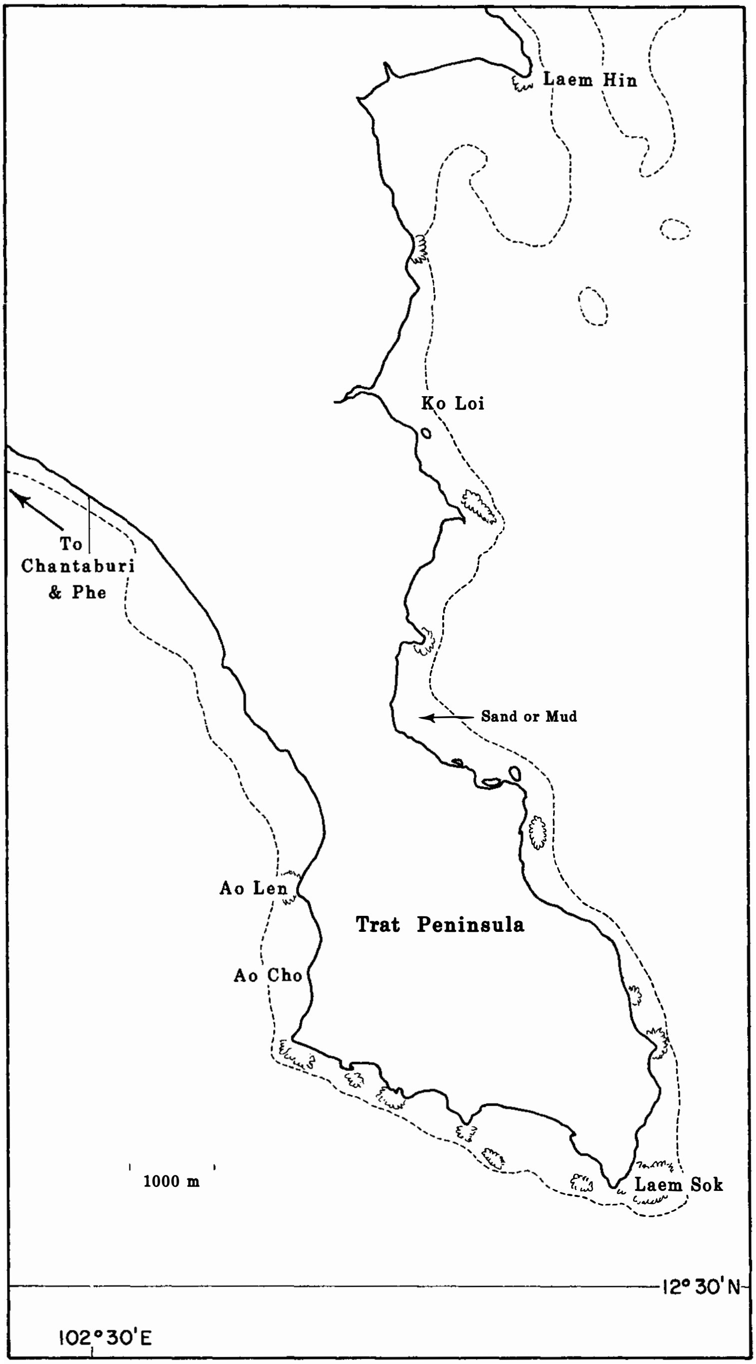


Fig. 14. Vicinity map of Trat Peninsula, Thailand, showing some of the collecting places, especially Ao Len, Ko Loi, and Laem Hin.

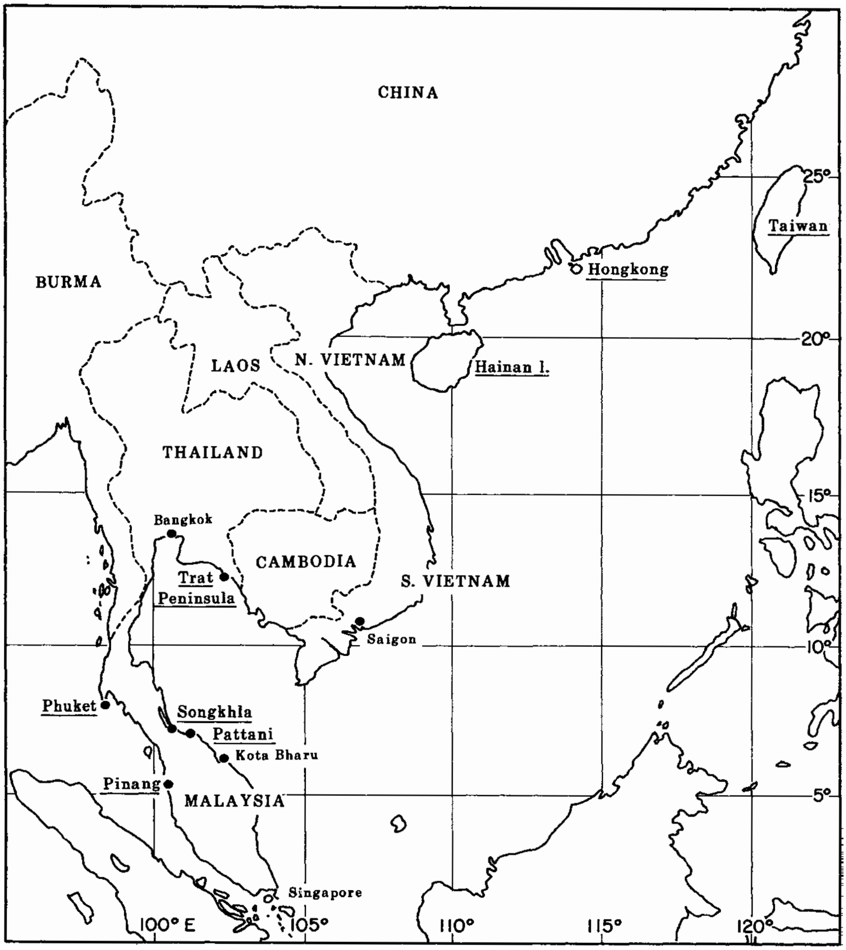


Fig. 15. Map of continental southeast Asia showing some of the collecting places (underlined) mentioned in this paper.

Remarks: Among species of *Polycavernosa, P. percurrens* most resembles *P. fastigiata* in stature and general appearance. It differs markedly in the low orders of branching and the thickness of the axes and branches of the tetrasporangial plants as compared with those of the gametophytes. Sporangial plants and gametophytes in *P. fastigiata* are similar to each other. Most of all, *P. percurrens* differs in the percurrent nature of the axis, lacking in *P. fastigiata*; the percurrent axis makes this species different from all other species of *Polycavernosa* that have been described.

Discussion

The recognition of eight taxa of Gracilariaceae from Thailand (Figs. 14–16) is not particularly helpful to those who are endeavoring to establish aquaculture of some of these species, as without doubt most of these taxa "look alike" to the uninitiated. As with

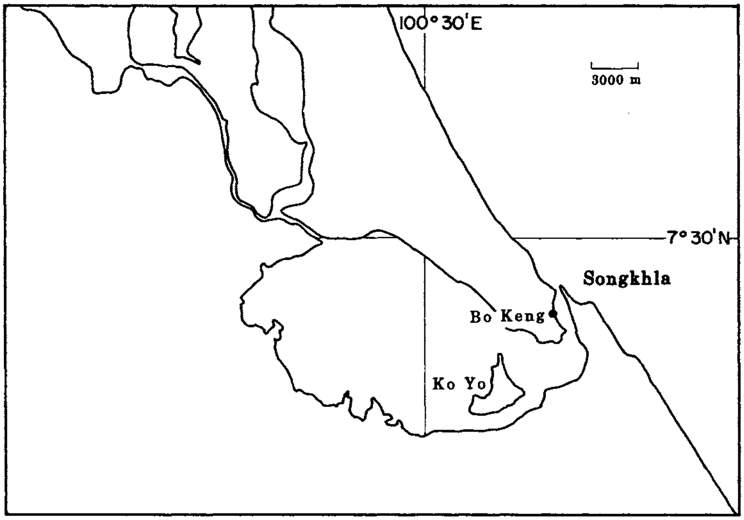


Fig. 16. Vicinity map of the region of Songkhla, Thailand, and a few of the nearby collecting places.

Gracilaria, however, as has been shown repeatedly (Hoyle 1978a, 1978b; Doty and Santos 1983), different species have different qualities of agar and different proportions of agar to agarose, making the marketability of the raw material vary with the inherent chemical contents of the cell walls. Few of these species have had the chemistry of their natural products analyzed, so their potential market value is unknown. It seems advisable to try to match species names to the chemistry of the plants so that one would have a known and perhaps predictable value for the raw material.

Acknowledgements

It is a pleasure to thank Jack Fisher and Thomas Mumford for the Thai specimens that are the basis of this paper. It is not always easy, while in the field, to collect, preserve, and otherwise take care of specimens for someone who is several thousand kilometers away. Because of lack of fieldwork in Thailand on my part, I may have made mistakes in the limits of the populations of the species given to me; in other words, I have performed the role of a "museum taxonomist." Nevertheless, these studies have shown that the Thai gracilarioids are far richer than previously known. Zhang Junfu and Xia Bangmei shared with me their knowledge of and experiences with southern Chinese gracilarioids, which have allowed me to recognize species outside the species' original range. I express my gratitude to Karla McDermid and her Latin teacher, Prof. Robert Ball, for putting into Latin the descriptions of the new species.

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SOME SPECIES OF *GRACILARIA* AND *POLYCAVERNOSA* FROM THE SIBOGA EXPEDITION

Isabella A. Abbott

Abstract

Herbarium specimens of marine algae belonging to the Gracilariaceae that had been collected on the Siboga expedition (1899–1900) were examined. The 31 sheets included only six of the total of 25 taxa reported by Weber-van Bosse for the Siboga algae. Among the six taxa, *Polycavernosa vanbosseae* is described as a new species for a misidentified *Gracilaria cylindrica*. Doubts are expressed as to the identity of southwest Pacific *G. arcuata* Zanardini and *G. blodgettii* Harvey. The most numerous specimens, previously identified as *G. lichenoides*, are recognized as *P. fastigiata* Chang et Xia.

Introduction

Some of the numerous specimens that make up the collections of *Gracilaria* and *Corallopsis* from the Siboga expedition (1899–1900) in the Indo-Malayan area were examined to determine whether more recent specimens from southeast Asia might have been named previously. Weber-van Bosse (1928) listed 20 species of *Gracilaria* and five species of *Corallopsis*. From the Leiden Herbarium (L), where the Weber-van Bosse specimens are kept, 31 numbers (sheets) were sent for examination, some of them containing more than one specimen. These taxa were distributed among *Corallopsis urvillei, Gracilaria arcuata, G. arcuata* var. *snackeyi, G. blodgettii, G. cylindrica*, and *G. edulis* (= *G. lichenoides*). Earlier, the *Gracilaria* collection in the Copenhagen Museum (C) and the Cryptogamic Herbarium, Paris Museum (PC), were also examined.

Japanese (Ohmi 1958, Yamamoto 1978) and Chinese (Chang and Xia 1976) workers have used some of the names that first had been applied to Pacific specimens by Weber-van Bosse (1928). Examples are *G. arcuata* (Zanardini 1858) originally from the Red Sea; *G. blodgettii* Harvey (Harvey 1853), originally from Florida; and *G. cylindrica* Børgesen (Børgesen 1920), originally from the Virgin Islands. There are two problems here: First, apparently neither Weber-van Bosse (1928) nor Ohmi (1958), nor Yamamoto (1978), nor Chang and Xia (1976) examined type material or topotype material. Not only did reports of spermatangial types in *G. blodgettii* by Schneider and Searles (1973) and Yamamoto (1978) conflict with those by Ohmi (1958) and Chang and Xia (1976), but even on sterile material, it is clear that many taxa bearing the same name are morphologically (genetically) different. The second problem deals with species limits. What constitutes, for example, *G. edulis* (Gmelin) Silva (Silva 1952)? Although this may be the earliest valid name for *G. lichenoides* (L.) Gmelin, an adequate description of the species, based on material that might be from near the type locality, is lacking. The problem is compounded by the fact that the type specimen of *Fucus edulis* is one or more illustrations (a lectotype, or perhaps a neotype to be chosen), and it has been very difficult to find a "perfect match" for any one of these illustrations. Yet, when *Gracilaria* specimens in various herbaria were examined, it was found that both collectors and those who subsequently named the specimens selected "*G. lichenoides*" for the bulk of the specimens from the western Pacific.

Description of the Species

Polycavernosa fastigiata Chang et Xia

Chang and Xia 1963, p. 120, pl. 1, figs. 1–12; pl. 2, figs. 1–6. Weber-van Bosse 1928, p. 436 [as *G. lichenoides* (L.) Gmelin].

The sterile specimens could be identified only because they are the size and have the branching pattern of *P. fastigiata* as recognized in hundreds of specimens from Malaysia and the Philippines. The only cystocarpic specimen, L 941.49.158 from New Guinea, is clearly in agreement with cystocarpic *P. fastigiata* from Hainan Island, its type locality. The remaining 10 specimens are from Baeka Cay (L 941.49.157); Taam (L 941.49.160); Savoe (two sheets with three packets, L 941.49.159, L 941.49.176); Makassar (L 941.49.164); Landoe, Rotti (L 941.49.180); Jedan (4 specimens, L 941.49.162); Roma (L 941.49.174); Sarasa (L 941.49.182); and the Gulf of Bima, Sumbawa (L 941.49.177). The following five specimens that were in the *G. lichenoides* file are not *P. fastigiata*: L 941.49.179 from Sarasa; L 941.49.6 and L 941.49.169 from Thursday Island (these are *Laurencia*, the latter mixed with another alga); L 941.19.173 from Sailoes; and L 941.49.13 from Aru Island, leg. W. Arnoldi (tetrasporangial). It would be very difficult to name these specimens.

Polycavernosa urvillei (Montagne) Xia et Abbott

Xia and Abbott 1987, p. 414.

Basionym: *Hydropuntia urvillei* Montagne (Montagne 1842, p. 7).

Synonym: *Corallopsis urvillei* (Montagne) J. Agardh (J. G. Agardh 1876, p. 410; Weber-van Bosse 1928, p. 440).

One of the numbers (L 939.69.939) has the stipitate rather beadlike ultimate branchlets of the specimens referred to as this species in Xia and Abbott (1987) and resembles the holotype from Torres Strait that is in the Montagne herbarium (P). Another number (L 939.69.958, with three specimens) is labelled *C. urvillei* (Montagne) J. Agardh f. *simplicior* but apparently was not published. These specimens resemble f. *elongata* Weber-van Bosse (Weber-van Bosse 1928, p. 440, fig. 178), and perhaps a mistake in labelling was made. They are 14–16 cm tall, with conspicuous axes 4–5 mm thick, and have third- or fourth-order branchlets that are flattened blades, unlike the teardrop-shaped, stipitate ultimate branchlets of *P. urvillei* from Malaysia. These two numbers are from Détroit de Selée, New Guinea. Alcohol-preserved specimens from this locality were also provided. The specimen of *C. urvillei* f. *cereus* J. Agardh, reported by Weber-van Bosse (1928, p. 440) from the Kei Islands, has been misplaced or lost (Prud'homme van Reine, pers. comm.). The third sheet (L 940.284.237) is a fragment from the Montagne Herbarium, origin not clear, but presumably the Torres Strait. It resembles the type material and the Leiden specimen L 939.69.939.

Polycavernosa vanbosseae Abbott, sp. nov. (Figs. 1, 2)

Gracilaria cylindrica of Weber-van Bosse (Weber-van Bosse 1928, p. 432), *non G. cylindrica* Børgesen (Børgesen 1920).

Thalli 12–14 cm alti, compressi; axes 2 mm diam.; ramificatio subdichotomas ramis lateralibus paulo angustatis sursum, interdum ramo angustato etiam basaliter. Cystocarpia circa 1 mm diam. in materia exsiccata, in sectione cellulis gonimoblasti gracilibus et elongatis. Basalia fila absorbentia gracilia, paucis bracchis lateralibus, superna fila absorbentia pauca, subtilia. Cellulae pericarpii rotundatae, 7–10 seriales.

The thallus is 12–14 cm tall, compressed; axes 2 mm in diameter, branching subdichotomous with lateral branches slightly tapering upward, sometimes with a branch tapering basally also. Cystocarps are about 1 mm in diameter in dried material, in section with slender and elongate gonimoblast cells. Basal absorbing filaments are slender, with few lateral arms; upper absorbing filaments few, delicate. Pericarp cells are rounded, in seven to ten rows.

Holotype: Cystocarpic specimen on sheet L 941.49.17, from 10–11 m depth off Jedan Island, Indonesia. Isotype under the same number and from the same collection (cystocarpic); syntype, a sporangial plant under the same number and from the same collection. Other specimens: L 941.49.11, several specimens (or parts of one plant?) on one sheet from Sapeh Bay, Sumbawa Island, Indonesia. All of the specimens examined are in the Leiden Herbarium. The species is named for Dr. Anna Weber-van Bosse, phycologist for the Siboga expedition.

The aforementioned description applies to the holotype and isotype, which are cystocarpic plants. They are taller than the tetrasporangial plant (also an isotype, presumably from the same collection, as it has the same accession number), with axes and laterals of nearly the same diameter. The tetrasporangial thallus is 3 mm wide through widest portions, with laterals about 1 mm in diameter, with second and third orders of branching tapering gradually to their bases, not stipitate but more conspicuously tapering than on cystocarpic plants. The cortex is one cell thick; medulla of thin-walled cells with abrupt transition from cortex; central medullary cells largest. Cystocarps are small; outside diameters of five that were measured on dried specimens were about 1 mm, between 150 and 250 μm in diameter of incompletely expanded cross section; scattered irregularly over the thallus. The gonimoblast tissue consists of slender, elongate cells, forming a slight central column in median longitudinal view; the base of the gonimoblast has a small sill of nearly isodiametric cells three to four rows thick; slender basal absorbing filaments with few lateral arms bridge this sill with the medulla, with a few at the lateral edges of cystocarp; upper absorbing filaments are scarce. Pericarp cells are small, with protoplasts about 8–10 μm in diameter, of seven to ten rows of rounded cells with thick walls, the innermost cell rows with thinner cell walls.

Remarks: Similar in gross morphology to type material (C) of *G. cylindrica* Børgesen from the Virgin Islands, though with less frequent branching, *P. vanbosseae* principally differs in the anatomy of the cystocarp. In *G. cylindrica*, upper absorbing filaments are conspicuous, and no basal ones occur. In the new species, upper absorbing filaments are scarce, and slender basal absorbing filaments are frequent. Pericarpic cells of *G. cylindrica* are thin-walled and have spherical to star-shaped contents, but they are spherical and with thick walls in *P. vanbosseae*.

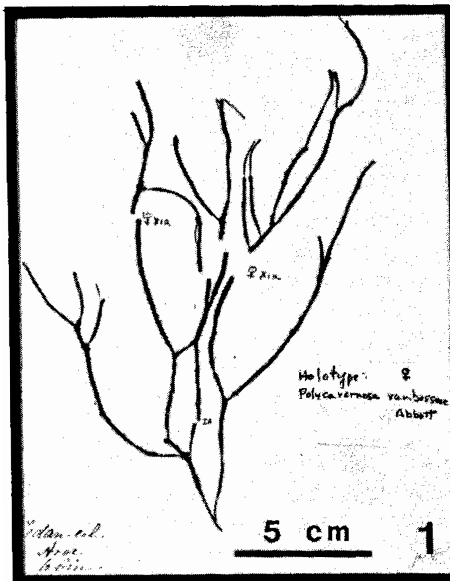
No spermatangial material was available to compare with the shallow textorii-type spermatangial arrangements of *G. cylindrica*.

Gracilaria arcuata Zanardini (Fig. 3)

Zanardini 1858, p. 265; Weber-van Bosse 1928, p. 429.

The specimens on the three sheets that are identified with this species are much alike: sparingly branched, the branches subdichotomous to trichotomous, tapering to an acuminate apex, or apex blunt (L 941.49.50 and L 941.49.51, six specimens in one packet, from the Sulu archipelago and L 941.49.46 from Jedan). They do not resemble the specimens illustrated by Okamura (1929–1932, pl. 272) and Yamamoto (1978, pl. 47, figs. 4, 5) for this species except in a very general way, and the illustrations of Chang and Xia (1976, p. 110) resemble *G. arcuata* var. *snackeyi* Weber-van Bosse rather than the Japanese interpretation of *G. arcuata* var. *arcuata*. They somewhat resemble Børgesen's illustration (Børgesen 1934, pl. 3) of Indian specimens that he identified as *G. arcuata*.

To my knowledge, no one has published on *G. arcuata* from the Red Sea, its type locality, in sufficient detail for an understanding of Zanardini's idea of this species. A search in some of the European herbaria has not yet uncovered authentic material of this species; I consider this search to be one of the important ones in Pacific and Indian Ocean



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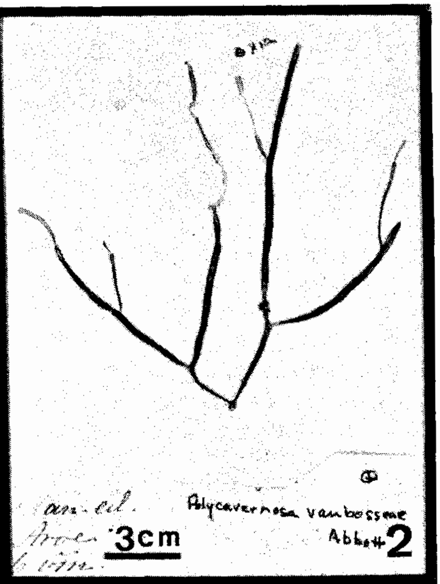

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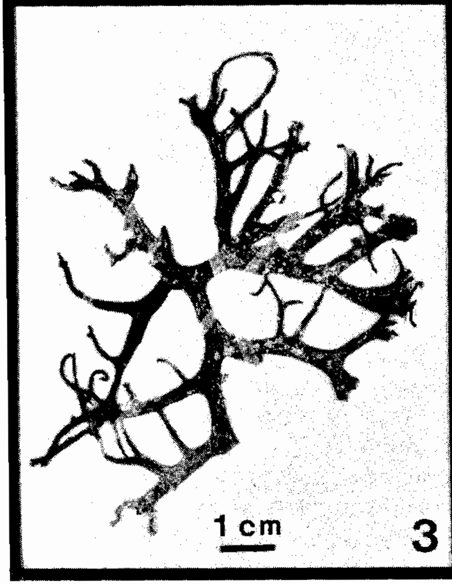

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Fig. 1. ***Polycavernosa vanbosseae*** **Abbott, cystocarpic thallus, holotype sheet (Leiden 941.49.17), from Siboga expedition.**

Fig. 2. ***Polycavernosa vanbosseae*** **Abbott, tetrasporangial thallus, isotype (Leiden 941.49.17) from Siboga expedition.**

Fig. 3. ***Gracilaria arcuata*** **Zanardini, from Siboga expedition from Sarasa (Leiden 941.49.49).**

Fig. 4. ***Gracilaria arcuata*** **var.** ***snackeyi*** **Weber-van Bosse (type?), from Brill Lighthouse near Makassar (Leiden 941.49.52).**

Gracilaria taxonomy because, at this time, specimens from various herbaria identified as this species differ greatly, leading to the realization that several taxa are involved.

Gracilaria arcuata var. *snackeyi* Weber-van Bosse (Fig. 4)

Weber-van Bosse 1928, p. 429.

From the material represented in the Leiden Herbarium from the Brill Lighthouse near Makassar (L 941.49.52, perhaps the type specimen of this variety) and from Sarasa (L 941.49.49), it is possible that this variety actually represents a distinct species. The thallus is described as cylindrical, but the specimen is flattened, with short, broad branches borne close together. The Sarasa specimen has secondary haptera, a condition also found by Børgesen (1952) for Mauritius specimens that he identified with this variety. The larger dimensions shown in Børgesen's fig. 35 (Børgesen 1952), and upon inspection of the specimens, the clearly decumbent and flattened nature of the thalli, suggest that Børgesen had a different species, neither the same species nor the same variety as *G. arcuata* var. *snackeyi*.

Gracilaria blodgettii Harvey

Harvey 1853, p. 111; Weber-van Bosse 1928, p. 430, fig. 174.

Many small, brittle pieces of the plant illustrated by Weber-van Bosse (1928, fig. 174), dried from alcohol preservative, are in a packet on sheet number L 941.49.43. A jar containing several plants in alcohol was also available. From the small dried pieces, sections showed clear verrucosa-type spermatangial conceptacles that were 52 x 78 µm, elongate-obovate. Liquid-preserved cystocarpic specimens showed reticulate gonimoblast tissue, a few upper absorbing filaments, and a pericarp of "cobwebby" cells (i.e., cells with several elongate, conspicuous secondary pit connections).

A comparison with an isotype of *G. blodgettii* from the Harvey Herbarium shows that this species has more slender branches with a different habit than is shown in the Weber-van Bosse illustration. Additionally, in my opinion, this isotype does not resemble what is currently identified as *G. blodgettii* by Reading and Schneider (1986) in its branching pattern and its slenderness. However, the isotype is tetrasporangial, and specimens that Dr. Schneider sent for my examination were spermatangial or cystocarpic. Plants identified as *G. blodgettii* by Schneider have spermatangia that grade from the textorii-type to verrucosa-type in the same plant. The plants here have only verrucosa-type spermatangial arrangements.

A comparison of the Weber-van Bosse specimen (from the coast of central Java) with Chinese material named *G. blodgettii* shows a number of similarities. The cross section is similar: two rows of small cortical cells followed inwardly by two to three layers of medium-sized cells, and then with a medulla of large, nearly uniform cylindrical to oval very thick-walled cells (to 26 µm thick). The cystocarps are similar, with elongate absorbing filaments and pericarps of cells with conspicuous secondary pit connections. However, the Chinese specimen illustrating this species (Chang and Xia 1976, fig. 28) is more densely branched than the Javanese plant, the gonimoblast filaments are different in structure, the carpospores of the Chinese plant have very conspicuous stellate plastids not present in the Javanese material, and the spermatangial conceptacles of the Chinese specimens are small and oval rather than elongate and obovate. These may be minute details and inconsequential if a whole suite of specimens were examined, but at present the name of this specimen cannot be given with certainty. It is concluded that neither the Chinese nor Javanese materials are the same as *G. blodgettii* from Florida.

Acknowledgements

Without the cooperation of Dr. W. F. Prud'homme van Reine, I could not have studied the Siboga material from the Leiden Herbarium (L), and I thank him for his help and interest. I appreciate loans also from Dr. Francoise Ardre, Cryptogamic Herbarium, Museum d'Histoire Naturelle, Paris (P and PC); the British Museum (Natural History), London (BM); from Dr. J. B. Hansen, Botanical Museum, Copenhagen (C); and Dr. Craig Schneider. I thank Karla McDermid for the Latin translation of *P. vanbosseae*, and I am grateful to Shawn Carper, Isabel Meneses, and Zeng Fen for aid in checking specimens of *P. fastigiata*.

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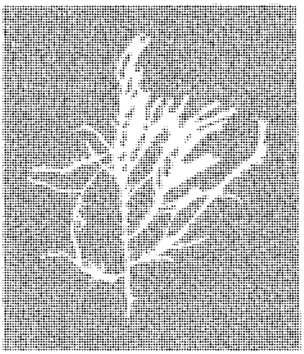
SECTION IV. *Eucheuma* (Rhodophyta, Solieriaceae)



INTRODUCTION

Isabella A. Abbott

The contribution of Doty (1985) and Doty and Norris (1985) on the taxonomy of some of the western Pacific and other species of *Eucheuma* (Solieriaceae, Gigartinales) in Volume 1 of this series reduced the chaos that existed with respect to the boundaries of species, the application of valid names of species, and the recognition of taxonomic categories within the genus. Focused on commercial species, the information from those papers is extended in this section by two papers. The first, by Doty, reorganizes the genus with a new tribe; a new genus, *Kappaphycus*; two new species; and six new combinations. In all, 18 seaweeds used commercially are treated. The second paper, by Cheney, describes the nomenclature, taxonomy and distribution, and excluded taxa of western Atlantic, Floridian, and Caribbean species of *Eucheuma*. The two papers allow us to make significant strides in the understanding and ordering of the troublesome taxonomy in *Eucheuma*, which, as with other genera that contain many species (e.g., *Ulva*), needs attention on a regional and then worldwide basis. This approach has been implemented in the studies of *Sargassum* and of *Gracilaria* and its relatives by this and the previous workshop.

Eucheuma, unlike *Ulva*, however, rarely is found fertile, and the very large, fleshy to cartilaginous thalli are difficult to dry and prepare as herbarium specimens, so many extant specimens are only small pieces of the original plant and not at all representative of the species. Only his approximately 25 years of work in the field and on his collections make it possible for Dr. Doty to give a kind of summary, a statement of the state of the art upon which others can build.

One of the criteria used by Doty in trying to bring as many features as possible to bear on species recognition is the use of the chemistry of the colloids found in these species. Taxonomists are rarely chemists but, for some taxa, creating teams of taxonomists and chemists has been effective. In *Laurencia* taxonomy, the team of William Fenical and James Norris has compared the elaborate terpinoids and other chemicals produced by this genus with the morphology on which a taxonomist usually depends. In *Eucheuma* and *Gracilaria* studies, the team of Maxwell Doty and Gertrudes Santos has matched many species with kinds of carrageenans and agars, respectively. In this volume, Zablackis and McDermid have contributed a paper on agar in *Laurencia*. Such teams may be necessary to continue these kinds of contributions to systematics of algal groups in the future.

It is because of Doty's encouragement that Cheney's paper is added to this volume. Although Cheney did not attend the Qingdao workshop, his studies on the western Atlantic-Caribbean complex of another species of *Eucheuma* are an appropriate and welcome addition to this volume.

PRODROMUS AD SYSTEMATICA EUCHEUMATOIDEORUM: A TRIBE OF COMMERCIAL SEAWEEDS RELATED TO *EUCHEUMA* (SOLIERIACEAE, GIGARTINALES)

Maxwell S. Doty

Abstract

Through formal listing of the recognized taxonomic entities and descriptions of new taxa and combinations of scientific names, the goal of having the taxonomy consistent for 18 seaweeds found in commerce as carrageenan-producing "cottonii," "spinosum," or "gelatinae" is approached. Illustrations, protologues, and distributions for all included taxa are given, with additional information for some less known or more problematic entities and topics. At the end a revised key is included for distinguishing the commonly recognized species.

The novelties published include *Eucheumatoideae* tribus nova (type genus: *Eucheuma* J. Agardh) and *Kappaphycus* genus novum (type species: *E. alvarezii* Doty). Additional species for all three remaining sections of *Eucheuma* are recognized. The publication of *E. amakusaensis* Okamura is completed (neotype: Doty No. 31613 in BISH). The following new species or new combinations are established: *E. kraftianum* Doty (holotype: Doty No. 24706 in BISH), *E. perplexum* Doty (holotype: Doty No. 31628 in BISH), *E. odontophorum* variety *mauritianum* (Børgesen) Doty (basionym: *E. speciosum* variety *mauritianum* Børgesen), *K. alvarezii* (Doty) Doty (basionym: *E. alvarezii* Doty), *K. inerme* (Schmitz) Doty (basionym: *E. inerme* Schmitz), *K. striatum* (Schmitz) Doty (basionym: *E. striatum* Schmitz), *K. procrusteanum* (Kraft) Doty (basionym: *E. procrusteanum* Kraft), and *K. cottonii* (Weber-van Bosse) Doty (basionym: *E. cottonii* Weber-van Bosse).

Introduction

The seaweed commonly referred to in the carrageenan industry as *Eucheuma* reaches the market (Doty and Norris 1985) as one of three kinds known in commerce by the nonscientific names "cottonii," "spinosum," or "gelatinae." As such, no generic name should be used with them. Their crops are almost entirely farmed, with the production of one, cottonii, now passing the first sale point of 50,000 dry tons per year. Perhaps more than 18 species are involved when the wild crop is considered. Most of them are not known well, not even taxonomically, and indeed only three species are of real commercial importance at present. The present work has been undertaken to provide preliminary solutions to the taxonomic problems faced by anyone undertaking more detailed work with these algae in commerce and in the various subdisciplines of biology.

Use of the carrageenans (Moss and Doty 1987) is increasing from 2% to 10% or more each year. Of the carrageenans known, beta, gamma, iota, kappa, mu, and nu types are recognized as being produced by one or another *Eucheuma* of the three aforementioned kinds. Incidentally, only a few other carrageenans have been described: lambda, which is a commercial product generally obtained from *Chondrus crispus* (Linnaeus) Stackhouse (Gigartinaceae), and an alpha, described by Zablackis and Santos (1986) from *Catenella nipae* Zanardini (Rhabdoniaceae). The mu carrageenan of Mueller and Rees (1968) and of Anderson et al. (1968) and the nu carrageenan of Stancioff and Stanley (1969) have been described but not isolated. Mshigeni and Semesi (1977), Doty and Santos (1978), Dawes (1979), and Green and Yaphe (1984a, 1984b), among others, have postulated distributions of these carrageenans among the eucheumoid species rather well. Although the chemical studies of these authors are welcomed, much of the work is fraught with uses of names contrary to the International Botanical Code, which requires use of those names in accord with both the type method and priority.

Expressions of commercial interest as well as the growing literature on scientific topics outside the competence of the present effort, such as in chemistry, physiology, ecology, biogeography, and the agronomics of cottonii, spinosum, and gelatinae, are likewise rife with taxonomic inconsistencies to such an extent that the names used should largely be ignored. Thus, having better taxonomy available is becoming critical.

Eucheuma was established by J. G. Agardh (1847) for seven species that now cover the gamut of those that bear the different major kinds of carrageenan. Unfortunately, despite the splendid individual pioneering efforts by J. G. Agardh (1847, 1852, 1876, 1892), Schmitz (1895), Weber-van Bosse (1913, 1926, 1928), and Yamada (1936), the taxonomy of the species is still poorly known. Recently Doty and Norris (1985) initiated a revision of *Eucheuma* by recognizing four sections: *Eucheuma*, *Anaxiferae, Gelatiformia*, and *Cottoniformia*. Yet, this approach was but a small step in view of the problems involved.

The original generic concept of *Eucheuma* was based on the relatively coarse, generally bushy, rigid nature of the thalli of most of the species then recognized and on their having three kinds of tissue (J. G. Agardh 1847, 1852, 1892; Harvey 1853, 1858–1863). These tissues (Fig. 1) were what could be called nowadays a rhizoidal medullary core (Fig. 1D), rotund medullary cells (Fig. 1C), and a cortex of radiating filaments (Fig. 1B) of elongated, much smaller cells. These attributes still provide the taxonomic criteria.

Size is of little value in these identifications; in fact, it is more often a deterrent to consistent taxonomy because the bulkiness of a thallus is usually such that only fronds or fragments are preserved in herbaria. The thalli are indeterminate in growth. Thus, all are found to range upward from 5 g in mass, below which the species cannot be determined. Often the commercial species are a few hundred grams in mass and 20–40 cm tall but can be much larger, by more than 50-fold (Doty 1985).

Before 1850, the reproductive structures of the red algae were, as a rule, not at all well described and were used infrequently in taxonomy. Applications of the improved microscopy of that period led immediately toward consistent usage of reproductive structures. For example, J. G. Agardh (1852) recognized the seriate arrangement of *Eucheuma* tetraspores (Fig. 2). Refinement is still going on. For example, Cheney and Dawes (1980) and Gabrielson (1983) have only recently adjusted earlier misimpressions of just where *Eucheuma* tetrasporangia attach to the cell families from which they originate, which raises the possibility that in the ontogeny of individual tetrasporangia, their primary pits shift as they mature, from being nearly basal to being lateral.

The overt female structure (Fig. 3) has been recognized superficially as a cystocarp for a long time. Within it, as in all close relatives of J. G. Agardh's *Eucheuma*, a fusion cell (Figs. 4A) arises. A variety of structures develop around it (Fig. 4B), from which, in due time, carpospores arise and leave the cystocarp through an ostiole. So little is known of the mechanics of what happens before the fusion cell appears that the reproductive ontogeny of this and earlier structures has little taxonomic value. Nothing of taxonomic value is known of the male structures.

The current understanding of the cystocarp's internal functional and dynamic morphology can be accepted as having begun with Harvey (1853) when he said the following of *E. isiforme*: "Conceptacles... placenta central, suspended in the cavity by numerous confervoid filaments connecting it on all sides with the walls of the conceptacle, cellular, often hollow within, bearing moniliform, densely crowded, simple or branched sporethreads on every side. Spores roundish oblong, the terminal one subpyriform. I have not seen tetraspores." Note the word "suspended" and Fig. 4B in the present text; the suspending confervoid filaments nowadays are called, at the suggestion of Kraft (1977), "traversing filaments." Gonimoblast filaments (Fig. 5) were called "spore threads"

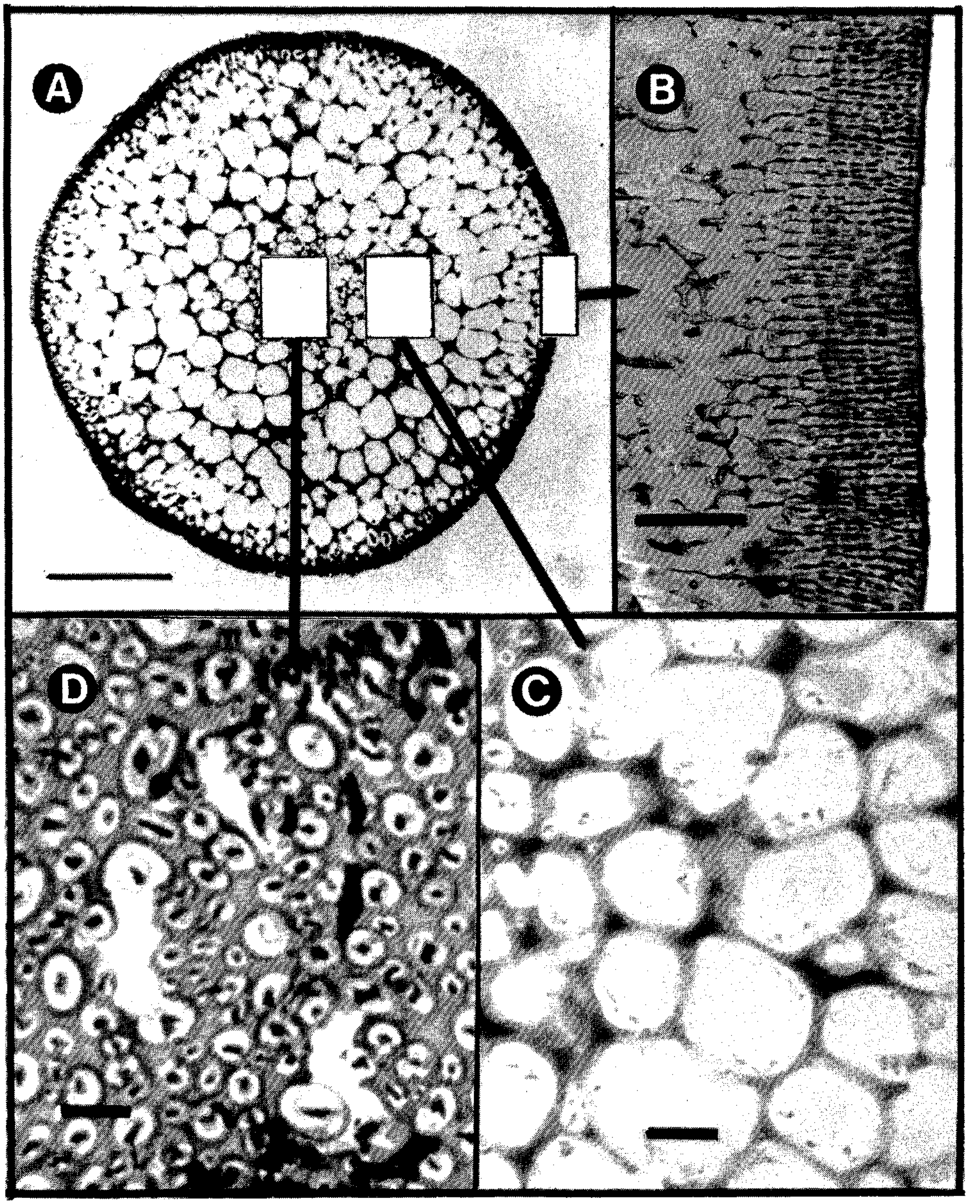


Fig. 1. The traditional three-tissue concept of the vegetative structure of a *Eucheuma* species. A, A cross section of a *Eucheuma speciosum* frond. (Voucher No. 24675; composite photograph No. 32942.23.) B, A section of cortex of *E. speciosum* shows the radiating cortical filaments. (Voucher No. 24406; photograph No. 32890.3.) C, A portion of the pseudoparenchymatous medulla of *E. speciosum.* (Voucher No. 24675; photograph No. 32942.23.) D, The central rhizoidal medullary core, or axis, of *E. serra.* (Voucher No. 24829B2; photograph No. 32899.17.) Scale bars: A = 500 μm; B = 100 μm; C and D = 25 μm.

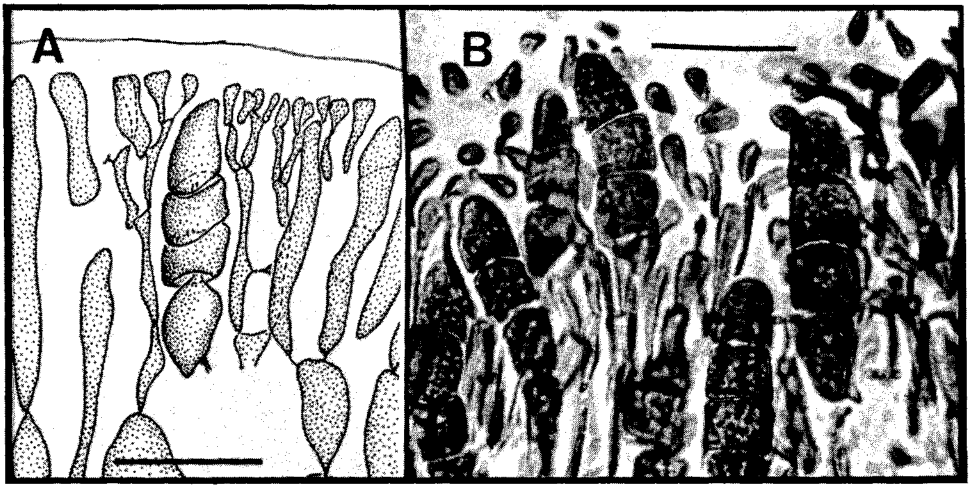


Fig. 2. The seriate tetrasporangia of *Eucheuma perplexum*. A, Camera lucida drawing of a cell group shows other cells nearby and subbasal pitting. (Voucher No. 31628; photograph No. 32941.19.) B, Several spore groups in a section of resoaked material. (Voucher No. 24829B2; photograph No. 32910.25.) Scale bars = 10 µm.

by Harvey, and "placenta" was indefinitely applied to the rest by both J. G. Agardh and Harvey.

Knowledge of the gross aspects of the reproductive and vegetative structures followed [e.g., J. G. Agardh 1876 (especially p. 598f), 1892; Schmitz 1895; Weber-van Bosse 1913, 1926, 1928; Kylin 1932, 1956], but further advances have been slow. Recent studies, such as those of Kraft (1969, 1972), Cheney and Dawes (1980), Gabrielson (1983), Gabrielson and Kraft (1984), Doty (1985), Norris (1985), Doty and Norris (1985), and others, have provided additional taxonomic, morphological, and variational details. Still more species are being described, for example, *E. procrusteanum* Kraft (Kraft 1969), *E. deformans* Gabrielson and Kraft (Gabrielson and Kraft 1984) and *E. alvarezii* Doty (Doty 1985), and all are being treated in physiological, floristic, and bibliographic works (e.g., Taylor 1960; Dawson 1961; Cheney and Babbel 1975, 1978; Velasquez et al. 1975; Glenn and Doty 1981; Mshigeni 1984; and Lewis and Norris 1987). Cheney (in this volume) has provided a long-needed taxonomic revision of the species of *Eucheuma* found in the Atlantic/Caribbean. All these publications have revealed the sore need for further and broader taxonomic revision to the tribal, generic, and species level.

The following text attempts to provide a systematic basis for yet more revisional and detailed studies of these seaweeds. Several taxonomic and nomenclatural novelties or adjustments are proposed to obtain application of the type method and other features of the International Code of Botanical Nomenclature and to provide guidance for future academically or commercially oriented studies in the field and laboratory. With some exceptions, the synonyms resulting from the costly and slow task of locating and studying the type specimens are not given in this preliminary treatment. Neither are the species included that are known to the author by their type specimens only.

Eucheumatoideae tribus nova (Family Solieriaceae)

Typice cortex cum familiis radiantibus cellularum parvarum et medulla cellularum amplarum parietibus crassis dense contiguis simul sed spatiis minoribus intercellulosis et

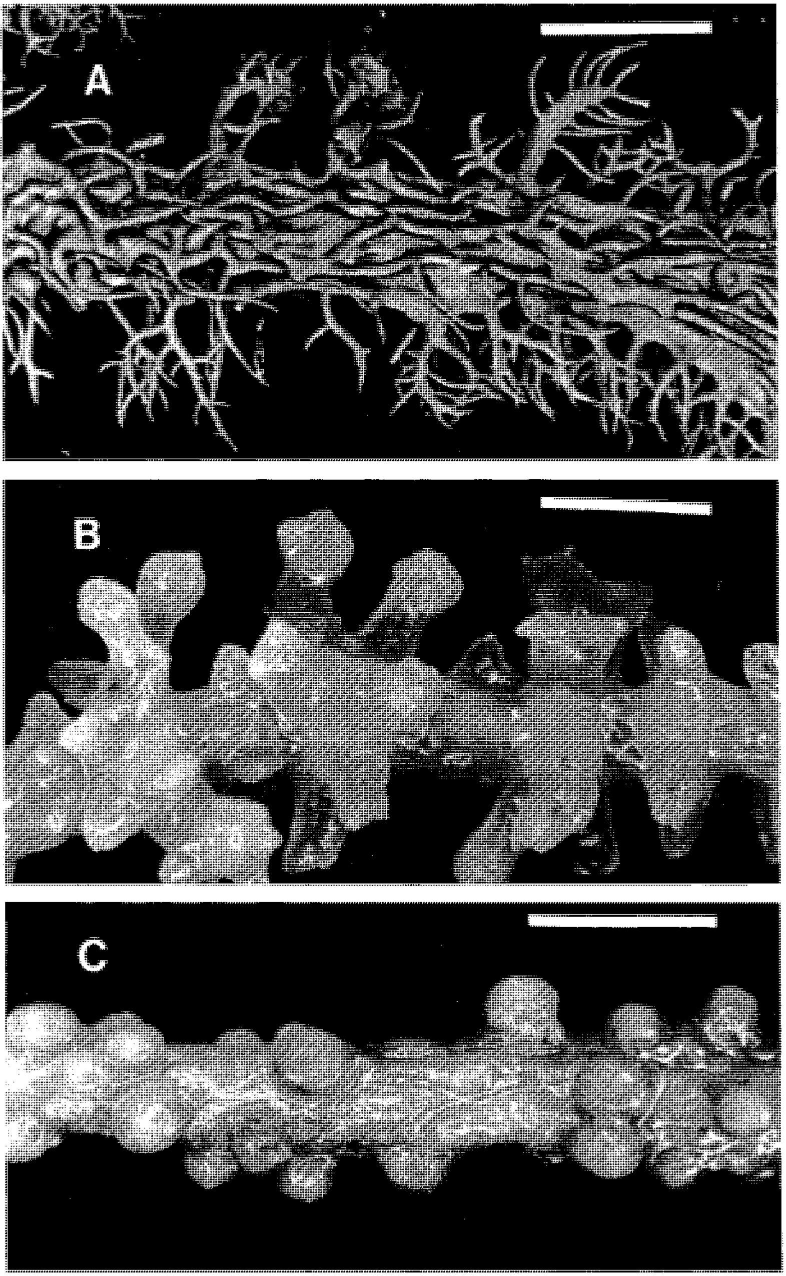


Fig. 3. Cystocarp positions on the thalli. A, *Eucheuma speciosum* on fertile spines borne on compressed segment margin. (Voucher No. 24156; photograph No. 32932.8.) B, *Eucheuma denticulatum* cystocarps subterminal on spines (Voucher No. 31439G; photograph No. 32941.3.) C, *Kappaphycus alvarezii* cystocarps directly on a resoaked main axis. Such may be somewhat constricted or cylindrical at the base. (Voucher No. 28727; photograph No. 32912.3.) Scale bars = 5 mm.

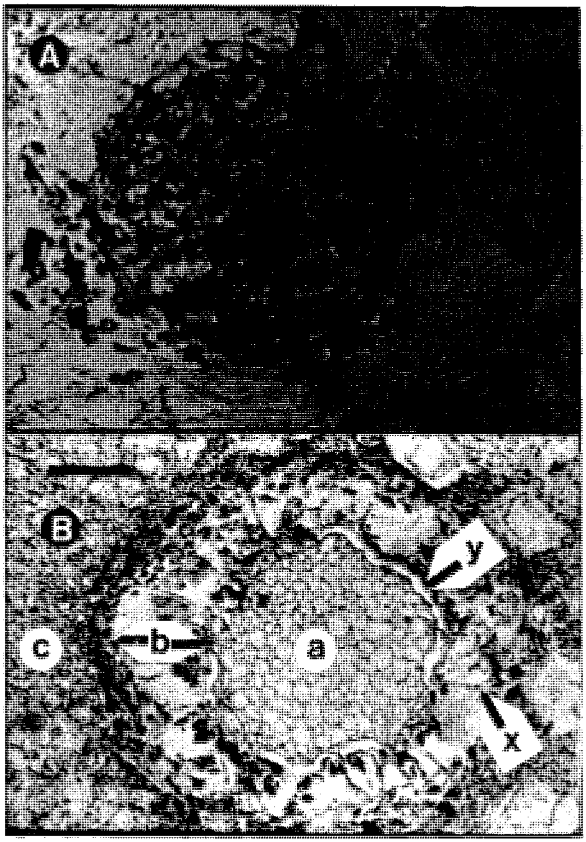


Fig. 4. Cystocarp contents in *Kappaphycus alvarezii*. A, A whole "fusion cell" dissected from a young cystocarp. (Voucher No. 32590; photograph No. 32626.11A.) B, Nearly equatorial section of placenta of *Eucheuma alvarezii* shows contents of fusion cell and other structural features. White arrows: a = fusion cell; b = placenta; c = pericarp; x = traversing filament; y = shrinkage space. (Voucher # 32730.A2; photograph No. 32884.22.) Scale bars: A = 50 µm; B = 100 µm.

axe hyphae vel rhizoidei praesentibus vel absentibus; gonimoblastus radialiter expandens intra texturas corticatas ubi cystocarpia ostiolis formata sunt; cystocarpia portata aut prope apices spinarum aut in axibus principalibus, plerumque strato speciali cellularum inter pericarpium et gonomoblastum; fila gonomoblasti radiantia ex ampla cellula sphaerica conjungenti. Aliter typicus Solieriaceae et Gigartinalis.

Type Genus: *Eucheuma* J. Agardh 1847.

Typically, cortex with radiating families (Doty and Norris 1985) of small cells; inner cortex and medulla of large, notably thick-walled cells densely packed together but with minor intercellular spaces, and a hyphal or rhizoidal central axis present or absent in the medulla.

Gonimoblast expanding radially within the cortical tissues as the ostiolate cystocarps are formed; cystocarps borne either at or near the tips of spines or on the branch axes, and, in time, gonimoblast surrounded by a placental envelope of filaments (Fig. 6), which initially lie next to the gonimoblast; from the placental envelope traversing filaments arise

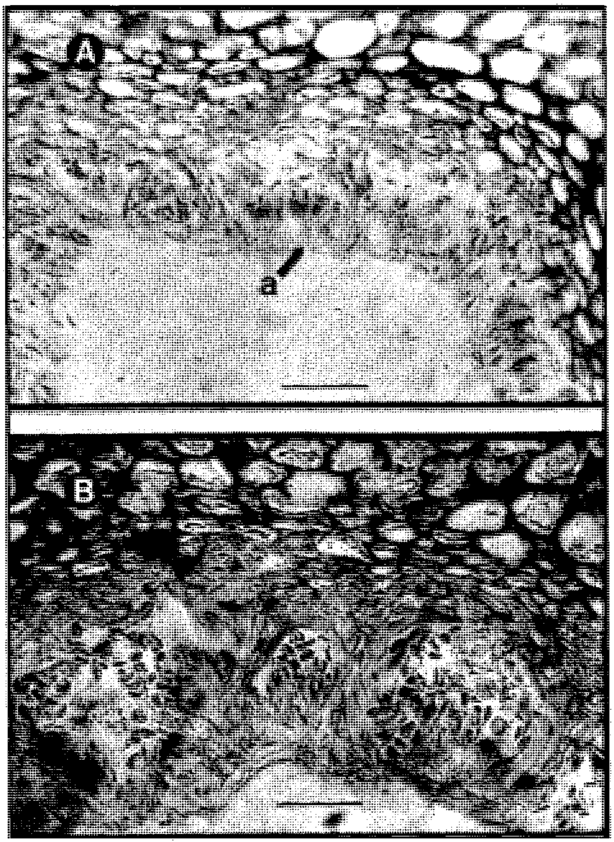


Fig. 5. Contents of the placenta show relationship of gonimoblast filaments and traversing filaments to the pericarp and fusion cell and between the latter gel (as what appears, in black and white, to be a characterless grey to black smudge). A, *Eucheuma denticulatum.* A gonimoblast filament system is shown at "a". (Voucher No. 31439M; photograph No. 32905.23.) B, *Eucheuma kraftianum.* (Voucher No. 24706A2; photograph No. 32888.22.) Scale bars = 100 μm.

in some abundance, and among them the gonimoblast filaments radiate from the large spherical "fusion cell" such that the gel-packed "faserhulle" of Kylin (1956), earlier described and figured by Harvey (1853), is formed between the gonimoblast and the pericarp. The gel in this layer must stabilize the positions (Figs. 4B and 5) of the structures in the pericarp lumen as do Harvey's "confervoid filaments."

To date this tribe is thought to consist of the classical genus *Eucheuma* with three sections and a new generic segregate described in the following. The criteria used by Doty and Norris (1985) in characterizing the major taxa in the Eucheumatoideae, (Table 1) stand tentatively revised. A common characteristic of all members of the tribe is their carrageenan-rich, cellularly dense, largely pseudoparenchymatous structure and, in addition to their other obvious solieriaceous attributes, the general presence of the special placental envelope. The existing knowledge of the reproductive details of the species of this tribe is so nearly a void that in specific taxonomy it is useless. Thus, understanding and use of the vegetative character of the species are preponderant, and vegetatively the

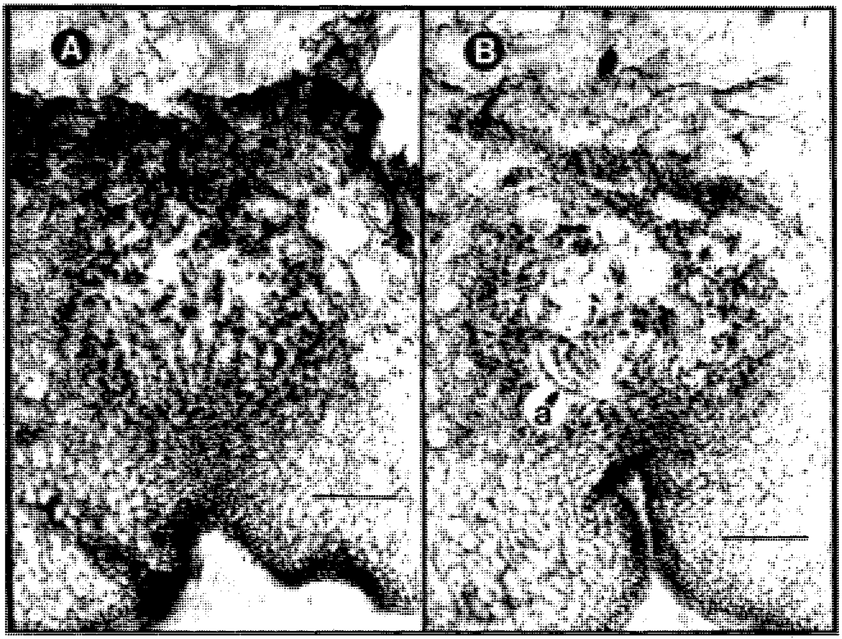


Fig. 6. The filamentous placental envelope lining the lumen of the pericarp and forming a cellular outer placental border in a *Kappaphycus alvarezii* cystocarp. Sections are tangential to and just inside the pericarp. The ostiole shows as an indentation in the margin of the section. A, Outer section. B, Inner section with a black arrow, a, pointing to an unbranched veil filament. A placental envelope filament. (Voucher No. 32730.A2; photograph Nos. 32882.4 and 32882.5, respectively.) Scale bars = 100 μm.

species in this tribe are often very plastic, though some (e.g., *E. gelatinae* and *E. speciosum*) are not. As a result, when the attributes of a taxon are read, the reader must bear in mind that they are tendencies, not absolutes. So, in Table 1, and in the descriptive paragraphs for the major taxa, what is said in absolute terms must carry the thought of "there is a tendency. . . ." It is hoped that this attitude will ease the lack of hard reproductive information. In the following sections, the practical taxonomy is based on vegetative anatomy at the species level; on a combination of vegetative, gel, and reproductive phenomena at the generic level, and on rather little adequate basis other than expediency at the tribal level. Perhaps no basis for phylogeny exists at all now. The systematic value of the hydrocolloidal wall materials is a great aid, but this information is rarely readily available to the taxonomist.

The nature of the nondamaged apical segment (i.e., the main axis where it extends beyond the first pair of spines, whorl of spines, or rebranched branch found below the thallus tip), the locations of the cystocarps, the presence or absence of an axial core (of hyphae or rhizoids), and the nature of the gel are major criteria (Table 1) used to distinguish two genera. The first three are "hand-lens criteria," that is, they can be used in the field. Thallus form, branching, blunt protuberances, and flattening are not of generic value, and thylles are only questionably so at this time. Important at the sectional and species level are the origins of the determinate spines (apices pointed) and protuberances (apices blunt) and the origins of the indeterminate branches. Secondary spine, protuberances, and branches, if any, arise later between the primary structures of the

Table 1. Typical Characteristics of the Major Taxa Within the Tribe Eucheumatoideae Resulting from their Vegetative Tendencies

Eucheuma section *Eucheuma*	*Eucheuma* section *Gelatiformia*
1. Fronds cylindrical; spines simple, their basal diameters less than their axis thickness	1. Fronds compressed; spines simple, their basal diameters equal their axis margin thickness
2. Spines in regularly spaced pairs or whorls first, but later others may appear scattered	2. Spines in rows, marginally first and later dorsally and ventrally on flatter faces or scattered
3. Branches generally from whorls, often opposite, irregular, or in pectinate series	3. Branches mostly marginal, pinnate, often opposite or irregular but not in pectinate series
4. Axial core rhizoidal	4. Axial core tortuous hyphal
5. Axial core cylindrical	5. Axial core often flattened
6. Iota carrageenan	6. Beta or other carrageenans
7. Cystocarps on laterals	7. Cystocarps on laterals
8. Generally one spine beyond cystocarp	8. Often several spines lateral on cystocarp or none

Eucheuma section *Anaxiferae*	*Kappaphycus*
1. Fronds cylindrical or dorsiventral, bearing compound spines	1. Fronds of many forms but commonly cylindrical, bearing simple blunt or spiny protuberances
2. Spines often scattered, in whorls or covering the thallus in various arrangements or densities	2. Protuberances irregularly arranged or, in some cases, appearing in rows so segments become angular
3. Branching generally from whorls and thus often opposite, whorled, or irregular	3. Branching irregular but sometimes irregularly pinnate or, by chance, opposite or falsely dichotomous
4. No hyphal or rhizoidal axial core in cylindrical axes	4. Hyphal axial core usually present and vaguely cylindrical
5. Iota carrageenan	5. Kappa carrageenan
6. Cystocarps on main axes	6. Cystocarps on main axes
7. Ultimately no spine on cystocarps	7. No lateral associated with cystocarp

same name. With age, segments tend to become proliferous of spines (Fig. 7A), protuberances, and branches and are of little taxonomic value.

In *Eucheuma*, primary determinate spines arise in pairs, whorls, or marginal rows near the tips of the branches. Some of the spines may become indeterminate and give rise to rebranched branches. Quasi-branching or really opposite branching (Fig. 8) is, thus, common. Later secondary determinate spines may arise (Fig. 7A) on the axes between the whorled spines, and on old thalli these secondary spines may, with age, produce secondary branches. Often, with age or (Fig. 7B) under some unusual circumstances, one or more primary spines may become secondary indeterminate branches. The cystocarps of the *Eucheuma* species tend to appear near the apices of spines (Fig. 3). In *Eucheuma* section *Eucheuma*, often the fertile spine elongates beyond the first cystocarp and produces one or more other cystocarps successively. However, these multicystocarpic spines remain small in diameter and differ distinctly from vegetative spines or axes. Also, in *Eucheuma* section *Gelatiformia*, the spines may produce more than one cystocarp but may branch in doing so, or the thallus may broaden laterally such that the fertile spine *anlage* are submerged in the vegetative structure, and thus the cystocarps appear sessile on the vegetative axis or are borne on unornamented podia. This section, however, may bear the most highly ornamented cystocarps seen in the tribe

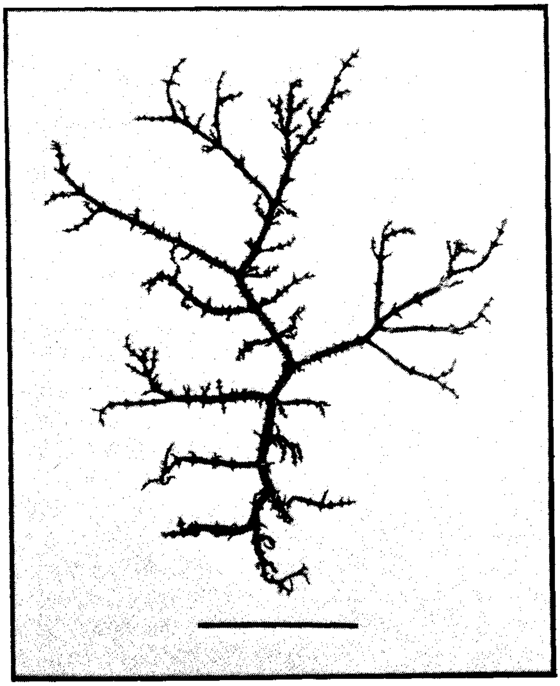


Fig. 7. Secondary spines and branches in *Eucheuma* species. A, Drawing of *Eucheuma denticulatum* showing uniform dense, nonwhorled, secondary spininess at the left. Secondary spines have obscured the primary spine whorls below, so whorls show only on the younger parts of the thallus at the right. (Voucher No. 14632; photograph No. 32944.12.) B, A proliferous form of *Eucheuma perplexum* from the southern tip of Taiwan. Branches arising secondarily from initially determinate spines. (Voucher No. 31642; photograph No. 32944.25.) Scale bars: A = 1 cm; B = 5 cm.

(Fig. 3). In *Eucheuma* section *Anaxiferae*, after initiating the production of cystocarps, the fertile spines become indeterminate and produce a non-spinelike vegetative axis bearing further fertile or vegetative spines. Thus, the cystocarps in this section may mature on vegetative axes and without ornamentation.

In *Kappaphycus*, no whorls are present; opposite branching is rare and appears only by chance. As a rule, neither rows of spines nor branches are seen unless some environmental cause has occurred. At the maximum expression of such orderliness of proliferations or spines, rows are seen, and they may cause the axial segments that bear them to deviate from cylindrical and become angular. In *Kappaphycus*, the indeterminate primary branches arise one at a time from near the tips of nondamaged axes. Secondary branches on the older segments are common. The cystocarps are borne as hemispheres directly on the main axes (Fig. 3C). At least in some cases or under some circumstances, it appears that production of cystocarps terminates growth in length of branches (e.g., *K. alvarezii*).

Morphological variability in response to the environment is wide within species and confuses the taxonomist who often has but one fragment of a thallus with which to work. It is postulated here that variation in form may range from strictly erect to markedly diffuse branching and to simple crusts in some species. This handicap, in the absence of adequate numbers of thalli grown under different circumstances, can be offset best by

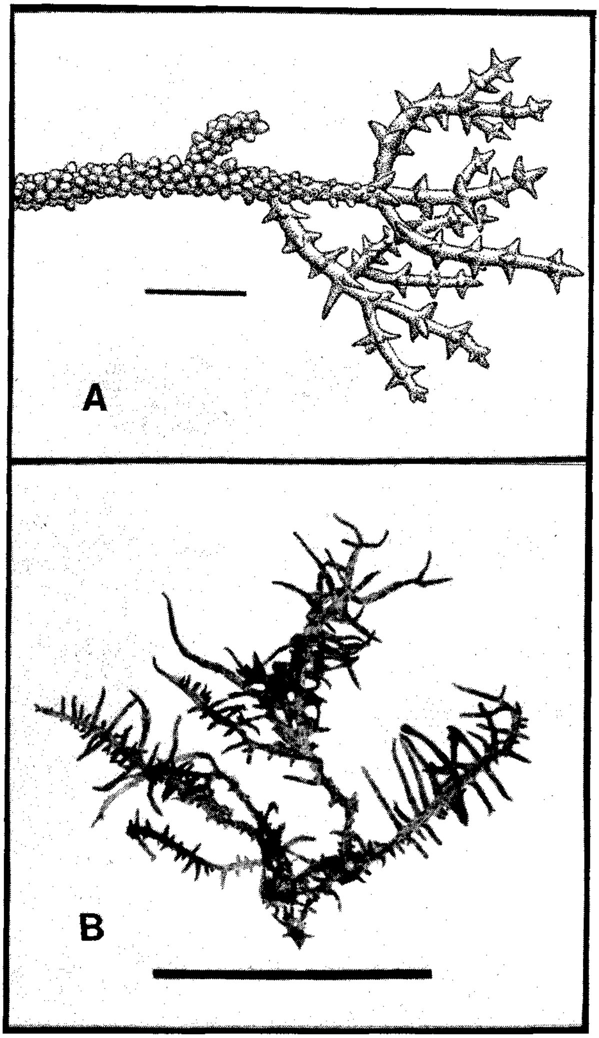


Fig. 8. A major frond of *Eucheuma denticulatum* with an unusually high frequency of opposite branching. (Voucher No. 14642; photograph No. 32938.19.) Scale bar = 5 cm.

ontogenetic studies of young materials such as are seen in most complete specimens. Given growth in the same habitat, the typical differences listed in Table 1 are obvious for the two genera and the *Eucheuma* sections (Fig. 9). The traditional differences recognized by J. G. Agardh (1876, 1892), as parts of keys rather than sections, and Weber-van Bosse's (1928) two sections, require understanding not provided by these two authors. Neither the superficial form nor the axial anatomy is taxonomically entirely reliable. For example, species completely lacking the "typical" axial core structures are found in both genera. At least three species appear to have crustose forms. In both genera, unilaterality is often seen but is suspected to be environmentally caused. The nature of the carrageenans at the generic or sectional level is a distinct help, but knowledge of the nature of these carrageenans is in a state of flux. Santos (pers.

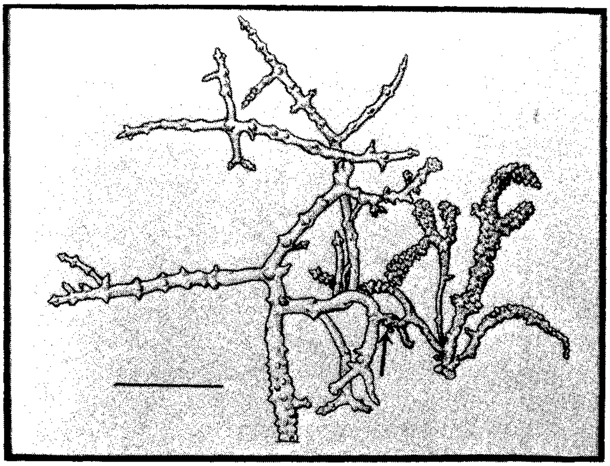


Fig. 9. Two thalli have grown together naturally where indicated by arrow. *Eucheuma denticulatum* shown at the left and a *Kappaphycus* at the right. (From material provided by Dimitri Stancioff; Voucher No. 24882; photograph No. 32941.5.) Scale bar = 2 cm.

commun.) has indicated the nature and variability of the fascinating beta-gamma-kappa carrageenan complex (Greer and Yaphe 1984b), and the possible precursor roles postulated by Stancioff and Stanley (1969) for mu and nu carrageenans are not at all settled.

If the aforementioned criteria are used with precaution, the two genera of this tribe can be separated by using the following key.[1]

Key to the Genera of Tribe Eucheumatoideae

Spines present in pairs, whorls, or lines usually at predictable places; spines simple or compound, becoming cylindrical in places, often displaced by branches; spines having densely rhizoidal axes; no hyphal structures arising from thylles; rhizoids abundant and forming a central medullary axial strand in most species; cystocarps at or replacing apices of spines; thalli producing iota or beta carrageenan preponderantly . . . . *Eucheuma*

Proliferations and spines absent or, if present, not in pairs, whorls, or lines at predictable places; tubercles and proliferations blunt and simple; if pointed, rarely becoming more than attenuate-conical and not becoming displaced by branches; proliferations and spines lacking densely rhizoidal axes; thylles present and often producing hyphae; hyphae, mixed with larger cells, forming a central medullary axial strand in most species, at least near the axis tips; cystocarps protruding from main axes; thalli producing kappa carrageenan preponderantly . . . . *Kappaphycus*

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[1] A precaution must be entered here. Only exceptionally in this text is other than the nature of an exsiccatum or exsiccata a point, unless speaking of function. The reader must be aware of the great difference between the results obtained from using exsiccatae (dried) and those obtained from using fresh or wet-preserved voucher materials. If the latter, whether alcoholic or aqueous as well as (Doty and Norris 1985) presence or lack of adequate cations (such as potassium or calcium) in either the preservation or study procedures makes big differences too. In field practices, of course, the researcher has living material, and it can be very different from the preserved form. Abbott has suggested that because type specimens are almost always exsiccata (singular noun exsiccatum), in taxonomic work or communications, the dried materials should be described as is done in the present text. In this connection, compare the appearance of the cystocarpic portion of *E. speciosum* in Fig. 3A with the wet preserved part having the living superficial form illustrated for this species and for *E. gelatinae* described later in this text.

***Kappaphycus* genus novum**

Thalli ramuli irregulariter, rotundi et kappa carrageenan ferentes. Cystocarpia in pagina segmentorum principalium. Gonimoblastus apparenter ex pagina sphaerica cellulae conjunctionis ut in typo *Eucheuma denticulatum* (Burman) Collins et Hervey. Medulla centralis tylosibus intercellularibus, aliquibus facientibus filamenta brevia irregularia tenuibus parietibus relative. Aliae proprietates ut in typo Solieriaceae, Gigartinales, Rhodophyta.

Typus est: *E. alvarezii* Doty (Doty 1985). See figures in Doty (1985) of the holotype and its varieties.

The name *Kappaphycus* is singular and neuter. It is composed of the Greek letter *kappa* (as written in the roman alphabet), which refers to the kappa carrageenan of the holotype, and the Greek noun *phycus* for seaweed. Phycus is used rather than *fucus marinus* as in the pure Latin of Lewis and Short (1958), because as a Latin noun itself, fucus does not refer to a seaweed. Also, because of the seaweed generic name *Fucus* Linnaeus, use of the word fucus can be confusing phycologically. The connecting vowel would normally be *o*, as preferred by the International Code of Botanical Nomenclature, but it intentionally is not used here.

This genus consists of members of the former *Eucheuma* section *Cottoniformia*. Their cystocarps (Fig. 3C) are borne on the main segments of the main axes. These species produce kappa carrageenan. The form and basic vegetative structure of the type species for *Kappaphycus* have been illustrated by Doty (1985, figs. 1–8) with respect to both external macroscopic and internal microscopic features. Branches arising as indeterminate knobs are produced solitarily, often seemingly at random. The inner cortex and axial region in the apical segments produce thylles that tend to become extended basally as hyphae in the axial region of the thallus. In one or more species (Weber-van Bosse 1913), any hypha-like structures seen right at the apex disappear shortly below, so no specialized central axial region of thick-walled hyphae is seen in them. Generally, a central axial region exists in which small and large cells are mixed. Otherwise, in older axes, no well-defined medulla and cortex are present internally.

The reproductive details are not clear at present, and the females do not tend to be less cylindrical than other thalli. The tetrsporangia become seriately divided and appear normal for the Solieriaceae.

The center of a maturing cystocarp in the holotype is occupied by a relatively huge spherical cell that radiates gonimoblast filaments. This cell is spoken of as a fusion cell by various authors, including J. G. Agardh (1876, 1892), who referred to the complex in Latin as the nucleus and the placenta. In living material, when a young pericarp is cut into, this fusion cell will often readily come out (Fig. 4B) as a rather turgid ball. It appears to contain a three-dimensional cytoplasmic reticulum illustrated in section and interpreted as not unlike soap bubbles filling a cup. The faces of the optically granular dissepiments between the "bubbles" apparently have no intrinsic characteristics of a cell wall other than position. This is not seen in resoaked dry material.

In the type species, between the pericarp and gonimoblast, a placental envelope, a layer of cellular filaments (Fig. 6), contributes to the faserhulle seen in this and many other members of the Solieriaceae. It is the nutritive tissue recognized by Kraft (1969) in *K. procrusteanum* cystocarps. A space filled with gel is seen between this pericarp envelope and the gonimoblast. In accordance with Harvey (1853), J. G. Agardh (1876, 1892), and Gabrielson (1983), this envelope, gel, space, and their contents (Figs. 5A, 5B) are termed here "placental" for now. Some of these authors may have used "placenta" for the relationship of the gonimoblast filament to the fusion cell wall in the sense that the ovules and placenta are related in a plant.

With the appearance of the placental space, filaments that remain sterile appear to span it from the surrounding pericarp lining to the fusion cell where they attach. Such traversing filaments are seen in *E. procrusteanum* (Kraft 1969) and as sterile gonimoblast filaments in *Eucheuma* (Gabrielson 1983) in mature cystocarp sections. At the same time that these filaments are seen embedded, at least in some cases, in relatively enduring gel, gonimoblast filaments are also seen (Fig. 5). They appear as though they have elongated into the placental space centrifugally, having branched and produced carpospores terminally. The carpospores appear initially to be solitary, in concatenation, or in dense clumps of undefined arrangement. In *Eucheuma*, the gel layering (Fig. 10) seen around the peripheral ends of young gonimoblast filament tips gives the impression that such layering could indicate gelation of wall material that might be homologous with sporangial walls. In any case, the gonimoblast filaments of both genera protrude into spaces that appear to be filled with a gel other than that surrounding the traversing filaments.

Possibly, the placental envelope (Fig. 6) arises relatively independently of the pericarp. In *K. alvarezii*, it appears to be a veil of unbranched filaments (e.g., "a" in Fig. 6B) covering the developing gonimoblast. From this tissue, which may be but one cell thick at first, the traversing filaments appear to be mainly of one cell or of one comparatively long, large-diameter cell with smaller cells at each end. In some cases, the peripheral end of such a cell has been seen oppositely pitted to two cells in a filament of the special layer of cells (placental envelope) lining the inner pericarp surface. When this is true, the traversing filaments thus appear to be intercalary in origin. However, if interpreted correctly, unlike those described for *Gracilaria truncata* Kraft (Kraft 1977), they originate from the placental envelope and thus are more nearly the sterile gonimoblast filaments Gabrielson (1983) described for *E. isiforme*.

The carpogonial branch, gonimoblasts, and development of carpospores are uncertain but appear to be within the limits of variation found for the Solieriaceae. The characteristics of the male plants are not known.

Only the most commonly recognized entities are included here. Some well-intentioned suggestions for synonymy are not followed. For example, Mshigeni (1984) suggested that the two entities recognized and named by Schmitz (1895) in the same paper, *K. inerme* and *K. striatum*, be considered synonyms under the latter name. Also, the numerous varieties recognized by such authors as Weber-van Bosse (1928) and Yamada (1936) are ignored for the present, along with the considerable number of the older binomials that, if they can be recognized from protologue materials at all, eventually may come to be applied appropriately. The type and other species are transferred as appropriate from the genus *Eucheuma* as follows.

Kappaphycus alvarezii (Doty) Doty nov. comb. (Figs. 3C, 4, 6, 11)

Basionym: *Eucheuma alvarezii* Doty (Doty 1985).

Holotype: The holotype specimen, bearing the Doty voucher No. 28727, is from the reef flat west of Karindingan Island on Creagh Reef, near Semporna, eastern Sabah, Malaysia, and is deposited in the B. P. Bishop Museum Herbarium, Honolulu, Hawaii.

Other Distribution: Sulu Sea, Sulu Archipelago, and adjacent areas. Distributed widely by humans in recent years.

Remarks: Although many details are missing, the life cycle appears to be triphasic, with the tetrasporic, female, and putative male phases similar in gross morphology. In view of the illustrated, recent work of Doty (1985), neither detail nor the variation in this

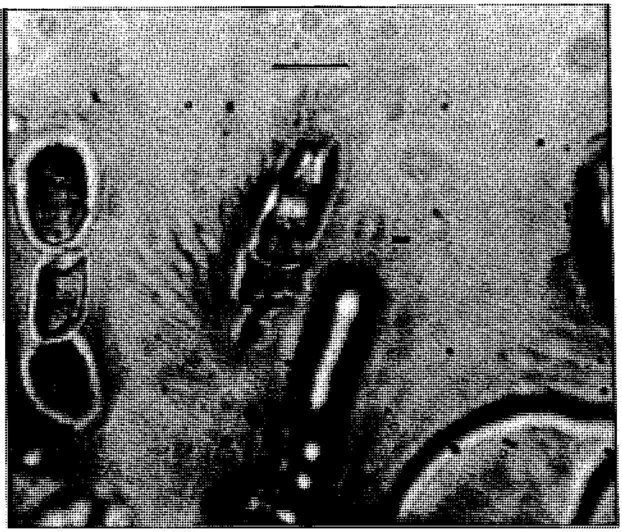


Fig. 10. Layering in the gel around the ends of young gonimoblast filaments in a section of *Eucheuma denticulatum* cut from a dried and resoaked commercial specimen. (Voucher No. 31439m; photograph No. 32942.12.) Scale bar = 5 μm.

species is provided here. (However, see the figures and the previous discussions and Fig. 11, which shows the farmed cottonii of commerce today.)

Kappaphycus inerme (Schmitz) Doty nov. comb. (Figs. 12, 13)

Basionym: *Eucheuma inerme* Schmitz (Schmitz 1895).

Holotype: The holotype specimen, Holst No. 1339 from Dar es Salaam, Tanzania, was originally deposited in the Berlin Herbarium and has probably been destroyed. Thus, as lectotype, an isotype specimen in the algal herbarium of the British Museum in London (Fig. 12B) bearing the same identification information is designated and accepted.

Distribution: East coast of Africa and southwestern Indian Ocean areas.

Remarks: Many of the specimens of *K. inerme* seen from Tanzania in the collections of Keto Mshigeni, G. F. Papenfuss, Robert Scagel, and others have a tendency for the erect branches to be inflated (see Fig. 13B) toward the apex. The same tendency is seen in some Philippine specimens not found in pools; thus it is uncertain as to whether light or genetics is the primary cause. Also, in *K. inerme*, in some cases, the central axial region has a rather regular border of cells of nearly uniform medium-sized cells that seems to be lacking in other *Kappaphycus* species. Thus, Mshigeni's (1984) treatment of these two species as synonyms may be justified, for little is known, other than size and perhaps range, that separates them. What could be a distinction between this species and *K. striatum* (Figs. 14A and 4B) is the base, if those specimens shown in Fig. 12 prove to be typical. It is thought that *K. striatum* generally has only a simple disc.

Kappaphycus striatum (Schmitz) Doty nov. comb. (Fig. 14)

Basionym: *Eucheuma striata* Schmitz (Schmitz 1895), which is usually written *E. striatum* Schmitz.

Holotype: Collected and preserved in alcohol by a Dr. Stuhlmann in Zanzibar. At Leiden there is an isotype received (Weber-van Bosse 1926) from H. Winkler of the

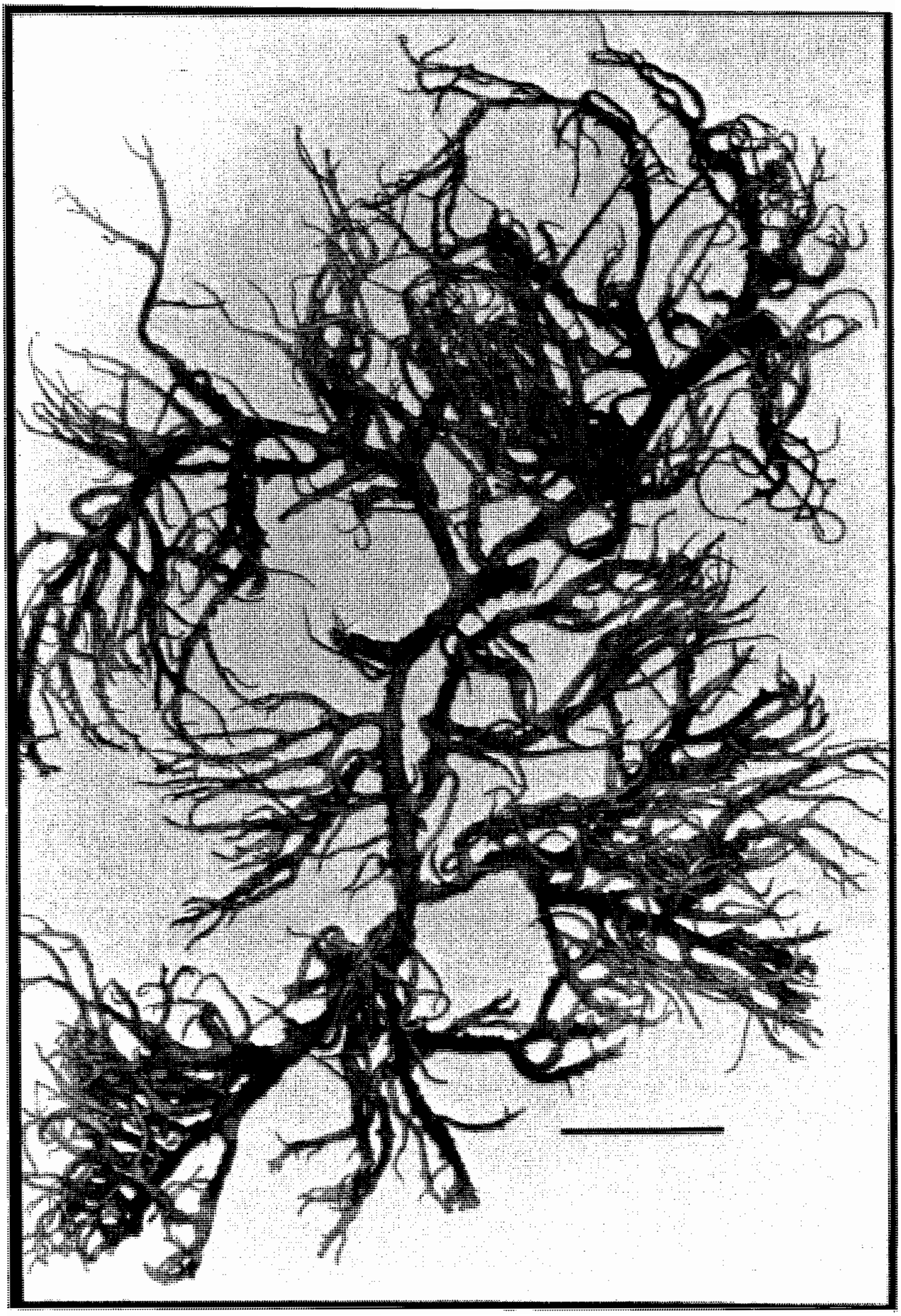


Fig. 11. *Kappaphycus alvarezii* Doty. Whole dried thallus farm-produced in Kosrae, Federated States of Micronesia. (Voucher No. 32630; photograph No. 32939.13.) Scale bar = 5 cm.

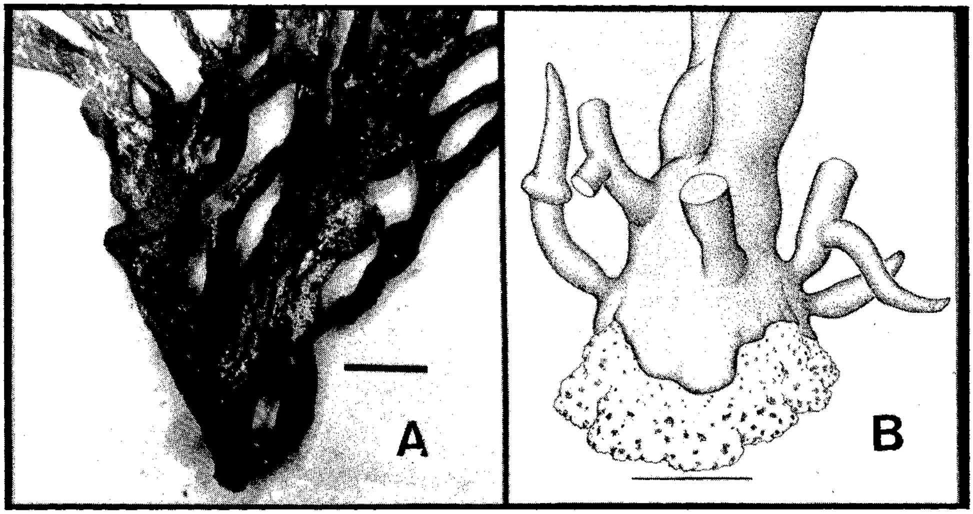


Fig. 12. Holdfasts of *Kappaphycus inerme*. A, Photograph of the base of the British Museum herbarium lectotype (isotype) specimen of Holst No. 1339 shows basal segments only. (Photograph No. 32943.7.) B, Drawing from holdfast of Papenfuss and Scagel collection PR-XV-2. (Photograph No. 32941.7.) Scale bars = 1 cm.

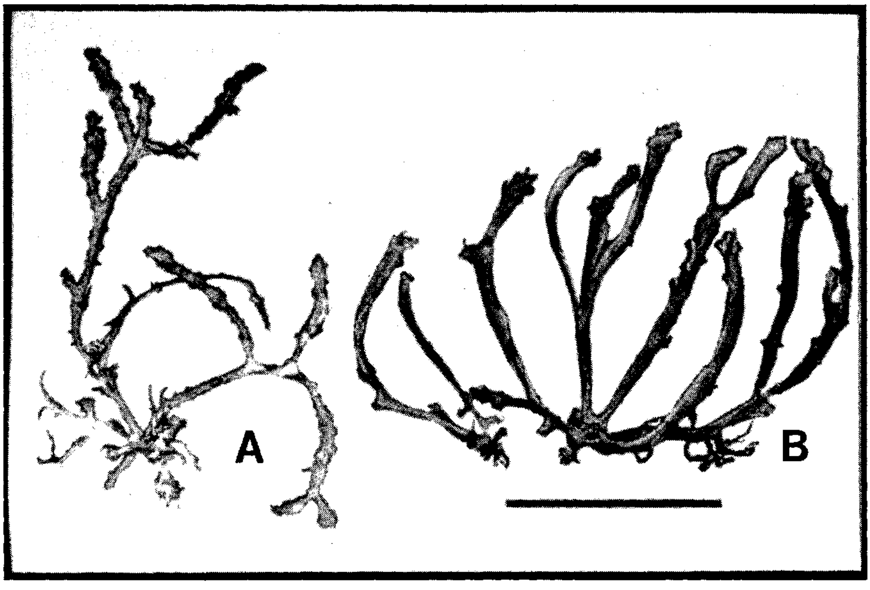


Fig. 13. Apically inflated fronds of *Kappaphycus inerme* showing their characteristic smooth, plain, long lower surfaces with few protuberances, gradually expanding axis, and but a few very slender proliferous branches from near the base. A, Normally inflated upwards. B, Apparently repeatedly tip damaged, perhaps by grazing; long basal frond segments largely arising from a horizontal older frond. (Collections made by G. F. Papenfuss and R. F. Scagel in Zanzibar; Voucher Nos. PR-XIV-75 and PR-XIV-2, respectively; photograph No. 32938.9.) Scale bar = 5 cm.

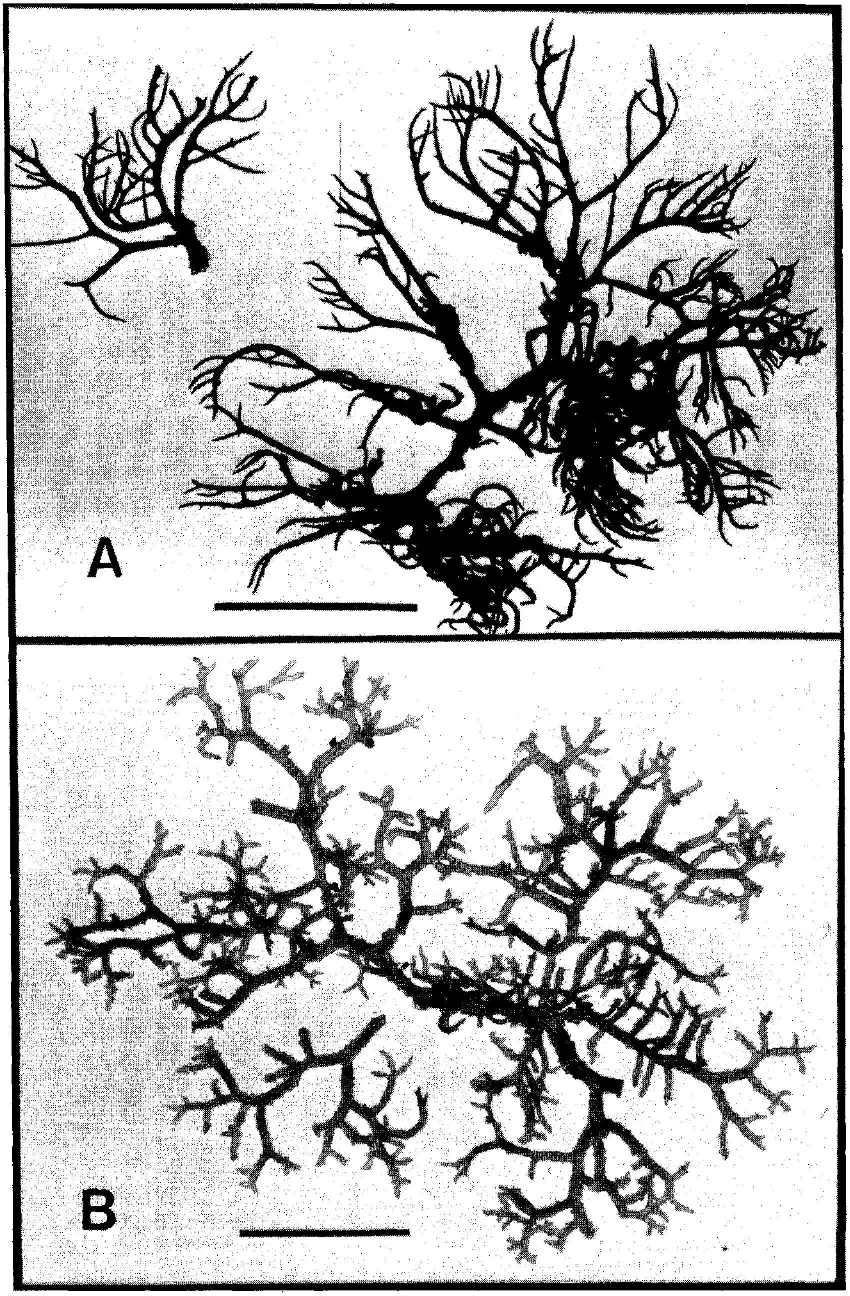


Fig. 14. Two common varieties of *Kappaphycus striatum.* A, The "elkhorn" variety common on clean reef flats in the Central Philippines. This specimen was a green thallus grown on a reef-flat farm. (Voucher No. 24792; photograph No. 32944.22.) B, The dichotomous variety common on muddy reef flats. (Voucher No. 16013; photograph No. 32942.8.) Scale bars = 5 cm.

Hamburg Herbarium. For the present study an exisiccatum 5 mm long, numbered H.H.27, was received from the same herbarium with "Holotype" stamped on its label and information that the alcohol-preserved material was available too. There is a tiny isotype, an exsicattum, in the British Museum.

Distribution: East Africa, Indonesia, eastern Sabah (Malaysia), Philippines, Belau, and Pohnpei (Federated States of Micronesia).

Remarks: The original cottonii farmed was this species, which is extremely variable. This species and the whole tribe are badly in need of further taxonomic study. The two forms illustrated are characteristic of reef flats (Fig. 14A) and mud flats (Fig. 14B), respectively. The second looks like the type specimen for *E. dichotomum* Weber-van Bosse (Weber-van Bosse 1928). The first is the elkhorn variety, which is very plastic, and was the first farmed strain of *Eucheuma*. Doty and Norris (1985) illustrated a putative form of this species having acute roughnesses on its principal segments. A major variant may be depicted under the name *E. edule* (Kuetzing) Weber-van Bosse (Weber-van Bosse 1926, fig. 33; 1928, fig. 170), but a type specimen for *Chondrus edulis*, Kuetzing's species, has not been seen. Certainly Kuetzing's (1868) description and figure of that species would be equally or more appropriate for either *Gracilaria eucheumoides* Harvey or *E. cottonii* Weber-van Bosse.

Kappaphycus procrusteanum (Kraft) Doty nov. comb. (Fig. 15)

Basionym: *Eucheuma procrusteanum* Kraft (Kraft 1969).

Type Specimen: Kraft No. 960 in the B. P. Bishop Museum, Honolulu, Hawaii.

Distribution: Central Philippines.

Remarks: This species (Fig. 15) is, at least phenotypically, quite variable. See Kraft (1969) for illustrations of the type specimen and cystocarps as well as a discussion of this often asymmetrically ovoid species.

Kappaphycus cottonii (Weber-van Bosse) Doty nov. comb. (Figs. 16)

Basionym: *Eucheuma cottonii* Weber-van Bosse (Weber-van Bosse 1913).

Lectotype: The lectotype specimen, collected by Stanley Gardiner in 26 fathoms of water at Saya de Malha in the Indian Ocean north of Mauritius, is deposited as No. 938.316-220 in the Leiden Herbarium; an isotype is deposited in the British Museum.

Distribution: Tanzania, to Hainan Island (China), Philippines, and Guam.

Remarks: Mshigeni (1984) is followed in treating *E. cottonii* Weber-van Bosse (Weber-van Bosse 1913) and *E. okamurai* Yamada (Yamada 1936) as taxonomically the same. In examinations of materials from the Japanese herbaria, Hainan Island (China), Tanzania, and elsewhere to which one or the other of these two names has been attached, no difference has been seen that would justify maintaining them as two specific entities.

Kappaphycus cottonii grows higher in the intertidal system than any other member of the tribe Eucheumoideae. Often it forms but a few prostrate branches on the top of a rock otherwise embedded in mud. If under such stress that it loses its normal straplike form, it would become what is recognized in the key to species as *E. crustiforme* or *E. horizontale*, both of which would be treated as synonyms of *K. cottonii* if taxonomic synonyms were being included in this paper.

Eucheuma J. Agardh 1847

Generally cylindrical to flattened, erect, bushy, fleshy thalli of large size for members of the Rhodophyta, reaching over 1 kg in mass. Some species prostrate. Producing

Fig. 15. Whole, very smooth frond of *Kappaphycus procrusteanum* with flat slender branches tapered to their tips. (Part of Gavino Trono collection No. 5793; Voucher No. 28256; photograph No. 32933.10.) Scale bar = 5 cm.

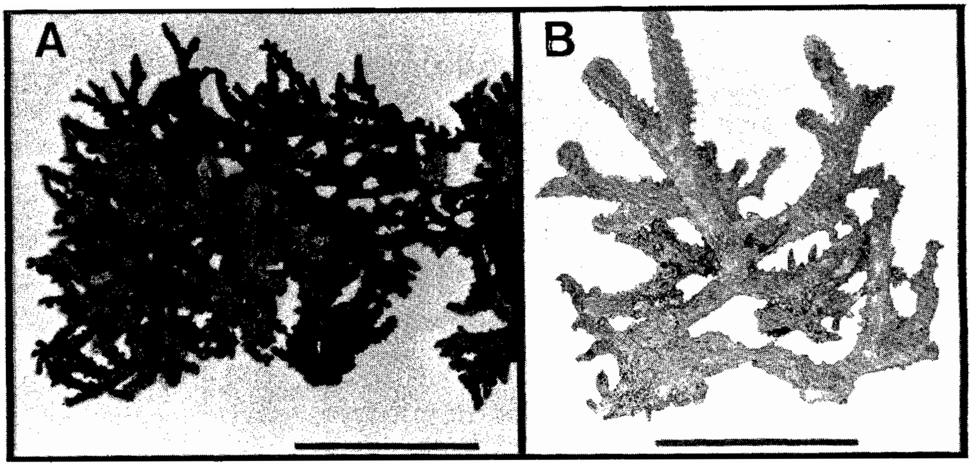


Fig. 16. Characteristic thalli of *Kappaphycus cottonii.* A, an elongated thallus in the form of a "head" collected by Gerald T. Kraft as No. 768. (Photograph No. 32932.25.) B, A whole, but simple, frond collected by Gavino Trono as No. 1995. (Photograph No. 32932.21.) Scale bars = 5 cm.

determinate spines in pairs or whorls at the apex. Branches arising largely through spines becoming indeterminate. Secondary spines produced irregularly or uniformly over the older surfaces. Classically distinguished as being composed of three tissues (Fig. 1): a central, dense axial core of rhizoids; a dense medulla of relatively isodiametric, large thick-walled cells surrounding the axial core; and a cortex consisting of radiating cellular filaments of small diameter.

Reproductively, *Eucheuma* is a member of the Gigartinalian family, Solieriaceae. There appears to be a tendency toward asymmetric compression, resulting in dorsiventrality and symmetric bilaterality, especially in female *Eucheuma* thalli. Gonimoblasts are produced from three-celled carpogonial branches in nemathecia near the apices of determinate spines (Gabrielson 1983). The mature gonimoblast is a relatively huge central cell (= *Fusionszelle* of Kylin 1956) from which radiate gonimoblast filaments (Fig. 5), as in *Kappaphycus*, which taper and branch toward a placental envelope (faserhulle) lining the pericarp. The envelope is in connection with the axial core of the cystocarp pedicel and possibly is several cells thick. Traversing filaments originating from intercalary envelope cells are slender, of small diameter, and in groups extending centripetally to the central gonimoblast "fusion" cell. Male plants are recognized definitely in only a few cases. Tetrasporangia divide seriately and are scattered in the outer cortex of the main axes.

Young cystocarps are produced in relation to spines (Fig. 3C) or terminating podia (= cystocarp terminated spines).

Cell walls are thick, composed of D-galactan carrageenans, of which beta, gamma, kappa, and iota forms are recognized largely on the basis of the presence or absence of their attached sulfate groups.

Lectotype: *Fucus denticulatus* N. L. Burman, based on specimen No. 1274-104 in the Linnean Herbarium in London, England.

Distribution: Western Caribbean, Gulf of California, and the warmer Indo-Pacific region.

J. G. Agardh (1852) provided a nice resume, written in Latin, of the conjectural older generic taxonomy and the list of synonyms resulting. It is as they are accepted today.

Three sections of the genus are recognized (Doty and Norris 1985) as being distinct from one another and typically having different sets of attributes (Table 1). No single attribute is sufficient to distinguish the sections or their species, and for that reason they are treated as sections representing vegetative tendencies rather than as separate genera.

EUCHEUMA SECTION *EUCHEUMA*

See Table 1 for characteristics.

This section represents a vegetative tendency to have indeterminate, cylindrical growth in length, with many determinate laterals appearing as spines from which most of the further orders of branches arise.

Eucheuma denticulatum (N. L. Burman) Collins et Hervey (Figs. 3B, 5A, 7A, 8–10)
Collins and Hervey, 1917.

Basionym: *Fucus denticulatus* N. L. Burman (Burman 1768, p. 28).

Lectotype: The specimen numbered 1274-104 in the Linnaean Herbarium, London, labeled "spinosus" in Linnaeus's handwriting. This same specimen also is accepted as the lectotype for *Fucus spinosus* Linnaeus because in publishing it without reference to specimens, Linnaeus (1771) cited the earlier validly published *Fucus denticulatus* N. L. Burman as a synonym. In accordance with Collins and Hervey (1917) and Dixon (1962), it is recognized that *Fucus muricatus* Gmelin (1768) was published after Burman's name, and so use of Burman's name is continued.

Type Locality: Uncertain, as Burman cited neither locations nor specimens, and there seem to be no specimens or recent reports of finding any *Eucheuma* anywhere in South Africa.

Distribution: From Mozambique northward to Djibouti, where it has been introduced; eastward across the Indian Ocean to Australia, where the specimens seen are largely from the northernmost small islands; Indonesia; eastern Malaysia; Philippines; and the related major island groups in the far western tropical Pacific to New Caledonia. This species has been distributed farther eastward recently by humans into the Pacific at least as far as Hawaii and Pohnpei (Federated States of Micronesia) and Christmas Island in easternmost Kiribati.

Remarks: *Eucheuma denticulatum* (Fig. 8) is an extremely variable species, the spinosum of the trade. Doty and Norris (1965) have illustrated other forms. Morphologically, this species differs from other similar species that have a dense strand of thick-walled rhizoids in their (axiferous) axial segments and generally terete axes. It bears spines in whorls at regular intervals (Figs. 7A, 8) and has spines that are more shortly conical. It is frequently oppositely branched (Fig. 8). This species is quick to attach apically by either spine or branch tips, and, thus, fragments broken from thalli reproduced from spores are often found arising from a prostrate old axis attached at several places. This species also may have a tendency to have branching that is less percurrent than that of other species of the section, which tend to be more erect, perhaps because these other species more often are annuals and thus arise from spores. *Eucheuma denticulatum* is a perennial and is reproduced largely by environmentally induced breakage and is spread by farming practices. Cystocarps are not often seen but are expected to be near the tips of lateral spines.

Eucheuma serra (J. Agardh) (Figs. 1D, 17)
J. G. Agardh, 1847.

Basionym: *Sphaerococcus serra* J. Agardh (J. G. Agardh 1841).

Type Locality: Mauritius.

Distribution: Perhaps overlapping the range of *E. denticulatum*.

Holotype: The holotype for *S. serra* J. Agardh is believed to have been illustrated by Kylin (1932, pl. 10, fig. 21) as Agardh Herbarium Specimen No. 34664, because on this sheet is written "*Fucus spinosus* Lin./ ex Ind. orient./ mis Mertens," possibly by Agardh himself. Certainly this is the specimen Agardh (1841) had at hand when describing the source of his material for *Sphaerococcus serra* as "Sph. spinosi nomine a Mertensio miss'ns, ramis oppositis ab ille diversus." Furthermore, it would seem from Areschoug's (1855) remarks on *E. nodulosum* (see also Weber-van Bosse 1928 [as *E. nodosum* {nom. nudum}]) and those of J. G. Agardh (1852, 1876, and 1892) that the specimen illustrated by Kylin must be accepted as the holotype for the species *S. serra* J. Agardh from Mauritius.

Remarks: This usually pale-colored entity (Fig. 17) often is seen among collections of *E. denticulatum*, from very bright calm water and from a geographically wide range of places. The forms range from those that are finely branched and erect to those that are slender and appear to have been prostrate. Sometimes *E. serra* has a redness about the basal segments that appears to be absent in *E. denticulatum* and, unlike the latter, it has a

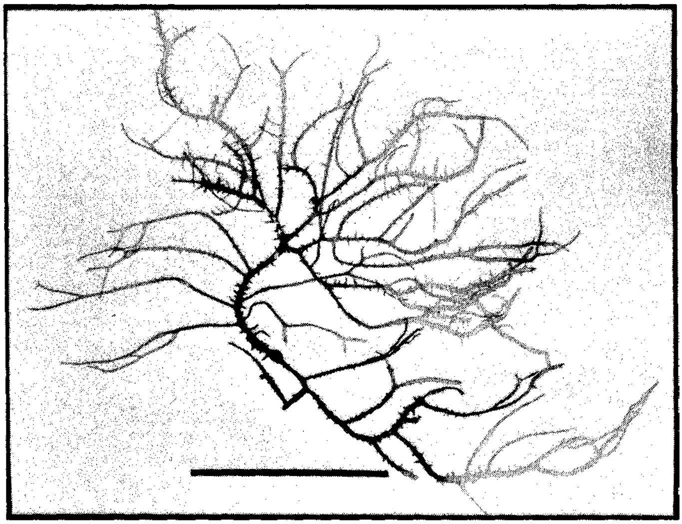


Fig. 17. *Eucheuma serra* J. Agardh. (Voucher No. KEM 356A; photograph No. 32944.21.) Scale bar = 5 cm.

tendency to become broadened and bilateral in the central parts of its apically flagellate main axes.

Initially J. G. Agardh (1847) published "*Gigartina serra* J. Ag." as the basionym for his *E. serra*. This is accepted as a "lapsus feder," for he later (1852) cited "*Sphaerococcus serra* J. Agardh (1841)" among his synonyms without mentioning a *G. serra* at all. The interposition of Kuetzing's view (1843, 1849), which was based on a specimen in Berlin, would not seem to affect the present application of *E. serra* (J. Agardh) J. Agardh.

Børgesen (1943, 1950) recognized the great confusion regarding the application of J. G. Agardh's *E. serra* and seems to have solved it correctly in agreement with the type specimen. To sample the confusion, it is necessary only to look at the splendid illustrations of seaweeds labeled *E. serra* in publications by Kylin (1932, pl. 10), Yamada (1936, figs. 1 and 2 and pls. 21 and 22 [perhaps two different species]), Børgesen (1943, figs. 15 and 16), Segawa (1957, fig. 398), and Gabrielson and Kraft (1984, figs. 6A and 8). In commenting on their application of the name, Gabrielson and Kraft correctly recognized the existence of a taxonomic problem.

Eucheuma isiforme (C. Agardh) J. Agardh (Figs. 18, 19B)

J. G. Agardh 1852.

Basionym: *Sphaerococcus isiformis* C. Agardh (C. A. Agardh 1822).

Holotype: Aspegren specimen in Lund No. 34654.

Distribution: The Caribbean and adjacent areas in general.

Remarks: This species comes in a wide variety of forms. Some bear numerous branches arising from whorls of spines and, when alive, have axes greater than about 4 mm in diameter. It is often difficult to distinguish this species (Fig. 18) from *E. denticulatum* without resorting to infrared spectroscopy of the gels. Many specimens seen are pale from water soaking after having been dried once or preserved in formalin. They are then often blunt-spined, as though the apices had been dissolved away, which is not

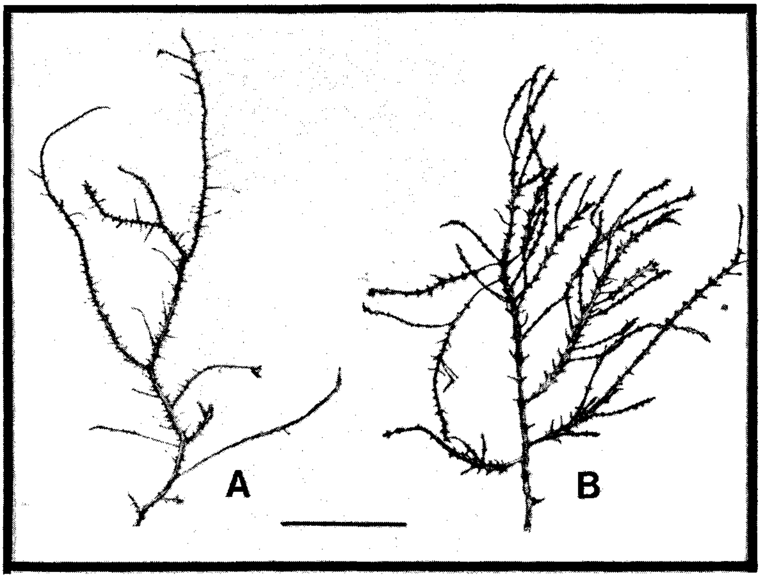


Fig. 18. Whole fronds of *Eucheuma isiforme*. A and B, A common red forms from deeper water. (A, Voucher No. 22702; received from Clinton Dawes as No. 4119 = Univ. of South Florida No. 79149. B, Voucher No. 22637. A and B, photograph No. 32940.19.) Scale bar = 5 cm.

surprising because they bear iota carrageenan. Such specimens of *E. denticulatum* are seen too, but they are usually a light yellow whereas those of *E. isiforme* are grayish.

Some specimens of *E. isiforme* tend to be a unique red color. Other rather non-*E. denticulatum* characteristics include the often irregular arrangement and attenuation (sometimes antenniferous) of the (apparently primary) spines. Other *E. isiforme* forms are relatively unbranched erect axes that apparently appear in tufts, with few lateral branches and with the spines scattered and the tips of the spines long and cylindrical. Some forms have few or no spines; this situation is also seen in other similarly slender *Eucheuma* species. (See Taylor 1960, Cheney and Dawes 1980, Cheney 1975, Cheney and Babbel 1978, Gabrielson 1983, and Cheney in the present publication for the recent literature and further information.)

Like both *E. denticulatum* and *E. uncinatum*, this species is reported to be terete (Taylor 1960) and to have its cystocarps positioned directly on the axial branches sometimes (Fig. 19B; Cheney 1975, fig. 10; Dawes et al. 1974, fig. 16), but for the most part they are borne near the tips of lateral determinate spines.

Eucheuma uncinatum Setchell et Gardner (Figs. 19D, 20)

Setchell and Gardner 1924.

Distribution: In the Gulf of California from Mazatlan to Puerta Galera, Mexico.

Remarks: This cylindrical, erect species, which matures at 25 to 50 cm tall, is quite different from *E. denticulatum* from the Indo-Pacific and *E. isiforme* from the Caribbean but far too widely variable in form and in the way the spines and cystocarps are borne to be characterized definitively without further study. Norris (1985) described the variability appropriately as "a dazzling array of morphological forms." Setchell and Gardner (1924, p. 748f, pls. 65–68) provided beautifully detailed photographs of variations, some under *E.*

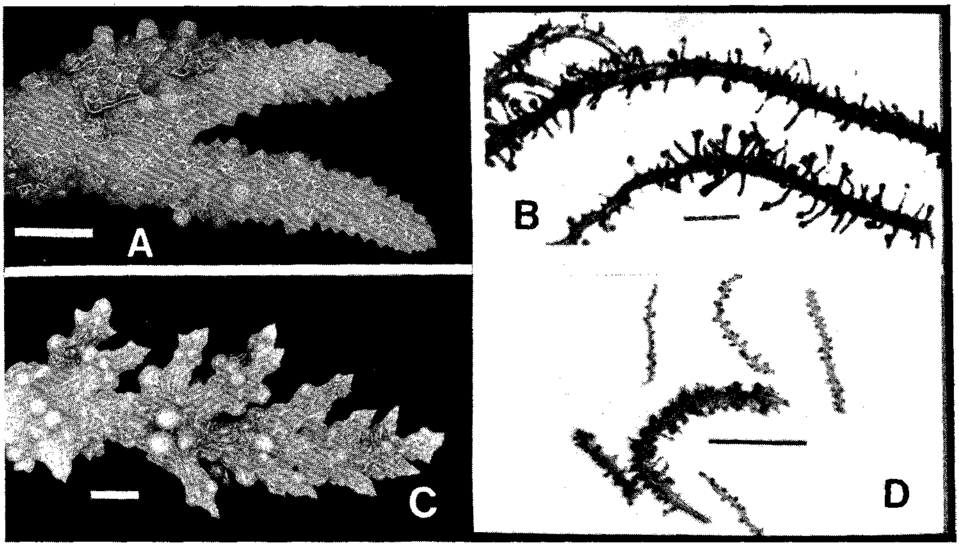


Fig. 19. Cystocarps of *Eucheuma* sections *Eucheuma* and *Anaxiferae*. A, a "spiny shoot" bearing the unornamented sessile mature cystocarps of *Eucheuma arnoldii* on its axis. (Gavino Trono Voucher No. 1001; Photograph No. 32943.19.) B, Cystocarps of *Eucheuma isiforme* largely at the tips of spines borne somewhat uni- to bilaterally on cylindrical main axes of exsiccata. (A reproduction of Cheney's (1975) fig. 10; photograph No. 32943.25.) C, The usually unornamented *Eucheuma amakusaensis* cystocarps borne on the axes of the indeterminate fertile spines, which, in turn, are bilaterally placed on the segment margins of the lectotype. (Voucher No. 31613; photograph No. 32932.2.) D, Xerograph of cystocarps of *Eucheuma uncinatum*. (Specimens selected from commercial lot No. R800 of Marine Colloids Division of FMC Corp.; Voucher No. 31437; photograph No. 32941.21.) Scale bars: A and C = 5 mm; B and D = 2 cm.

johnstonii Setchell et Gardner, which they described along with *E. uncinatum*. Dawson (1944, p. 288) generally is followed in combining the two species. Some of its mannerisms of growth and other features resemble those of certain species placed in *Eucheuma* section *Gelatiformia* (see following sections). For example, the cystocarps (Fig. 19D) are borne directly on the axes, at the bases of spines in other cases, or subterminally toward the ends of spines. When the cystocarp-bearing spines are protracted (e.g., 2 cm long), they may bear cystocarps along their axes also. In the latter case, those toward the tips are smaller and presumably younger.

Norris (1985) provided the characteristics that would distinguish this species (Fig. 20) from others of the genus. Among the critical reproductive attributes are the tetrasporangia that appear (Setchell and Gardner 1924, pl. 25, fig. 42) to produce two large, probably viable, and, terminally, two very small sporelike division products of the parent sporangial cytoplast. Additionally, the cystocarps produce spores in the absence of the fusion cell known in essentially all other species of *Eucheuma*, including *E. denticulatum* and *E. isiforme* (Norris 1985).

EUCHEUMA SECTION *ANAXIFERAE* WEBER-VAN BOSSE

Eucheuma section *Anaxiferae* was treated earlier (Doty and Norris 1985) as including one species, and thus *E. arnoldii* Weber-van Bosse is designated as the type species for

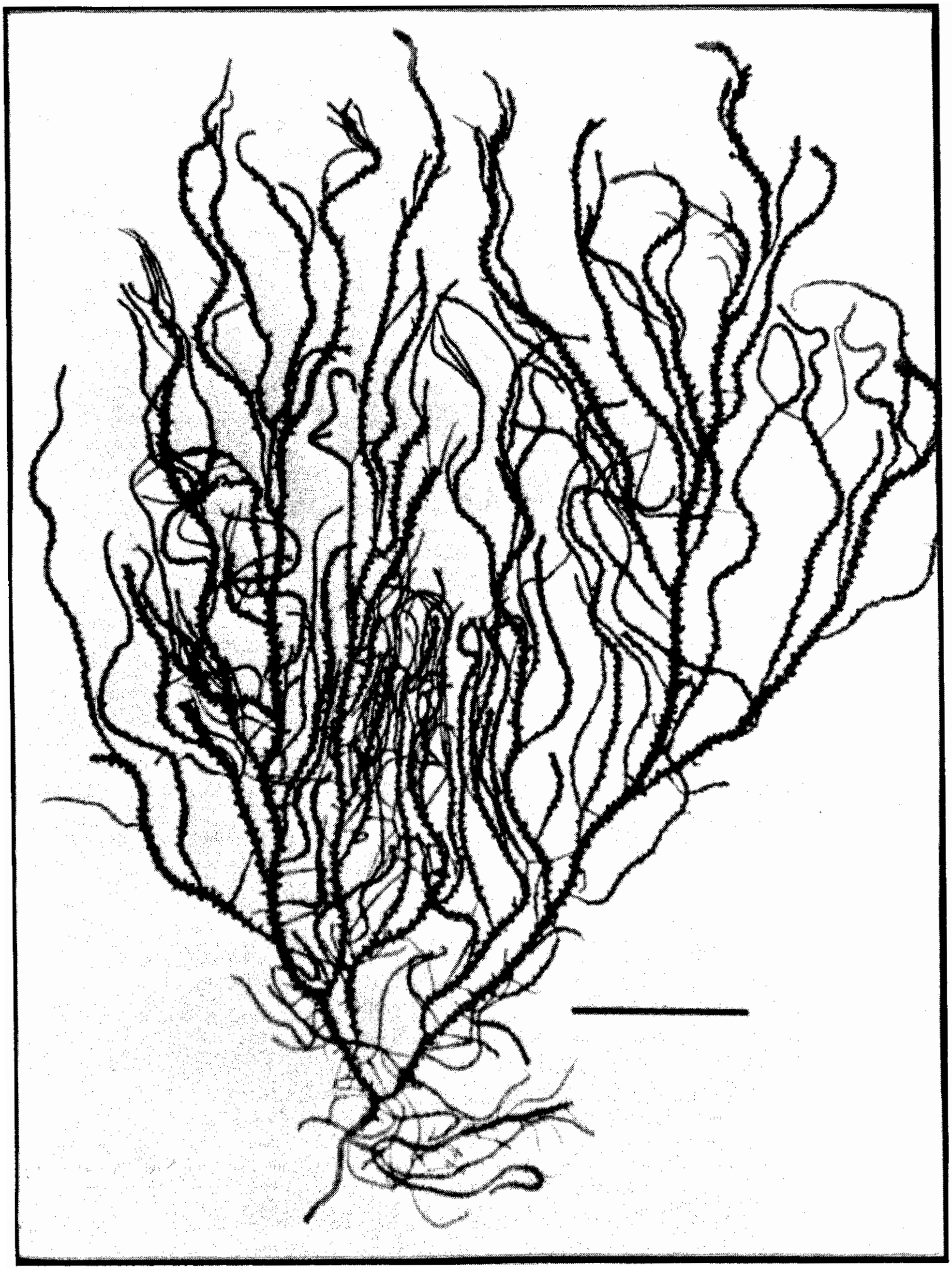


Fig. 20. ***Eucheuma uncinatum*****. Xerograph shows slender basal segment, broader central area, and flexuous apical region. (Voucher No. 31437; photograph No. 32935.23.) Scale bar = 5 cm.**

the section. The principal characteristics of the section are listed in Table 1. This section is distinguished by the vegetative tendencies for indeterminate growth of the fertile cystocarp-bearing spines and for lack of differentiation in the central medullary tissue. One result is that, though the cystocarps first appear subapically on the apically compound fertile spines, indeterminate apical growth results in the older cystocarps being both unornamented and sessile on axes of vegetative appearance.

As usual in the tribe Eucheumatoideae, plasticity is extensive, and the specific limits, especially within *E. arnoldii*, require study.

Eucheuma arnoldii Weber-van Bosse (Figs. 19A, 21)

Weber-van Bosse 1928.

Holotype: Herb. Lugd. Bat. No. 938.7-440. Both wet-preserved and exsiccata. The holotype was illustrated by Weber-van Bosse (1928). In accordance with Kraft (1972), *E. arnoldii* is accepted as having a wide range of varieties. See Fig. 21 for two of the varieties. See Fig. 19A for cystocarps, which appear subapically on spines but mature on short vegetative axes.

Distribution: From northern Queensland to the southern Ryukyus and Taiwan.

Eucheuma amakusaensis Okamura sp. ineditae (Figs 19C, 22)

Okamura 1956.

Thalli erecti sed magis late effusi horizontaliter quam verticaliter. Axes principales aliquantum dorsiventraliter compressi et bilateraliter spinosi. Ut in typo, *E. arnoldii*, spinae sunt compositae.

Neotype: Doty voucher No. 31613 (Fig. 22) from collections collected and forwarded by Iwao Shinmura, Kagoshima Prefectural Fisheries Experimental Station, Kagoshima, Japan, and now deposited in the B. P. Bishop Museum Herbarium as No. 508860. In accordance with Segawa (1957), it may be that Collection No. 19766 in the herbarium of the Faculty of Science, Hokkaido University, will prove appropriate as a lectotype. Presumably it is a specimen from this collection that Segawa has illustrated.

Distribution: Southern Japan, Taiwan, and probably, Philippines.

Remarks: At least in the 1956 edition of Okamura (1956, p. 594), there is neither a Latin description nor mention of materials for *E. amakusaensis.* Thus, the Latin description given here is provided to complete the valid publication of this name.

The thalli are actually erect on very short basal segments (Fig. 22B) but spread far wider horizontally than tall vertically. The horizontal main axes are somewhat dorsiventrally compressed and bilaterally spinose. This species was not treated by Doty and Santos (1978), but since then it has been found that the haploid and diploid thalli both produce an iota carrageenan (unpublished data). The nonornamented sessile mature cystocarps (Fig. 19C) have the same origin as those of the previous species. See also Ohmi and Shinmura, 1978, and Shinmura, 1975.

EUCHEUMA SECTION *GELATIFORMIA* DOTY AND NORRIS

Thalli horizontal or erect; fronds compressed and dorsiventrally asymmetrical, bilateral, arising from a crustose base; pinnae often opposite and cylindrical to compressed or flat, not in whorls; tissue components with an outer radiating, usually filamentous, cortex, inner nonfilamentous cortex and pseudoparenchymatous medulla with an axial core of tortuous rhizoids that is cylindrical in cylindrical parts of the thallus and compressed or flattened where the thallus is less than cylindrical.

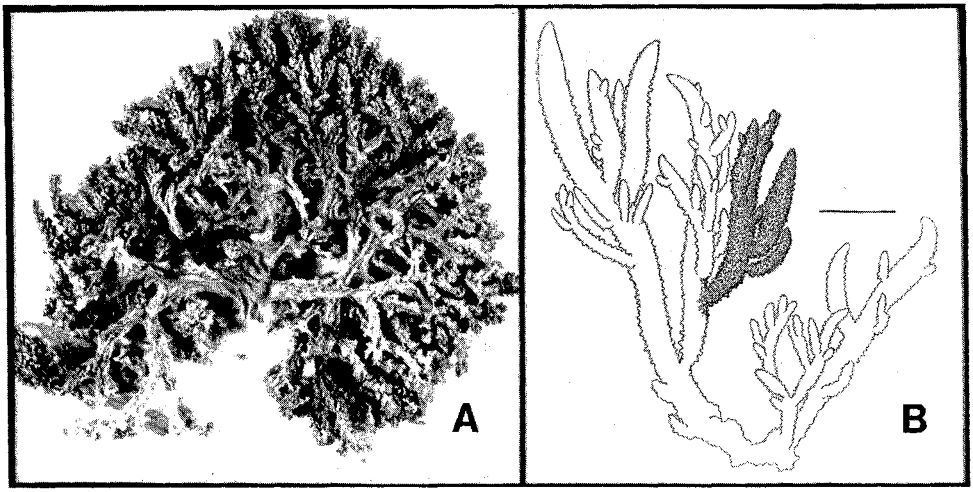


Fig. 21. Whole specimens of *Eucheuma arnoldii.* A, Drawing of a branch of a *Eucheuma arnoldii* variety *alcyonida* from Caluya Island, Philippines. (Voucher No. 24531; photograph No. 32941.9.) B, The collection mentioned in the protologue for *Eucheuma cupressoideum* Weber-van Bosse from the Farlow Herbarium collections by H. L. Clark in the Torres Straits, accepted as the lectotype for that species and for photograph No. 32929.12. Scale bar = 1 cm.

Tetrasporangia borne largely on the main axes but may be clustered near and on determinate laterals. Cystocarps borne near apices of determinate lateral branchlets. Containing beta and other carrageenans.

Type Species: *Fucus gelatinus* Esper (Esper 1797).

The members of this section are morphologically distinct from those in *Eucheuma* sections *Eucheuma* and *Anaxiferae* in having a core of rhizoids that is compressed somewhere or in bearing beta carrageenan. In at least the type species for the section, the principal wall material is beta carrageenan; gamma and kappa carrageenans are minor but significantly weighable components. In other species of the section that have beta carrageenan, some kind other than beta may be preponderant. In each of the other three groups of Table 1, the species have but one carrageenan, either iota or kappa, in significant quantities.

This section is distinguished by its vegetative tendencies toward broadening of the axes laterally and segmentation such that cylindrical genicula separate bilateral compressed intergenicula or branches. For the present, several carrageenan types are included because of the lack of consistent information on the gel. The axial type is thought to be distinctive.

The dried thalli of *E. kraftianum* and *E. perplexum* are rather quickly destroyed by immersion in water, whereas those of the other species of this section are relatively resistant to it. This has possibly prevented both the scientific recognition and the commercial use of *E. kraftianum* and *E. perplexum.* Several of the more common of them (probably also including members of *Eucheuma* section *Anaxiferae*) have reached the processing companies under the name of *E. gelatinae*, with the hope that it would yield a kappa carrageenan with some furcellaran-like properties. Yet, when processed, what was received has yielded not kappa carrageenan but a quickly water-suspendable material that was thought at the time to be an iota carrageenan.

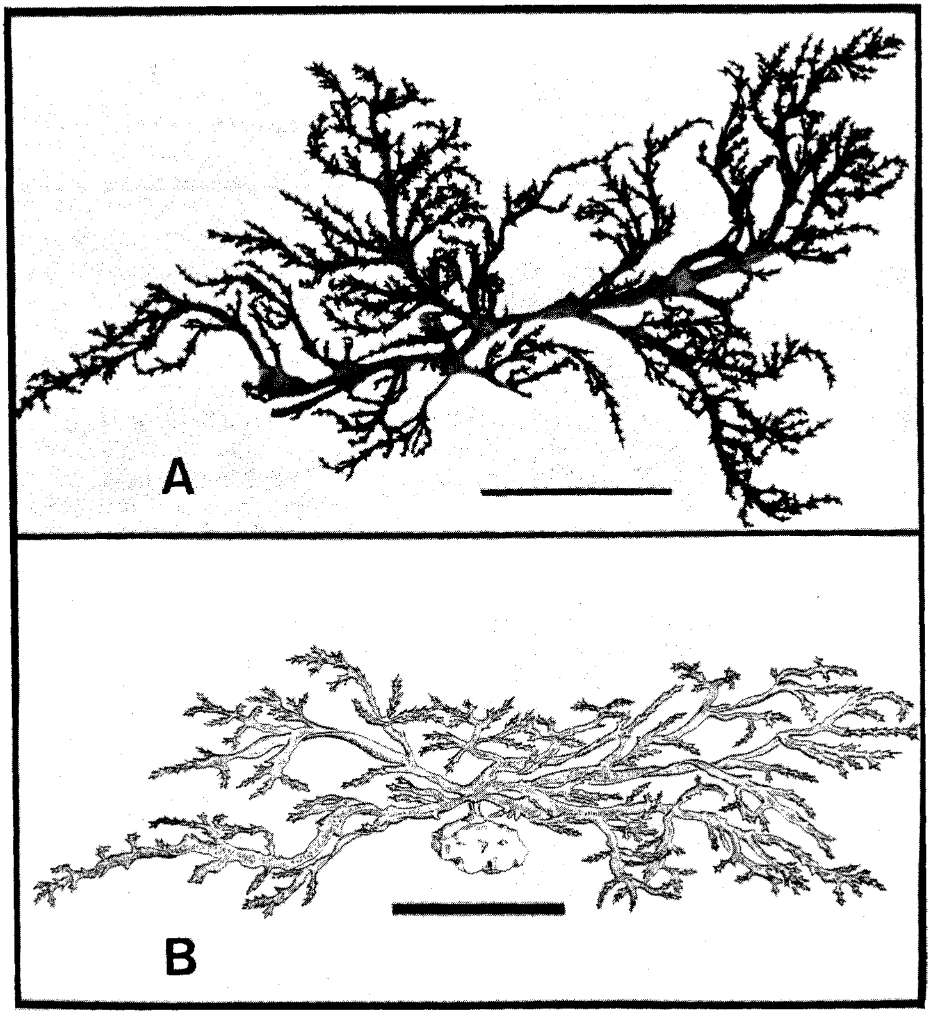


Fig. 22. ***Eucheuma amakusaensis*** **Okamura. Lectotype voucher No. 31613 in the Bishop Museum Herbarium No. 508860. A, Photograph No. 32932.23 of one specimen in the lectotype collection. B, The specimen in A drawn in side view to show the spatial relationships of the holdfast, the short erect basal segment, the substratum, and the bilaterally branched, flattened horizontal lateral axes. (Material provided by Iwao Shinmura; photograph No. 32941.15 and drawing by Ismael Trono) Scale bars = 5 cm.**

Recently Greer and Yaphe (1984b) discovered that *E. gelatinae* produces a mixture of kappa, gamma, and beta carrageenans. Their determinations were made on disaccharide hydrolysates, and no physically discrete weighable amounts of beta or gamma carrageenan were obtained. This is added evidence favoring the hypothesis that in the biological production of the dominant kappa, iota, and beta carrageenans, mu, nu, and gamma carrageenans, respectively, appear as natural precursors. Beta carrageenan, which lacks sulfate groups, is relatively nonionic and may become commercially important for this reason.

Eucheuma gelatinae (Esper) J. Agardh (Figs. 23, 24A)

J. G. Agardh 1847.

Basionym: *Fucus gelatinus* Esper (Esper 1797).

Lectotype: In the Hamburg Herbarium (Fig. 23A). Note: Specimen No. 34697 in the Agardh Herbarium at Lund could be a part of this same collection and thus is accepted as a lectotype-isotype for the present species.

Distribution: Largely eastern Philippines and southern China. Many, if not most, of the records in the literature of this species are misleading.

Remarks: Although this species is seen frequently, it has received little study or description of it in its natural habitat. Its thalli (Fig. 23B) are leathery and, like the other principal species of the genus, are pliable and bend away from the direction in which the waves and surges of seawater come over the intertidal rocks on which it grows.

The branches of *E. gelatinae* arise irregularly from proliferations that initially may be merely simple dentations, knobs, or cylindrical protrusions up to a very few millimeters long. On some flattened parts of the lectotype (Fig. 23A), there appear to be compressed tubercles. Usually the apical and central or horizontal segments are primarily laterally dentate and determinate. Where the fronds are vertical, their apical (flat) and basal (cylindrical) segments are often smooth. Those that are more permanently horizontal are smooth only above, with many cylindrical proliferations from their lower surfaces.

The cystocarps are borne toward ends of proliferations on the lower surface (Fig. 24A). The report of Schmitz (1895) that the proliferations are chiefly on the dorsal surface is subject to question. However, with age, apically some fronds may be so generally proliferous from the rebranching of the initially simple lateral and ventral outgrowths that fertility *seems* present without regard to which surface is concerned. In the case of horizontal fronds, some, especially lateral, dentations are seen in various stages of becoming flat and indeterminate like their parent axis.

Eucheuma perplexum species nova (Figs. 2, 7B, 24E, 25–27)

Thalli erecti ad repentes, segmenta basilaria cylindrata sed axes mox compressi desuper et series marginales spinarum ferrentes quae oppositae vel dispersae sunt; ramificatio opposita vel irregulariter pinnata; axes fasciculo medulloso rhizoidei praesenti et compresso in ramis planioribus; tetrasporangia inventa in axibus principalibus; cystocarpia strato speciali cellularum inter pericarpium et gonimoblastum. Producentes iota carrageenan.

Holotype: Doty No. 31628, deposited in the B. P. Bishop Museum Herbarium as No. 508858.

Type Locality: Patotsu at the northern end of Taiwan.

Distribution: Philippines, southern Japan, Tanzania, and, to be expected, from Lord Howe Island and Queensland (Australia).

Typically, thalli (Fig. 25A) initially sprawl from a small crustose base and intertangle with other objects. Later the fertile cystocarpic branches may become erect (Fig. 26) and up to about 5 cm tall and the attachments compound (Fig. 27B) at the type locality (Fig. 27A). Basal segments are cylindrical, but distally the axial segments soon become compressed, gradually broadening and bearing marginal spines scattered, or spines appearing in nearly opposite pairs. Later additional spines may appear, especially on the margins; the dorsal and ventral surfaces remain relatively plain or with but few scattered spines. Branching is opposite or irregularly pinnate. Axial segments become gradually broader from being cylindrical and 1 mm in diameter to strongly dorsiventrally compressed and 4 to 7 mm wide before narrowing to the apex; away from the base they become more

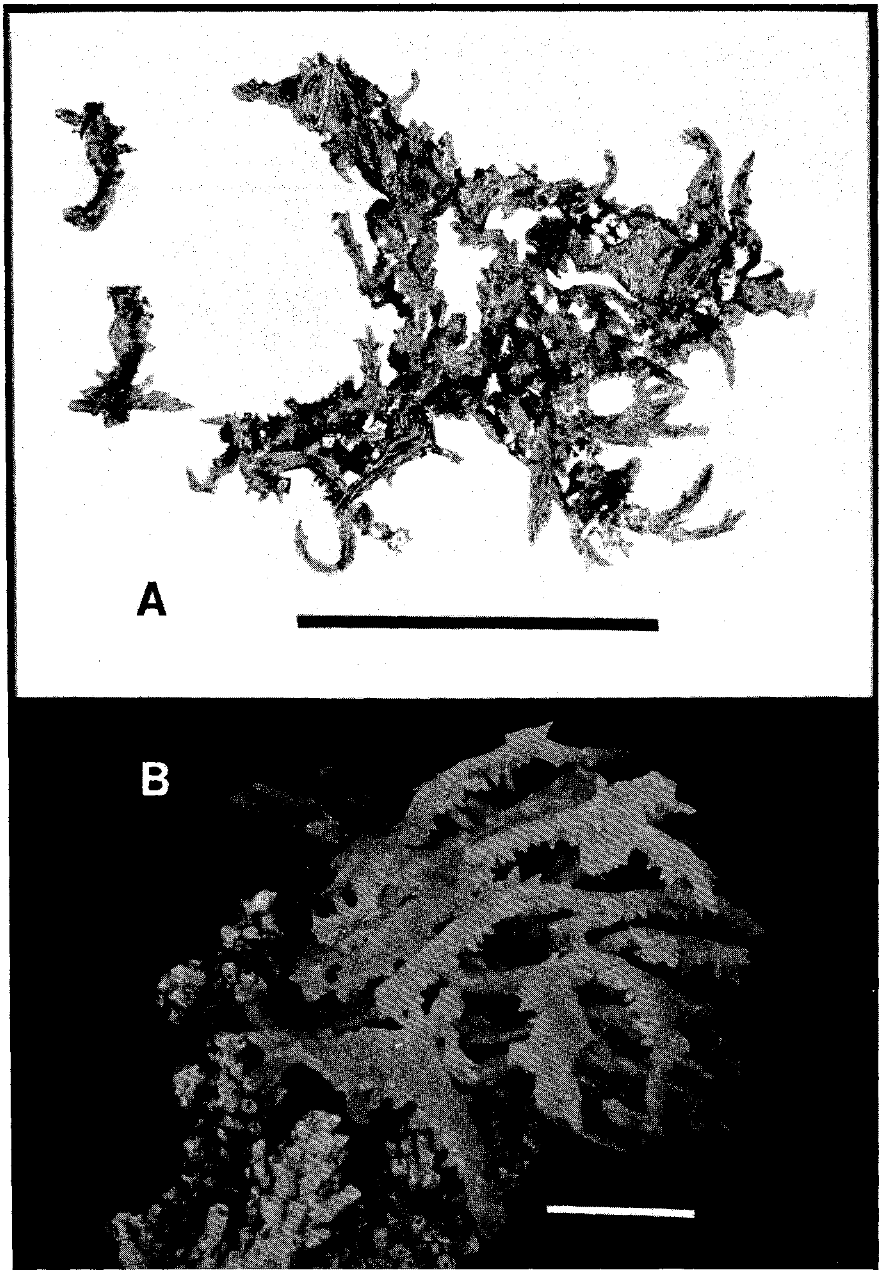


Fig. 23. *Eucheuma gelatinae.* A, One of the many specimens of *Fucus gelatinae* Esper in the collection selected as the lectotype and curated in the Hamburg Herbarium. (Retouched photograph No. 32935.15.) B, The natural orientation of a *Eucheuma gelatinae* specimen as viewed from the side. (Collected at Hainan Island, China, by Fen Tseng; Voucher No. 32763 in B. P. Bishop Museum; photograph No. 32938.6.) Scale bars: A = 2.5 cm; B = 5 cm.

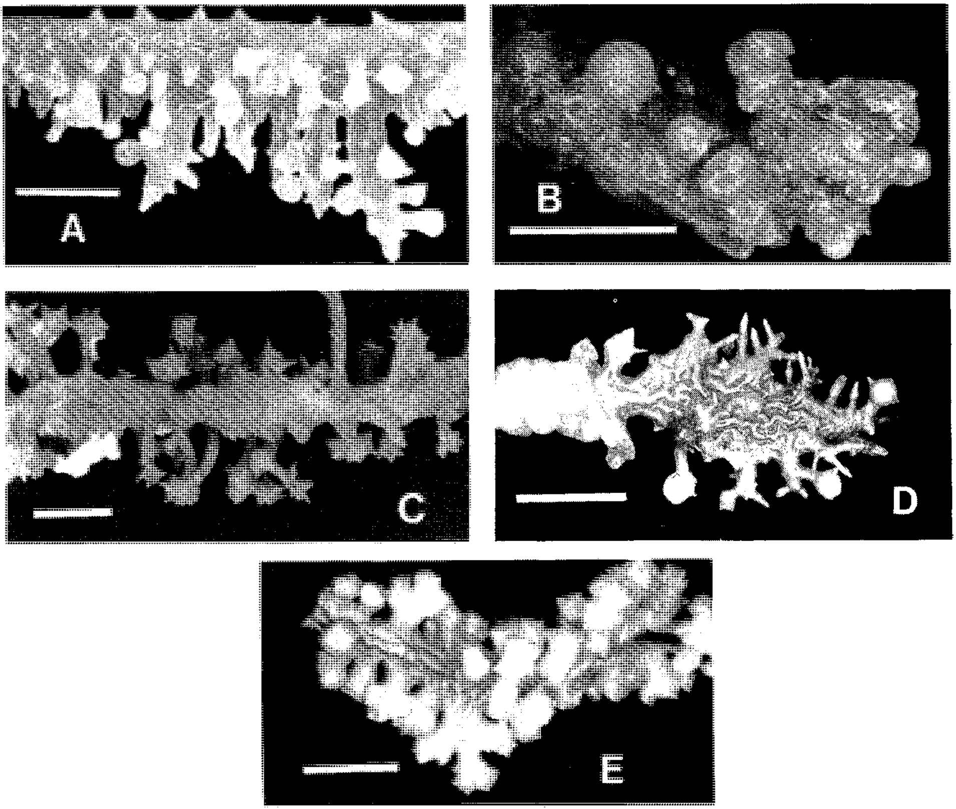


Fig. 24. Cystocarps of *Eucheuma* section *Gelatiformia*. A, Cystocarps and the lower surface of a fertile segment of *Eucheuma gelatinae*. Note the sparse row of reduced spines showing on the segment's near margin. (Voucher No. 32903; photograph No. 32912.16.) B, The largely nonornamented cystocarps of *Eucheuma platycladum* borne mostly on stalks (but sometimes sessile) on the flat under surface of a flat thallus fragment. Sometimes ornamented with spines. (Voucher No. KEM 352A; photograph No. 32912.20.) C, The conspicuous multispinose cystocarps of *Eucheuma kraftianum* borne on the margins of the uppermost broadened segments. In some cases, the spines are simple; in others, compound or, even, indeterminate. (Voucher No. 24706; photograph No. 32912.11.) D, Multispinose cystocarps of *Eucheuma speciosum*, which may be nearly alate at times and borne on one or both margins of the upper broader (intergenicular) segments of the main axes. (Voucher No. 24094; photograph No. 32940.23.) E, Cystocarps of *Eucheuma perplexum* borne largely on the branch margins. (Voucher No. 31628; photograph No. 32943.23.) Scale bars = 5 mm.

irregular in width, often being distinctly broadened opposite branch bases. A medullary rhizoidal core is present, more circular in more cylindrical segments and more compressed in flatter segments. Tetrasporangia (Fig. 7B), are found on main axes. At maturity, the terminal members of tetrasporangial groups of *E. perplexum* are usually bluntly rounded and otherwise rotund-cylindrical as are the central two. Thus, in such cases of resoaked material (as shown in Fig. 7B), it is suspected that most of the groups shown are immature rather than mature, and they tend to be reduced at both ends as in *E. uncinatum* or only the inner end. Often in resoaked material of *Eucheuma*, the mature tetrasporangia squeeze out of the tissues in which they grew, as though the gel around them had become more soluble in water during the drying and resoaking process.

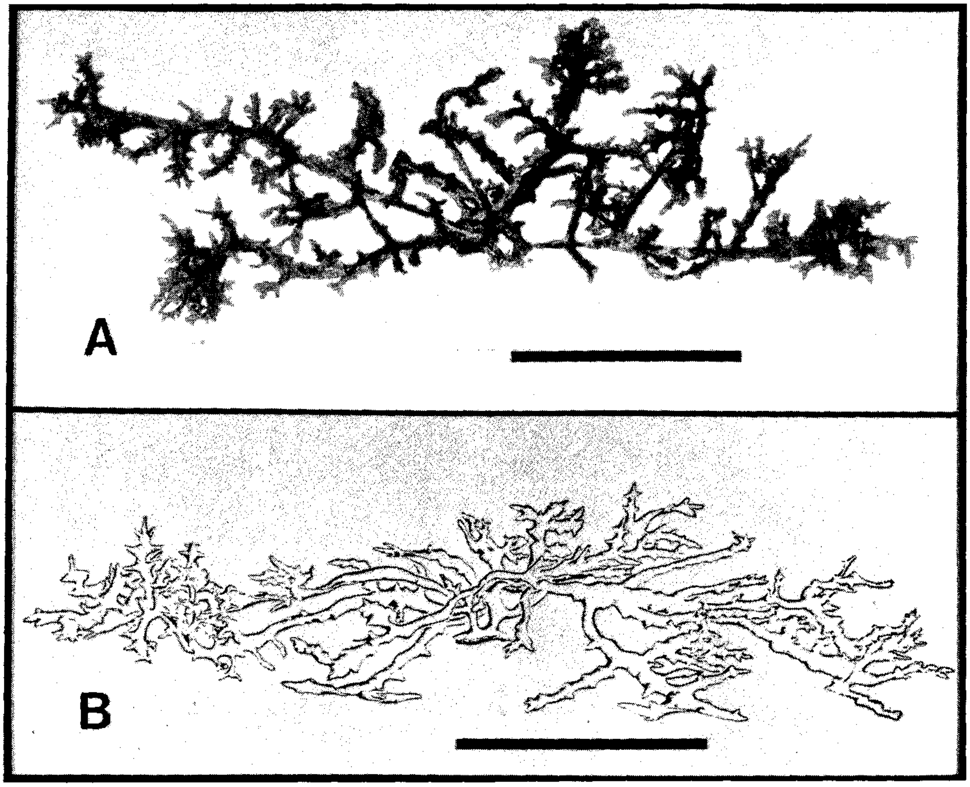


Fig. 25. Part of protologue and an isotype of *Eucheuma perplexum*. A, Tetrasporic or young thallus. (Photo No. 32933.18.) B, Drawing shows horizontal habit of tetrasporic or young forms. (Voucher No. 31628, Sheet 6 of 13; part of holotype preparation deposited in the B. P. Bishop Museum Herbarium as No. 508858; photograph No. 32941.13.) Scale bars = 3 cm.

Cystocarps (Fig. 24E) are on or near the tips of multi-spinose determinate cylindrical proliferations that are borne mostly on the margins of the flattened axes but occasionally arise from either of the flat surfaces. Cystocarps have pericarp lined internally with a placental envelope of cells on the surface facing the gonimoblast. The presence of iota carrageenan has been identified by the cold-water solubility of old branches and by the infrared adsorption of their gels.

The cystocarps initially are mere hemispherical protuberances among similar, but pointed, radiating spines at the tips of the fertile proliferations; later the cystocarps become larger than the spines though remaining smooth apically. Ostioles are not conspicuous. The cystocarp-bearing spines are capitate, not winged as in *E. speciosum* and some other species. The spines bearing cystocarps often bear several small sharp points, with the spine itself terminating as an assymetrically larger sharp point.

Remarks: In species of *Eucheuma* section *Gelatiformia*, such as *E. gelatinae*, the cystocarpic proliferations are mostly on the ventral surface of the segments that bear them. In most other species of *Eucheuma* section *Eucheuma* (e.g., in *E. serra* and *E. denticulatum*), the fertile axes are cylindrical or nearly so, and the spines bearing cystocarps are not generally unilateral or on one flatter side. However, Dawes et al.

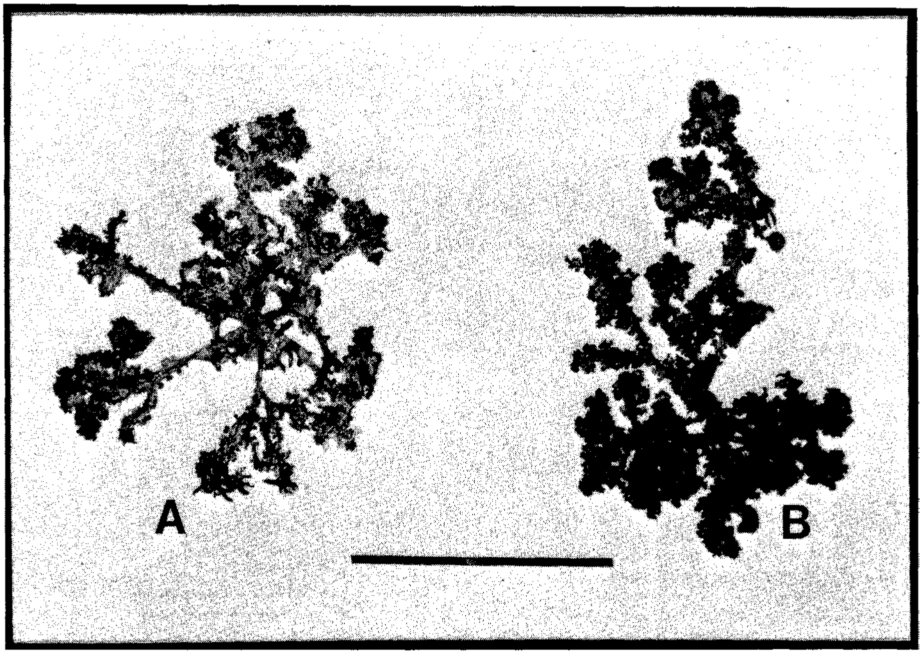


Fig. 26. Isotypes of *Eucheuma perplexum* from Patotsu near Keelung in northern Taiwan. A and B, Cystocarpic thalli "H" and "J," respectively, from the holotype preparation. (Voucher No. 31628, Sheet 7 of 13, deposited in the B. P. Bishop Museum Herbarium as No. 508858; photograph No. 32932.14.) Scale bar = 5 cm.

(1974, fig. 16) have illustrated such a bilateral form for *E. isiforme* variety *denudatum* Cheney (elsewhere in this publication), and this form has been seen in the present and other, even cylindrical, species.

Eucheuma serra as described and pictured in Gabrielson and Kraft (1984) shows some of the characteristics of *E. perplexum*, as do the illustrations of seaweeds illustrated under that name by Yamada (1936), Segawa (1957), Arasaki (1964), and Chihara (1970, 1975). See Gabrielson and Kraft (1984) also for its distinction from *E. deformans* Gabrielson et Kraft, a unique species illustrated also by Kraft and Woelkerling (1981, fig. 42B), which seems not to have appeared in commercial lots of seaweed. Although smaller, *E. perplexum* recalls some forms of *E. amakusaensis* in habit.

A final note on distinguishing *E. perplexum* from *E. serra* and *E. denticulatum*: A major branch of the last two entities is broadest where it leaves the parent axis and is cylindrical or gently tapers to very near its apex whether bearing pairs of spines or not. The major branches of *E. perplexum* tend to broaden noticeably from near their bases if they bear a row of spines along each margin. Likewise, the spines are not rigorously paired in *E. perplexum*; their bases are as thick as their parent axis segment; and below the apical segment, usually the distance from one marginal spine to the next is shorter than the length of the longer of the two spines. In *E. serra*, the pairing of spines is quite rigorous; the bases of the spines are smaller in diameter than their parent axis segment; and below the apical segment, usually the distance from any one spine to the next is distinctly greater than the length of either spine. Finally, *E. perplexum* is often clearly red or very dark at its base, whereas *E. serra* is often pale yellowish.

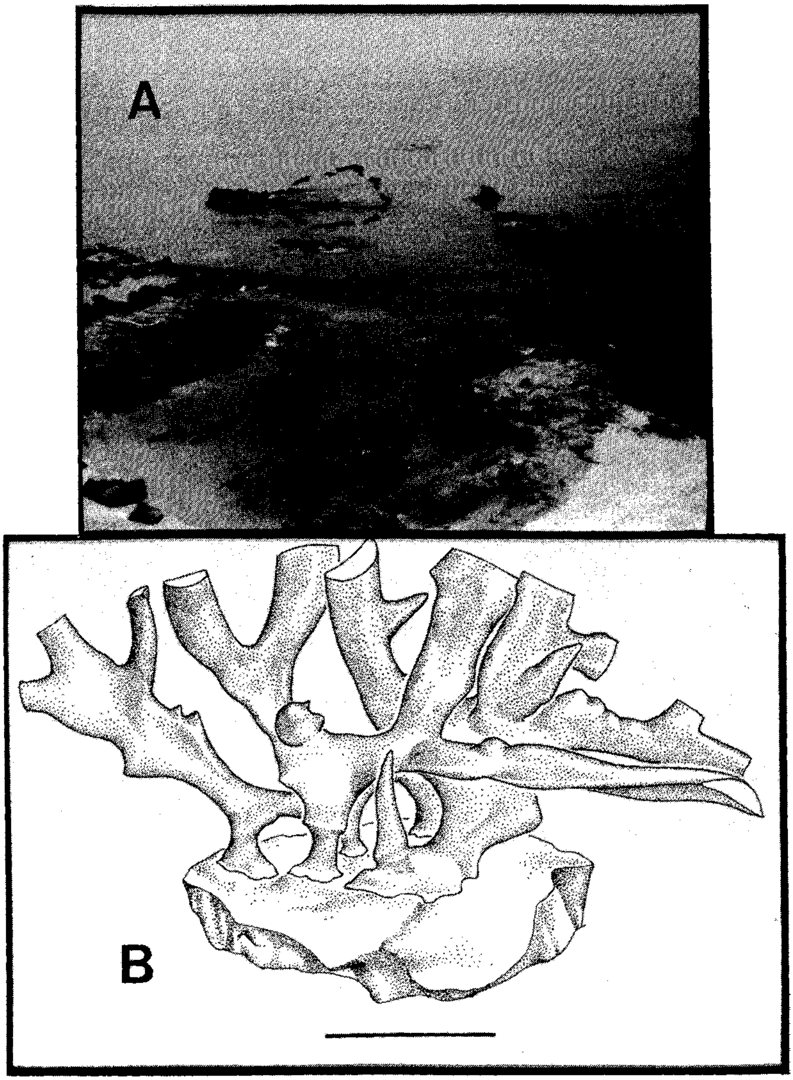


Fig. 27. Habitat and older base of *Eucheuma perplexum*. A, The type locality for *E. perplexum* taken looking north from the highway at the type locality at Patotsu, northernmost Taiwan. The specific rock and its nearby area from which the collection by Wen Young Tseng was made from the area are circumscribed by a dashed line. (Photograph No. 32940.15.) B, Drawing of an older compound holdfast of *E. perplexum* with somethat rhizoidal fleshy attachments from which young fronds arise. (Voucher No. 31628, Sheet 3 of 13; photograph No. 32941.17.) Scale bar = 1 cm.

Eucheuma kraftianum species nova (Figs. 5B, 24C, 28)

Thalli fere plani, irregulariter pinnatiramosi pinnis saepe non longioribus quam latitudine laminae. Cystocarpia prope apices pinnarum lateralium. Tetrasporangia immersa in segmentis principalibus. Axes centrales rhizinae asymmetrice compressi. Parietes cellulae continentes prompte frigicam solubilem aquaticam materiam gelatinae.

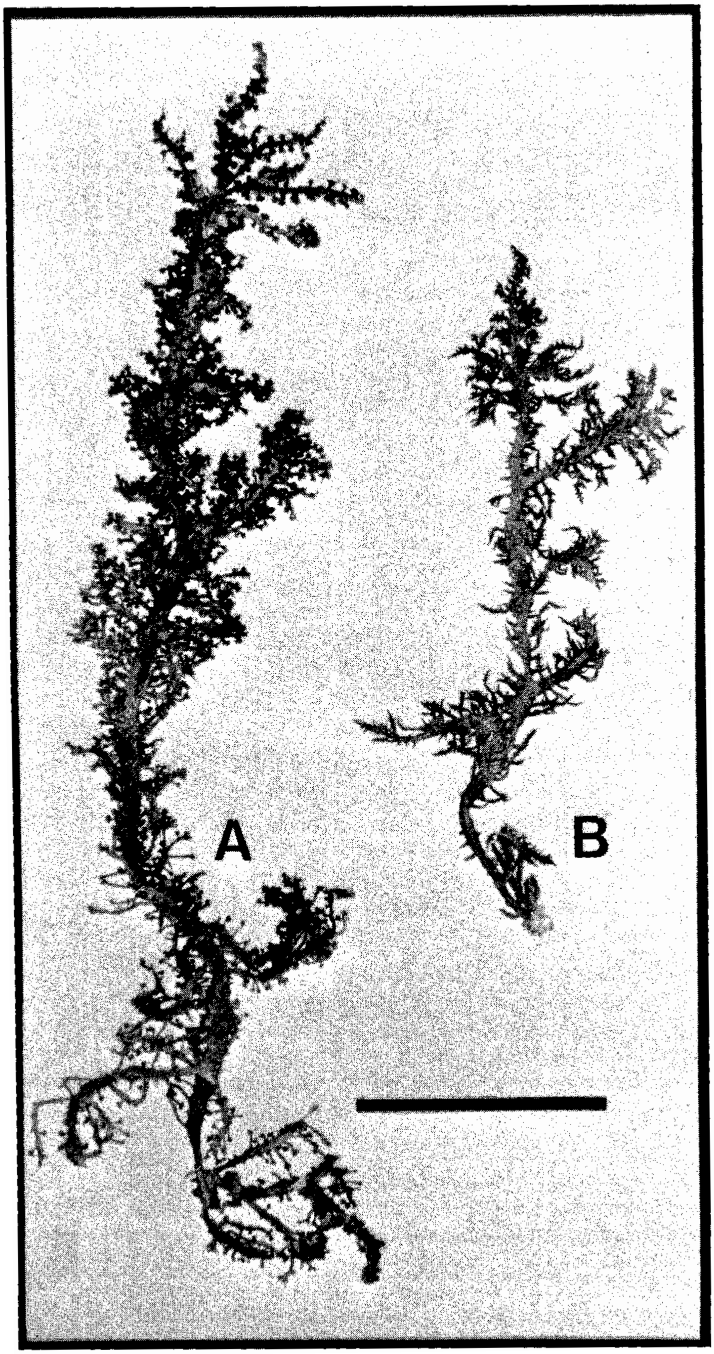


Fig. 28. Part of the holotype preparation of *Eucheuma kraftianum* deposited as No. 508859 in the B. P. Bishop Museum Herbarium. (Voucher No. 24706; photograph No. 32933.21.) A, Cystocarpic. B, Tetrasporic. Scale bar = 5 cm.

Holotype: A preparation on one herbarium sheet bearing two specimens and the Doty Voucher No. 24706 in the B. P. Bishop Museum Herbarium as No. 508859.

Type Locality: Central Indonesia.

Distribution: Lombok Straits and nearby. However, commercial samples without reliable locations have been seen with other origins given.

Eucheuma kraftianum thalli are frondose (Fig. 28) in appearance because of the frequency of indeterminate branches arising from the main axes and often because of crowded, short determinate branches. Fronds are up to 20 cm tall, with fewer than 10 arising from a rhizomatous crust or cushionlike holdfast as cylindrical basal segments that often branch at sharp narrow angles; lower axial segments initially are flattened asymmetrically and irregularly pinnately branched, thence upwards often another (a third) row of proliferations arises on one flatter surface, and with their growth the fronds may tend to become somewhat three-sided and twisted, whereas the apical axial segments are flattened and dentate marginally and mostly less than 0.5 cm broad and 0.2 cm thick; soft and flexuous when alive. The main axes lack segmentation. The central rhizoidal medullary axis is compressed asymmetrically wherever the axis is not cylindrical.

Cystocarps are borne (Fig. 24C) very near the tips of lateral cylindrical determinate pinnae. Tetrasporangia are immersed in the main segment surfaces.

Remarks: This species was referred to by Doty and Santos (1978) as *Eucheuma* species ineditae and was said to contain iota carrageenan. The thalli soften more readily in cold water than do, for example, *E. denticulatum* thalli.

According to the collectors, *E. kraftianum* has been found (Claude Wolfe, pers. commun.) as deep as 25 m on steeply sloped bottoms. However, it has been seen on the reef flats near Benoa on the island of Bali, Indonesia. At this latter site, it is found in the very shallow subtidal rills or grooves that largely run at right angles across the outer margin of the reef flat. The thalli seen growing on the bottoms of the rills were much larger than those growing higher on their sides.

Eucheuma speciosum (Sonder) J. Agardh 1847 (Figs. 1, 3A, 24D, 29–31)

J. G. Agardh 1847.

Basionym: *Gigartina speciosa* Sonder (Sonder 1845).

Lectotype: Preiss No. 2565 in the Lund Herbarium.

Distribution: Western Australia.

Remarks: The type material was apparently a large collection from which isotypes were widely distributed. This species is distinctive and rather well represented in the herbaria where seen. Yet, some confusion may exist as to the holotype, as authors treating this species have had different specimens at hand. For example, in the Leiden Herbarium collection, No. 938.92-314 has both type and Kuetzing Herbarium labels attached, the latter bearing the name *Gigartina ornata* Kuetzing. So it might be suspected that it is the holotype for *G. ornata* Kuetzing. Though Kuetzing (1868) listed the earlier *G. speciosa* Sonder (Sonder 1845) as a synonym, it is questionable whether it should be chosen as the lectotype because Sonder may not have had that specimen in mind at all. The Hamburg Herbarium has specimens from Preiss's Collection No. 2565 bearing the name *E. speciosum* (Sonder) J. Agardh. The label of one of them (Fig. 30A) is stamped "Holotype," another (Fig. 30B) similarly, as the holotype for *E. speciosum* variety *denudatum* Sonder. In any case, both of these names are based on the one in the Preiss collections but referred to only by Sonder (on p. 28 in *Alp. Preiss*, 1845 or 1846) by No. 2565. Sonder's herbarium is now in the National Herbarium of Victoria, Melbourne, Australia, and contains specimens filed under this name. In the Agardh Herbarium,

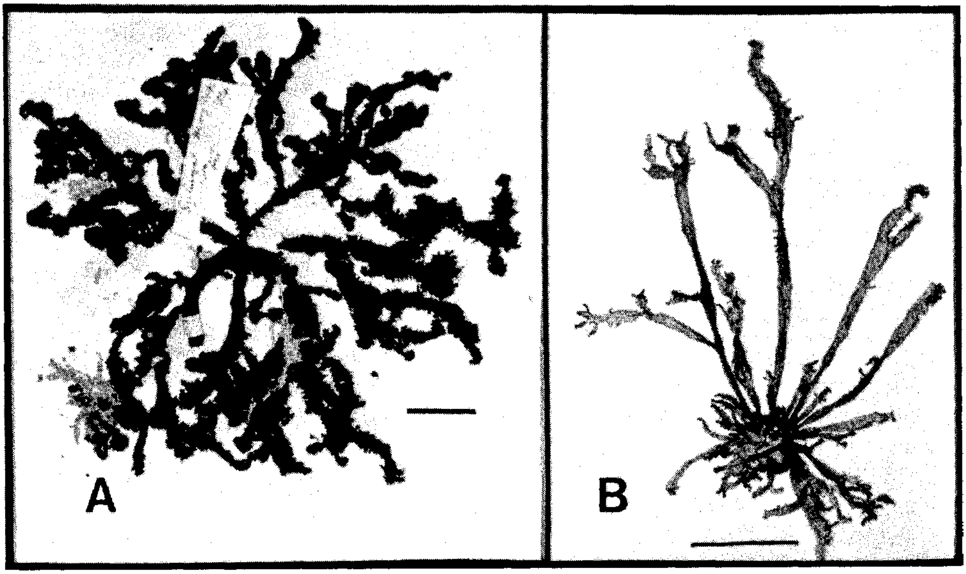


Fig. 29. *Eucheuma speciosum*. A, Isotype. (Voucher No. 34703 in Lund; photograph No. 32941.24.) B, Downward view of the obscured base of a thallus having, as characteristic, many erect or ambient stiff fronds. (Photograph No. 32933.8.) Scale bars = 5 cm.

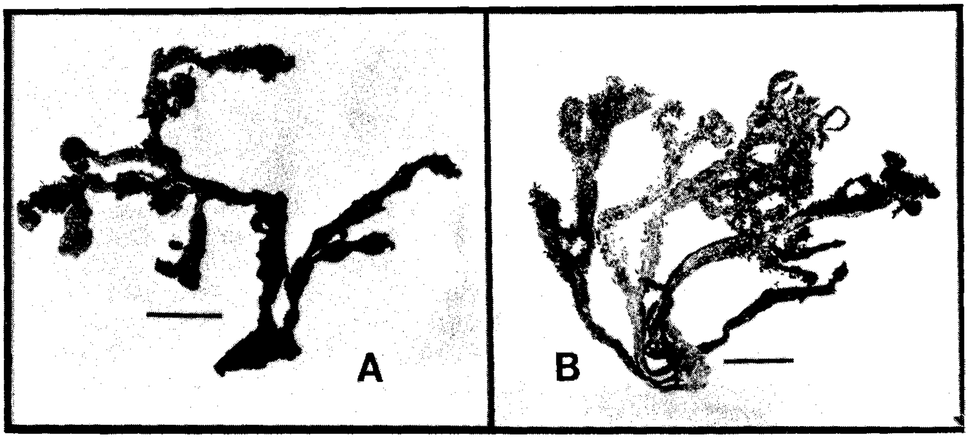


Fig. 30. *Eucheuma speciosum* (Sonder) J. Agardh specimens at Bremen. Both are exciccata from the Preiss collection No. 2565 and the Binder Herbarium, and both have "HOLOTYPUS" stamped on their labels. They also bear reprints of Sonder's (1845) valid publication of the respective names in *Gigartina*. Vouchers bearing the loan number 440, items 19 and 20 respectively. Photographs provided by the Hamburg Herbarium without scale. No scale provided. A, "*Eucheuma speciosum* (Sond.) J. Ag." (Photograph No. 32941.22.) B, *E. speciosum* beta *denudatum* with "basi-nuda" but the latter crossed off. (Photograph No. 32941.23.) Scale bars = 5 cm.

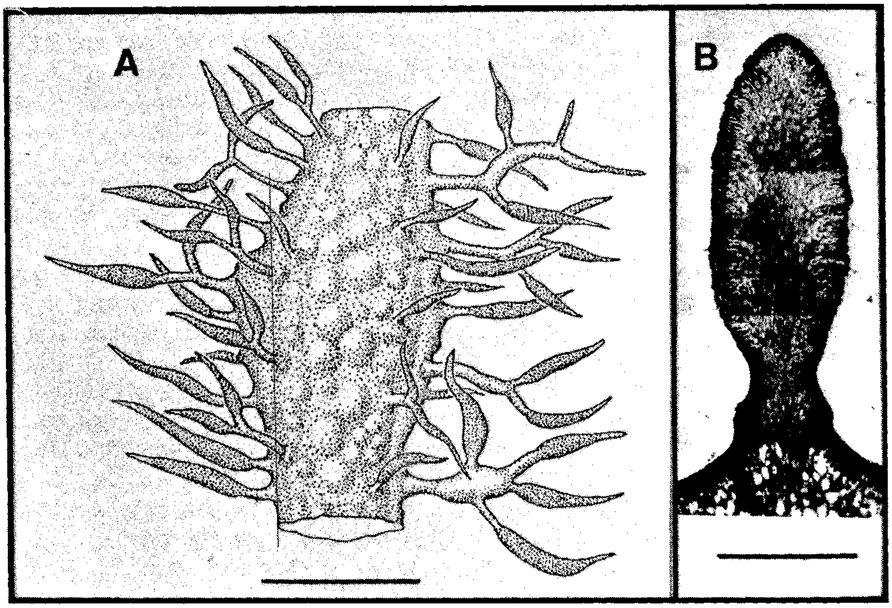


Fig. 31. Tetrasporic propagula of *Eucheuma speciosum.* A, Drawing of a segment of a main axis shows the placement and a variety of tetrasporic propagulae. (Voucher No. 24647 preserved in formalin and then isopropyl alcohol; photograph No. 32941.11.) B, Near medial frontal section. (Voucher No. 24410; photograph No. 32944.6.) Scale bars = 1 mm.

Collection No. 34703 (Fig. 29A) bears related labeling and direct reference to J. G. Agardh (1852, p. 628). They all seem to represent this entity well (e.g., Kuetzing 1868, p. 3, pl. 6, figs. c and d; Harvey 1858–1863, pl. 44, which shows details of the cystocarp nicely) as do other isotypes deposited in various other herbaria. (See also Fig. 30, which shows isotypes labeled holotype in the Hamburg Herbarium.)

This species is unique in many ways, for example, by the thick crustose base (Fig. 29B) from which over 50 fronds may arise, by the extremes in ornamentation of the cystocarps (Figs. 3A, 24D), and by the tetrasporangia possibly being restricted to rather simple lanceolate marginal propagulae with a morphologically specialized constriction (Fig. 31) at their bases. The extreme in development of the three-tissue cross-sectional anatomy (Fig. 1A) is a further example of the isolation of this species from the rest. Yet, some of the apparent affinities it has to other species of this section and especially to the following three cannot be ignored.

Eucheuma odontophorum Børgesen (Figs. 32–35)

Børgesen 1943.

Type Specimen: No. 835 in Herbarium Botanicum Hauniense, Universitetets Botaniska Museum, Kobenhavn.

Type Locality: Flat Island, Mauritius, in 25 fathoms of water.

Distribution: Mauritius and East Africa (Mshigeni 1984).

Remarks: This species was said to contain kappa carrageenan by Doty and Santos (1978); the material used for their study (MSD Voucher No. 31077) was *E. odontophorum* variety *mauritianum.* At that time, the existence of beta carrageenan was not known.

Eucheuma odontophorum (Fig. 32) has affinities with *E. speciosum*, but the prominent strong or long tapered, often ciliose spines, its segmental form, and possible mode of quasi-sympodial production of new segments set it off from that and other species distinctly. The "set" of a few large cells in the periphery of the axial core is seen in some other axiferous species and is especially like that of *E. speciosum*. In Fig. 33, note the rhizoids in the tip of the damaged spine shown. Fig. 34 emphasizes the often very short intergenicular segments that are rotund in cross sections of live materials and that, as Mshgeni (1984) has noted, are turned down at their two ends. The genicula (the obvious parts of segments) between are cylindrical and smooth.

Not enough is known about *E. odontophorum* to circumscribe it in any detail. The type specimen (see Børgesen's illustrations) and the only other collection seen (Fig. 32) is of thin, axiferous, strap-shaped, fragmentary blades ornamented only by lateral teeth so as to look like a juvenile form of *E. platycladum* (described in the next section). Only the two collections are known of the typical form; both were probably adrift and look very much alike, though the type specimen was from 49 m and that in Fig. 32 from 50 cm.

Eucheuma odontophorum variety *mauritianum* (Børgesen) nov. comb. (Basionym: *Eucheuma speciosum* variety *mauritianum* Børgesen [Børgesen 1943]) can be distinguished (Fig. 35), as Mshigeni (1984) has suggested, by its spiny segments that are compressed slightly and at maturity usually are downwardly arched terminally. A typical specimen, Voucher No. 22838, is deposited in the B. P. Bishop Museum as No. 508857. Cystocarpic thallus, No. 31077, from Point aux Roches, Souillac, Mauritius, for the gel work of Doty and Santos (1978), shows that the stalked cystocarps are almost entirely on what appears to be the ventral surface. They are largely nonspiny, but occasionally one has a few small spines on its surfaces. The axiferous segments of this variety have been seen attached apically to the substratum, forming a podium, which it had overgrown in producing the next segment. At times, it is difficult to distinguish this variety from the linear, possibly nonprostrate, more compressed, and flatter form of *E. odontorphorum* variety *odontophorum*, which seems not to be attached apically.

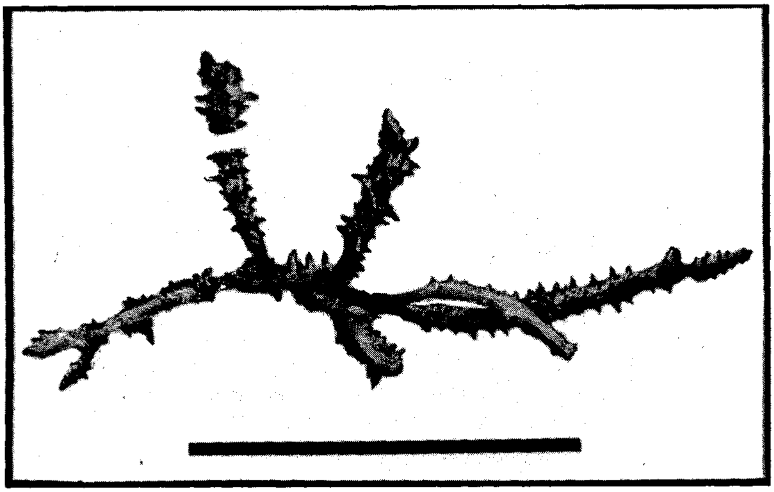


Fig. 32. *Eucheuma odontophorum* Børgesen. Xerograph of a fragment found lying loose in a reef flat pool at Pointe Roche Noire, near Tombeau Bay, Mauritius. (Voucher No. 22813; photograph No. 32935.19.) Scale bar = 5 cm.

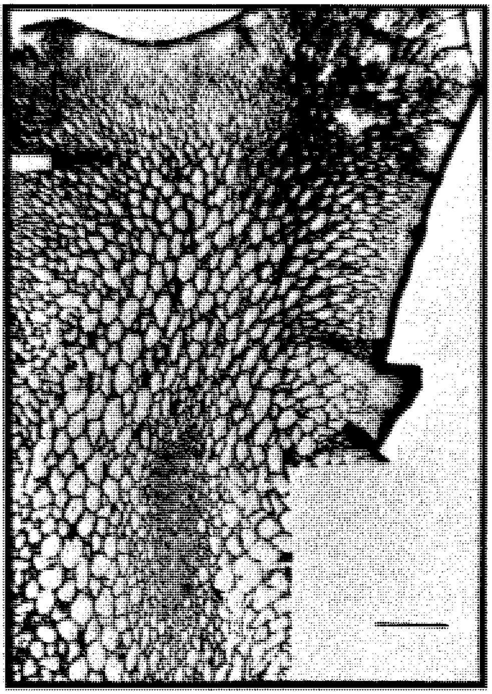


Fig. 33. Composite photographic illustration of the cross section of an unusually flat, resoaked segment *Eucheuma odontophorum* variety *mauritianum* shows the characteristic central axis and the rhizoidal, though damaged, tip of a young spine. (Collected at Pointe aux Roches near Souillac on the south coast of Mauritius by MSD in October 1971; Voucher No. 31077A; photograph No. 32944.9.) Scale bar = 5 cm.

Eucheuma platycladum Schmitz (Figs. 24B, 36, 37)
Schmitz 1895.

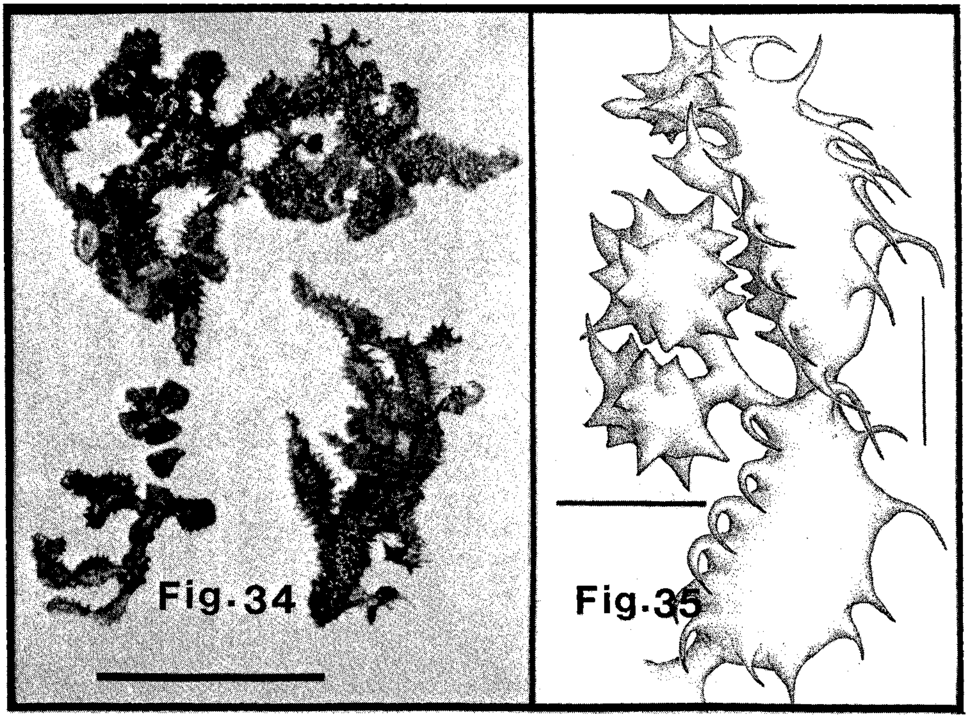
Type Specimen: Holst No. 1340 from Dar es Salaam. The type is believed to have been at Dalheim.

Distribution: East Africa.

Remarks: This prostrate species (Fig. 36) appears to broaden from strap-shaped to deltoid young horizontal branches and become expanded blades that are anaxiferous, often misshapen, horizontal, strongly compressed or flat and rigid. The blades may bear tubercles or spines on all surfaces.

The cystocarps (Fig. 24B) are borne at the apices of pedicels (spines) on one surface. A very few cystocarps may appear on the other surfaces. Schmitz (1895) stated that the cystocarps appear on the upper surface, but they are observed on the lower, though too few cystocarpic specimens have been seen to be sure. Until lots of holdfasts and thalli are available for study or the thalli are seen in the field, this simple attribute cannot be known with certainty.

The placement of *E. platycladum* among the sections is unsatisfactory. There are mixed reports of its being anaxiferous as well as axiferous. The spine and branch tips of this species have the typical tortuous rhizoids of *Eucheuma* section *Gelatiformia* (Fig. 37), and here and there the rhizoids reach the central area. In the central medullary area, which otherwise may appear anaxiferous, some rhizoids seem to join and become parallel



Figs. 34 and 35. Fig. 34, Fronds of *Eucheuma odontophorum* variety *mauritianum*. (From a collection No. 16487 made at Pointe aux Roches on the south coast, Mauritius by Joseph Gueho, Mauritius Sugar Industry Research Institute, October 1974; Voucher No. 22838; photograph No. 32933.2.) Scale bar = 500 μm. Fig. 35, Drawing of typical young and mature segments of *E. odontophorum* variety *mauritianum*. (Voucher No. R-LXX-21 collected by G. F. Pappenfuss and Robert Scagel; photograph No. 32939.21.) Scale bar = 5 mm.

with the other elements, and then fewer are seen centrally as the frond broadens.

The determination by Doty and Santos (1978) that *E. platycladum* is a kappa carrageenan species occurred before the discovery of beta carrageenan, and so far there has been no opportunity to reexamine its carrageenan. It is hoped that Mshigeni and Semesi (unpublished data) have done so with the information of Greer and Yaphe (1984b) in mind. Though the gel in *E. platycladum* may be kappa carrageenan, and the morphology of the medullary axis is truly distinct or anaxiferous, this species is placed here, for most of its cystocarps are sessile or terminal on podia rather than subterminal on a spine. It is suggested that perhaps these cystocarp positions may have arisen from the cystocarps having originated in subterminal positions on spine *anlage* that are lost in the broadening of the thalli as the initial cystocarp position is lost in the longitudinal indeterminate elongation of the spines in *Eucheuma* section *Anaxiferae*.

Summary Comments

The taxonomic information given here is provided, though very imperfect, to facilitate and encourage the work of others to better distinguish the taxa involved. For the most part, descriptions of species are now based on a few voucher specimens. (However,

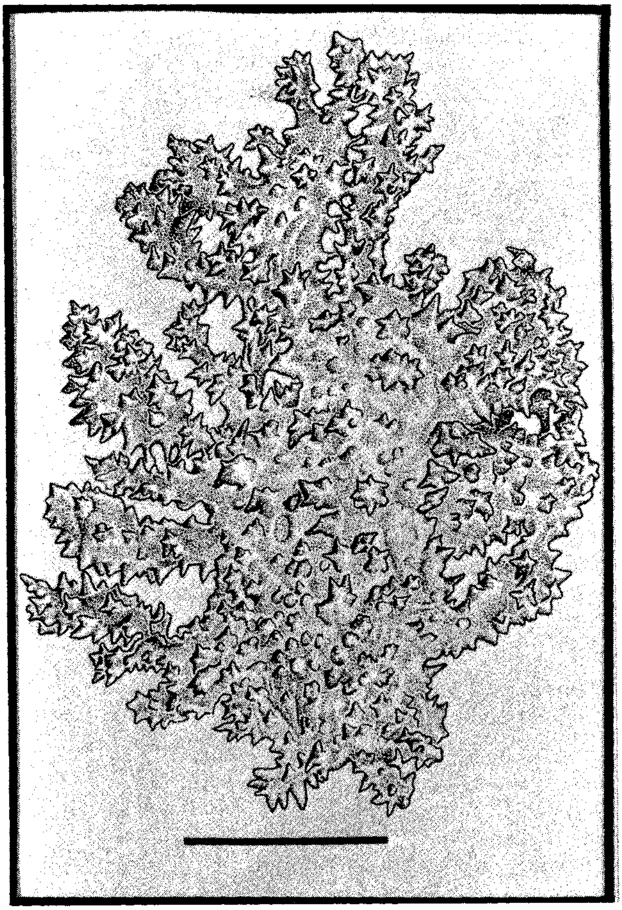


Fig. 36. Drawing of *Eucheuma platycladum* Schmitz. (Voucher No. Mshigeni 392B; photograph No. 32939.23; xerograph.) Scale bar = 5 mm.

older descriptions may have been based on still fewer specimens.) Circumscribing most of the species, with some exception, would be impossible now. Meanwhile, recognizing the characteristic variations that appear in the specific natural and cultural environments and describing them in quantitative terms as vegetative tendencies may be rewarding. For example, it could lead to understandings, via experimentation, of causes and effects.

Somewhat the same can be said for the biogeographic information. Doing it well means using one set of taxonomic criteria, yet even the criteria given in this study and the putative key are seriously deficient in many ways. For example, obviously *E. serra, E. perplexum*, and *E. kraftianum* are related structurally and, perhaps, by the nature of their gels, and *E. platycladum* may be quite wrongly understood. Before real progress can be made, much more information must be available on the anatomy, reproduction, and carrageenans of the principal individual species of the Eucheumoideae.

Lack of time has allowed error and redundancy to creep in. Fully aware of many simple informational gaps that would seem easily removable with means at hand, this chapter is appropriately considered but a prodromus or forerunner of things to come.

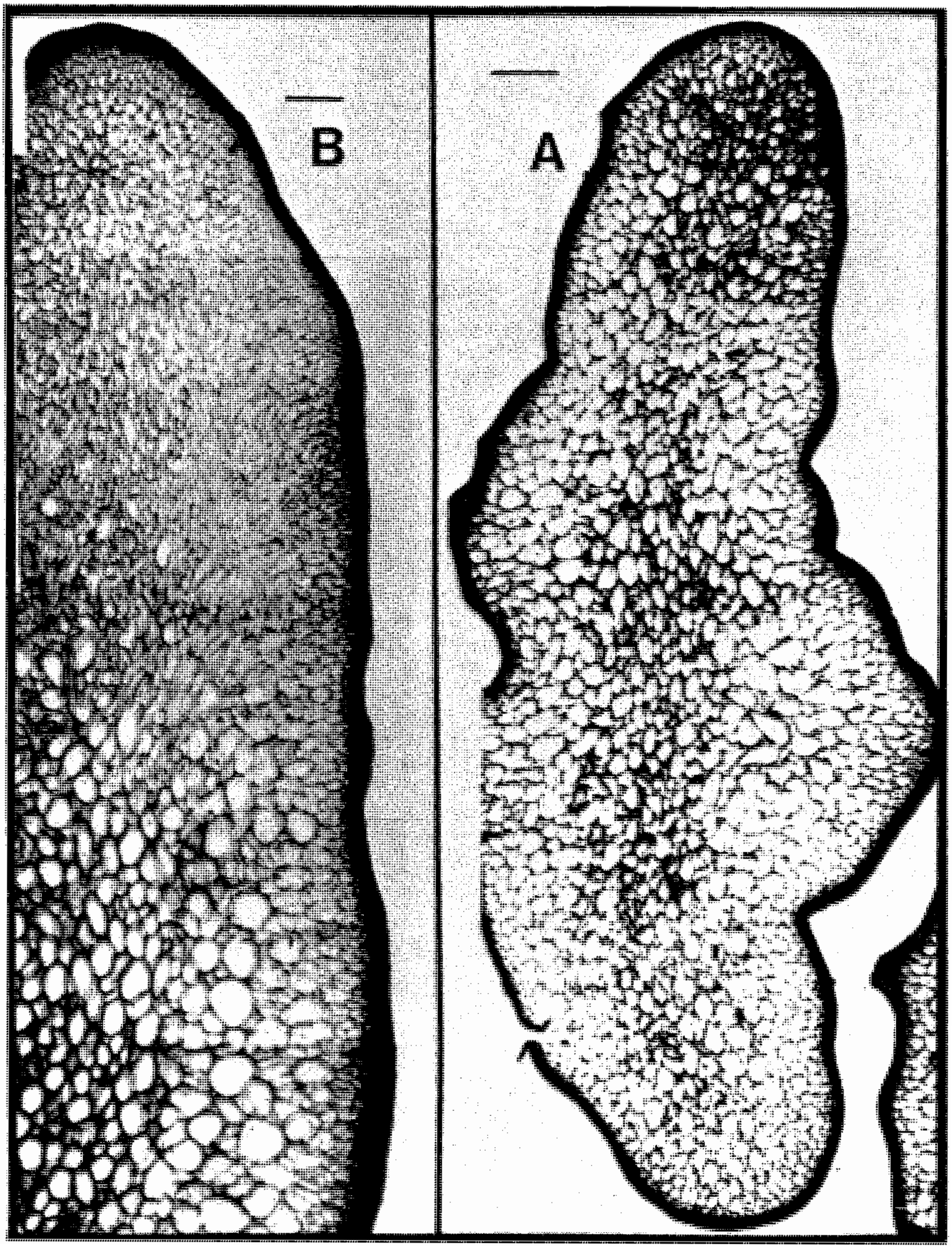


Fig. 37. Cross sections through main intergeniculae of *Eucheuma platycladum* in two different resoaked collections. Note rhizoids in tips present as small circular cells with central lumen filled (black) with cytoplasm. A, A more slender thallus, presumably younger. (Voucher No. PR-XIII-29.3 collected by Papenfuss and Scagel; photograph No. 32944.15.) B, A broader, presumably older thallus. (Voucher No. PR-XIII-29.1; photograph No. 32944.1.) Scale bars = 250 µm.

Putative Key to the Species Often Treated as *Eucheuma*

It is hoped that this key will prove to be a workable, practical guide to the species. It is based on relatively obvious vegetative features only and thus is weak in this respect. "Determinate," in reference to branches or branching, is defined as "not giving rise to indeterminate branches." "Branch(es)" and "branching" are used to mean, respectively, "what they are" and "what they do or have done." "Basal segment" is that part of a seaweed axis between the holdfast and the first indeterminate branch. Two species of *Gracilaria* are included because they are easily and often mistaken for *Eucheuma* species. The key is only to the type variety; thus, nonspiny varieties of typically spiny species are not included.

1. Axes bearing spines in whorls some place *or* spines rebranching (compound) and scattered *or* densely covering the cylindrical axis (rarely spines in remote pairs asymmetrically placed on a slightly compressed axis or spiny bilaterally and anaxiferous); axis cylindrical or nearly so and not segmented by constrictions; in all species most cystocarps on stalks or spines 2
1. Axes smooth *or* bearing simple primary spines in rows (marginal if axiferous) *or* bearing tuberculate to cylindrical protuberances; axes compressed or cylindrical, often separated into segments by constrictions; cystocarps borne variously 8
    2. Branches neither at regularly predictable places nor the result of development of a spine in one of the whorls; spines curving toward the branch apex and remaining determinate; presumably producing agar; (not included in this study) . . . . *Gracilaria aculeata* (Hering) Papenfuss (eastern South Africa).
    2. Branches frequently at predictable places along an axis; spines straight, some spines elongating into indeterminate branches; producing an iota carrageenan 3
3. Mature spines rebranched, in discrete whorls or covering axis segments completely; anaxiferous (Section *Anaxiferae*) 4
3. Mature spines simple, in whorls or widely spaced pairs some place on the axis; axiferous (Section *Eucheuma*) 5
    4. Fronds spreading laterally from the basal segment more than upwards; branches compressed so as to be dorsiventral . . . . *Eucheuma amakusaensis* Okamura (southern Japan and Taiwan).
    4. Fronds spreading upward from the thallus base more than horizontally; branches cylindrical, not dorsiventral . . . . *Eucheuma arnoldii* Weber-van Bosse (western subtropical Pacific).
5. Spines scattered or mostly in pairs toward the apex of the thallus; in some cases no fusion cell at cystocarp center 6
5. Spines irregular or in whorls of three or more toward the apex of the thallus; fusion cell central in cystocarp 7
    6. Densely spiny; spines not in pairs; no fusion cell in cystocarp . . . . *Eucheuma uncinatum* Setchell et Gardner (Mazatlan northward in the Gulf of California
    6. Spines in remote pairs asymmetrically placed on the axis or solitary . . . . *Eucheuma serra* J. Agardh (Indo-Pacific, probably overlapping the native range of *E. denticulatum*).
7. Spines in whorls some place; producing ideal iota carrageenan . . . . *Eucheuma denticulatum* (N. L. Burman) Collins et Hervey (eastern Africa to western warmer Pacific west of Micronesia but distributed by humans still farther east).
7. Spines in whorls or scattered; producing a deviant iota carrageenan . . . . *Eucheuma isiforme* (C. Agardh) J. Agardh (Caribbean and related Atlantic areas).
    8. Thalli compressed to flattened above the basal segment 9
    8. Thalli cylindrical at least above the basal segment, branching irregular, not usually pinnate 18
9. Thallus with blunt protuberances and branches irregular in origin, often from near the bases of the fronds 10

9. Thallus with conical spines and branches commonly arising from the indeterminate growth of some of them, often bilaterally 13

10. Erect blades; recumbent perhaps but neither decurrent nor prostrate .... *Kappaphycus procrusteanum* (Kraft) Doty (in this publication) (Central Philippines).

10. Prostrate, irregular in form, or with linear segments sometimes in heads, or decumbent, or decurrent from their place of origin 11

11. Thalli irregular horizontal crusts. (Includes *E. horizontale, E. striatum* forms, and *E. cottonii* forms but not discussed in this publication) .... *Eucheuma crustiforme* Weber-van Bosse (Indian Ocean to southern Japan).

11. Thalli of linear segments 12

12. Cortex with small cells among the medullary cells; producing a hard kappa carrageenan; cystocarps, as well as the seriate tetrasporangia, scattered on main axes .... *Kappaphycus cottonii* (Weber-van Bosse) Doty (in this publication) (Tanzania eastward to Guam).

12. Cortex without small cells among the medullary cells; producing a soft agaroid gel; cystocarps at bases of short laterals; cruciate tetrasporangia common on ventral surface; warmer Pacific (not elsewhere in this study) .... *Gracilaria eucheumoides* Harvey (western warmer Pacific).

13. Generally several fronds erect from a fleshy prostrate base; with or without marginal spines; axiferous 14

13. Generally horizontal or prostrate at least above the basal segment; flattened parts bilaterally spiny 16

14. Major segments soft, readily pliable, flattened .... *Eucheuma kraftianum* Doty (in this publication) (central Indonesia).

14. Major segments rigid, compressed 15

15. Largely prostrate, covered with long conical spines or smooth with strong marginal teeth; axiferous .... *Eucheuma odontophorum* (Børgesen) Doty (in this publication) (Mauritius).

15. Largely erect, often only marginal spines conspicuous .... *Eucheuma speciosum* (Sonder) J. Agardh (Western Australia).

16. Thallus generally prostrate and with quickly broadening deltoid apical segments; anaxiferous; producing kappa carrageenan preponderantly; East Africa .... *Eucheuma platycladum* Schmitz (Tanzania).

16. Thalli generally at least partially erect and of linear segments; axiferous; producing carrageenans other than kappa 17

17. Broadest segments with many proliferations or spines on their ventral surfaces; cystocarpic spines largely on ventral surface; producing beta carrageenan preponderantly .... *Eucheuma gelatinae* (Esper) J. Agardh (southern Japan, southern China to Indonesia).

17. Broadest segments about equally proliferous of spines on both surfaces; cystocarpic spines largely on margins; producing iota carrageenan preponderantly .... *Eucheuma perplexum* Doty (in this publication) (eastern Australia to Taiwan and southern Japan).

18. Short secondary branches forcipate near major shoot apices and these, in deflecting the original axis, may produce cervicornate branching; blunt knobs or acute spines of uniform length are often present; often spine tips turned downward apically or spines so arranged in rows as to obscure the roundness of the axis; branching generally close and axils angular; apices generally directed toward the light and plagiotropic, not inflated above their bases, often of uniform diameter to near the apically quickly tapered or inflated tips; often conspicuously, secondary indeterminate branches arise from the shaded lower interior segments and these significantly increasing the density of the branching; medullary core of axial hyphae tending to disappear as the branches reach 5 mm in diameter .... *Kappaphycus striatum* (Schmitz) Doty (in this publication) (Indo-Pacific to Belau and eastward to Pohnpei, Federated States of Micronesia).

18. Short secondary branches absent near major shoot apices and when present neither forcipate nor deflecting the long, straight apical segment; uppermost segments tending to be smoothly cylindrical with only indeterminate branches and these neither in rows nor obscuring the basic roundness of the segments; other kinds of branches usually absent or only denticulations; branching generally open and the 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 19

19. Branches reaching the surface of the thallus often inflated above their midparts or apically . . . . *Kappaphycus inerme* (Schmitz) Doty (in this publication) (East Africa and southwestern Indian Ocean).

19. Branches reaching the surface of the thallus rarely inflated above their midparts . . . . *Kappaphycus alvarezii* (Doty) Doty (in this publication) (Sulu Sea and related areas; farmed and widely distributed by humans).

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THE GENUS *EUCHEUMA* J. AGARDH IN FLORIDA AND THE CARIBBEAN

Donald P. Cheney

Abstract

The six previously reported species of *Eucheuma* (Solieriaceae, Rhodophyta) from Florida and the Caribbean are examined. For *E. isiforme* (C. Agardh) J. Agardh, a new variety is created for spineless plants previously known from the Florida areas as *E. nudum* J. Agardh. Other taxa, *E. acanthocladum* (Harvey) J. Agardh, *E. gelidium* (J. Agardh) J. Agardh, *E. echinocarpum* Areschoug, and *E. schrammii* (Crouan and Crouan) J. Agardh, are removed from *Eucheuma*. *E. nudum* is removed from the flora of the Florida-Caribbean basin. These transfers leave *E. isiforme* with its two varieties as the only *Eucheuma* in this region. *E. denticulatum* (Burman f.) Collins et Hervey is considered to be a distinct but closely related species to *E. isiforme*.

Introduction

Six species of *Eucheuma* (Solieriaceae, Rhodophyta) are reported from the western Atlantic and the Caribbean by Taylor (1960), and though widely distributed in the island groups of the Caribbean, they are not especially abundant in any one place. The commonest species is *E. isiforme* (C. Agardh) J. Agardh (1847), which was placed by Doty and Norris (1985) in *Eucheuma* section *Eucheuma*. This paper is divided into several sections: Nomenclature, Taxonomy and Distribution, and Excluded Species.

Nomenclature

Eucheuma isiforme (C. Agardh) J. Agardh

J. G. Agardh 1847, p. 6.

Basionym: *Sphaerococcus isiformis* C. Agardh (C. A. Agardh 1822, p. 271).

Whorled spines are emphasized in the brief original description of *S. isiformis* to distinguish it from *S. spinosus* (L.) C. Agardh (C. A. Agardh 1822). Only one specimen in the Agardh Herbarium (LD) bears the same collection information that appears in this description: "West Indies" and Herb. Aspegren, which is in the handwriting of C. Agardh. This specimen (LD 34654, fig. 22) is to be considered the holotype in keeping with Article 7 ICBN and the recommendations of Rollins (1972). This specimen bears few whorled spines, and I consider it atypical of the species.

A large number of specimens from Key West, Florida, collected by W. H. Harvey and others, are also identified in the Agardh Herbarium and appear to form the basis of J. Agardh's (1847) concept of the species when he transferred this taxon to *Eucheuma*.

The general morphology of the original collection as a whole, and the type specimen in particular, closely resembles that of plants identifiable as *E. denticulatum* (Burman f.) Collins et Hervey. Dixon (1962) has shown that *E. denticulatum* (Burman f.) Collins et Hervey, based on *Fucus denticulatus* Burman f. (Burman 1768), has priority over *E. muricatum* (Gmelin) Weber-van Bosse (Weber-van Bosse 1928), based upon *Fucus muricatus* Gmelin (Gmelin 1768). *F. denticulatus* Burman f. was published in April, and *F. muricatus* Gmelin in May 1768. *Eucheuma spinosum* (L.) J. Agardh (basionym, *Fucus spinosus* Linne (Linne 1771)) is a later homonym of *F. spinosus* Gmelin (Gmelin 1768).

The basionyms of *E. denticulatum, E. muricatum*, and *E. spinosum*, whether they are conspecific or not, all antedate C. Agardh's *S. isiformis*, and if all of these were considered to be the same species, *E. denticulatum* would have to be the name used. The continued separation of *E. isiforme* and *E. denticulatum* is, in fact, open to question in view of the considerable overlap in their morphological variation. Their continued separation is also of considerable practical interest because, at present, the only *Eucheuma* species listed by the Food Chemicals Codex (1972) as permissible sources of carrageenan for human use are *E. spinosum* and *E. cottonii*.

Originally, *E. isiforme* and *E. denticulatum* (as *S. isiformis* and *S. spinosus*, respectively) apparently were separated primarily on the basis of whorled spines in the first species. This feature, however, is inconsistent, for plants with whorled and unwhorled spines clearly occur in both species.

When two geographically isolated species cannot be clearly distinguished morphologically, two taxonomic alternatives are available: The two species can be combined and the morphological variants distinguished at a subspecific level, or the species can be maintained and recognized as part of a species complex. Collins and Hervey (1917) suggested that *E. isiforme* and *E. spinosum* be combined as *E. denticulatum* (Burman) Collins et Hervey. However, because they apparently had not examined type material and were perhaps unfamiliar with *E. spinosum*, their argument for conspecificity should be taken with reservation. Until the problem can be studied further, and more biosystematic information is available, the recognition of *E. isiforme* and *E. denticulatum* as geographically isolated species of a closely related species complex is favored.

As treated in this paper, all species belonging to this complex that are found in the Florida and Caribbean region are to be recognized as *E. isiforme*. This opinion includes the report of *E. spinosum* from the Atlantic Ocean by Maze and Schramm (1870–1877, p. 229). Specimens referred to by those authors (Numbers 73 and 814, BM) were examined and judged to belong to *E. isiforme* as circumscribed here.

Taxonomy and Distribution

Eucheuma isiforme (C. Agardh) J. Agardh (Figs. 1–4)

Description: Plants generally 12–50 cm tall, erect or becoming procumbent with age; generally with a single main axis arising from a prominent discoid holdfast; procumbent plants frequently bearing additional secondary holdfasts. Axes terete throughout. Branching of two to four orders, generally irregular throughout; main branches similar to, and often indistinguishable from, the main axis, 3–6 mm in diameter; branches and branchlets smooth to very spinose; ultimate projections highly variable in length, number, shape and pattern; color golden-yellow to dark red; texture cartilaginous.

Lower portions of thallus in cross section consisting of three to five rows of densely pigmented outer cortical cells, five to eight rows of unpigmented inner cortical cells, and a densely compacted filamentous medulla; total width of the cortex generally 2.5–5.0 times that of the medulla.

Plants dioecious. Carpogonial branches three-celled (Fig. 2), borne in the outer cortex; auxiliary cells distant, borne inside or adjacent to the outer cortex. Cystocarps with a single, large, central fusion cell, surrounded by radiating gonimoblasts, which give rise to single, terminal, ellipsoidal to spherical carpospores. Gonimoblasts surrounded by a prominent nutritive tissue or "Faserhülle," which is connected to the fusion cell by numerous sterile filaments. Cystocarps stalked, embedded in special papillae of variable length, found throughout the plant. Male plants rare; spermatia borne singly on elongated spermatangial cells; spermatangia (Fig. 3) occurring in sori, generally found in upper parts of plants. Tetrasporangia (Fig. 4) 10–20 μm wide by 35–60 μm long, arising from the outermost layers of the cortex, zonately divided, found throughout the plant, especially the upper parts.

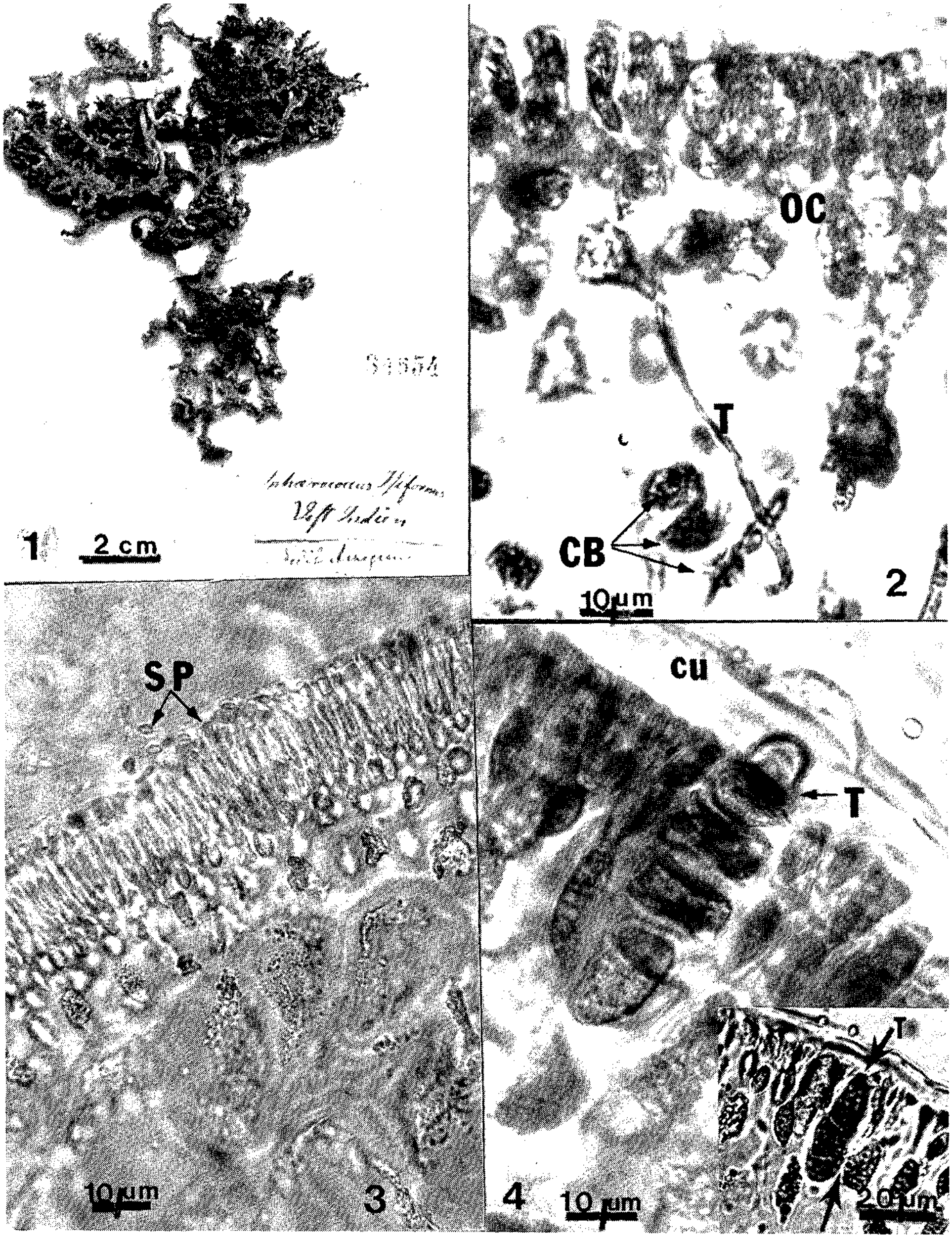


Fig. 1–4. ***Eucheuma isiforme*****. Fig. 1, Holotype (LD) of *Eucheuma isiforme* (C. Agardh) J. Agardh. Fig. 2, Three-celled carpogonial branch (CB) and trichogyne (T) located within the outer cortex (OC). Fig. 3, Spermatangial sorus of a male plant showing elongated spermatangial mother cells and terminal spermatangia (SP). Fig. 4, Cross section of a tetrasporangial plant showing a mature, zonately divided tetrasporangium (T) beginning to push through cuticle (CU). Inset shows a tetrasporangium (T) connected by lateral pit connection (*arrow*) to adjacent cortical cell.**

Remarks: *Eucheuma isiforme* has been shown in a related study (Cheney and Dawes, unpublished) to include a far greater range of morphological variation than had been ascribed to it previously. Two extremes in the overall range of morphology can be easily distinguished: the spinose plants originally recognized as *E. isiforme (sensu stricto)*, and the spineless plants previously reported as *E. nudum* by Dawes and coworkers (e.g., Dawes et al. 1974, Dawes et al. 1976, Dawes et al. 1977, Moon and Dawes 1976). The principal morphological differences between these two growth forms have been shown through transplantation studies to be genetically fixed rather than environmentally induced. For the sake of providing a practical means of distinguishing these two growth forms by name, they are accordingly assigned varietal status. Recognition of more than two varieties or of additional subspecific categories would appear to be impractical because of the more or less continuous nature of the morphological variation within the species.

Key to the Varieties of *Eucheuma isiforme*

1. Plants spinose throughout; spines all of approximately the same length, generally less than 3 cm long, distributed randomly in a radial pattern or more frequently in whorls . . . . *E. isiforme* var. *isiforme*
2. Plants with few or no spines; branches smooth except for infrequent ultimate laterals, which are generally up to 6 cm long or more and randomly distributed in a bilateral or radial fashion . . . . *E. isiforme* var. *denudatum*

Description of the Species

Eucheuma isiforme (C. Agardh) J. Agardh var. *isiforme* (Fig. 1)

Synonyms: *Sphaerococcus isiformis* C. Agardh (C. A. Agardh 1822, p. 271). *Gigartina isiformis* (C. Agardh) Endlicher (Endlicher 1843, p. 42). *Eucheuma isiforme* (C. Agardh) J. Agardh (J. G. Agardh 1847, p. 6, as *E. isiformis*). *Hypnea wurdemannii* Harvey (Harvey 1853, p. 119) *nomen nudum.*

Type Locality: West Indies, exact locality and date unknown; specimen given by Aspegren.

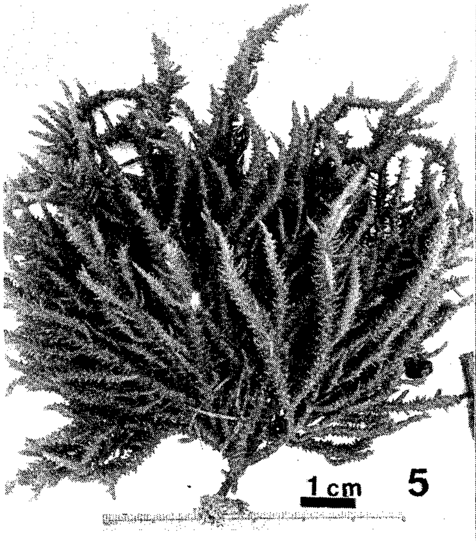
Holotype: Herb. Agardh 34654 (LD), fig. 22; isotype: (S) (Fig. 1).

Description: Plants (Fig. 5) generally erect, 12–25 (up to 35) cm tall. Branching abundant throughout, to three or four orders. Branches conspicuously spinose, generally bearing from 5 to 15 spines per centimeter of branch length. Spines usually of uniform length throughout, short, 1–2 (up to 3) cm long, and pointed; however, in some cases, blunt and nodulous. Spines distributed randomly in a radial fashion or, more commonly, in regularly spaced whorls. Plants typically golden-yellow.

Distribution: Florida: throughout the Florida Keys, the Dry Tortugas, and offshore the west coast from very deep water (see the following). Atlantic Ocean and Caribbean Sea: Bermuda, Bahamas, Cuba, Puerto Rico, Virgin Islands, Lesser Antilles, Barbuda, Tortola, Mexico, and Belize. Reported also from Hispanola and St. Barthelemy (Taylor 1933, 1962, 1969); however, specimens not seen. Probably found throughout the Caribbean Sea. Additional references are provided in Cheney (1975).

Habitat: Attached to limestone, rock, and coral substratum; typically in shallow water, 1–4 m deep, although reported from depths as great as 73 m (Dawes and Van Breedveld 1969). In shallow water, generally found in sites where considerable water movement is present because of currents.

Specimens Examined (not all cited): Bermuda: Tuckertown, iv 1912, Collins s.n. (= Collins et al. 1912, fasc. 38:1886, C, FH, L, NY, UC, US); Tucker's Town Bay, 15 iii 1949,



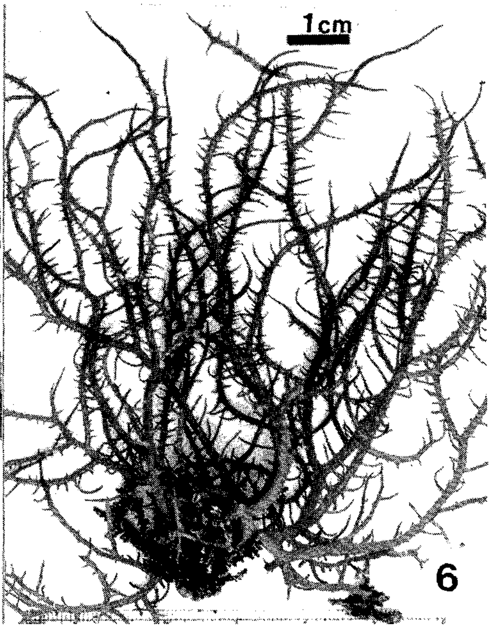


Fig. 5. Habit of *Eucheuma isiforme* var. *isiforme* from Molasses Key, Florida.
Fig. 6. Habit of *Eucheuma isiforme* "Bahia Honda form."

Taylor and Bernatowicz 49-274 (FH, UC, US); Walsingham Area, west side of Castle Harbor, 6 iv 1949, Bernatowicz 49-635 (FH, UC, US); Castle Harbor, viii 1913, Collins s.n. (FH, NY); s.d., Kern 58, 78 (DUB); Castle Island, south side, 28 iii 1949, Taylor and Bernatowicz 49-506 (UC, US); Bailey's Bay, sublittoral, 14 vi 1900, Howe 110 (NY); Gibbet Island, 27 iii 1921, Hervey 27 (NY); Bailey's Bay, 18 i 1913, Hervey s.n. (L, UC); St. George Island, Whalebone Bay, 25 iv 1953, Bernatowicz 53-262 (L); 30 fathoms off Bermuda, Moseley s.n. (BM). Florida: Monroe County: Key West, 10, 15, i 1895, Hall s.n. (NY); s.d., Messina 182 (B, NY, UC); s.d., Harvey 45 (NY); s.d., Collins s.n. (UC): 22 x 1895, Bolton 56 (FH); Hooper s.n. (Exsic. Amer. Bor. 12, C, FH, L, NY, S, UC, US); iii 1872, Melvill s.n. (FH); ii 1850, Harvey s.n. (BM, DUB, S, UC); s.d. Messina s.n. (= Collins et al. 1895, fasc. 2:92, C, L, NY, US); West Summerland Key, i–iii 1947, Stephenson s.n. (UC); Big Pine Key, Long Beach, 26 iii 1952, Killip 42060A (US); 4 i 1954, Killip 43422 (US); 13 ii 1952, Killip 41920 (US); Indian Key, iv 1896, Curtiss s.n. (MB, C, MO in UC, NY): Bahia Honda Key, north of old CCC camp, Overseas Highway, southeast of road, 5 iv 1943, Humm s.n. (DUKE); vii 1850, Tuomey 16 (DUB); Content Keys, north side, 18 iii 1967, Croley 918 (US); 24 ix 1966, Dawes, Croley, Lawrence 649 (UC, US); Indian Key, 22 vii 1932, Schmitt 56 (US); Pinellas County: Clearwater Beach, 21 viii 1924, Taylor 36 (US). Dry Tortugas: Garden Key, 10 vi 1924, Taylor 101 (NY); Bird Key, 23 vi 1926, Taylor 1457 (NY); 1873, Ingalls s.n. (NY, UC); Bush Key, on flats inside, 9 vi 1926, Taylor 1242 (C, FH, L, UC). Dade County: Biscayne Key, xi 1897, Thaxter s.n. (F). Hernan Cortez Cruise 17: station xiv, depth to 25 ft, 19–24 iv 1965, Dawes 2612 (UC, US); station v, depth to 25 ft, 19–24 iv 1965, Dawes 2326 (US). Mexico: Cozumel, Q. Roo, Punta Palancar, 12 viii 1966, Tirado 345 (US). Bahamas: Stocking Island: Exuma Harbor, unattached, 26 ii 1905, Howe 4169 (BM, C, FH, L, MO in UC, NY, US); Exuma Chain:

Great Guana Cay, 21 ii 1905, Howe 4062 (NY). Cuba: Hicacos Peninsula, east of Xanadu, i 1957, Schmitt 834 (US); west of Havana, viii 1927, Leon 13084 (NY). Puerto Rico: La Perguera, 0.75 miles seaward from Media Luna reef, to 55 ft depth, 3 iii 1979, Mathieson s.n. (NHA 41,952); 0.5 miles seaward from Margarita Reef, to 80 ft depth, 5 iii 1979, Mathieson s.n. (NHA 42,014). Virgin Islands: St. John off Annaberg, 14 iii 1906, Børgesen 1984 (C); St. Thomas, 8 iii 1906, Børgesen 1883 (C): St. John, 1905–1906, Børgesen 1964 (C). Guadeloupe: St. Martin, iii 1869, Maze 814 (BM) (as *E. spinosum*); St. Martin, 4 xii 1856, Maze 73 (BM) (as *E. spinosum*); 31 viii 1870, Maze 1584, 1990 (BM) (as *E. nudum*). Barbuda: Gravenor Landing, along shore in honeycomb coral rock, 28 iv 1958, Schmitt 26 (US); Cocoa Point, 27 iv 1959, Cowan 95 (US). Tortola: Frenchman Cay, dredged, viii 1969, Almodovar 5961 (DUKE, L, NY, UC). Belize (= British Honduras): Middle Key, Glover's Reef, 8–30 ft, 29 vii 1972, Dawes (USF); Glover's Reef, 22 vii 1972, Dawes 8208 (USF). Additional specimens are cited in Cheney (1975).

Remarks: The typical variety is distinguished by its highly branched and typically spinose appearance. Occasionally, plants can be found that have lost most of their spines, particularly in the lower parts of the plants; however, this is rare and appears to be related to aging and/or reproductive maturation. Plant length and color are variable, largely due to differences in habitat conditions. Plants found in deep water tend to be more elongated and darker red than shallow-water plants, which are typically golden-yellow.

Dawes et al. (1974) described a unique growth form of *E. isiforme*, referred to as the Bahia Honda form (= *Eucheuma* sp. in Dawes et al. 1977), previously noted by Harvey (1853). Because of its very spinose nature, the Bahia Honda form clearly falls within the circumscription of the typical variety. It is known only from Bahia Honda Key and is undeserving of formal taxonomic recognition (for a recent definition of formae, see Semple 1974). It is suggested that these plants be referred to as simply the Bahia Honda form (Fig. 6) of var. *isiforme*.

Eucheuma isiforme (C. Agardh) J. Agardh var. *denudatum* Cheney, var. nov. (Fig. 7)

E. isiforme (C. Agardh) J. Agardh var. *denudatum* Cheney (*nomen nudum*) in Moon and Dawes 1976, p. 165.

Plantae 16–40 (50) cm alt., erectae, ex unico haptero principale natae, aut procumbentes, numerosa haptera secondaria, a ramis producta, habentes. Ramificatio plerumque sparsa, usque ad duo tresve ordines. Ramelli laterales ramorum rari, plerumque 4 vel pauciores in uno centimetro longitudinis rami, perspicue sine spinis. Ramelli laterales ultimi 6–15 cm vel plures, attenuati, irregulariter in uno plano aut, rarius, in modo radiato aut subradiato distributi. Plantae typi colore atrorubrae.

Description: Plants 16–40 (up to 50) cm tall; erect, with a single main holdfast, or procumbent with numerous secondary holdfasts produced from branches. Branching generally sparse, to two to three orders. Branches with infrequent laterals, generally four or fewer per centimeter of branch length, conspicuously spineless. Ultimate laterals 6–15 cm long or longer and tapering, distributed irregularly in a single plane or, less frequently, in a radial or subradial fashion. Plants typically red.

Type Locality: Florida: Indian River County, Riomar Reef, Vero Beach (27° 60′ N, 80° 35′W), attached to sabellarid worm reef, 2–5 m deep, March 21, 1974.

Holotype: Cheney 74-27 (USF), fig. 24; isotype: (US).

Distribution: Florida: offshore the west coast from Florida Bay north to Alligator Point and Apalachee Bay, and on the east coast from Vero Beach to Juno Beach. North Carolina: southeast of Cape Fear, off Frying Pan Shoals. Mexico: Yucatan (specimens probably of deep-water origin). See Cheney (1975) for references.

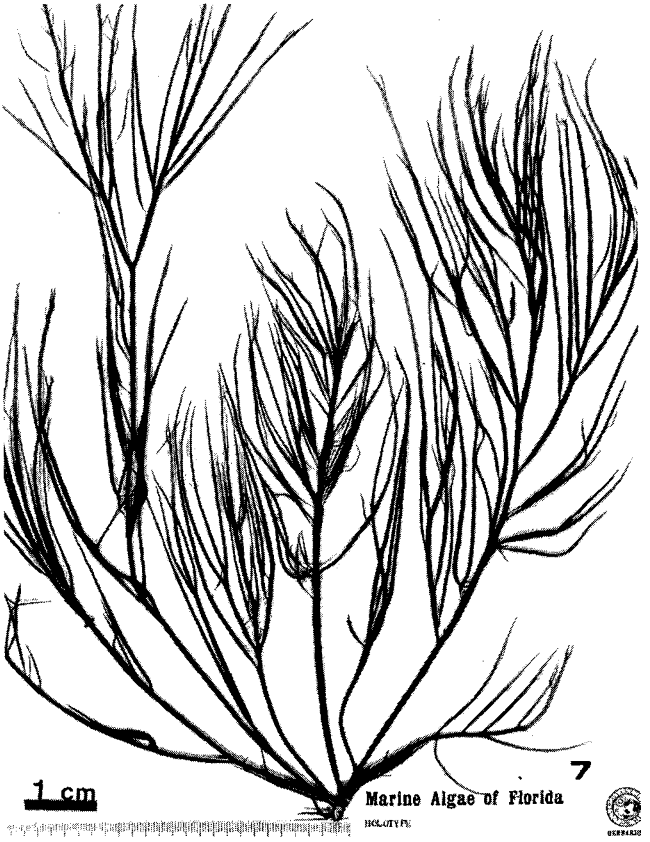


Fig. 7. Holotype of *Eucheuma isiforme* (C. Agardh) J. Agardh var. *denudatum* Cheney var. nov.

Habitat: Found offshore North Carolina (Schneider 1976, as *E. isiforme*) and the west coast of Florida in depths of 23–41 m and 10–35 m, respectively; attached to shell, rock, and coral rubble along the tops of limestone and coral-reef outcroppings. On the east coast of Florida, found attached to sabellarid worm reefs and associated rubble, in sites of generally reduced water clarity, to depths of 2–5 m.

Specimens Examined (not all cited); North Carolina: Station 17662, depth 26 m, 2 viii 1971, Searles and Schneider s.n. (DUKE); Station 17090, depth 25 m, 25 v 1971 Searles and Schneider s.n. (DUKE, UC). Florida: s.d. Farlow s.n. (C, BM); Palm Beach County: Jupiter, ix 1895, Curtiss s.n. (BM, C, FH, MO in UC, NY, US); Franklin County: Alligator Point, 8 xi 1950, Miles s.n. (DUKE) (as *E. acanthocladum*); Lee County: Boco Grande, near range light, 20 xii 1955, Earle s.n. (DUKE) (as *E. acanthocladum*); Brevard County: Indian River, ii 1880, Curtiss s.n. (FH); Melbourne, xi 1900, Marsh s.n. (FH); xi 1871, Curtiss s.n. (FH), 2 specimens; St. Johns County: St. Augustine, s.d. Hall s.n. (NY); Hourglass Cruises: west coast station v, 25 ft, 19–24 iv 1965, Dawes 2327 (US). Mexico: Yucatan: Progreso, 5 iv 1865, Schott 287 (BM); Progreso, 7 iv 1865, Schott 441 (US); Celestun, Schott s.n. (US); Campeche, 1839, Linden s.n. (BM).

Remarks: This variety is distinguished from variety *isiforme* by its more elongated and spineless appearance. Ultimate laterals are of variable length throughout the plant, as opposed to the short spines found in variety *isiforme*, which are all of approximately the same length. The relative abundance of ultimate laterals varies both within and between populations.

Plants from the east and west coasts of Florida show several minor morphological differences; however, I do not consider them deserving of formal taxonomic distinction at this time. Plants from the shallow-water sites on the east coast frequently are more elongated and have fewer laterals than plants from the west coast. Furthermore, laterals of the east coast plants are typically constricted at the base and tapered at the end, giving a spindle-shaped appearance.

Plants placed in this variety have been misidentified and reported in the literature as *E. acanthocladum* (Dawes et al. 1967, Dawes and Van Breedveld 1969) and, more frequently, as *E. nudum* (e.g., Dawes 1974, Dawes et al. 1974, Dawes et al. 1976). Examination of type material of *E. nudum*, however, has established that although the two are very similar in morphology, *E. nudum* and *E. isiforme* var. *denudatum* are clearly separate entities. Because of the confusion that has surrounded *E. nudum* in the past, a clarification of this species is included here.

Eucheuma nudum was first described by J. G. Agardh in 1852. It was separated from the other species primarily on the basis of its terete, spineless, conical-tipped branches ("*ramis elongatis inermibus, apicibus conicis*"). No collection information was provided in the original description, or in a later one (J. G. Agardh 1876). However, Agardh (1876) referred to its resemblance to *Chondrus vermicularis* Kützing as illustrated by Kützing (1867, pl. 61), which was reported from the Sandwich Islands (the Hawaiian Islands). In his final treatment, Agardh (1892) described the locale of *E. nudum* as the Sandwich Islands and the Pacific Ocean "superiore ad Californiam."

Examination of the *Eucheuma* specimens found at the Agardh Herbarium (LD) suggests that J. G. Agardh's interpretation of the species *E. nudum* was probably based on a limited amount of material. The most complete specimen, LD 34628, agrees well with Agardh's original description and is the only specimen to bear the citation of the original description in Agardh's hand (i.e., "*Eucheuma nudum* J. Ag., Sp. Alg. p. 625"). Kylin (1932, p. 23, pl. 9, fig. 18) illustrated this specimen and cited it as the "original examplar." My studies have confirmed Kylin's opinion. Consequently, LD 34628 is to be considered the lectotype of the species.

This specimen (LD 34628) has the same growth habit as plants described herein as *E. isiforme* var. *denudatum*; however, it has a very different anatomy. Cross sections of the main axis of the lectotype of *E. nudum* did not show the dense medulla typical of variety *denudatum* plants but rather indistinct cortical and medullary regions that consisted of large amounts of small rhizoidal cells with large cortical cells scattered throughout. This suggests that the type specimen is probably from the Indian or western Pacific Oceans, where this type of anaxiferous construction has been reported for other *Eucheuma* species, such as *E. vermiculare* and *E. striatum* (Doty 1970, Kraft 1969, Weber-van Bosse 1928). Doty (1970) and Kraft (1969) in their treatments of the Philippine species of *Eucheuma* recognized an *E. striatum* complex that includes *E. vermiculare* (Kützing) Weber-van Bosse, *E. edule* (Kützing) Weber-van Bosse, *E. crassum* Zanardini, *E. cervicorne* Weber-van Bosse, *E. dichotomum* and *E. simplex* Weber-van Bosse, and *E. striatum*. It now appears that *E. nudum* may also be part of this complex. It shows particularly close affinities to *E. vermiculare* (Kützing) Weber-van Bosse. Clearly, the plants from Florida previously identified as *E. nudum* have nothing to do with this species.

I also conclude that J. G. Agardh's references to California (J. G. Agardh 1892, p. 121) were based on either an incorrect determination or an inappropriate interpretation of species limits and should be excluded from the circumscription of the species *E. nudum*.[1]

Excluded Species

1. *Eucheuma acanthocladum* (Harvey) J. Agardh (J. G. Agardh 1876, p. 600).
2. *Eucheuma echinocarpum* Areschoug (Areschoug 1854).
3. *Eucheuma gelidium* (J. Agardh) J. Agardh (J. G. Agardh 1847, p. 16).

Examination of reproductive material of *E. acanthocladum, E. echinocarpum*, and *E. gelidium* has revealed that all three species possess a cystocarp construction that consists of a central sterile tissue instead of a fusion cell. This makes it necessary to remove them from the genus *Eucheuma*. The conspecificity of *E. acanthocladum* with *E. gelidium* and the correct generic placement of these three species will be described in a forthcoming paper (Gabrielson and Cheney 1987).

4. *Eucheuma schrammii* (Crouan et Crouan) J. Agardh (J. G. Agardh 1892, p. 124).

Mychodea schrammii Crouan et Crouan (Maze and Schramm 1870–1877).

Type Locality: Guadeloupe: Crosier (Point Laverdare) and Moule, January and April (no year given), Maze Coll. no 138, 1st Series 1609.

Lectotype: Herbarium Agardh 34680 (LD), vide Kylin (1932, p. 24); isotypes: BM, P.

Type material of this species from the Agardh Herbarium (LD) and BM has been examined, including two specimens (one from each herbarium) that are cystocarpic. Examination of the cystocarps of these specimens revealed a small-celled, placentate cystocarp construction. It is suggested, therefore, that this species be placed in a new genus, *Meristiella*.

Acknowledgements

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[1] *Eucheuma nudum* was identified by W. A. Setchell (in herbario) from Hawaii, but Abbott (1980), on examining the same specimen, identified it as *Gracilaria* species. No specimen that resembles Kützing's *C. vermicularis* has been seen from the Hawaiian Islands or from California (Abbott and Hollenberg 1976), and it is suggested here that the location cited by Kützing (1867) as "archipelago sundico," cited also by J. G. Agardh (1876), is not the Sandwich Islands (Hawaiian Islands) but the Sunda Islands, approximately 5 to 10° S and 110° E, in the heart of *Eucheuma* species distribution.

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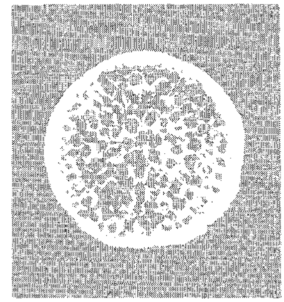
SECTION V. *Laurencia* (Rhodophyta, Rhodomelaceae)



INTRODUCTION

Karla J. McDermid

Laurencia is a genus of small to medium-sized red algae, members of the order Ceramiales, family Rhodomelaceae. *Laurencia* species are found worldwide, primarily in warmer waters, and often constitute a considerable part of tropical and subtropical floras (Taylor 1960, Pham-hoang 1969, Cribb 1983, Lewis 1984). The species grow in a variety of habitats, including the intertidal and subtidal zones; in tidepools; on reef flats; in protected or exposed locations; and on stones, rocks, dead coral, and other seaweeds. Tseng (1943) noted that *Laurencia* "generally prefer places where the current is rapid and the water comparatively clear" (p. 186). Frequently characterized as "turf-forming" (Hay 1981), *Laurencia* species can dominate the hard substrata in some marine communities. Fish and invertebrates may graze on *Laurencia* species, and these *Laurencia*-herbivore interactions are a controversial ecological topic (Norris and Fenical 1985). Renewed systematic treatment of the genus is long overdue, and it is hoped that its inclusion in this workshop marks a rebirth of the taxonomy of *Laurencia*, a seaweed with great scientific and commercial potential.

At its establishment, the genus *Laurencia* encompassed only eight species (Lamouroux 1813) distinguished by their purple-reddish color and globular reproductive tubercles (cystocarps) on the terminal portions of cylindrical branches. Species of *Laurencia* also share other distinctive characters: (1) blunt branch tips terminating in a small depression containing a single apical cell, (2) trichoblasts or hairs that arise in this pit, (3) corticated polysiphonous axes, (4) spermatangial conceptacles, and (5) tetrahedrally divided tetrasporangia in the cortex. In addition, a *Polysiphonia*-type, triphasic isomorphic life history is common to *Laurencia* species (Notoya et al. 1978, McDermid unpublished). Cytologically, about nine species of *Laurencia* have been studied, and they seem to have equable haploid chromosome counts, ranging from n = 26 to n = 32 (Austin 1959, Cordeiro-Marino et al. 1983, Yabu 1985).

J. G. Agardh (1863, 1876) accepted 38 species of *Laurencia* and divided them into four sections on the basis of branching pattern and the terete or compressed nature of the branches. De Toni (1903, 1924) later increased the number to 52 recognized species. In 1931, Yamada reported on 64 species of *Laurencia*. Dawson (1962) enumerated the new taxa described since De Toni's work, bringing the total to 121 species. Since 1962 many new species have been described by Hollenberg and Abbott (1965), Saito (1969b), Saito and Womersley (1974), Schnetter (1975), Zhang and Xia (1980), Rodríguez de Rios (1981), Ganzon-Fortes (1982), Cribb (1983), and Cordeiro-Marino and Fujii (1985). Now the number of *Laurencia* species approaches 140. Harvey (1860) wrote, "I fear the *species* of *Laurencia* have been too much multiplied," and yet many *Laurencia* remain undescribed. In addition, the reportedly cosmopolitan species (i.e., *L. obtusa* [Hudson] Lamouroux, *L. paniculata* [C. Agardh] J. Agardh, and *L. papillosa* [Forsskål] Greville) need critical reevaluation that is based on knowledge of the type material, *Laurencia* biochemistry, and algal biogeography.

The genus was rearranged systematically into four sections by Yamada (1931), who emphasized differences in cortical cell shape in cross section (Figs. 1 and 2) and the presence or absence of lenticular thickenings (Fig. 3) in the medulla. Other characteristics were considered important at the species level, such as projecting cortical cells of ultimate branchlets (Fig. 4), compound stichidial branches, percurrent main axis, branchlet shape, frond margins, branching, size, texture, and color. In 1967, Saito proposed two subgenera distinguished by tetrasporangial arrangement (Figs. 5 and 6) and the presence or absence of secondary pit connections (Fig. 7) between cortical cells. These subgenera were divided further into sections on the basis of lenticular thickenings, thallus shape, and cortical cell shape. Saito (1969a) formed the "Spectabilis Group" for six species of *Laurencia* from California that shared several unique characteristics: (1) tetrasporangial initials cut off *adaxially* from the mother (pericentral) cell; (2) deep, pocketlike lateral spermatangial conceptacles; (3) parallel tetrasporangia; and (4) no secondary pit connections in the cortex. Saito suggested that the "Spectabilis Group" might have subgeneric standing because other *Laurencia* species uniformly seem to have *abaxial* tetrasporangial initials and bowl-shaped, terminal spermatangial conceptacles. However, this problem has not been resolved. In 1974, Saito and Womersley redefined the section *Pinnatifidae* of the subgenus *Laurencia* and introduced a new section, *Planae*, of the same subgenus. Recently, another new section, *Articulatae*, in the subgenus *Chondrophycae*[1] was established by Zhang and Xia (1985). Thus, the species of *Laurencia* currently are classified as shown in Table 1.

Although the genus *Laurencia* has a long history, and worldwide distribution, the taxonomy of the genus remains poorly understood. Variability, both morphological and anatomical, is common in the species. In fact, in the first description of the genus, Lamouroux (1813) emphasized that "the *Laurencia* vary a lot; they differ equally in the diverse stages of their growth, thus rendering their synonomy very obscure" (p. 130). Harvey (1860) also noted that young plants may not resemble older ones. Yamada (1931) recognized that the "external habit of the frond as well as the stichidial branches are very variable according to the conditions under which they grow" (p. 185). Cribb (1958, 1983) pointed out considerable within-species variation of projection of cortical cells, presence of lenticular thickenings, branching, frond texture, tereteness, and even secondary pit connections. He dismissed most characters as being of limited taxonomic value, except the nature of attachment and the size and shape of cortical cells. Saito and Womersley

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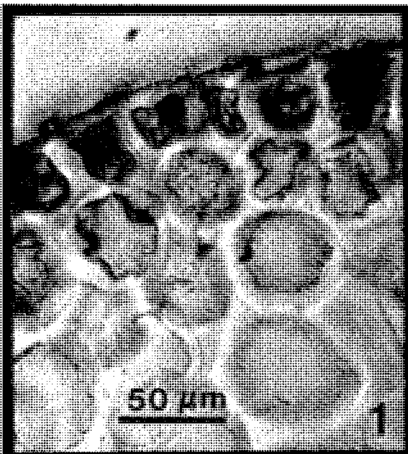
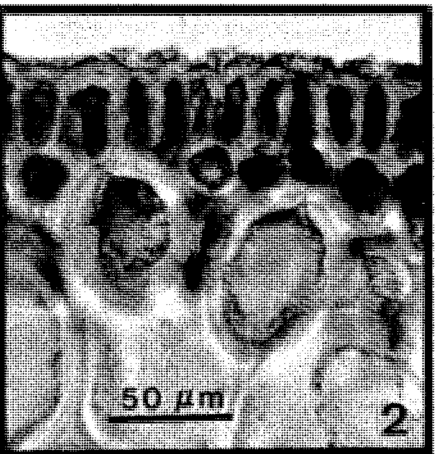
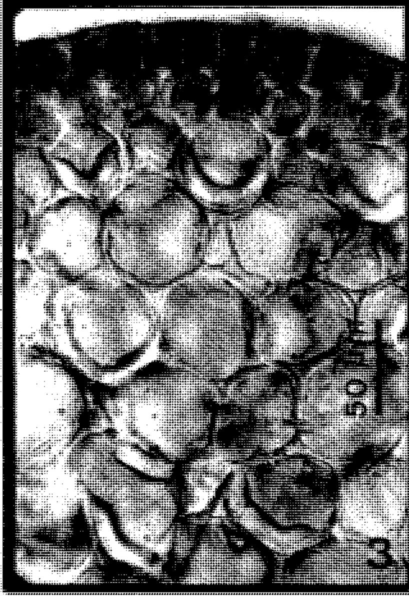
[1] In this paper, the subgenus *Chondrophycus* (Saito 1967) has been corrected to *Chondrophycae* so that the adjective ending is plural and agrees in gender with the genus name (*Laurencia*: feminine gender), in accordance with Article 21.2 ICBN (Voss et al. 1983). In Latin, the plural feminine ending is -ae.







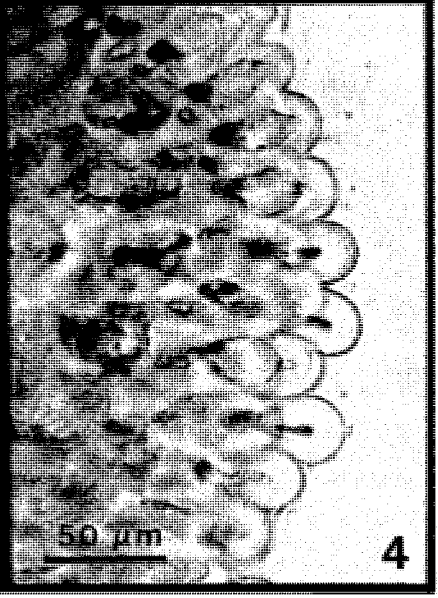
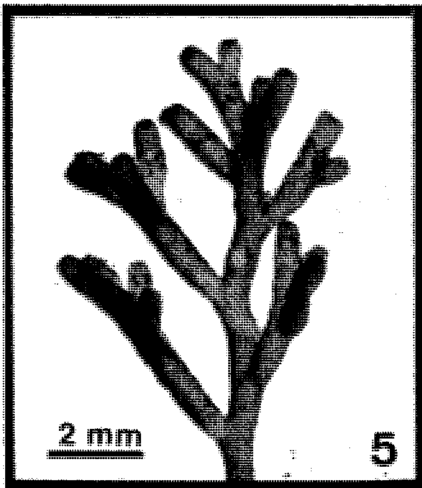


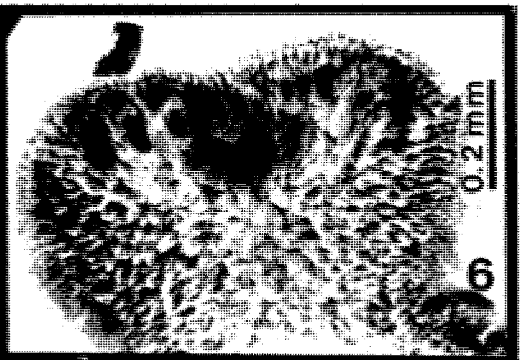
Fig. 1. Subquadrate cortical cells in the cross section of *Laurencia majuscula* (Harvey) Lucas (KM 2030).

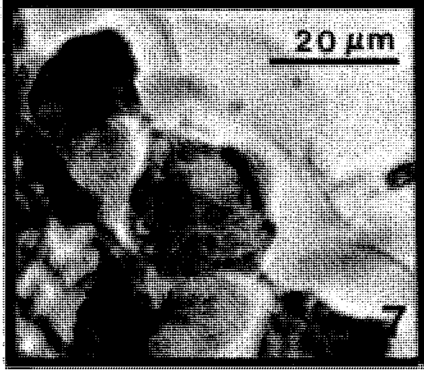
Fig. 2. Radially elongated cortical cells in the cross section of *Laurencia parvipapillata* Tseng (KM 1054).

Fig. 3. Lenticular thickenings in medullary cells in the cross section of *Laurencia nidifica* J. Agardh (KM 1057).

Fig. 4. Projecting cortical cells in a branchlet of *Laurencia dotyi* Saito (KM 1037).







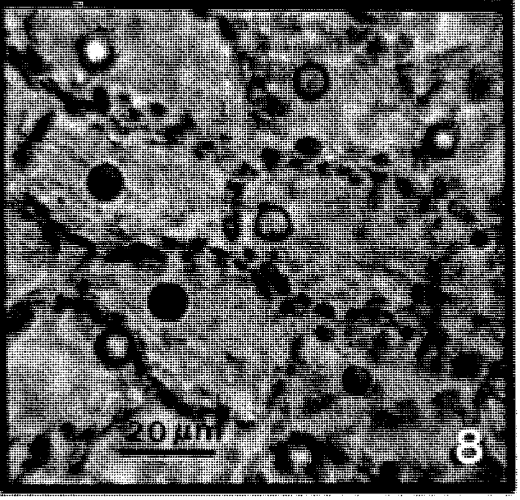


Fig. 5. Parallel-type tetrasporangial arrangement in *Laurencia mariannensis* Yamada (KM 909). Branchlets continue to elongate as tetrasporangia are produced; thus, mature tetrasporangia are aligned on lateral surfaces of branchlets, parallel to the central axis.

Fig. 6. Right angle-type tetrasporangial arrangement in *Laurencia parvipapillata* Tseng (KM 1054). Tetrasporangia mature at a more rapid rate than branch elongation, and mature tetrasporangia ring the apical pit in a plane perpendicular to the central axis.

Fig. 7. Secondary pit connections between the cortical cells of *Laurencia majuscula* (Harvey) Lucas (KM 592) in longitudinal section.

Fig. 8. "Corps en cerise" or cherry bodies in cortical cells in surface view of fresh *Laurencia brachyclados* Pilger (cultured gametophyte).

(1974) acknowledged the variability of lenticular thickenings and stated that "it is thus not practical to separate the section *Forsterianae* of this feature" (p. 817). In essence, the genus is left with very few reliable diagnostic features that apply to all species. However, the presence of intracellular, refringent, globular inclusions within cortical and trichoblast cells, known as "corps en cerise" or "cherry bodies" (Fig. 8) (Feldmann and Feldmann 1950), may be a taxonomically valuable character. "Corps en cerise" primarily are reported in members of the subgenus *Laurencia*, those species with terete thallus shape and parallel-type tetrasporangial arrangement (Bodard 1968, Notoya et al. 1978, Saito

Table 1. Basis of Current Classification of *Laurencia*.

Subgenus	TET INI	TET ARR	2° PC	LENT	THALLUS	RAD ELONG CORT
Subgenus *Laurencia*						
Section *Laurencia*	Abaxial	Parallel	+	–	Terete	–
Section *Fosterianae*	Abaxial	Parallel	+	+	Terete	–
Section *Pinnatifidae*	Adaxial	Parallel	+	+/–	Compressed	–
Section *Planae*	Abaxial	Parallel	+	+/–	Compressed	–
Subgenus *Chondrophycae*						
Section *Chondrophycae*	Abaxial	Right-angle	–	–	Terete/compressed	–
Section *Palisadae*	Abaxial	Right-angle	–	–	Terete/compressed	+
Section *Articulatae*	Abaxial?	Right-angle	–	+	Terete	–
Spectabilis Group	Adaxial	Parallel	–	–	Compressed	–

Note: TET INI = tetrasporangial initial; TET ARR = tetrasporangial arrangement; 2° PC = secondary pit connections in cortex; LENT = lenticular thickenings in medulla; THALLUS = shape of thallus; RAD ELONG CORT = radially elongated cortical-cell shape.

1980, Young et al. 1980, McDermid this volume). Unfortunately, one shortcoming of "corps en cerise" is that they are poorly preserved in dried specimens, probably because of the volatile nature of their contents (see following information). Therefore, the taxonomic usefulness of "corps en cerise" is limited to fresh material.

Despite the problems of classification and identification, the biochemical components of *Laurencia* make this genus the "most studied of all algal genera" (Erickson 1983, p. 132) by chemists. Since the first report on the chemistry of natural products of *L. glandulifera* Kützing (Obota and Fukushi 1953), more than 250 compounds have been isolated from *Laurencia* species. Sesquiterpenoids, diterpenoids, and acetylenic nonterpenoids form the three major classes of *Laurencia*-derived compounds, many of which contain bromine and chlorine (halogens). Crude extracts of some *Laurencia* and their purified organic compounds have been found to show antibacterial or antifungal activity (Aubert et al. 1979, Diaz-Piferrer 1979, Glombitza 1979, Hoppe 1982, Erickson 1983). The "corps en cerise" appear to be the site of synthesis and/or storage of the halogenated natural products characteristic of some *Laurencia* species (Howard and Fenical 1980, Young et al. 1980).

The unique chemistry of the genus often provides clues to its taxonomy. It is thought that at least one compound in the suite of chemical compounds made by each species of *Laurencia* is species-specific (Fenical and Norris 1975). In addition, culture and field studies of several *Laurencia* species have revealed that synthesis of halogenated terpenoids is not greatly affected by physical environmental factors (Howard et al. 1980).

When Fenical and Norris (1975) applied chemistry to *Laurencia* taxonomy, they separated three forms of *L. pacifica* Kylin from the Gulf of California into three species. Similarly, two morphologically identical, but chemically different, populations of *L. snyderae* Dawson from southern California may deserve taxonomic distinction (Howard et al. 1980). Three forms of *L. nidifica* J. Agardh in Hawaii that have significant within-species chemical variations (Erickson 1983) deserve reinvestigation. Samples of *L. obtusa* from Spain, Greece, Italy, England, Tenerife Island, the Black Sea, and China contain quite diverse chemicals (Erickson 1983) and may represent seven individual species, or at least demand reexamination at the morphological level required for taxonomy.

Laurencia species are also a source of phycocolloids (O'Colla 1962, Hoppe 1979). The water-soluble polysaccharides of *L. pinnatifida* (Gmelin) Lamouroux have been studied extensively by Bowker and Turvey (1968a, 1968b) and characterized as agar. *Laurencia flexilis* Setchell from Hainan Island, China, yielded agar (36.4% of dry weight of seaweed) with a gel strength of 458 g/cm^2 for the alkali-treated fraction (Xia and Zhang 1982, Wu and Zeng 1985). At least one Hawaiian species of *Laurencia* has been found to contain agar with an agarose fraction (Zablackis and McDermid this volume). In contrast, *L. papillosa* from Tanzania reportedly yielded a colloid similar to lambda-carrageenan (Mshigeni and Nzalalila 1977); however, the infrared spectra and negative optical rotation values presented suggest the presence of a sulfated agar (G. A. Santos, pers. commun. 12-XII-1986). Several *Laurencia* species from the Caribbean were also said to produce carrageenan-type gels (Diaz-Piferrer 1979). Clearly, the colloid chemistry of the genus needs investigation.

Laurencia is used in a variety of other ways. In Hawaii many "limu" or seaweeds are eaten, including *Laurencia* species. "Limu lipeepee" or *L. dotyi* Saito and "limu maneoneo" or *L. nidifica* give a peppery flavor to raw fish or liver dishes (Abbott 1984). *Laurencia obtusa* or "sangau" is eaten in parts of Indonesia (Zaneveld 1959, Hoppe 1969). *Laurencia papillosa*, called "tartariptip" or "layalaya," is consumed by some Filipinos (Zaneveld 1959). "Pepper dulse" is the name for *L. pinnatifida*, which is used as a spice in Scotland and Ireland (Lamouroux 1813, Chapman and Chapman 1980) and chewed like tobacco in Iceland (Hoppe 1969). In addition, *Laurencia* species are used by neurobiologists and invertebrate zoologists who work with sea hares (Aplysidae) that require a diet of *Laurencia* for normal growth and metamorphosis (Switzer-Dunlap and Hadfield 1977).

Laurencia remains a complex genus, taxonomically, chemically, and ecologically. Much information can be gathered from thorough study of the systematics of the genus *Laurencia*—information that is necessary and valuable for science and industry.

Acknowledgements

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LAURENCIA FROM THE HAWAIIAN ISLANDS: KEY, ANNOTATED LIST, AND DISTRIBUTION OF THE SPECIES

Karla J. McDermid

Introduction

The Hawaiian Islands are home to 15 or more species of *Laurencia* (Rhodomelaceae, Ceramiales). Species of *Laurencia* in Hawaii are found from the high intertidal to at least as deep as 20 m on both limestone and basalt substrata. *Laurencia* are often a major component of the intertidal "algal turf." As common and sometimes dominant members of marine communities in Hawaii, *Laurencia* species may have important roles in seaweed-seaweed and seaweed-animal interactions.

Since prehistoric time, *Laurencia* has been collected for human consumption in Hawaii (Reed 1907, Abbott 1984). The first known scientific collections of Hawaiian *Laurencia* were made in the 1800s, and some of these valuable specimens are in the B. P. Bishop Museum Herbarium (BISH) (Abbott 1980), Agardh Herbarium (LD), and the Grunow Collection (W) (abbreviations for herbaria follow Holmgren and Keuken 1974). A few species of *Laurencia* that occur in Hawaii were studied by Yamada (1931). However, the first to focus on the Hawaiian members of this genus was Saito (1969). He reported 17 species of *Laurencia* in the Hawaiian flora.

The genus, as a whole, needs more taxonomic and systematic attention, especially in Hawaii where phycologists, ecologists, and chemists are actively collecting, studying, culturing, and biochemically analyzing the many species of *Laurencia*.

Key to the Species of Hawaiian *Laurencia*

1. Thallus terete 2
1. Thallus compressed, at least in older parts 12
    2. Cortical cells radially elongated in transverse section 3
    2. Cortical cells not radially elongated 4
3. Branches often arcuate . . . . *L. yamadana*
3. Branches paniculate . . . . *L. paniculata*
    4. Thallus composed of sparsely branched axes arising from a basal crust . . . . *L.* sp. "crustiformans"
    4. Thallus composed of much-branched axes arising from small discoid or stoloniferous holdfasts 5
5. Lenticular thickenings present in medullary cells 6
5. Lenticular thickenings absent in medullary cells 9
    6. Thallus less than 1 cm tall, creeping, with large half eggshell-shaped lenticular thickenings . . . . *L. decumbens*
    6. Thallus more than 1 cm tall 7
7. Cortical cells protruding 8
7. Cortical cells not protruding . . . . *L. nidifica*
    8. Branching dichotomo-corymbose, thallus 1–2 cm tall . . . . *L. galtsoffii*
    8. Branching paniculate, thallus to 5 cm tall . . . . *L. mariannensis*
9. Cortical cells protruding . . . . *L. majuscula*
9. Cortical cells not protruding 10
    10. Thallus cartilaginous, ultimate branchlets wartlike, tetrasporangia right angle-type, secondary pit connections absent . . . . *L. cartilaginea*
    10. Thallus soft, tetrasporangia parallel-type, secondary pit connections present 11

11. Thallus bright green except tetrasporangia, axis 0.7–1.0 mm in diameter .... *L.* sp. "green"
11. Thallus red, axis 0.1 mm in diameter .... *L. brachyclados*

12. Cortical cells protruding, at least near apex 13
12. Cortical cells not protruding 14

13. Cortical cells radially elongated in transverse section, cortical cells externally conical throughout thallus .... *L. parvipapillata*
13. Cortical cells subquadrate in transverse section, cortical cells externally hemispherical .... *L. dotyi*

14. Thallus up to 2 mm broad, margins smooth .... *L. succisa*
14. Thallus up to 5 mm broad, margins undulate .... *L. undulata*

List and Distribution of Hawaiian Species of *Laurencia*

This information is the result of a compilation of literature citations, the examination of dried herbarium material, and the collection of fresh specimens. Hawaiian localities are listed from northernmost to southernmost islands. Abbreviations for herbaria follow Holmgren and Keuken (1974). Other abbreviations include KM for K. McDermid, RT for R. Tsuda, and MSD for M. S. Doty. A comparison of some vegetative and reproductive characteristics of Hawaiian *Laurencia* is shown in Table 1.

Laurencia brachyclados Pilger (Figs. 1, 2)
Pilger 1922, p. 6, figs. 9–10.
Yamada 1931, p. 216.
Type Locality: Annobon Island, Guinea, West Africa.
Type Specimen: (not examined).
Hawaiian Distribution: Oahu: Waikiki (KM 966, tetrasporophyte, April 18, 1986); Molokai: Kalaupapa (KM 1073, tetrasporophyte, August 7, 1986).
Other Distribution: Vietnam (Dawson 1954, p. 458, fig. 61; Pham-hoang 1969, p. 282, fig. 2.213).
Remarks: This species represents a new record for Hawaii. Hawaiian plants collected in the field and cultured in the laboratory agree very well with Pilger's description and figures, as well as those of subsequent authors.

Laurencia cartilaginea Yamada (Fig. 3)
Yamada 1931, p. 230, pl. 19, fig. a, text fig. O.
Type Locality: Mogi, Fukuoka Prefecture, Japan.
Type Specimen: SAP T1 (examined) (Fig. 4).
Hawaiian Distribution: Oahu (Saito 1969, p. 154, fig. 8b).
Other Distribution: Japan (Saito 1967, p. 53, pls. 17–18, text figs. 43–47); Vietnam (Pham-hoang 1969, p. 280, fig. 2.210); Singapore (Saito 1969, p. 154); Caroline Islands (Trono 1969, p. 89); Philippines (Cordero 1977, p. 206, fig. 221); and Xisha Islands, China (Zhang and Xia 1985, p. 60, text fig. 7, pl. 1, fig. 5).
Representative Hawaiian Specimens: KM 655, Oahu, June 5, 1984; KM 764, Oahu, October 14, 1984; KM 863, Oahu, tetrasporophyte, September 14, 1985.
Remarks: Hawaiian specimens seem smaller and less cartilaginous than the type specimen from Japan and the Chinese specimens I have examined.

Laurencia decumbens Kützing (Figs 5, 6)
Kützing 1865, p. 18, pl. 51, figs. a, b.
Yamada 1931, p. 195.
Type Locality: New Caledonia.
Type Specimen: Kützing Herbarium (L) (not examined).
Hawaiian Distribution: Kauai and Oahu (Saito 1969, p. 151, fig. 4d).
Other Distribution: Mauritius (Børgesen 1945, p. 50, figs. 25–27); Xisha Islands, China (Zhang and Xia 1985, p. 55, text fig. 3, pl. 1, fig. 8).
Representative Hawaiian Specimens: KM 671, Oahu, tetrasporophtyte, June 11, 1984; KM 719, Oahu, tetrasporophyte, August 8, 1984; KM 851, Oahu, June 29, 1985; KM 945, Oahu, tetrasporophyte, March 15, 1986.
Remarks: This species is often overlooked because of its small size and habit of growing intertwined with other species in dense mats.

Laurencia dotyi Saito (Figs. 7, 8)

Saito 1969, p. 154, figs. 9a–9c, 10a, 10b.

Type Locality: Kaneohe Bay, Oahu, Hawaiian Islands.

Type Specimen: BISH 430052 (examined). (Fig. 9).

Hawaiian Distribution: Kauai, Oahu, Molokai, and Maui (Saito 1969, p. 154); Hawaiian Islands (Abbott and Williamson 1974, p. 18; Abbott 1984, p. 30); additionally, Laysan (RT 573 at BISH) and Niihau (UC 622843).

Representative Hawaiian Specimens: KM 683, Oahu, tetrasporophyte, June 29, 1984; KM 978, Oahu, April 26, 1986; KM 1037, Oahu, female and tetrasporophyte, April 22, 1986; KM 1091, Molokai, tetrasporophyte, August 7, 1986.

Remarks: This species is very common in Hawaii. Degree of protrusion of cortical cells, thallus tereteness, and iridescent color show some variability.

Laurencia galtsoffii Howe (Figs. 10, 11)

Howe 1934, p. 39, fig. 5.

Type Locality: Pearl and Hermes Reef, northwest Hawaiian Islands.

Type Specimen: NY s.n. (examined) (Fig. 12).

Hawaiian Distribution: Pearl and Hermes Reef (Tsuda 1966, p. 9); Laysan and Kauai (Saito 1969, p. 151, fig. 4b).

Other Distribution: Xisha Islands, China (Zhang and Xia 1985, p. 56, text fig. 4, pl. 1, fig. 6).

Representative Hawaiian Specimens: KM 2003, Kauai, tetrasporophyte, August 22, 1986.

Remarks: The Hawaiian distribution of this species seems limited to the northern Hawaiian Islands.

Laurencia majuscula (Harvey) Lucas (Figs. 13, 14)

Lucas 1935, p. 223.

Yamada 1931, p. 223, pl. 16, fig. c.

Basionym: *L. obtusa* (Hudson) Lamouroux var. *majuscula* Harvey (Harvey 1863, p. xxvi).

Type Locality: Western Australia.

Type Specimen: Harvey's Australian Algae No. 236? (not examined).

Hawaiian Distribution: Laysan (as *L. obtusa*, Tsuda 1965, p. 19); Pearl and Hermes Reef, French Frigate Shoals, Necker, and Kure Atoll (as *L. obtusa*, Tsuda 1966, p. 9); Midway, Laysan, Kauai, Oahu, and Maui (Saito 1969, p. 149); Maro Reef (Balazs 1979, p. 110); additionally, Molokai (KM 1096) and Hawaii (MSD 10040 at BISH).

Other Distribution: Southern Japan, India, and perhaps the warm Atlantic (as *L. obtusa* var. *majuscula*, Yamada 1931, p. 223, pl. 16, fig. c); India (as *L. obtusa* var. *majuscula*, Børgesen 1933, p. 135; 1939, p. 120); Hong Kong (as *L. obtusa* var. *majuscula*, Tseng 1943, p. 200); Caroline Islands (Trono 1969, p. 90; Tsuda 1972, p. 10; Tsuda and Belk 1972, p. 4); Philippines (Cordero 1977, p. 210, fig. 227); Australia (Lucas and Perrin 1947, p. 249; Saito and Womersley 1974, p. 819, figs. 1a, 6; Cribb 1983, p. 120, pl. 37, fig. 3); Xisha Islands, China (Zhang and Xia 1985, p. 55, text fig. 2, pl. 1, fig. 4).

Representative Hawaiian Specimens: KM 619, Oahu, May 13, 1984; KM 717, Oahu, tetrasporophyte, August 18, 1984; KM 859, Oahu, tetrasporophyte, September 14, 1985; KM 1096, Molokai, tetrasporophyte, August 7, 1986; KM 2001, Kauai, tetrasporophyte, August 22, 1986.

Remarks: This species is quite variable in size in Hawaii, yet it agrees with specimens I have seen from Australia.

Laurencia mariannensis Yamada (Figs. 15, 16)

Yamada 1931, p. 200, pl. 5, fig. b, text figs. F, G.

Type Locality: Saipan, Marianas Islands.

Type Specimen: SAP 13874 (examined) (Fig. 17).

Hawaiian Distribution: Pearl and Hermes Reef (as *L. obtusa*, Tusda 1965, p. 19); Laysan and Lanai (Saito 1969, p. 151); additionally, Oahu (UC 623242) and Molokai (UC 622830).

Other Distribution: Caroline Islands (Taylor 1950, p. 144, pl. 55, fig. 1; Dawson 1956, p. 60, fig. 66; Abbott 1961, p. 5; Trono 1969, p. 90); Marshall Islands (Dawson 1957, p. 124); Gilbert Islands and Philippines (Saito 1969, p. 151); eastern Australia (Cribb 1983, p. 121, pl. 37, fig. 1); Xisha Islands, China (Zhang and Xia 1985, p. 57, text fig. 5).

Representative Hawaiian Specimens: KM 826, Oahu, tetrasporophyte, April 20, 1985; KM 909, Oahu, female, male, and tetrasporophyte, November 24, 1985.

Remarks: This species is found in shallow subtidal areas, primarily on dead coral heads.

Table 1. Comparison of Hawaiian *Laurencia* Species

Taxon	Habit	Main Axes	Cortical Cells	Lenticular Thickenings	Tetrasporangial Arrangement
L. brachyclados	uprights with creeping axes; alternate-corymbose branching; rose-red; 0.8-3 cm tall	terete; 0.1 mm diam.	2° pit connections present; non-projecting; sub-quadrate*; 16.1 µm diam.**; corps en cerise present	absent	parallel
L. cartilaginea	erect thallus from discoid holdfast; alternate-opposite, dense branching; red-brown; 3-7.5 cm tall	terete; 1 mm diam.	2° pit connections absent; non-projecting; sub-quadrate; ? µm diam. ? corps en cerise	absent	right-angle
L. decumbens	creeping thallus; mainly secund branching; tan-fawn; 0.3-1.5 cm tall	terete; 0.05-0.1 mm diam.	2° pit connections present; non-projecting; sub-quadrate; 19.7 µm diam. ? corps en cerise	present	parallel
L. dotyi	erect axes from discoid holdfast; alternate-opposite branching; tan-red brown with iridescence; 1.5-4.5 cm tall	compressed terete; 1-1.25 mm diam.	2° pit connections absent; projecting at apex; sub-quadrate; 19.7 µm diam.; no corps en cerise	absent	right-angle
L. galtsoffii	little tufts; dichotomo-corymbose branching; rose-red; 2 cm tall	terete; 0.5-1 mm diam.	2° pit connections present; projecting all over thallus; sub-quadrate; 20.8 µm diam.; corps en cerise present	present	parallel
L. majuscula	erect thallus from entangled holdfast; dense, alternate branching; blood-red; 3-11 cm tall	terete; 0.9-1.6 mm diam.	2° pit connections present; projecting; sub-quadrate; 19.2 µm diam.; corps en cerise present	absent	parallel
L. mariannensis	creeping; alternate-paniculate branching; rose-red; 1-4 cm tall	terete; 0.2 mm diam.	2° pit connections present; projecting; sub-quadrate; 9.7 µm diam.; corps en cerise present	present	parallel

L. nidifica	erect thallus from stoloniferous holdfast; alternate-opposite branching; straw-pinkish; 3-8 cm tall	terete; 0.5-1 mm diam.	2° pit connections present; non-projecting; sub-quadrate; 13.9 µm diam.; corps en cerise present	present	parallel
L. paniculata	erect thallus from discoid holdfast; paniculate branching; red-brown; 3-6 cm tall	terete; 0.8 mm diam.	2° pit connections absent; non-projecting; radially elongated; ? µm diam.; ? corps en cerise	absent	right-angle
L. parvipapillata	semi-prostrate; sub-opposite branching; dark red; 5 cm long	strongly compressed; 2 mm diam.	2° pit connections absent to rare; projecting all over thallus; radially elongated; 7-8 µm diam.; no corps en cerise	absent	right-angle
L. succisa	erect axes from discoid holdfast; alternate branching; dark red; 2.5-4 cm tall	compressed; 1.5 mm diam.	2° pit connections absent; non-projecting; sub-quadrate; 14.1 µm diam.; no corps en cerise	absent	right-angle
L. undulata	erect thallus from discoid holdfast; alternate branching; red-brown; 5-6.5 cm tall	semi-compressed; 1-1.5 mm diam.; thallus sometimes broadened to 2.5 mm	2° pit connections absent; non-projecting; sub-quadrate; ? µm diam.; ? corps en cerise	absent	right-angle
L. yamadana	clumps from discoid holdfast; arcuate branches with tips re-attaching; alternate branching; dark red brown; 1.5-4 cm tall	terete; 0.5-0.9 mm diam.	2° pit connections absent; non-projecting; radially elongated; 12.6 µm diam.; no corps en cerise	absent	right-angle
L. sp. "crustiformans"	upright axes from a crust; sparsely branched; dark red-brown; 1-3 cm tall	terete; 0.5 mm diam.	2° pit connections present; non-projecting; sub-quadrate; 12.6 µm diam.; corps en cerise small & scarce	absent	right-angle
L. sp. "green"	entangled cushion or erect thallus with stoloniferous holdfast; alternate branching; bright green; 2-5.5 cm tall	terete; 0.7-1 mm diam.	2° pit connections present; non-projecting; sub-quadrate; 22.5 µm diam.; corps en cerise present	absent	parallel

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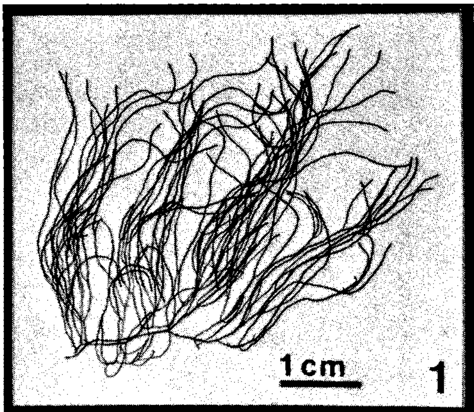
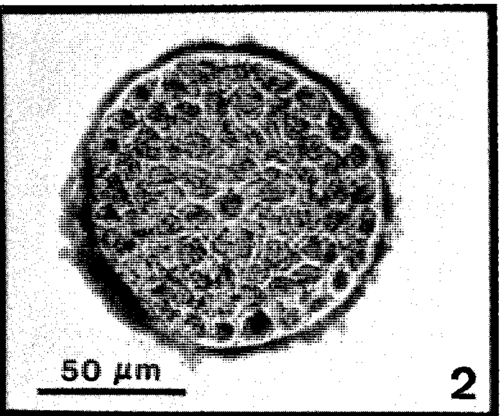
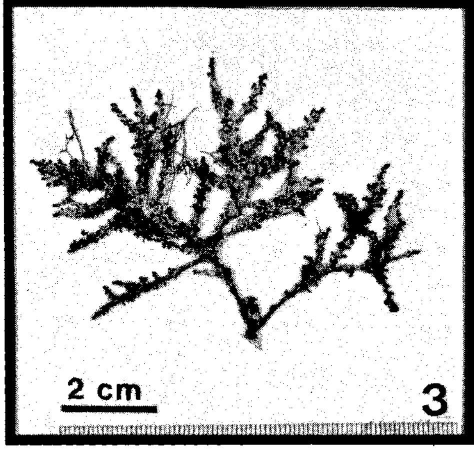
* cortical cell shape in cross-section

** cortical cell size in cross-section







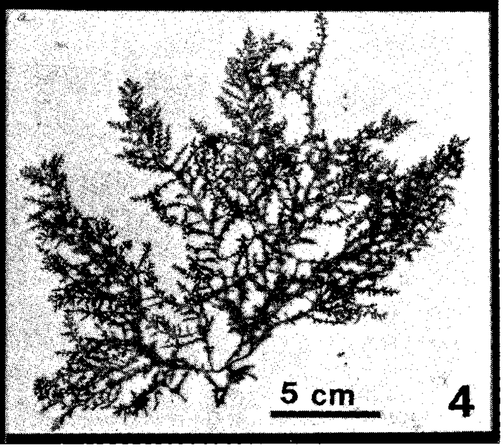


Fig. 1. *Laurencia brachyclados*, fresh cultured tetrasporophyte.

Fig. 2. *Laurencia brachyclados*, cross section of cultured gametophyte.

Fig. 3. *Laurencia cartilaginea*, dried, MSD 14759, Oahu.

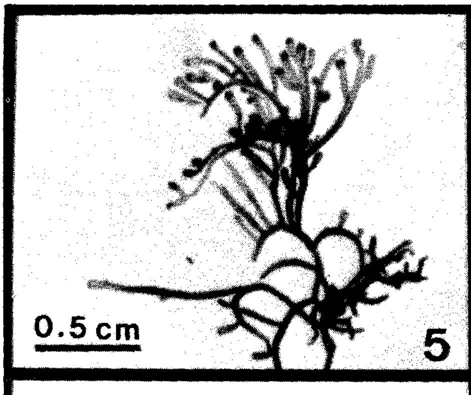
Fig. 4. *Laurencia cartilaginea*, dried, Holotype, SAP T1, Japan.

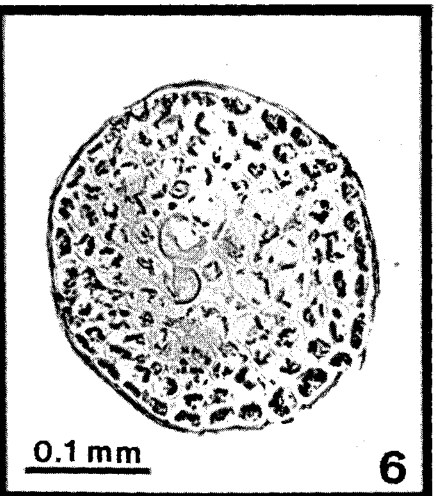
Laurencia nidifica J. Agardh (Figs. 18, 19)
J. G. Agardh 1863, p. 749; 1876, p. 649.
Yamada 1931, p. 202.
Type Locality: Oahu, Hawaiian Islands.
Type Specimen: LD 36628 (examined) (Fig. 20).

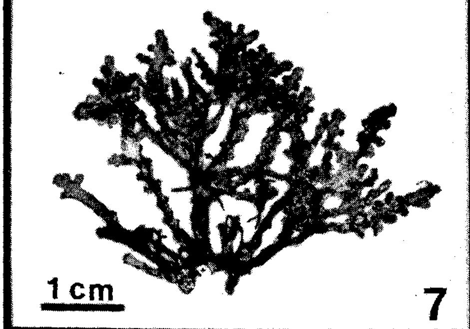
Hawaiian Distribution: Laysan (as *L. obtusa*, Tsuda 1965, p. 19); Oahu (Chamberlain 1880, p. 33; as *L. paniculata*, Chamberlain 1880, p. 33; Neal 1930, p. 70, fig. 19a; Abbott 1980, p. 105); Hawaiian Islands (De Toni 1903, p. 785; Lemmerman 1905, p. 661; MacCaughey 1918, p. 147; Yamada 1931, p. 202; Abbott and Williamson 1974, p. 19, fig. 14; Magruder and Hunt 1979, p. 81; Abbott 1984, p. 32, fig. 16); Kauai, Oahu, Molokai, and Lanai (Saito 1969, p. 152, fig. 5); additionally, Maui (MSD 28139 at BISH).

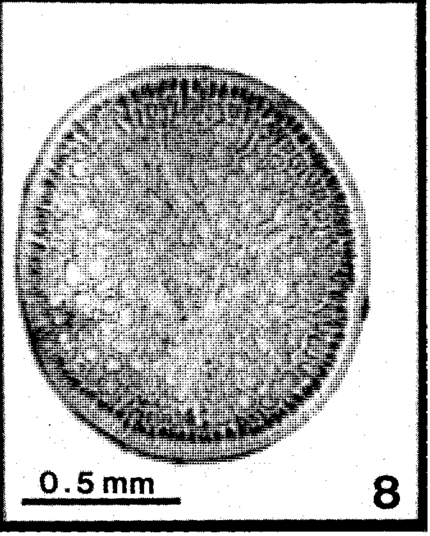
Other Distribution: Aldabra, Indian Ocean (Weber-van Bosse 1913, p. 121); Celebes (Weber-van Bosse 1923, p. 341); Mauritius (Børgesen 1945, p. 47, figs. 21–24); eastern Australia (Cribb 1958, p. 168, pl. 5, fig. 12, pl. 6, figs. 1–3); Vietnam (Pham-hoang 1969, p. 284, fig. 2.215); Japan (Saito 1978, p. 12, fig. 1).

Representative Hawaiian Specimens: KM 714, Oahu, tetrasporophyte, August 10, 1984; KM 832, Oahu, tetrasporophyte, May 21, 1985; KM 853, Oahu, female, July 23, 1985; KM 902, Oahu,









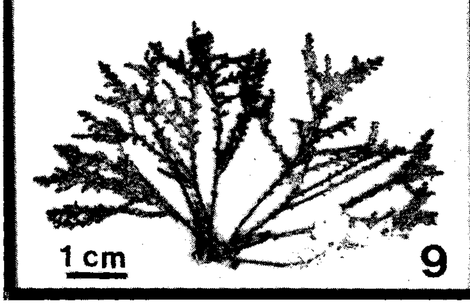


Fig. 5. *Laurencia decumbens*, dried, KM 802, Oahu.

Fig. 6. *Laurencia decumbens*, cross section, KM 851, Oahu.

Fig. 7. *Laurencia dotyi*, dried, KM 751, Oahu.

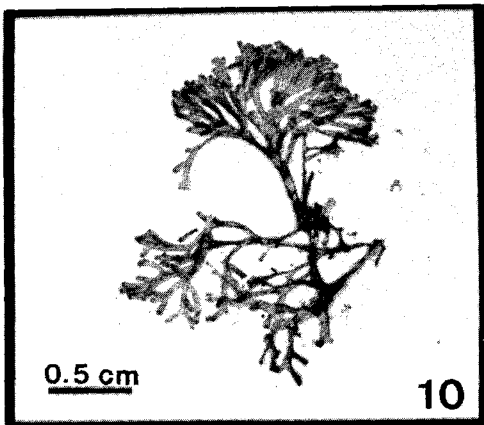
Fig. 8. *Laurencia dotyi*, cross section, KM 1037, Oahu.

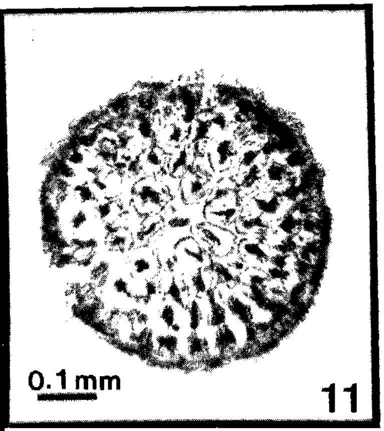
Fig. 9. *Laurencia dotyi*, dried, Holotype, BISH 430052, Oahu.

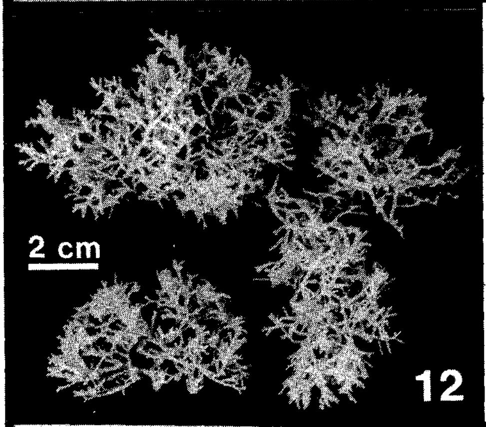
male, October 31, 1985; KM 911, Oahu, female, November 24, 1985; KM 1095, Molokai, tetrasporophyte, August 7, 1986; KM 2002, Kauai, tetrasporophyte, August 22, 1986.

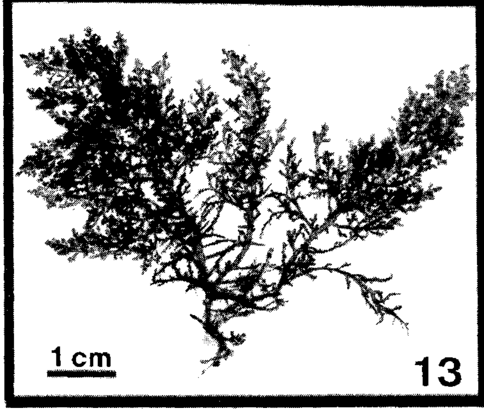
Remarks: This species is common in Hawaii. It is variable in color, but usually pale green to straw-colored with pink tips. It has a distinctive odor.

Laurencia paniculata (C. Agardh) J. Agardh (Fig. 21)
J. G. Agardh 1863, p. 755; 1876, p. 651.
Yamada 1931, p. 192, pl. 3, fig. a.
Basionym: *Chondria obtusa* var. *paniculata* C. Agardh (C. A. Agardh 1822, p. 343).









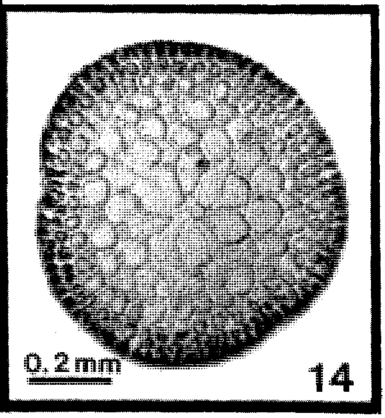


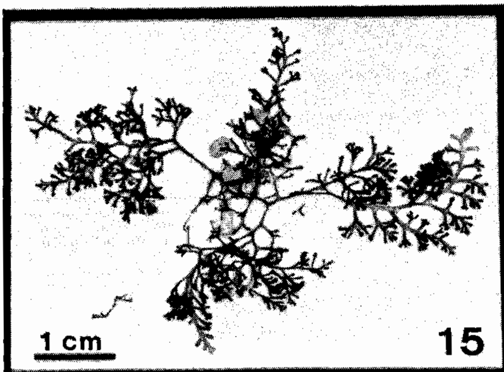
Fig. 10. ***Laurencia galtsoffii*, dried, MSD 10250, Kauai.**

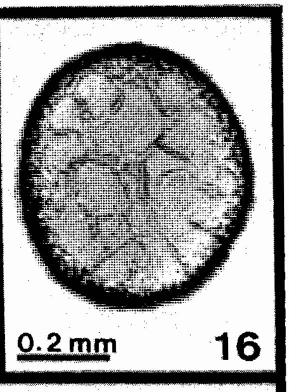
Fig. 11. ***Laurencia galtsoffii*, cross section, KM 2003, Kauai.**

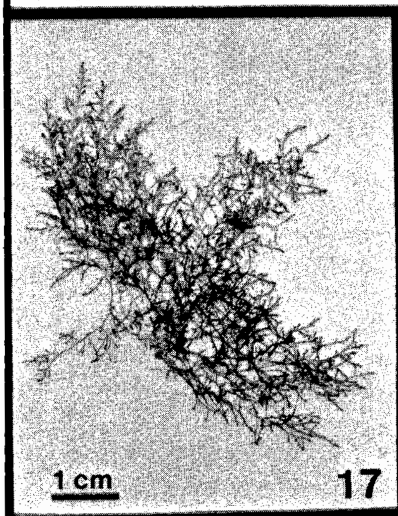
Fig. 12. ***Laurencia galtsoffii*, liquid-preserved before pressing, Holotype, NY s.n., Pearl and Hermes Reef.**

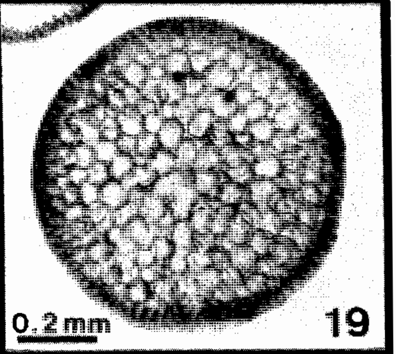
Fig. 13. ***Laurencia majuscula*, dried, KM 698, Oahu.**

Fig. 14. ***Laurencia majuscula*, cross section, KM 2030, Oahu.**









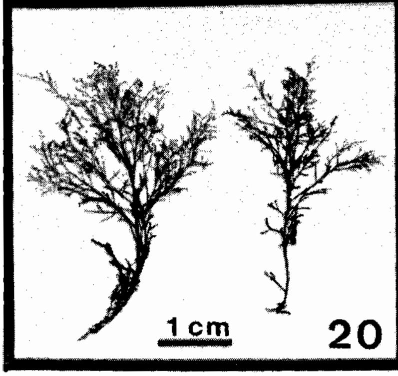


Fig. 15. ***Laurencia mariannensis*****, dried, KM 909, Oahu.**

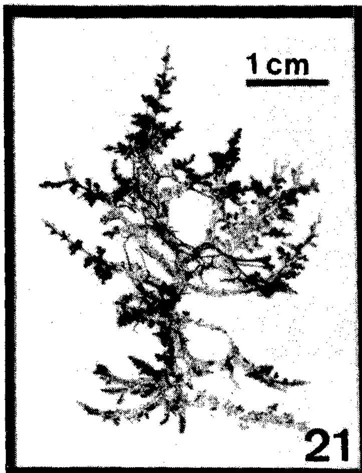
Fig. 16. ***Laurencia mariannensis*****, cross section, KM 909, Oahu.**

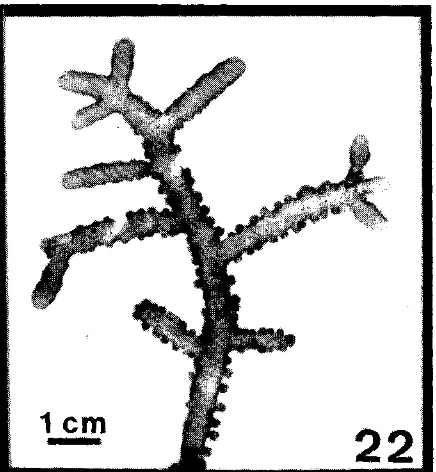
Fig. 17. ***Laurencia mariannensis*****, dried, Holotype, SAP 13874, Saipan.**

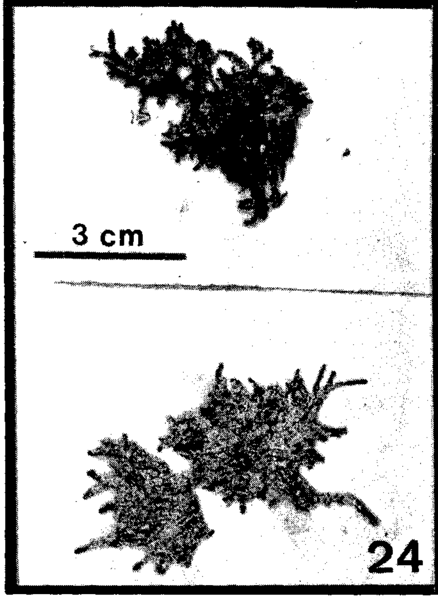
Fig. 18. ***Laurencia nidifica*****, dried, KM 3-IX, Oahu.**

Fig. 19. ***Laurencia nidifica*****, cross section, KM 1057, Oahu.**

Fig. 20. ***Laurencia nidifica*****, dried, Holotype, LD 36628, Oahu.**







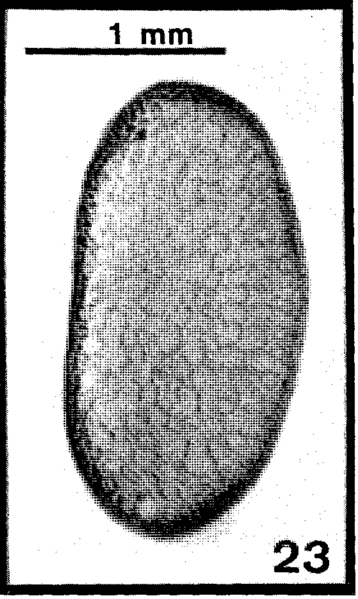


Fig. 21. ***Laurencia paniculata*, dried, MSD 14773, Oahu.**

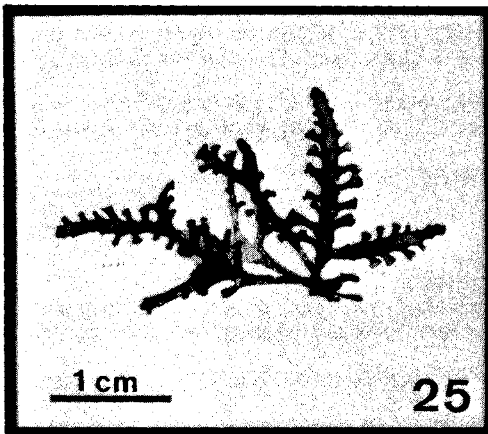
Fig. 22. ***Laurencia parvipapillata*, fresh, KM 932, Oahu.**

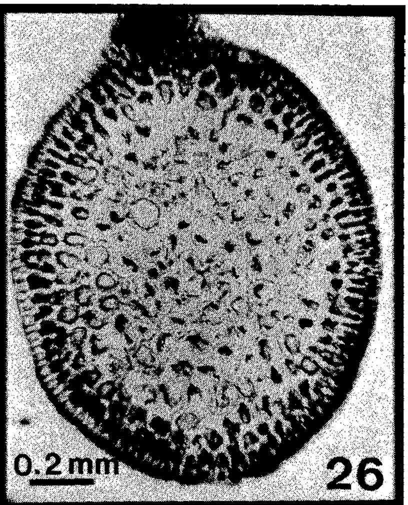
Fig. 23. ***Laurencia parvipapillata*, cross section, KM 1054, Oahu.**

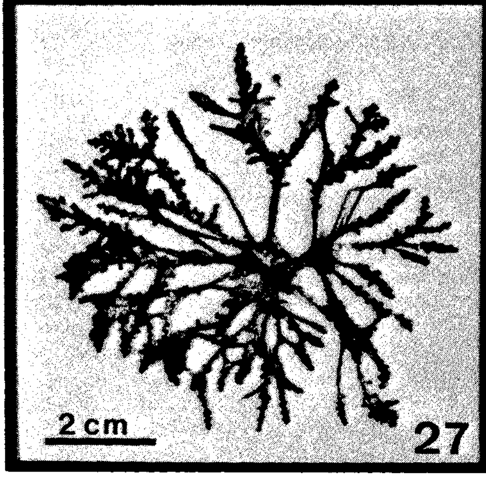
Fig. 24. ***Laurencia parvipapillata*, dried, Holotype, ATS 30, Hong Kong.**

Type Locality: Trieste, Adriatic Sea.
Type Specimen: LD 36711, specimen on right (not examined).
Synonym: *L. thuyoides* Kützing (Kützing 1865, p. 26, pl. 74, figs. a, b).
Hawaiian Distribution: Oahu and Lanai (Saito 1969, p. 158).

Other Distribution: Europe (Hauck 1885, p. 206; Falkenberg 1901, p. 247; De Toni 1903, p. 788; Funk 1927, p. 448, fig. 47; New Caldeonia (as *L. thuyoides*, Kützing 1865, p. 26); Bali, Borneo, Celebes, and New Guinea (Weber-van Bosse 1923, p. 342); Florida (Taylor 1928, p. 180); Iranian Gulf (Børgesen 1939, p. 119, fig. 33); Hong Kong (Tseng 1943, p. 191); Vietnam (Dawson 1954, p.







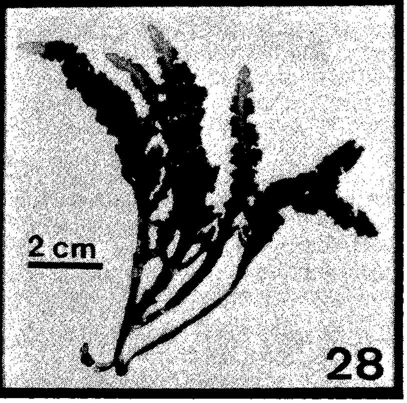


Fig. 25. *Laurencia succisa*, dried, MSD 14809, Oahu.

Fig. 26. *Laurencia succisa*, cross section, KM 903, Oahu.

Fig. 27. *Laurencia undulata*, dried, MSD 14823, Oahu.

Fig. 28. *Laurencia undulata*, dried, Holotype, SAP 13869, Japan.

458, figs. 6a, 6c, 6d; Pham-hoang 1969, p. 276); southern Australia (Saito and Womersley 1974, p. 845, figs. 5d, 25); Gilbert Islands (Tsuda 1964, p. 10); Philippines (Trono and Put 1982, p. 24).

Representative Hawaiian Specimens: I have not collected this species myself.

Remarks: The Hawaiian plants are identified with this Adriatic species with much reservation. They agree somewhat with J. G. Agardh's description but are not as thick and coarse as the type that was examined and photographed by Yamada. The range of variation in this species in Hawaii and worldwide needs to be explored.

Laurencia parvipapillata Tseng (Figs. 22, 23)

Tseng 1943, p. 204, pl. 4.

Type Locality: Hong Kong.

Type Specimen: ATS 30 (Fig. 24).

Hawaiian Distribution: Midway (Buggeln 1965, p. 9); Midway, Oahu, Maui, and Hawaii (Saito 1969, p. 159, fig. 11c); Hawaiian Islands (Abbott and Williamson 1974, p. 18); Hawaii (Abbott 1980, p. 105); additionally, Molokai (KM 1090).

Other Distribution: Vietnam (Dawson 1954, p. 458, fig. 61g; Pham-hoang 1969, p. 277, fig. 2.206); Caroline Islands (Dawson 1957, p. 124; Tsuda 1972, p. 10); Philippines (Saito 1969, p. 159); eastern Australia (Cribb 1983, p. 123, pl. 35, figs. 1–3, pl. 41, figs. 1, 2); Xisha Islands, China (Zhang and Xia 1985, p. 64, text fig. 10, pl. 1, fig. 3).

Representative Hawaiian Specimens: KM 624, Molokai, May 16, 1984; KM 847, Oahu, June 29, 1985; KM 1054, Oahu, tetrasporophyte, September 1, 1986; KM 1061, Molokai, male, August 7, 1986.

Remarks: Hawaiian specimens clearly correspond to the type material from China.

Laurencia succisa Cribb (Figs. 25, 26)

Cribb 1958, p. 163, pl. 1, figs. 1–3.

Type Locality: Queensland, eastern Australia.

Type Specimen: Ball Bay 22.v.1956 (not examined).

Hawaiian Distribution: Kauai, Oahu, Lanai, and Maui (Saito 1969, p. 157); Hawaiian Islands (Abbott and Williamson 1974, p. 18; Magruder and Hunt 1979, p. 81; Abbott 1984, p. 30, fig. 15); additionally, Hawaii (MSD 10054 at BISH).

Other Distribution: North Marianas Islands (Tsuda and Tobias 1977, p. 157); eastern Australia (Cribb 1983, p. 126, pl. 35, fig. 4).

Representative Hawaiian Specimens: KM 691, Oahu, tetrasporophyte, July 10, 1984; KM 934, Oahu, February 17, 1986.

Remarks: In the field, this species is often difficult to distinguish from *L. dotyi.*

Laurencia undulata Yamada (Fig. 27)

Yamada 1931, p. 243, pl. 29, fig. a, text fig. T.

Type Locality: Enoshima, Kanagawa Prefecture, Japan.

Type Specimen: SAP 13869 (examined) (Fig. 28).

Hawaiian Distribution: Oahu (Saito 1969, p. 157, fig. 8a).

Other Distribution: Hong Kong (Tseng 1943, p. 206); Japan (Saito 1967, p. 59, pl. 3, figs. 4–6, pl. 4, figs. 5–7, text figs. 48, 49).

Representative Hawaiian Specimens: I have not collected this species myself.

Remarks: Saito reported this species from Hawaii but expressed concern about its similarity to Hawaiian *L. cartilaginea.* The Japanese type material possesses distinct, broad, "inflated" branches that are rare in Hawaiian specimens. Hawaiian specimens of *L. undulata* and *L. succisa* appear to me to be quite similar. I have never observed any fresh specimens of Hawaiian *L. undulata*; therefore, I include *L. undulata* in this list with reservation.

Laurencia yamadana Howe (Figs. 29, 30)

Howe 1934, p. 37, fig. 4.

Type Locality: Kaneohe Bay, Oahu, Hawaiian Islands.

Type Specimen: NY s. n. (examined) (Fig. 31)

Synonyms: *Laurencia amabilis* Yamada (Yamada and Segawa 1953, p. 13, figs. 6, 7).

Hawaiian Distribution: Oahu, Molokai, and Maui (Saito 1969, p. 157, fig. 11a); Laysan, Oahu, and Maui (as *L. surculigera*, Saito 1969, p. 157, fig. 11b).

Other Distribution: Hachijo Island, Japan (as *L. amabilis*, Yamada and Segawa 1953, p. 13, figs. 6, 7); Caroline Islands (Trono 1969, p. 89).

Representative Hawaiian Specimens: KM 650, Oahu, May 19, 1984; KM 887, Kauai, tetrasporophyte, October 18, 1985; KM 923, Oahu, female and tetrasporophyte, January 18, 1986; KM 987, Oahu, tetrasporophyte, May 8, 1986.

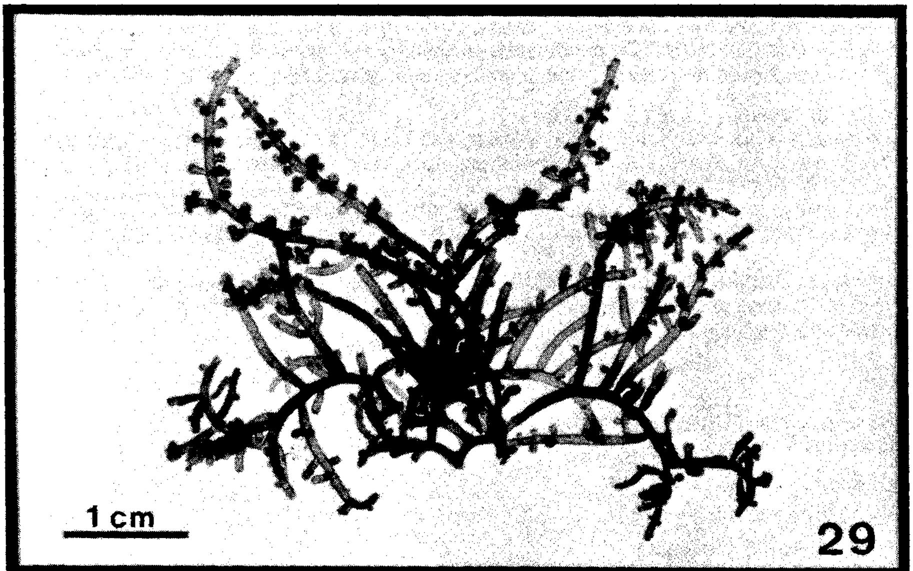
Remarks: Previously, *L. surculigera* was reported from Hawaii by Saito; however, Hawaiian specimens do not resemble the holotype of *L. surculigera* (ATS 32) in China. They do agree with the holotype and other specimens of *L. yamadana.*

Laurencia sp. "crustiformans" (Figs. 32, 33)

Hawaiian Distribution: Kauai, Oahu, Molokai, and Maui (as *Laurencia obtusa* variety *rigidula*, Saito 1969, p. 150); Hawaiian Islands (as *Laurencia obtusa*, Magruder and Hunt 1979, p. 81); additionally, Hawaii (KM 2021).

Other Distribution: perhaps Mauritius (as *L. obtusa* var. *rigidula*, Børgesen 1945, p. 58, figs. 34, 35); Fiji ? (as *L. obtusa* var. *rigidula*, Saito 1969, 150).

Representative Hawaiian Specimens: KM 670, Oahu, tetrasporophyte, June 11, 1984; KM 886, Kauai, October 18, 1985; KM 895, Oahu, October 31, 1985; KM 1092, Molokai, August 7, 1986; KM 2021, Hawaii, female, November 29, 1986.



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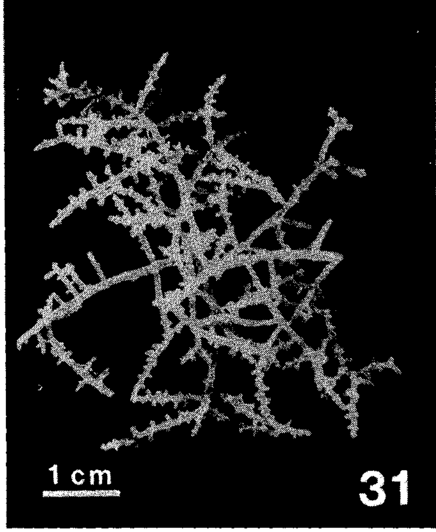

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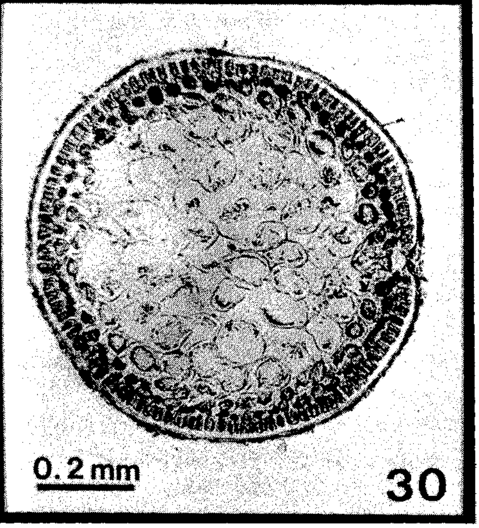

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Fig. 29. *Laurencia yamadana*, liquid-preserved, KM 848, Oahu.
Fig. 30. *Laurencia yamadana*, cross section, KM 923, Oahu.
Fig. 31. *Laurencia yamadana*, dried, Holotype, NY s.n., Oahu.

Remarks: This species forms a dense "turf" in exposed intertidal areas. The Hawaiian material does not resemble the type material of *L. obtusa* variety *rigidula* (W) from Samoa, which was described by Grunow (1873/1874, p. 45) and examined by Yamada (1931, p. 225), in size, branching, branching order, tetrasporangial arrangement, or holdfast morphology.

Laurencia sp. "green" (Figs. 34, 35)

Hawaiian Distribution: Kauai, Oahu, Molokai, and Lanai, (as *L. nidifica* in part, Saito 1969, p. 152, fig. 5); Hawaiian Islands (as *L. nidifica* in part, Abbott and Williamson 1974, p. 19; as *L. nidifica* in part, Abbott 1984, p. 32, fig. 16).

Representative Hawaiian Specimens: KM 871, Oahu, October 12, 1985; KM 892, Kauai, October 18, 1986; KM 958, Oahu, tetrasporophyte, April 13, 1986; KM 1094, Molokai, August 7, 1986.

Remarks: Saito included a green morph under *L. nidifica*; however, these green plants lack lenticular thickenings, and their biochemical compounds are different from those of *L. nidifica* (K. McDermid unpublished data).

Uncertain Records in Hawaii

Laurencia corymbosa J. Agardh
Laysan (Tsuda 1965, p. 19).

L. flagellifera J. Agardh
Maui (Saito 1969, p. 159).

L. obtusa (Hudson) Lamouroux
Hawaiian Islands (Chamberlain 1880, p. 33; MacCaughey 1918, p. 147); Laysan (Reinbold 1899, p. 296; Lemmermann 1905, p. 662).

L. obtusa variety *densa* Yamada
Midway (Buggeln 1965, p. 9).

L. obtusata (no reference found)
Hawaiian Islands (Reed 1907, p. 87).

L. papillosa (Forsskål) Greville
Hawaiian Islands (Lemmermann 1905, p. 662; Reed 1907, p. 87; MacCaughey 1918, p. 147).

L. perforata (Bory) Montagne
Hawaiian Islands (Chamberlain 1880, p. 33; Reed 1907, p. 87; MacCaughey 1918, p. 148); Laysan (Tsuda 1965, p. 20).

L. pinnatifida (Gmelin) Lamouroux
Hawaiian Islands (Reed 1907, p. 87; MacCaughey 1918, p. 148).

L. pinnatifida variety *densa* Lamouroux
Hawaiian Islands (MacCaughey 1918, p. 148).

L. pinnatifida osmunda (no reference found)
Hawaiian Islands (Reed 1907, p. 87).

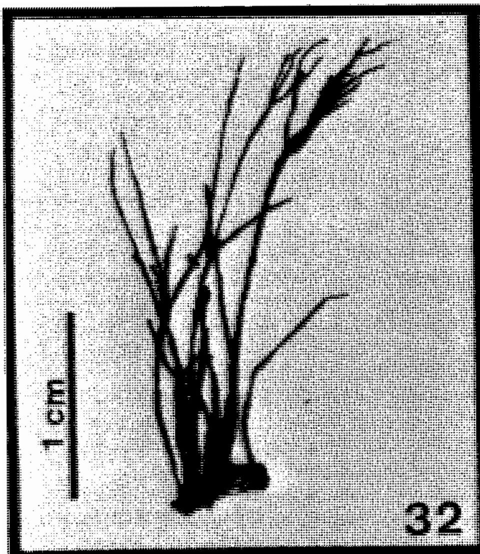
L. pygmaea Weber-van Bosse
Laysan (Tsuda 1965, p. 20).

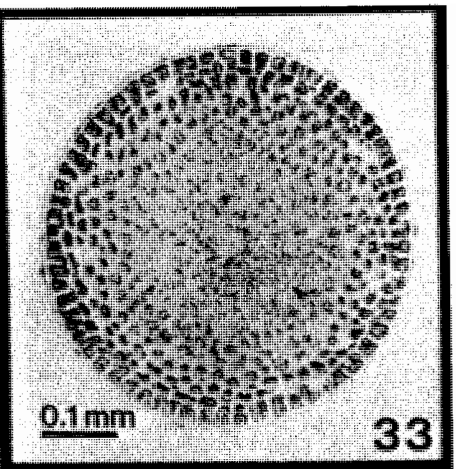
L. subsimplex Tseng
Midway (Saito 1969, p. 15, fig. 4c).

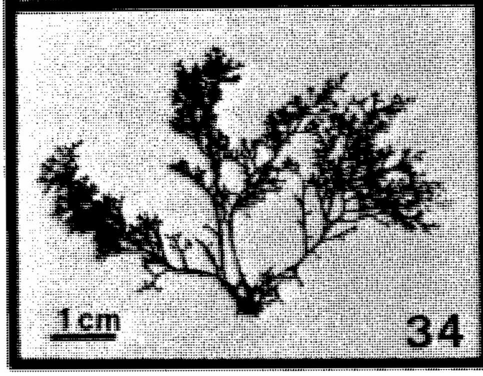
L. tenera Tseng
Oahu (Saito 1969, p. 150, fig 4a).

L. vaga Kützing
Laysan (Reinbold 1899, p. 296; Lemmermann 1905, p. 662); Hawaiian Islands (MacCaughey 1918, p. 147).

L. virgata J. Agardh
Hawaiian Islands (Chamberlain 1880, p. 33; Reed 1907, p. 87; MacCaughey 1918, p. 148).







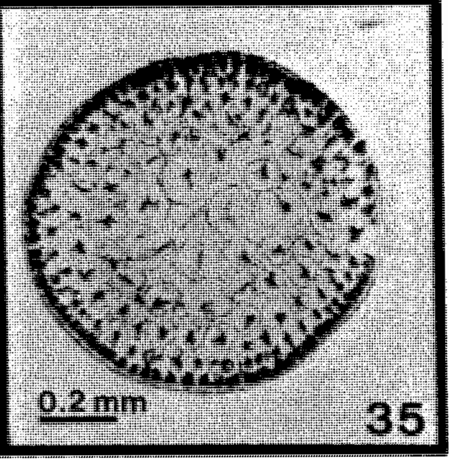


Fig. 32. *Laurencia* sp. "crustiformans," dried, KM 534, Oahu.

Fig. 33. *Laurencia* sp. "crustiformans," cross section, KM 1046, Oahu.

Fig. 34. *Laurencia* sp. "green," dried, KM 995, Oahu.

Fig. 35. *Laurencia* sp. "green," cross section, KM 1056, Oahu.

Acknowledgements

This paper could not have been written without the generous loans and/or hospitality of many herbaria. Thanks go to S. Sohmer and W. H. Magruder of the B. P. Bishop Museum (BISH), F. Ardré of the Muséum National d'Histoire Naturelle (PC), J. J. Bert for a visit to the Lamouroux Herbarium (CN), T. Yoshida for use of Yamada specimens (SAP), P. C. Silva in Berkeley (UC), the New York Botanical Garden (NY) for Howe material, the Botanical Museum in Lund (LD) for Agardh specimens, the Wien Naturhistorisches Museum (W) for Grunow collections, and the Institute of Oceanology Herbarium in Qingdao (ATS) for Tseng specimens. I am also grateful to R. T. Tsuda, G. T. Kraft, and I. A. Abbott for sharing their private *Laurencia* collections.

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

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

Abstract

The 30 reported species of *Laurencia* from China are presented in a key and are listed, with the distribution within China given. This is our first key to these species in English. It may help others to know how we understand the relationships of the species as they occur in China.

Key to the Species of Chinese *Laurencia*

1. Thallus gelatinous to very succulent in substance . . . . *L. subsimplex*
1. Thallus firm to cartilaginous 2

    2. Secondary longitudinal pit connections present between cortical cells, tetrasporangial arrangement of the parallel type 3
    2. Secondary pit connections absent, tetrasporangial arrangement of the right angle-type 18

3. Axes and branches terete or subterete 4
3. Axes and branches distinctly compressed 9

    4. Lenticular thickenings absent in the walls of the medullary cells 5
    4. Lenticular thickenings present in the walls of the medullary cells 10

5. Cortical cells projecting above the surface near the end of the ultimate branchlets . . . . *L. majuscula*
5. Cortical cells not projecting 6

    6. Frond less than 1 cm tall when mature . . . . *L. tenera*
    6. Frond more than 1 cm tall when mature 7

7. Slightly but constantly compressed . . . . *L. hongkongensis*
7. Frond usually terete 8

    8. Frond fleshy, generally purplish pink or dark purple . . . . *L. obtusa*
    8. Frond very rigid, dark brown, or black at the bases; branchlets corymbose upwards, ultimate branchlets closely arranged . . . . *L. flexilis* var. *tropica*

9. Branches distichous throughout, superficial cortical cells projecting near the ends of branchlets . . . . *L. pinnata*
9. Branches distichous at first, becoming polystichous and finally obscure in pattern; superficial cortical cells not projecting . . . . *L. chinensis*

    10. Superficial cortical cells projecting near the ends of ultimate branchlets 11
    10. Superficial cortical cells not projecting 13

11. Thallus cushionlike, less than 2 cm tall . . . . *L. galtsoffii*
11. Thallus not cushionlike, more than 2 cm tall 12

    12. Main branches alternate, ultimate branchlets clustered, radially placed . . . . *L. silvai*
    12. Main branches subdichotomous, ultimate branchlets not clustered . . . . *L. mariannensis*

13. Frond thin and delicate, branching usually secund . . . . *L. decumbens*
13. Fronds robust, axes percurrent 14

    14. Principal axis with numerous soft, protuberant branchlets . . . . *L. nipponica*
    14. Axes without soft, protuberant branchlets 15

15. Branches tristichous (in three vertical ranks) . . . . *L. tristicha*
15. Branches otherwise 16

    16. Thallus dwarf, loosely intricate at the base . . . . *L. venusta*
    16. Thallus large, basally densely intricate or entangled 17

17. Branchlets often opposite or in whorls . . . . *L. okamurai*
17. Branchlets nearly distichous . . . . *L. japonica*

  18. Cortical cells neither elongated radially nor arranged like palisade cells in transverse section of branchlets 19
  18. Cortical cells elongated radially and arranged like palisade cells in transverse section of branchlets 23

19. Lenticular thickenings present in the walls of the medullary cells 20
19. Lenticular thickenings absent 21

  20. Branching generally unilateral, branches and branchlets often more or less curving toward the substratum, articulate (jointed) here and there . . . . *L. articulata*
  20. Branching generally verticillate, not articulate . . . . *L. verticillata*

21. Frond never compressed, ultimate branchlets cylindrical, shortened, or wartlike . . . . *L. cartilaginea*
21. Frond generally compressed except in ultimate branchlets 22

  22. Frond small, up to 4 cm high and 2 mm broad, cartilaginous; outer cortical cells projecting near ends of branchlets; margin of fertile branchlets not undulate . . . . *L. parvipapillata*
  22. Frond large, up to 7 cm high and 4 mm broad, fleshy; outer cortical cells not projecting; margin of fertile branches undulate . . . . *L. undulata*

23. Branches dividing close to base from a short stalk, branchlets pinnate . . . . *L. palisada*
23. Branches arising otherwise; not stalked; not pinnate 24

  24. Branchlets crowding the apices, fanlike, or irregularly fingerlike, closely set, more or less in two ranks . . . . *L. longicaulis*
  24. Branchlets more loosely and evenly disposed, with irregularly set branchlets in more than two ranks 25

25. Ultimate branchlets turbinate, strongly swollen at tips, crowded on minor branches . . . . *L. jejuna*
25. Ultimate branchlets subcylindrical or subclavate, not crowded on minor branches 26

  26. Ultimate branchlets 3 mm or more in length, lower ones several times longer than upper ones . . . . *L. surculigera*
  26. Ultimate branchlets less than 3 mm in length 27

27. Cystocarp conical 28
27. Cystocarp ovoid or nearly spherical 29

  28. Thallus thin and soft, ultimate branchlets clavate . . . . *L. capituliformis*
  28. Thallus firm and rigid, ultimate branchlets wartlike but disposed very loosely . . . . *L. paniculata*

29. Thallus thick and rigid, in age branches and branchlets densely covered with small wartlike ultimate branchlets; cystocarp ovoid . . . . *L. intermedia*
29. Thallus subcartilaginous, branches densely covered with wartlike ultimate branchlets even when young; cystocarp nearly spherical . . . . *L. papillosa*

List and Distribution of Chinese Species of *Laurencia*

Laurencia articulata Tseng
Distribution: Hong Kong (Tseng 1943); Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. capituliformis Yamada
Distribution: Penglai, Shangong Province (Howe 1934).

L. cartilaginea Yamada
Distribution: Hong Kong (Tseng et al. 1980); Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. chinensis Tseng
Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983).

L. decumbens Kützing
Distribution: Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. flexilis Setchell variety *tropica* (Yamada) Xia et Zhang
Distribution: Wengchang, Hainan Island, Guangdong Province (Xia and Zhang 1982; Tseng et al. 1983); Taiwan (Yamada 1931, as *L. tropica*).

L. galtsoffii Howe
Distribution: Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. hongkongensis Tseng, Chang, Xia et Xia
Distribution: Hong Kong (Tseng et al. 1980, 1983).

L. intermedia Yamada
Distribution: Qingdao, Shandong Province (Howe 1934); Huanghai Sea coast (Tseng et al. 1983).

L. japonica Yamada
Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983); Pingtan, Fujian Province (Zhou and Chen 1983).

L. jejuna Tseng
Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983).

L. longicaulis Tseng
Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983).

L. majuscula (Harvey) Lucas
Distribution: Hong Kong (Tseng 1943, as *L. obtusa* variety *majuscula*); Xisha Islands, Guangdong Province (Zhang and Xia 1985); Hong Kong and Guangdong Province (Tseng et al. 1983).

L. mariannensis Yamada
Distribution: Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. nipponica Yamada
Distribution: Yentai, Shandong Province (Yamada 1931).

L. obtusa (Hudson) Lamouroux.
Distribution: Beidaihe, Hebei Province (Collins 1919; Howe 1924); Yentai, Shandong Province (Howe 1934); Pingtan, Fujian Province (Zhou and Chen 1983); widely distributed on entire sea coast (Zhang and Xia 1985).

L. okamurai Yamada
Distribution: Xiamen, Fujian Province (Yamada 1931); Beidaihe, Hebei Province (Grubb 1932a, 1932b); Huanghai Sea coast (Tseng et al. 1983).

L. palisada Yamada
Distribution: Taiwan Province (Yamada 1931).

L. paniculata (Agardh) J. Agardh
Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983).

L. papillosa (Forsskål) Greville
Distribution: Qingdao, Shandong Province (Tseng and Li 1935); Xiamen, Fujian Province (Cotton 1915; Tseng 1936); Pingtan, Xiamen and Dongshan, Fujian Province (Zhou and Chen 1983); Taiwan Province (Okamura 1931).

L. parvipapillata Tseng
Distribution: Hong Kong (Tseng 1943); Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. pinnata Yamada
Distribution: Chengshan, Yushan and Nanji, Zhejiang Province (Hang and Sun 1983); Xisha Islands, Guangdong Province (Zhang and Xia 1985).

L. silvai Zhang et Xia

Distribution: Xisha Islands, Guangdong Province (Zhang and Xia 1983, 1985; Zhang and Xia 1980 and Tseng et al. 1983, as *L. fasciculata*).

L. subsimplex Tseng

Distribution: Hong Kong (Tseng 1943).

L. surculigera Tseng

Distribution: Hong Kong (Tseng 1943; Tseng et al. 1983).

L. tenera Tseng

Distribution: Hong Kong (Tseng 1943).

L. tristicha Tseng, Chang, Xia et Xia

Distribution: Hong Kong (Tseng et al. 1980, 1983).

L. venusta Yamada

Distribution: Taiwan Province (Okamura 1931); Jinjiang, Fujian Province (Zhou and Chen 1983).

L. verticillata Zhang et Xia

Distribution: Xisha Islands, Guangdong Province (Zhang and Xia 1980, 1985; Tseng et al. 1983).

L. undulata Yamada

Distribution: Hong Kong (Tseng 1943; Tseng et al. 1980, 1983); Nanji, Zhejiang Province (Hang and Sun 1983); Pingtan, Fujian Province (Zhou and Chen 1983).

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AGAR FROM A SPECIES OF *LAURENCIA*, A RED SEAWEED FROM THE HAWAIIAN ISLANDS

Earl K. Zablackis and Karla J. McDermid

Abstract

The cell-wall polysaccharide of an undescribed species of the red algal genus *Laurencia* from Hawaii was extracted. Chemical, physical, and infrared analyses indicated a sulfated agar with an agarose fraction. The clean anhydrous yield of agar was 14.9%.

Introduction

Agar and agarose are widely used and highly valued algal natural products for industry and many fields of biological research. Agar is a sulfated galactan with a repeating disaccharide backbone of 3-linked β-D-galactopyranose and 4-linked α-L-galactopyranose, with the latter residue often in the form of a 3,6-anhydrofuranoid ring (Izumi 1973). Various positions along the chain may be sulfated, O-methylated, or have pyruvic acid residues as cyclic ketals on the 3-O-substituted D-galactose residue (Lahaye et al. 1986). Agarose, the industrially more valuable fraction, consists of the repeating disaccharide 4-O-3,6-anhydro-α-L-galactopyranose and 3-O-β-D-galactopyranose and may also have substituted groups, as in agar (LaHaye et al. 1986).

The search continues for more and/or alternative sources of agar and agarose. Most chemical research on the red algal genus *Laurencia* (Rhodomelaceae, Ceramiales) has focused on the unique secondary metabolites synthesized by these seaweeds (Howard and Fenical 1980, Erickson 1983); however, only a handful of studies have investigated the cell-wall polysaccharides (O'Colla 1962, Bowker and Turvey 1968a, 1968b, Mshigeni and Nzalalila 1977, Diaz-Piferrer 1979, Wu and Zeng 1985). To our knowledge, the polysaccharide chemistry of the Hawaiian *Laurencia* species has not been explored. Many species of *Laurencia* in Hawaii have a cartilaginous texture, but the taxon studied here (which will be described as new by McDermid) is the toughest and most wiry. These "scrub-brush–like" qualities suggested that this alga might contain a significant amount of phycocolloid that had a high gel strength. This species is a common component of red algal turf and is found in exposed intertidal and shallow subtidal zones (to 1.5 m deep) on limestone and basalt substrata. This alga can also be cultured in the laboratory (McDermid, unpublished data).

Here we report the presence of a sulfated agar from the hot-water extract of this species of *Laurencia* from Hawaii.

Materials and Methods

The seaweed samples used in the analyses were collected in July 1986 on intertidal limestone benches south of Kaneilio Point on the western coast of Oahu Island, Hawaii. Voucher specimens (KM 1026) are in the B. P. Bishop Museum, (BISH), Honolulu, Hawaii.

The seaweeds were rinsed in saltwater and cleaned of epiphytes. Only the upright axes, not the basal crust, were used in this study. Samples were air-dried in the dark for 48 hr.

The clean, dry seaweed (30 g) was placed in a stainless steel pot and heated under strong alkaline conditions (500 ml of 3% NaOH) on a boiling water bath for 3 hr. After heating, the alkaline liquid was removed, and the seaweed was washed three to four times with water until the washings were about pH 7. Then the seaweed was mixed with 500 ml water, adjusted to pH 6.3 with 10% glacial acetic acid, and heated for 1 hr on a boiling water bath. The mixture was then blended in a blender, and the resulting thick paste and washings were returned to the pot and boiled for 2 hr. During the last 30 min of boiling, 75 g of filter aid (diatomaceous earth) was added, and the mixture was stirred continuously for the remaining time. This mixture was filtered hot under pressure (60–80 psi), and the cake was washed with 100 ml of hot water. The filtrate and washings were combined, poured into a shallow pan, and frozen overnight. The frozen agar gel was thawed and washed thoroughly with water until the agar mixture was colorless. Then the agar was washed once with 85% isopropanol, twice with 95% isopropanol, and dried at 60°C. The dried agar flakes were ground to a 40-mesh powder. Agarose was extracted from the agar powder by the method of Blethen (1966), as used by Santos and Doty (1983).

The gel strength of a 1.5% agar gel that had been cooled at 10°C for 2 hr was determined by using a Marine Colloids gel tester with an 11-mm plunger. The 3,6-anhydrogalactose was measured by the resorcinol method of Yaphe and Arsenault (1965). The sulfate content was determined by the turbidometric method of Tabatabai (1974), as modified by Craigie et al. (1984). Films for infrared determinations were prepared by drying a 0.2% solution on mercury (Santos and Doty 1975) and were analyzed with a Beckman IR 10 spectrophotometer.

Results

This *Laurencia* species produced a 14.9% clean anhydrous yield of agar. The agar contained 32.2% 3,6-anhydrogalactose and 5.3% sulfate. The gel strength was 389 g cm^{-2}. The infrared spectrum (Fig. 1A) showed that the extract of this species of *Laurencia* was of the agar type. The spectrum had prominent peaks at 1240 cm^{-1}, 930 cm^{-1}, and 897 cm^{-1}, indicative of the S-O stretching vibration, 3,6-anhydrogalactose, and β-D-galactopyranosyl groups, respectively. A minute agarose fraction (less than 1% clean anhydrous yield) was recovered and used for infrared films. The infrared spectrum of this agarose fraction (Fig. 1B) was comparable to that of a standard agarose (Fig. 1C).

Discussion

A few species of *Laurencia* have been examined for their hot-water–soluble extracts. Bowker and Turvey (1968a, 1968b) described a sulfated and methylated extract of the agar type from European *L. pinnatifida* (Gmelin) Lamouroux. This extract was later shown to be slightly degraded by an agarase from the bacterium *Cytophaga* (Turvey and Christison 1967, Duckworth and Turvey 1969), thus verifying the agar nature of the polysaccharide. *Laurencia flexilis* Setchell from Hainan Island, China, was shown to contain an agar with a gel strength of 458 g cm^{-2} (Wu and Zeng 1985). One species from Tanzania, *L. papillosa* (Forsskål) Greville, has been reported as having a lambda carrageenan (Mshigeni and Nzalalila 1977). However, the phycocolloid had an optical rotation characteristic of an agar, and infrared spectra suggested that it was a sulfated agar.

The Hawaiian material becomes the third species of *Laurencia* to have the hot-water–soluble extract characterized as an agar. The sulfate content is lower and the 3,6-anhydrogalactose content is higher than the values reported for *L. papillosa* (Mshigeni and Nzalalila 1977), whereas the gel strength is lower than that reported for *L. flexilis* (Wu and Zeng 1985). Unfortunately, the values for sulfate and 3,6-anhydrogalactose were not listed for the Chinese taxon.

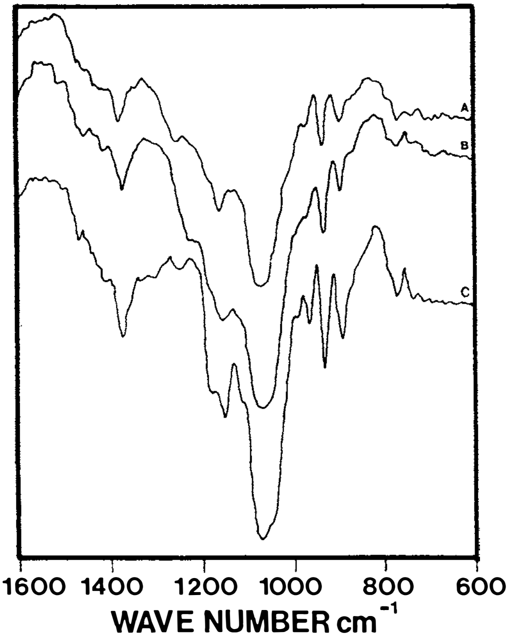

Fig. 1. Infrared spectra. A = agar from a Hawaiian *Laurencia* species (KM 1026); B = an agarose fraction of KM 1026; C = agarose standard from Marine Colloids.

The sulfate content, 3,6-anhydrogalactose content, and gel strength of the Hawaiian *Laurencia* are comparable to those of agar from *Gracilaria cylindrica* (Doty and Santos 1983). However, the yield and percentage of agarose are lower than those reported for *Gracilaria* species (Santos and Doty 1982, 1983).

Infrared analysis is not as useful a tool for agars as it is for carrageenans. Nevertheless, the spectra presented here do show that the agar extract of the Hawaiian *Laurencia* species is similar to the agar extract of *Gracilaria salicornia* (Santos and Doty 1982). Complete characterization of the agar and agarose extracts of the *Laurencia* samples would include sequential water and ethanol extractions and analysis of the fractions by nuclear magnetic resonance spectroscopy. Lahaye et al. (1986) have shown that this procedure is a powerful method for characterizing agars and determining the heterogeneous nature of agar polymers.

It is obvious that different species of *Laurencia* produce various types of cell-wall polysaccharides. In fact, *L. nidifica* J. Agardh and *L. yamadana* Howe, two taxa that co-occur in the algal turf community with the species studied here, produce distinctly different hot-water–soluble extracts (Zablackis and McDermid, unpublished data). Characterization of the cell-wall polysaccharides of *Laurencia* species might be valuable to the systematics of this complex group of algae. Moreover, although the yield of agarose was small in this material, further study of *Laurencia* phycocolloids may reveal other sources of commercially useful agarose.

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SECTION VI. Taxonomic Index