TAXONOMY OF ECONOMIC SEAWEEDS

With reference to the Pacific and other locations

Volume IX

Isabella A. Abbott and Karla J. McDermid, Editors

A Publication of the
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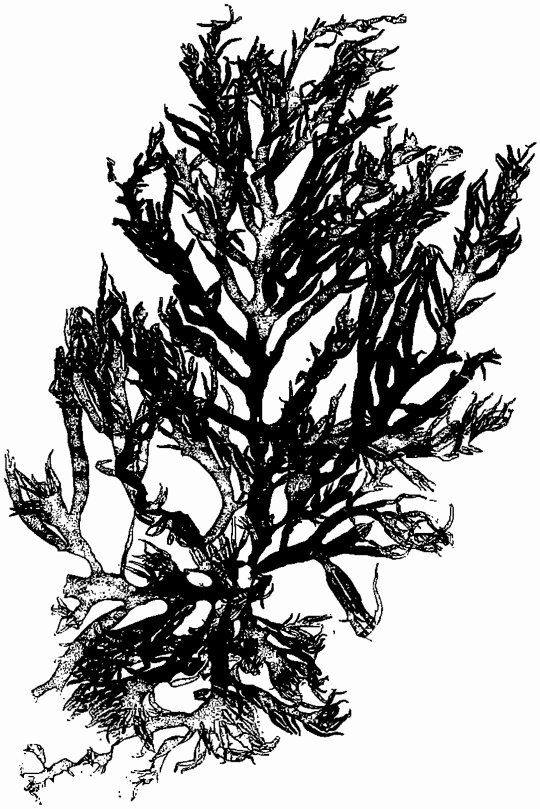
Isabella A. Abbott and Karla J. McDermid, Editors
Results of an international workshop sponsored by the Hawaii Sea Grant College Program and California Sea Grant College Program and hosted by the University of Hawaii at Hilo, May 22–29, 2002.



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Foreword

E. Gordon Grau
Director, University of Hawaii Sea Grant College Program

In May 2002, we proudly sponsored the ninth biennial Workshop on Taxonomy and Diversity of Economic Seaweeds in Hilo, Hawaii. The first workshop in this series on the taxonomy of commercially interesting seaweed species was held in Guam in 1985. For nearly twenty years, through the efforts of Dr. Isabella Abbott, international participants have come together to work to better understand the taxonomy of seaweeds that are important as sources of food, hydrocolloids, marine natural products, and aquacultured crops. The Hilo Workshop continued and expanded upon these valuable collaborations. With support from the University of Hawaii Sea Grant College Program, California Sea Grant, and the University of Hawaii, 26 seaweed experts from universities and scientific institutions in Australia, Chile, Guam, Japan, the People's Republic of China, South Korea, Thailand, the United States, and Vietnam gathered for the weeklong workshop. Participants focused on identification of species in selected economically useful genera, such as *Dictyota*, *Sargassum*, *Caulerpa*, *Codium*, *Gelidium*, *Gelidiella*, *Gracilaria*, *Halymenia*, *Hypnea*, and *Laurencia*. To encourage a successful future, the Workshop intended to train up-and-coming scientists while facilitating discussion about introducing more students to the fields of phycology and taxonomy. The results of this productive workshop are evident in these proceedings edited by Dr. Isabella Abbott and Dr. Karla McDermid. To achieve sustainable use and wise stewardship of marine resources, science-based information must be shared both within and beyond the scientific community through activities such as the May 2002 Workshop and associated proceedings. Our hope is that scientists will continue to build upon the legacy of this series.

Pioneer Participants of the First Workshop, Guam (1985), and the Ninth Workshop, Hilo (2002)

left to right: Roy Tsuda, Jim Norris, Jim Sullivan, Isabella Abbott, Bernabé Santelices, Tadao Yoshida, Xia Bangmei

Preface

Isabella A. Abbott, Coeditor

Anyone who was at the Hilo Sea Grant Workshop would know that Karla McDermid planned the logistics of welcoming, transportation, housing, meals. These things don't happen by themselves but because someone was planning ahead and being thoughtful to the smallest details. I want everyone to know that, while I gave advice and help when asked, I didn't volunteer my person to be there to help her all along the way. Therefore, the great success and enjoyment of that Workshop (and please note the productivity published in the pages that follow) everyone owes to Karla. Should we be able to obtain funding to hold other future Workshops, she will be more than adequate at leading them, and I strongly recommend that you don't let her get away!

I did put in time on the Workshop papers, and we (Karla and I) are proud of the good product that we have turned out, but of course most of you have published with us previously, so you knew what to do. Thank you all for cooperating with us.

I plan to take a back seat from now on; 18 years has been long enough, and I need the time to finish two grants so that I can do some traveling and some things other than writing about seaweeds. But of course I will help Karla should the Workshops continue. I very much enjoy working with her.

It has been fun and a privilege to lead this Workshop. Its impact will be lasting, not the least getting our Asian colleagues to think and write in English so that westerners can see what is happening in algae in the western Pacific and adjoining seas. There is no question that if Jim Sullivan didn't have the vision to push this through, it would never have happened; it is too hard to raise funds plus run a big meeting and edit the writing of those whose first language is not English. It has been more rewarding for me than most of you know, and I want to thank all of you for good memories.

Aloha from Isabella Abbott
October 28, 2003

Introduction: Looking Back, Looking Forward

Karla J. McDermid, Workshop Convenor and Coeditor

In May 2002, phycologists from around the world discovered the University of Hawaii–Hilo. Each day started with early morning fieldtrips at low tide and ended with dinner at a different Hilo restaurant. A first priority was to provide a rich collaborative learning experience. Every day we worked on the selected genera, and the Marine Science Building labs and rooms were open twelve hours a day. The dual-head microscopes allowed true teamwork: two taxonomists could view the same slides at the same time! The teams examined hundreds of specimens including dried herbarium specimens and preserved material brought from their home countries, as well as fresh Hawaiian samples. Special presentations were made by Paul Silva, Bernabé Santelices, John Huisman, Anong Chirapart, and UH–Hilo students on a variety of topics including *Codium* taxonomy, red algal coalescence, the marine flora of Australia, seaweed research in Thailand, and nutritional composition of Hawaiian macroalgae. On the last afternoon, Group Summary Presentations were made. Some of this workshop's accomplishments were discovery of new species, new regional records, and clarification of the characteristics of known species. At the farewell dinner, the Mayor of Hawaii County, who had always wanted to be a marine biologist, exhorted us to "keep doing what we do, because it is so important for the ocean and the world."

An equally meaningful goal for this workshop was to discuss the challenges ahead in the field of seaweed taxonomy. At dinner one night, we all filled out questionnaires and talked about our answers. The first question was "How did you get interested in studying seaweeds?" An overwhelming majority of us answered that it was a special teacher or a class that "introduced us to the seaweed world." Some of the responses were:

> "I met a good teacher."
> "A professor with a grant invited me to join the group studying marine macroalgae."

"A teacher who took us for collection of marine algae."
"A field course where I was given an algal project."

For others, what drew them to phycology was finding *Caulerpa* on the seashore, a gift of an algal guidebook, or the purchase of a mask and snorkel.

A second question asked was "How can we get more students involved in seaweed research, especially taxonomy?" "Money" was the most common response, including more money for thesis work, for training programs and research assistantships. One person outlined the solution: "Get more small grants, hire students; they work on seaweeds and become interested in whatever they know best." Others talked about how to capture students' interests:

"Encourage by example and select students who are 'natural' collectors."
"Tell students how important taxonomy is and relate it to biotechnology."
"Teach about the importance of seaweeds to world climate, marine ecology, etc."
"Make better connections with the applied aspects of taxonomy."
"Work with students and infect them with your enthusiasm."

An excellent idea suggested more than once was that every participant of future workshops bring a student. Another common answer was that we need to publish more books that illustrate the importance of taxonomy—more floras, surveys, interactive keys, photo books, guidebooks. Each of us must try harder to show how taxonomy provides the basis for testing and answering questions in field ecology, population genetics, physiology, phylogenetics, aquaculture, natural products chemistry, biogeography, biotechnology, and conservation biology. One participant warned that we must act, because "when the present seaweed specialists are no longer here, there will be no one to identify the algae others are working on." It was agreed that we must reach out to students as others in the past reached out and mentored us: through good teaching, memorable classes, research projects, student jobs, and personal inspiration.

Taxonomy, the science of classification of organisms, is part of human nature and our desire to sort and group things we observe. Aristotle and other ancient Greeks named and classified creatures, indigenous cultures worldwide developed their own working taxonomy systems, and about 250 years ago Linnaeus introduced binomial nomenclature, still used today. In an article in *Nature,* Godfray argued that taxonomy is facing a crisis because of reduced funding, poor distribution of information, lack of clearly achievable goals, and little attention paid to the non-specialists who use the information.[1] The author advised that, in order to survive, descriptive taxonomy must reinvent itself as a 21st-century web-based, information science under a single

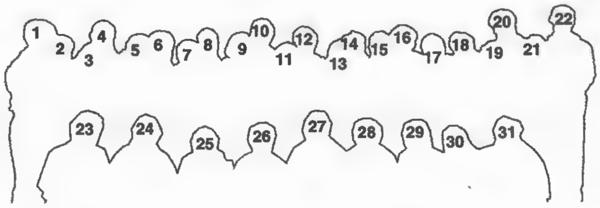
---

[1] H. Charles J. Godfray, Challenges for taxonomy, Nature 417:17–19, 2002.

administration. Others see the future of taxonomy primarily in molecular genetics, with species' identities determined more by gene sequences and much less by morphology or anatomy. However, even if taxonomy evolves into a DNA-dominated, web-based science, there will always be a need for scientists who can cut sections, make a microscope slide, and interpret anatomical features; for researchers who can recognize species in the ocean and on an herbarium sheet; and for holotypes, paratypes, and isotypes that document the ocean's biodiversity. A recently conducted search using the Web of Science found that articles in *Taxonomy of Economic Seaweeds* Volumes 1–7 had been cited 347 times. Clearly the results of the taxonomic workshops have been useful, not only to the participants but also to a wider audience. We must continue to provide high-quality information on the taxonomy and diversity of economical valuable seaweeds.

Acknowledgments

Many, many people helped make this workshop a success. We thank Chancellor Rose Tseng of UH–Hilo, Dr. Gordon Grau, Hawaii Sea Grant Director, and Dr. Russell Moll, California Sea Grant Director, for funding the workshop through three separate grants. We are grateful to the Research Corporation of the University of Hawaii staff for patiently guiding us through budget and fiscal details: thanks Doreen Koizumi, Keri Ann Tomita, Paula Gealon, and David Lovell. We appreciate the *aloha* (kindness, love) shown by Clifford Kaneshiro, UH–Hilo Bookstore Manager, and Miles Nagata, UH–Hilo Housing Director, as well as Auxiliary Service, College of Arts and Sciences, and College of Agriculture, Forestry and Natural Resources. Auntie Ulu Garmon, who gave the opening chant, and Pualani Kanaka'ole Kanahele and the Hạlau o Kekuhi, who performed *Ka'uluwehi o ke kai* (the lush vegetation of the sea), made the workshop *pono* (complete, right). The smoothness of daily operations of the workshop was largely due to the tireless student volunteers: Yumi Kamada, Sara McCutcheon, Marybeth Murphy, Jeremy Polloi, and especially to Brooke Stuercke, who organized their efforts. Words do not fully express our gratitude to John Thomas, editor extraordinaire. We thank the David and Lucile Packard Foundation, the Minority Biomedical Research Support Program, and Dr. Mary Donohue, Assistant Director of Hawaii Sea Grant for their financial support of the publication of this volume. Finally, we say *mahalo nui loa* (thank you very much) to all the participants of this workshop, who made it so much fun and so very productive.



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Notes

About Chinese Names

In accordance with the national change made in China in 1987, Chinese names are listed with surname first, no comma, and given name last, with a different spelling than before. A good example of old style and new style is Chang, C. F. (old), vs. Zhang Junfu (new). For another example, Lu Baoren's first name is Baoren. Because he is known in the West as C. K. Tseng, Dr. Tseng has asked us to list his name in this Western style.

About Vietnamese Names

In this volume, we use whole names (all three pieces of the name) for Vietnamese authors at first mention in the text and in the Literature Cited (references) section. When we speak to them, we use the last of the three name pieces as their "familiar" name. The reason that many of our Vietnamese colleagues use their third name is that Vietnam has only a very few family names, and the "familiar" name is the one that distinguishes each individual. You would be surprised to find that Pham Hoang Ho is listed as Ho about as many times as he is listed as Pham in the literature. But he never explained what the order of names meant. Now, we know; so please observe this usage.

Listing Species Names

In accordance with the practices of the international journal *Taxon* and the adoption of this practice in volume 4 of the workshop series, reference to place of publication follows author name(s) of nomenclature of species, basionyms, synonyms, types, and so forth and is not listed in the Literature Cited sections (references). On the other hand, if the species and author(s) are listed in the text, for example, in the discussion, this citation is listed in Literature Cited. An example is as follows:

Sargasum ilicifolium (Turner) C. Agardh, Sp. algarum, p. 11, 1820.
Basionym: *Fucus ilicifolius* Turner, Fuci...vol. 1, p. 113, pl. 51, 1808.

The order is species name, author name, place of publication (i.e., name of either book or journal), volume number, page number(s), plate or figure number(s), and date. If this style is followed, no one will ever create an illegitimate name, many of which occur because an author did not provide the exact reference in which the species are described. Article 33.2 of the International Code of Botanical Nomenclature states: "A new combination... for a previously and validly published name is not validly published unless its basionym...is clearly indicated and a full and direct reference given to its author and place of valid publication with page or plate reference and date."

Literature Cited

In this volume, all references to volumes from the eight previous workshops are listed in nomenclature setups and in Literature Cited as "Tax. Econ. Seaweeds 1 (or 2, 3, 4, 5, 6, 7, or 8)," followed by page and figure numbers, instead of giving the whole citation including editor, place of publication, and so forth. Inasmuch as the entire citation for each volume takes five lines of type, it will save a lot of ink and paper if we shorten the references within the volume. The entire citations are given here for reference:

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

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

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

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

Taxonomy of economic seaweeds: with reference to some Pacific species, vol. 5. I. A. Abbott, ed. [i–ii] + iii–xx + 1–254, 1995. California Sea Grant College System, University of California, La Jolla, Calif. Report No. T-CSGCP-035.

Taxonomy of economic seaweeds: with reference to some Pacific species, vol. 6. I. A. Abbott, ed. [i–ii] + iii–xviii + 1–212, 1997. California Sea Grant College System, University of California, La Jolla, Calif. Report No. T-040; ISBN 1-888691-04-2.

Taxonomy of economic seaweeds: with reference to some Pacific species, vol. 7. I. A. Abbott, ed. [i–ii] + iii–xviii + 1–181, 1999. California Sea Grant College System, University of California, La Jolla, Calif. Report No. T-044; ISBN 1-888691-08-5.

Taxonomy of economic seaweeds: with reference to some Pacific species, vol. 8. I. A. Abbott and K. McDermid, eds. [i–ii] + iii–xviii + 1–332, 2002. California Sea Grant College System, University of California, La Jolla, Calif. Report No. T-048; ISBN 1-888691-07-7.

INTRODUCTION: DEFINING CURRENT TAXONOMY

Isabella A. Abbott

"Taxonomy of Economic Seaweeds" has been the short cut to describe what the past nine Workshops have been doing for 18 years. We all think we know how to define that word "taxonomy," and we usually say it means to put a correct name, or give a correct name, to an organism, in our case an alga. At our first meeting in Guam, taxonomy meant writing up the species in our respective algal floras; it became clear almost immediately that many names we were using were incorrect (mostly superceded by studies in far-off places, or published in journals we never heard of). Sometimes the person we were sitting next to was a specialist in the group of algae under consideration, and we didn't know that. We are all specialists in one degree or another. But as of the Vietnam Workshop (the 8th, held in 1999) we have been moved, perhaps because we weren't paying too much attention, into the 21st century by papers that included molecular genetics, which is to say, quantitative phylogenetics, which is technically a step beyond phylogeny from a strictly morphological perspective.

Foreseeing this change for many of us is a giant step since we are still preoccupied with "old-fashioned" taxonomy based on morphology and anatomy. We can rather easily find new species in our floras, and we can always take an alga that has had an incorrect name when it was listed from our flora and give a correct name to it.

But things have changed rather precipitously: the morphological tools we know well are only part of the contribution to taxonomy that is concerned with naming taxa.

In the course of the Workshops, all of us have learned to acknowledge that there are rules of nomenclature we must adhere to, but we can't learn them all at once. (That's true, learn a few rules at a time—learn them so well that you can argue with others about them! That will give you courage to learn a few more!) Knowing the rules gives you a very strong bridge on which to stand—morphologically strong. Understanding them will give you the best foundation for being able to interpret and understand the impact of molecular studies upon "old-fashioned" taxonomy. As you will see when you read Dr. Silva's chapter, it took him a very long time to figure out all of this—he is a good leader to follow.

CLASSIFICATION, TAXONOMY, AND PHYLOGENY AND THEIR RELATION TO NOMENCLATURE, WITH SPECIAL REFERENCE TO ALGAE

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Abstract

Classification is the orderly arrangement of objects. Classifying is instinctive behavior that pervades our everyday life, consciously or subconsciously. Everyday classifications usually comprise coordinate classes. Taxonomy is the theory and practice of describing, naming, and classifying objects, especially organisms. The taxonomic structure in biological classifications is a pyramid of taxa, each taxon being coordinate with other taxa of the same rank and subordinate to a more broadly circumscribed taxon immediately above it. The species, although basic in this structure, lacks a universally accepted definition.

Phylogeny is the evolutionary history of a particular group of organisms. The phylogenetic structure is a cladogram, which is a diagrammatic representation of the hypothetical evolutionary branchings of a lineage during divergence from its ancestral stock. Each branch (clade) represents a monophyletic taxon or group of taxa sharing a closer common ancestry with one another than with members of any other clade. Phylogenetic information is of great importance in developing a taxonomic structure, but it is questionable whether all taxa must be monophyletic.

Nomenclature is the formation and application of names of taxa and thus is a verbal expression of a taxonomic structure. The principles of priority and typification are of paramount importance in botanical nomenclature. Because the phylogenetic structure is composed of clades rather than taxa, traditional taxonomic nomenclature is not applicable.

With general acceptance that the deepest clades in the Tree of Life represent several different major groups, each phylogenetically equivalent to the traditional animal and plant kingdoms, the necessity of addressing the uncertainties and inadequacies of existing nomenclatural codes has arisen.

Classification

Classification is the orderly arrangement of objects. We live in a classified world. Everything we are, everything we do, everything we eat, is classified. We go through life arranging or organizing various objects or processes according to some scheme that best suits our particular purpose. Classifying is instinctive behavior that allows us to cope with the bewildering world around us. Classifying enables us to establish routines, which give us more time for productive activity. A well-organized person keeps utensils for food preparation in one drawer and utensils for cooking in another drawer. A well-organized person keeps old clothes suitable for work around the house or in the garden separate from clothes that are usually worn to the office or laboratory and separate also from dress-up clothes. In all of these everyday classifications, many of which are undertaken subconsciously, the classes are coordinate, lying side-by-side on a single level.

Taxonomy

Taxonomy is the theory and practice of describing, naming, and classifying objects. The term, which is derived from the Greek word *taxis* (order, rank, row, arrangement), is applied almost exclusively to the description, naming, and classification of organisms. Taxonomy has evolved, and will continue to evolve, through interaction of three processes: (a) progressive addition, modification, and abandonment of criteria suggested by information obtained by means of continually improving observational and analytical instruments and techniques; (b) discovery of organisms with combinations of characteristics that do not fit existing definitions of taxonomic units; and (c) changing philosophical concepts. Taxonomy is sometimes defined as a science, but as I have detailed elsewhere (Silva 1982, 1984), taxonomy, like the practice of medicine, is an art based on supposedly unassailable scientific data. Taxonomic decisions, such as whether to treat *Caulerpella* as a distinct genus or as a subgenus of *Caulerpa,* are opinions, not facts. The practice of taxonomy is strongly influenced by many extrinsic factors, related both to the taxonomist and to the group of organisms being classified. Our taxonomic system is a synthesis of countless taxonomic decisions of varying importance. Every taxonomist relies heavily on the contributions of other authors, both past and present, and therefore must be cognizant of taxonomic history in order to make meaningful additions to the classifiction of a particular group of organisms.

Taxonomic classification results in the recognition of units that may be visualized as boxes and are termed *taxa* (sing. *taxon*). A taxon is coordinate with other taxa of the same rank (e.g., species in a genus) but subordinate to the taxon immediately above it. In the resulting hierarchical pyramid, the most narrowly defined taxa are at the bottom and higher taxa are successively larger and more broadly defined. This hierarchical system of classification has great powers of prediction and recall. For example, if someone hands you a large brown seaweed that has a holdfast, a stipe, and a blade, you would have good reason to assume that it is a member of the Laminariales. Solely on the basis of gross morphology, you could deduce its method of development and life history. Knowing that it is a brown alga further allows you to deduce cytological and biochemical characteristics.

Classification involving hierarchical arrangement of taxa developed through observation. Greek and Roman naturalists were aware of plants and animals that formed groups based on morphological similarities. Cats, dogs, lilies, mints, oaks, pines, and many other natural groups were discerned. Within each of these natural groups, individual members were recognized and named, resulting in the first step toward a hierarchical system of classification.

Standardization of Taxonomic Categories

During the two millennia after the early Greek and Roman naturalists, the number of steps in the hierarchy was increased, but the terms applied to these steps varied from one author to another. To standardize these terms and their hierarchical arrangement, as well as to answer other questions in naming and classifying plants, the committee appointed by the Société botanique de France to organize an internationl botanical congress in Paris in 1867 asked the well-known Swiss botanist Alphonse de Candolle (1806–1893) to prepare a set of rules governing botanical nomenclature that could be discussed at the congress. Candolle was unbelievably prompt, returning a draft within a few weeks (Candolle 1867a). Based in large part on the writings of Linnaeus, Candolle's *Lois de la nomenclature botanique* (Candolle 1867b), which was adopted by the congress, dealt mainly with the formation of names. A hierarchy of taxonomic categories was also established, but the terms and the Latin terminations of the names in those categories were not brought into agreement with present-day usage until the first of the current series of codes was adopted by the Second International Botanical Congress meeting in Vienna in 1905.

The principal categories in botanical classification from top to bottom are now standardized as *kingdom, phylum* or *division, class, order, family, genus,* and *species.*

Concepts of the Principal Categories in Botanical Classification

The concept of *species* as a particular kind of organism is of ancient origin. Well-known European plants such as *Laurus nobilis* (laurel or bay tree) were well defined and named by Greek and Roman authors. The concept of species is also an integral part of those biological classifications that lay outside the realm of Western civilization, such as those constructed by Amazonian Indians, Polynesians, or Chinese. Ironically, although the category species is basic in the taxonomic structure and is the category most likely and most easily visualized as a collection of individual organisms, its definition is the most elusive and controversial of all categories. The zoological requirement that the members of a species share a common breeding pool to which they are confined cannot be applied to plants. Some plant species comprise several reproductively isolated strains. Conversely, some plant species are promiscuous and freely produce hybrids in nature.

The usefulness of recognizing infraspecific taxa within polymorphic species has long been appreciated. *Variety (varietas)* is the most commonly used infraspecific category in botanical classification, in which it represents a morphologically variant population (growth form, color form), usually without geographic correlation. Trivial variants, such as color forms, are often recognized taxonomically within a variety by being assigned to the category *form (forma). Subspecies* is the only infraspecific category recognized in zoological classification, in which it represents an incipient species, almost always with geographic correlation. The zoological concept of subspecies is gradually entering botanical classification (see, e.g., the treatment of *Sargassum ringgoldianum* by Yoshida 1983). Plant taxonomists dealing with complex species sometimes have recognized both subspecies and varieties as well as forms. Weber-van Bosse (1898), for example, in treating *Caulerpa racemosa,* recognized 2 subspecies, 20 varieties, and 6 forms.

The concept of *genus* as a group of species that share certain morphological features, such as details of fructification, was suggested by classical writers in their groupings of oaks and maples but did not become a part of modern taxonomy until the 17th century. The category was firmly established by Joseph Pitton de Tournefort (1656–1708), a botanist at Montpellier, who built on the ideas of John Ray (1627–1705), the father of British botany, and August Rivinus (1652–1723), a botanist and physician from Leipzig.

The concept of *family* as a group of genera that share certain morphological features arose simultaneously with the concept of genus. Interpretation of the publications of authors of the 17th, 18th, and early 19th centuries is hampered by their use of the term *ordo* (pl. *ordines*) to apply to the modern concept of family. Tournefort was as important in establishing the concept of family as he was in establishing the concept of genus, building on the work of his teacher, Pierre Magnol (1638–1715), who first used the term *familia* in the modern sense.

The concept of *order* as a group of families that share certain morphological features was slow to develop but became well established during the late 1800s and early 1900s through the work of Adolf Engler (1844–1930) and his associates in Berlin. Authors in the early 1800s applied various terms to these taxa, including *alliance* and *series (Reihe).*

The concept of *class* as a group of orders that share certain morphological features developed almost entirely in the 20th century. Modern classes are based not only on morphology but on ultrastructure, biochemistry, and molecular phylogeny.

The concept of *phylum* is zoological, being suggested by the large number of organisms that vary widely in structure but have a similar underlying pattern (e.g., molluscs, coelenterates, annelid worms). The concept of *division* arose in the late 1800s among German and Austrian botanists, the term meaning literally a division *(Abteilung)* of the plant kingdom. Rarely, both categories were recognized in the same classification. Most 20th-century botanists, however, used the terms interchangeably, and the current International Code of Botanical Nomenclature (ICBN) (Greuter et al. 2000) sanctions this interchangeability.

The concept of *kingdom* is an ancient one, as even the least clever person could tell the difference between plants and animals. Dividing all organisms into only two kingdoms, however, is not in agreement with present-day knowledge. An ever-increasing amount of information regarding the ultrastructure, biochemistry, and molecular phylogeny of a vast assemblage of organisms that are neither typical higher plants nor typical higher animals supports the recognition of several kingdoms (e.g., Copeland 1938; Smith 1950; Whittaker 1969; Leedale 1974; Whittaker and Margulis 1978). Moving in the opposite direction, Dillon (1963) placed all living organisms in a single kingdom, for which he chose the name Plantae, "since groups always recognized as plants make up the larger portion of the phylogenetic tree."

Effect of Linnaeus on the Recognition of Taxonomic Categories

Carl Linnaeus (1707–1778), the great Swedish naturalist, is rightfully credited with imposing order on the chaotic taxonomic situation that faced him at the beginning of his illustrious career. His most important botanical publication was *Species plantarum* (Linnaeus 1753) and his most important zoological publication was *Systema naturae* (Linnaeus 1758). Linnaeus divided the animal kingdom into six classes: Mammalia, Aves, Amphibia, Pisces, Insecta, and Vermes. Five of these classes are in use at the present time, only Vermes having disappeared in the taxonomic rubbish bin. Linnaeus was intentionally not so successful at delineating major taxonomic groups of plants. For the plant kingdom, he instituted his celebrated "sexual system," based on the number and position of stamens and pistils. The artificiality of this scheme was appreciated by Linnaeus, who considered it an acceptable downside in adopting a classification that was remarkably user-friendly, as testified by the hundreds of floristic accounts that were inspired by *Species plantarum.*

It should be emphasized that the Linnaean botanical classes have nothing to do with presently accepted classes, such as Phaeophyceae or Rhodophyceae. In *Species plantarum,* the 24th class bears the name Cryptogamia and contains those plants without obvious sexual reproduction. This class Cryptogamia is divided into Filices, Musci, Algae, and Fungi. The rank of these taxa is not indicated in *Species plantarum,* but they are indicated as *ordines* in *Genera plantarum* (Linnaeus 1754) and were treated as families by authors in the late 18th and early 19th centuries. Within the first 23 classes, the concept of family was set aside. The so-called sexual system, being based on arbitrary characters, often fractionated groupings of genera that Linnaeus would have recognized as families had he not chosen an artifical system of classification.

Development of Taxonomic Structure

During the 250 years that have elapsed since the publication of *Species plantarum,* vast changes have taken place in the taxonomic structure for plants in general and algae in particular. Sophistication of taxonomy is directly correlated with increasing availability of comparative attributes. Gross morphological characters of the 18th century were greatly amplified by anatomical characters in the 19th century and ultrastructural details in the 20th century thanks to improvements in light microscopy and the development of electron microscopy. Scanning electron microscopy (SEM) has revolutionized the taxonomy of diatoms and coccolithophorids. Whereas holes in the diatom frustule can be discerned with the light microscope, SEM enables the taxonomist to see the complex structure in the chambers underlying the holes. Transmission electron microscopy (TEM) has revolutionized taxonomy at ranks above that of family by providing static and dynamic details of ultrastructure deemed to be of paramount phylogenetic significance.

Biochemical characters were added to morphological characters during the last half of the 20th century, giving rise to chemotaxonomic techniques such as electrophoretic comparison of isozymes. These techniques were widely used in the classification of higher plants, especially at the level of species, but occasionally they were applied to algae (e.g., Lindstrom and Cole 1992).

All taxonomists have attempted to produce "natural" systems of classification, but the only agreement among the classifications is the assumption that "naturalness" is expressed by morphological similarity. Whether or not a taxonomist believed in evolution, the resulting classification was intuitively phyletic. The taxonomist decided intuitively the taxonomic value or evolutionary significance of each character and character state.

Attempts to quantify similarities and differences by comparing measurements of a large number of equally weighted characters, scored consistently for all groups under consideration, led to the practice of numerical taxonomy (also called taximetrics), which soon evolved into the sophisticated field of phenetics. The digital computer, which underwent rapid development in the second half of the 20th century, provided the necessary tool for analyzing complex interrelationships among multiple characters and character states. These interrelationships may be expressed graphically by several different kinds of diagrams (phenograms).

Phylogeny

Phylogeny is the evolutionary history of a particular group of organisms. Because evolution is observable only at the level of species and infraspecific taxa, phylogeny is constructed from a series of hypotheses concerning the inheritance of shared characters or character states and the origin of new characters or character states. Phylogeny has been expressed graphically in various ways, most important being dendrograms ("trees"), which were first used by Haeckel (1866: pls. I–VIII), the German naturalist who coined the terms *phylum* and *phylogeny*. In the first century of their use, dendrograms were intuitive, drawn freehand, and often with few branches (see, e.g., Silva 1956). Although phenetic studies involve characters and character states without regard to their origin, phylogenetic relationships may nevertheless be inferred from phenograms.

Dissatisfaction with both the phyletic and phenetic approaches to classification led to the development of cladistics, which has been defined as "the concepts and methods for determining branching patterns of evolutionary history" (Stuessy 1980). Unlike phenetic analyses, in which all characters are assigned equal weight, cladistic analyses are based on characters selected for their assumed phylogenetic importance. Whether a particular character state is primitive or derived must also be decided subjectively. The use of cladistics has been greatly enhanced by the addition of molecular data to traditional morphological, anatomical, cytological, and biochemical characters. Comparison of the nucleotides in a particular part of the genome among individuals representing different taxa is believed to be an objective source of phylogenetic information.

The graphic expression of a cladistic analysis is a branching diagram called a cladogram. As narrowly defined, a cladogram merely represents the relationships among characters and character states from which a range of phylogenetic inferences may be made. As broadly defined, a cladogram represents the evolutionary branchings of a lineage during divergence from its ancestral stock. In this sense it is a dendrogram (phylogenetic "tree"). Large numbers of cladograms can be generated by computer, differing according to the algorithm selected. The fallibility of basing phylogeny on a single part of the genome is obvious, so that cladograms generated from combined traditional and molecular data engender far more confidence than those based on a single data set. Classifications developed by the cladistic method are based on phylogenetic hypotheses. Recency of common ancestry rather than phenetic similarity is the sole criterion for delineating taxa.

The goals of molecular studies vary. Studies that focus on details of the genome per se are of little or no interest to a taxonomist. Studies that are primarily concerned with phylogenetic relationships may or may not concern the taxonomist, depending on their context. Studies that are made with a taxonomic problem in mind (e.g., the resolution of species within a genus) are of paramount interest (see, e.g., Hughey et al. 2001).

Effect of Phylogenetic Information on Taxonomy

Taxonomy and phylogeny, while not mutually exclusive, are significantly different. The building block of a taxonomic classification is the taxon, whereas the structural unit of a phylogenetic classification is the clade. A clade is a branch of a cladogram that may be either single and terminal or a collection of all branches, both terminal and intercalary, that are derived from a particular point of divergence. Because all organisms in the clade share a common ancestry, the taxon represented by the clade is said to be monophyletic. Many traditional taxa, by contrast, are paraphyletic, combining phenetically similar but phylogenetically unrelated organisms. The degree to which a clade dips into the cladogram corresponds to taxonomic rank, with very deep clades corresponding to higher taxa.

The authors of most phylogenetic papers, after demonstrating that certain taxa are paraphyletic, hesitate to offer taxonomic revisions. Their caution is warranted by a lack of consensus as to the relationship between phylogeny and taxonomy. Arguments have been made both for and against the position that all taxa must be monophyletic (see Brummitt 2002). When we are shown that the terminal clades representing various species of *Ulva* and *Enteromorpha* interdigitate, as do those of *Porphyra* and *Bangia* as well as those of *Grateloupia* and *Prionitis,* we must carefully consider the consequences of merging genera purely for the sake of achieving a monophyletic classification.

Nomenclature

Nomenclature is the formation and application of names used to express a classification. Taxonomic nomenclature has been developed over the past 250 years and its rules are universally accepted. By contrast, phylogenetic nomenclature is in its infancy. A proposed "PhyloCode" (http://www.ohiou.edu/phylocode/) has evoked much controversy regarding the relationship between phylogenetic and taxonomic nomenclature (Cantino 2000; Forey 2002). Phylogenetic nomenclature deals with the naming of clades or the taxa they represent in the absence of a hierarchical classification.

One of several innovations of Linnaeus that stimulated floristic exploration to such a remarkable extent in the latter part of the 18th century was his consistent use of the binomial system of naming species. Initially, a specific epithet was appended to a generic name as a kind of shorthand to save Linnaeus precious time. He called the epithet a *nomen trivium* ("trivial name") and did not intend for it to replace the *nomen specificum,* which was a descriptive phrase. Linnaeus soon recognized the great mnemonic value of trivial names, which he then treated as specific names. Linnaeus saved additional time by using a binomial system of citing literature. Thus, "Tourn. inst." referred to Tournefort's *Institutiones rei herbariae* (1700) and "Tourn. cor." referred to *Corollarium institutionum rei herbariae* (1703) by that same author.

Nomenclatural Codes

The binomial system of nomenclature underlies all three codes that have been produced to govern the naming of organisms, namely, the International Code of Botanical Nomenclature (ICBN), the International Code of Zoological Nomenclature (ICZN), and the International Code of Nomenclature of Bacteria (ICNB). The current edition of the ICBN (Greuter et al. 2000) is called the St. Louis Code because it incorporates changes authorized by the Nomenclature Section of the International Botanical Congress meeting at St. Louis in 1999. The St. Louis congress was the 16th in the present-day series. Although several so-called international botanical congresses were convened in Europe prior to 1900, usually with the participation or even instigation of horticulturists, the Paris congress of 1900 is considered the first in the present-day series because it established a mechanism for convening future congresses (Table 1).

Table 1. Sites and Dates of Modern International Botanical Congresses

1.	Paris	1900	9.	Montreal	1959
2.	Vienna	1905	10.	Edinburgh	1964
3.	Brussels	1910	11.	Seattle	1969
4.	Ithaca	1926	12.	Leningrad	1975
5.	Cambridge	1930	13.	Sydney	1981
6.	Amsterdam	1935	14.	Berlin	1987
7.	Stockholm	1950	15.	Tokyo (Yokohama)	1993
8.	Paris	1954	16.	St. Louis	1999

The origin and development of the first ICBN established the procedure for producing subsequent editions. The Paris congress in 1900 appointed an international commission on botanical nomenclature headed by John Briquet, a prominent Swiss botanist, who was given the title "Rapporteur général." Briquet solicited proposals for emending Candolle's *Lois de la nomenclature botanique* and then published them, together with his analysis of each proposal and the text recommended by the commission (Briquet 1905). This document, which was debated at the Second International Botanical Congress (Vienna, 1905), served as the basis for the Vienna Code (Briquet 1906), the first in the present-day series. Briquet's *Texte synoptique* (Briquet 1905) established a precedent for all future congresses.

The procedures for producing revised editions of the ICBN have been entrusted to the International Association for Plant Taxonomy beginning with the Paris congress of 1954. Prior to each International Botanical Congress, proposals to change the current ICBN are solicited, assembled, and analyzed by the Rapporter général in a document called "Synopsis of proposals," patterned after Briquet's *Texte synoptique.* These proposals are then discussed by the Nomenclature Section of the International Botanical Congress, which meets a week preceding the general congress. The Nomenclature Section, after sifting through the numerous published proposals as well as those made from the floor during the meeting, accepts a few proposals, with or without emendation, and then makes recommendations to the general congress, which routinely accepts them at the closing plenary session. A new edition of the ICBN is then prepared by an editorial committee appointed by the Nomenclature Section.

Rudiments of Botanical Nomenclature

The ICBN offers two hurdles for anyone attempting to publish a scientific name. The first hurdle is called *effective publication,* for which standards are set forth to ensure that the publication containing the new name is available to the taxonomic community in general. Although electronic publication has the potential for inducing far greater readerships than even the most popular scientific books or journals, the taxonomic community has not yet felt sufficiently comfortable with it to accept it as effective publication.

The second hurdle is called *valid publication,* for which standards are set forth to guarantee that a new name is published with adequate supporting information. Requirements have been tightened progressively so that the date of publication must be kept in mind when determining whether a name has been validly published (Table 2). Certain of these requirements have been modified to accommodate the nomenclature of non-fossil algae. For example, the requirement for a Latin diagnosis when publishing names of taxa at all ranks is postponed from January 1, 1935 (applicable to all other plants except fossils) to January 1, 1958. In another example, the requirement for an illustration when publishing names of species and infraspecific taxa applies only to algae among non-fossil plants.

Table 2. Requirements for Valid Publication of Extant Algae

1 May 1753. Description (in any language) and/or illustration for genera, species, and infraspecific taxa; description (in any language) for taxa at all other ranks
1 January 1908. Description (in any language) for taxa at all ranks, with or without illustration
1 January 1953. Rank of taxon must be clearly stated; alternative names are no longer valid; basionym or replaced name must be clearly indicated with a direct reference to its author and place of publication (including page or plate reference) and date
1 January 1958. Description must be in Latin; illustration required for specific and infraspecific taxa; type must be indicated
January 1990. Depository of type specimen must be stated; the word typus or its equivalent in a modern language must accompany designation of type

The starting point for valid nomenclature is the publication of the first edition of *Species plantarum,* arbitrarily set at May 1, 1753. Certain groups of algae (filamentous blue-greens, desmids, Oedogoniaceae) have been assigned later starting points.

Although the designation of species by appending an adjectival or substantival epithet to a generic name is of paramount importance in botanical nomenclature, epithets are also used in infrageneric and infraspecific names. In infrageneric names, an epithet or more than one epithet is appended to a generic name with an indication of the rank of each infrageneric taxon (subgenus, section, subsection). In infraspecific names, an epithet or more than one epithet is appended to a specific name with an indication of the rank of each infraspecific taxon (subspecies, variety, subvariety, form, subform). Adjectival specific epithets must conform grammatically to the gender of the generic name. Thus, the epithet in *Fucus capillaceus* S. G. Gmelin becomes *capillaceum* when the species is transferred from *Fucus* (a masculine noun) to *Gelidium* (a neuter noun) and *capillacea* when the species is transferred to *Pterocladia* or *Pterocladiella* (both feminine nouns). Stearn's *Botanical Latin*

(1992) is indispensable in determining the correct endings of a particular adjective.

Infrageneric and infraspecific taxa may be moved vertically (to a different rank within the genus or species) or horizontally (to a different genus or species). If the epithet is retained in the name of the transported taxon, the author of that epithet is cited in parentheses preceding the transporting author. Thus, *Botryocladia* (J. Agardh) Kylin (*Chrysymenia* sect. *Botryocladua* J. Agardh) and *Botryocladia leptopoda* (J. Agardh) Kylin (*Chrysymenia uvaria* var. *leptopoda* J. Agardh) are examples of vertical transfer (both upward), whereas *Turbinaria vulgaris* var. *decurrens* (Bory) J. Agardh (*Turbinaria decurrens* Bory) is a downward transfer and *Turbinaria turbinata* (Linnaeus) Kuntze (*Fucus turbinatus* Linnaeus) is a lateral transfer.

Names of taxa above the rank of genus are monomials. Grammatically, they are plural adjectives treated as substantives. Thus, Ceramiaceae is a curtailment of the phrase "Algae Ceramiaceae," meaning "Algae pertaining to *Ceramium*." This dual grammatical nature leads to editorial uncertainty: is the word *Ceramiaceae* singular or plural? The answer depends on whether the taxon is considered as a box or as a group of organisms within the box. Thus: "Of the four families that constitute the Ceramiales, the Ceramiaceae was the first to be recognized taxonomically. In general, Ceramiaceae are beautiful algae."

In the writings of Linnaeus and subsequent authors in the first half of the 19th century, nomenclature was concerned chiefly with the formation and propriety of names. It was only when it became necessary to fractionate the overly broad Linnaean genera that the focus of nomenclature changed from formation to application. When a genus is divided into two or more parts, which part should retain the original name? Since 1930 the answer has been governed by the type method, by which a name is attached to its type. Prior to 1930, the application of a name was determined by circumscription, allowing a name to be applied to widely varying taxa.

Each taxonomic group with a particular circumscription, position, and rank can bear only one *correct* name. If more than one name is available, the earliest is the correct name. To be available, a name must be validly published and legitimate, that is, not in violation of any rule.

The principle of priority can be sidestepped by means of nomenclatural conservation, a process by which an incorrect name is conserved against earlier homonyms or synonyms. Arguments for conserving a particular name must be published. Upon publication, the proposal is referred to the pertinent nomenclature committee of the International Association for Plant Taxonomy (e.g., Committee for Algae). The committee decides whether the proposal is worthy of support. Its recommendation is transmitted to the General Committee of the International Association for Plant Taxonomy, which usually approves it without comment. A slate of recommendations, for and against proposals for conservation, after being approved by the Nomenclature

Section of an International Botanical Congress, is presented to the general congress for acceptance at the closing plenary session.

So far, 158 generic names of algae have been conserved against earlier homonyms or earlier heterotypic synonyms, which are listed as rejected names. In addition, 14 generic names have been conserved with types that preserve traditional application of the names, and 8 generic names have been conserved to preserve traditional orthography. At ranks other than genus, 22 family names and 11 specific names of algae have been conserved.

The principle of priority may also be sidestepped by direct rejection of specific names (Art. 56). So far, only one algal name has been rejected: *Ulva simplicissima* Clemente 1807, which threatened to displace the very well known name *Scytosiphon lomentaria* (Lynbye) Link (*Chorda lomentaria* Lyngbye 1819).

Illegitimate Names

There are two types of illegitimate names. *Later homonyms* constitute the first type. The epithet of a later homonym may be rescued by transferring the name to a different genus in which the resultant binomial is not a later homonym. Thus, *Fucus fimbriatus* Turner 1810, a later homonym of *Fucus fimbriatus* S. G. Gmelin 1768, is illegitimate and may not serve as a basionym. The epithet was rescued in 1813 by Lamouroux, who transferred Turner's species to *Delesseria*. This was the first such tramsfer, with the result that *Delesseria fimbriata* Lamouroux 1813 is treated as a new (and legitimate) name for *Fucus fimbriatus* Turner. The species dates from 1813 rather than from 1810, and the possibility that a substitute name or synonym was published between those dates must be taken into consideration. In this example, no substitute names or synonyms are available. All subsequent combinations with *F. fimbriatus* Turner as the intended basionym are treated as being based on *Delesseria fimbriata* Lamouroux. The currently accepted name of this species is *Osmundaria fimbriata* (Lamouroux) R. Norris.

Similarly, *Dasya harveyi* Kützing 1864 is a later homonym of *Dasya harveyi* Ashmead 1858. The epithet was rescued in 1893 by Schmitz, who transferred Kützing's species to *Lophocladia,* but not before Kuntze had published a substitute name *(Baillouviana kuetzingii)* in 1891. The correct name for this species is *Lophocladia kuetzingii* (Kuntze) P. C. Silva rather than *L. harveyi* (Kützing) Schmitz.

Superfluous names constitute the second type of illegitimate name. A superfluous name is one in which the original treatment (protologue) includes the citation of an available name or the type of an uncited available name that should have been adopted. The epithet of a superfluous name can be rescued only by an author who transfers the species to another genus and simultaneously excludes from the circumscription of that species the type of the name whose citation in the protologue resulted in a superfluous name. Thus, *Fucus sinuosus* Goodenough et Woodward 1797 is superfluous because

Fucus crenatus S. G. Gmelin 1768 was cited as a synonym in the protologue. When Lamouroux transferred the species to *Delesseria,* he did not rescue the epithet because he did not exclude *Fucus crenatus* from the circumscription of the species. Several other authors published combinations with *Fucus sinuosus* as the intended basionym but without excluding *Fucus crenatus.* All of these binomials are illegitimate because in each case the author should have adopted the epithet *crenatus.* Because *Fucus sinuosus* is illegitimate and thus may not serve as a basionym, these intended combinations are to be accredited directly to the combining author and without citing Goodenough et Woodward in parentheses (e.g., *Delesseria sinuosa* Lamouroux).

Formation of Names

Although the ICBN permits arbitrary formation of generic names and specific epithets, proposers of new names should show consideration for the taxonomic community by choosing names that are not only pronounceable but also euphonious. Generic names are best formed from Greek word elements and should look like nouns. Specific epithets may either be nouns in apposition to the generic name or adjectives modifying the generic name. If adjectival, they are best formed from Latin word elements. Brown's *Composition of Scientific Words* (1956) is very helpful, if not indispensable, both in forming new names and in determining the etymology of existing names.

The recently published generic name *Playaensis* is so blatantly a geographical adjective that it is difficult to think of it as a noun, while the epithet of the type species, *circumfimbria,* plays the ungrammatical role of a noun in apposition to an adjective. Retaining the author's choice of Latin for both the generic name and the specific epithet, I suggest that *Laplaya circumfimbriata* would have been suitable, with the generic name a noun recalling the habitat (*playa,* a Spanish word for sandy place, treated as Latin), and the specific epithet a Latin adjective (past participle) describing an important characteristic.

In my opinion, authors should avoid the use of names designed to display their erudition or to make a case for political correctness. Above all, authors should avoid burdening botanical nomenclature with barbarisms. The epithet of the recently published *Amphidinium yuroogurrum* is derived from the word *yuroogurra* in the language of the Eora, the indigenous people of Botany Bay, Australia, but knowing its derivation is of no mnemonic value since the Eora language is not within the cognizance of the average phycologist. Treating Spanish adjectives as Group A Latin adjectives with the endings *-us*, *-a*, and *-um* (e.g., *bonitus, bonita, bonitum*) may be only a mild affront to grammatical sensibility, but the "twist" in *Rhizosolenia twistata* is definitely jarring.

Unsolved Taxonomic and Nomenclatural Problems

There is no across-the-board answer to the question of when and to what extent phylogeny should be incorporated in taxonomy. It seems reasonable to assume that, in the absence of serious nomenclatural consequences, incorporation would be highly desirable. Because cladistic classification involves the naming of clades whereas taxonomic classification involves the naming of taxa, the two nomenclatures are separate and serve different purposes.

An ever-increasing body of molecular and ultrastructural data fully supports the taxonomic recognition of several kingdoms. The ICBN and ICZN were developed to express the taxonomy of "typical" higher plants and animals, respectively, and thus fail to address many problems that face taxonomists who deal with other groups of organisms. Bacteria, which traditionally have been assigned to the plant kingdom, are covered by the recently developed International Code of Nomenclature of Bacteria, which is patterned after the ICBN with modifications to accommodate microbiological methods of research.

Although all flagellates were brought into the plant kingdom by Senn (1900), only the Volvocales sensu lato have been consistently treated under the ICBN. Silicoflagellates, dinoflagellates, euglenoids, chloromonads, and chrysomonads have often, if not usually, been treated under the ICZN. In many instances the authors failed to state which code they were using, causing uncertainty as to the validity (or availability) of the newly published names since botanical and zoological rules differ in this regard.

The existence of multikingdom classifications with only three nomenclatural codes is obviously problematic. Possible solutions have been discussed by Blackwell and Powell (1999). One solution would be to have a single code covering all organisms, a draft of which has been circulated as the BioCode (http://www.rom.on.ca/biodiversity/biocode/biocode1997.html). There is general agreement that this plan is not feasible in the face of 250 years of botanical and zoological traditions. Another solution would be to develop a code for each kingdom, a plan for which there is not much enthusiasm, partly because there is no consensus as to the circumscription of the various kingdoms. A third solution would be for an international commission to assign each major group of organisms to one or another of the three codes, ignoring taxonomic and phylogenetic considerations.

Alternatively, we could continue the present practice of allowing authors to choose which code they are using. A name available under one code but not under the other code could be conserved to ensure that a single taxon does not bear two correct names. For example, *Spirodinium* is a later homonym in zoological nomenclature, but it is the correct name for a genus of dinoflagellates in botanical nomenclature. To settle this conflict, *Gyrodinium,* which was published as a substitute name for *Spirodinium*, has been conserved under the ICBN with the concomitant rejection of *Spirodinium*.

The root of most interregnal problems is homonymy. Although ideally a generic name should have only one application in all of biology, in fact there are hundreds of correct names of plants that are also correct names of animals. We may not be bothered by the fact that *Eisenia* has been applied both to a kelp and to an annelid worm, but trying to read an ecological account of coral reefs in Madagascar where the dominant alga is *Turbinaria* and the dominant coral is also *Turbinaria* is bothersome. A more serious situation is the conflict between *Peranema* Dujardin 1841, a well-known colorless euglenoid, and *Peranema* D. Don 1825, a well-known fern. In this intractable situation we must accept the homonymous use of *Peranema,* fortified by the taxonomic distance between euglenoids and ferns.

Conclusion

Some problems in integrating phylogeny with taxonomy and expressing the resulting classification in nomenclature have been discussed. In bringing classification, phylogeny, and nomenclature into harmony, taxonomists must be willing to deviate from ideology, which under certain circumstances must yield to practicality.

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Literature Cited

Blackwell, W. H., and Powell, M. J. 1999. Reconciling kingdoms with codes of nomenclature: Is it necessary? Syst. Biol. 48:406–412.

Briquet, J. 1905. Texte synoptique des documents destinés à servir de base aux débats du Congrès international de Nomenclature botanique de Vienne. Berlin. 161 pp.

Briquet, J. 1906. Règles internationales de la Nomenclature botanique adoptées par le Congrès international de Botanique de Vienne 1905.... Jena. 99 pp.

Brown, R. W. 1956. Composition of scientific words....rev. ed. Smithsonian Institution, Washington, D.C. 882 pp.

Brummitt, R. K. 2002. How to chop up a tree. Taxon 51:31–41.

Candolle, A. de. 1867a. Lois de la nomenclature botanique. Paris. 60 pp.

Candolle, A. de. 1867b. Lois de la nomenclature botanique adoptées par le Congrès international de Botanique tenu à Paris en août 1867.... Genève. 64 pp.

Cantino, P. D. 2000. Phylogenetic nomenclature: Addressing some concerns. Taxon 49:85–93.

Copeland, H. F. 1938. The kingdoms of organisms. Quart. Rev. Biol. 13:383–420.

Dillon, L. S. 1963. A reclassification of the major groups of organisms based upon comparative cytology. Syst. Zool. 12:71–82.

Forey, P. L. 2002. *PhyloCode*—pain, no gain. Taxon 51:43–54.

Greuter, W. G. et al. (eds.). 2000. International Code of Botanical Nomenclature (Saint Louis Code). Koeltz, Königstein, Germany. [Regnum Vegetabile 138]

Haeckel, E. 1866. Generelle morphologie der organismen, Vol. 2. G. Reimer, Berlin. clx + 462 pp. 8 pls.

Hughey, J. R., Silva, P. C., and Hommersand, M. H. 2001. Solving taxonomic and nomenclatural problems in Pacific Gigartinaceae (Rhodophyta) using DNA from type material. J. Phycol. 37:1091–1109.

Leedale, G. F. 1974. How many are the kingdoms of organisms? Taxon 23:261–270.

Lindstrom, S. C., and Cole, K. M. 1992. The *Porphyra lanceolata–P. pseudolanceolata* (Bangiales, Rhodophyta) complex unmasked: Recognition of new species based on isozymes, morphology, chromosomes and distributions. Phycologia 31:431–448.

Linnaeus, C. 1753. Species plantarum.... Holmiae [Stockholm]. [xii +] 1200 + [31] pp.

Linnaeus, C. 1754. Genera plantarum.... Editio quinta. Holmiae [Stockholm]. [xxxii +] 500 + [22] pp.

Linnaeus, C. 1758. Systema naturae per regna tria naturae.... Editio decima. Holmiae [Stockholm]. Vol. 1. [i–iv +] [1]–823 [824 = Errata] pp.

Senn, G. 1900. Flagellata. In: Engler, A., and Prantl, K. (eds.), Die natürlichen Pflanzenfamilien.... I. Teil, Abt. 1a, pp. 93–188. Leipzig.

Silva, P. C. 1956. Evaluation of the Protista as a group of living organisms. Micropaleontology 2:294–295.

Silva, P. C. 1982. Taxonomic classification of algae. In: Mitsui, A., and Black, C. C., Jr. (eds.), CRC handbook of biosolar resources. Vol. 1, pt. 1, Basic principles, pp. 523–564. CRC Press, Boca Raton, Florida.

Silva, P. C. 1984. The role of extrinsic factors in the past and future of green algal systematics. In: Irvine, D. E. G., and John, D. M. (eds.), Systematics of the green algae, pp. 419–433. Academic Press, London.

Smith, G. M. 1950. The fresh-water algae of the United States. 2d ed. McGraw-Hill, New York. vii + 719 pp.

Stearn, W. T. 1992. Botanical Latin.... 4th ed. David & Charles, Newton Abbot [England]. xiv + 546 pp.

Stuessy, T. F. 1980. Cladistics and plant systematics: Problems and prospects. Introduction. Syst. Bot. 5:109–111.

Weber-van Bosse, A. 1898. Monographie des Caulerpes. Ann. Jard. Bot. Buitenzorg 15:243–401.

Whittaker, R. H. 1969. New concepts of kingdoms of organisms. Science 163:150–160.

Whittaker, R. H., and Margulis, L. 1978. Protist classification and the kingdoms of organisms. BioSystems 10:3–18.

Yoshida, T. 1983. Japanese species of *Sargassum* subgenus *Bactrophycus* (Phaeophyta, Fucales). J. Fac. Sci. Hokkaido Univ., ser. 5, Bot. 13:99–246.

Section II. Caulerpales

INTRODUCTION

Isabella A. Abbott

Among the tropical green algae, two genera, *Caulerpa* and *Codium,* are definitely of commercial value, the former in the Philippines and Japan, the latter in the Hawaiian Islands, Japan, and Korea. Some other places such as Samoa and Tonga may consume moderate amounts of *Caulerpa,* but these specimens are usually collected by householders, not purchased. For the most part, they are eaten raw or pickled, and in Polynesia they are covered with coconut cream and grated fresh coconut; that makes those who might turn up their noses at the thought of eating raw seaweeds absolutely relish the experience! There are many preparations in the Philippines for using fresh *Caulerpa* in salad, mostly with the fresh seaweed as the main ingredient of the dish; in southern Japan, *Caulerpa* and *Codium* are treated rather similarly as vinegared and flavored "pickled" seaweed. *Codium* is used in rather large amounts in some parts of Korea in the flavorful *kim chee* preparation.

The Hawaiian Islands are thought to be rather too cool for the best *Caulerpa* development, and although there are 14 species being described from the Islands in this section, they are not common in the field, and their sizes are much smaller than in locations nearer the equator. (On the other hand, *Codium* species, which are not described in this volume, are numerous in Hawaii, with 4 species being named as new this year).

ANNOTATED CHECKLIST OF SPECIES OF *CAULERPA* AND *CAULERPELLA* (BRYOPSIDALES, CAULERPACEAE) FROM VIETNAM, THAILAND, AND THE HAWAIIAN ISLANDS

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Karla J. McDermid

Abstract

Herbarium specimens and recent collections of *Caulerpa* and *Caulerpella* from Vietnam, Thailand, and the Hawaiian Islands were examined and compared. Eleven species were present at all three locations: *Caulerpa cupressoides, C. lentillifera, C. macrophysa, C. microphysa, C. peltata, C. racemosa, C. serrulata, C. sertularioides, C. taxifolia, C. verticillata,* and *Caulerpella ambigua*. *Caulerpa antoensis, C. cupressoides, C. elongata*, and *C. nummularia* are new records for the Hawaiian Islands.

Introduction

The genus *Caulerpa* (=creeping stem) was described by Lamouroux (1809) on the basis of 10 species, whose thalli consist of erect axes arising from creeping stolons attached to the substratum by rhizoids. The erect axes, also known as uprights or assimilators, show a variety of sizes, shapes, and branching. Branchlets or ramuli are often present on the central axes. Thalli are siphonous, with no crosswalls, and a network of cell wall in-growths called trabeculae provide support. During reproduction, the entire plant content converts to biflagellate zoospores (holocarpic). Other early workers continued to define additional species, notably Kützing (1849), who listed 41 species. Jacob Agardh (1872) organized *Caulerpa* into 13 tribes. Weber-van Bosse (1898) monographed the genus, bringing together descriptions and drawings for the entire array of named species and varieties. Svedelius (1906) discussed the ecology and biogeography of *Caulerpa* in his report on the genus in Ceylon. He described and illustrated 21 species and many varieties. Børgesen listed 11 species of *Caulerpa* from the Danish West Indies in 1913, then (1940) described 5 species from Mauritius. *Caulerpa* specimens from Java and the Philippines are reported in Gilbert (1942) and more recently in Meñez and Calumpong (1982). Yamada (1940, 1944a,b) worked on *Caulerpa* from Pohnpei and Ant Atoll in Micronesia. Taylor reported on *Caulerpa* from the northern Marshall Islands (1950) and the Andaman Sea (1965), as well as the Indian Ocean (1967).

A more recent series of papers on Caulerpales from the southwestern Pacific by Coppejans and colleagues provide useful keys, drawings, and descriptions (Coppejans 1992; Coppejans and Beeckman 1989, 1990; Coppejans et al. 1994; Coppejans and Meinesz 1988, Coppejans and Prud'homme van Reine 1992). Rather than using the term "variety," these workers use the term "ecad," which does not have taxonomic standing. Their term may, however, more accurately reflect the ecologically variable forms of *Caulerpa*.

Caulerpa species are notoriously variable, which has led to the description of a great number of varieties, subspecies, forms, and ecads, many of which intergrade. Culture studies have produced more than one "variety" growing from a single stolon; they have also shown significant changes in morphology under different environmental conditions such as light, temperature, salinity, or turbulence (Ohba et al. 1992; Carruthers et al. 1993). Thus, the status of such varieties is unclear, and this probably will remain so until genetic analyses are carried out.

Caulerpella ambigua (Okamura) Prud'homme van Reine et Lokhorst, was separated from *Caulerpa* and placed in a new genus because it is nonholocarpic: its reproductive branchlets are separated from the main axis by a wall (Prud'homme van Reine and Lokhorst 1992). South and N'Yeurt (1993) discussed *Caulerpella* specimens from Fiji, and the genus is also known from Vietnam, Thailand, and the Hawaiian Islands. The distinction between the two genera has been confirmed by the recent molecular work of Fama et al. (2002).

Various species of Caulerpa have been used economically (Chamberlain 1998; Payri et al. 2000; Littler and Littler 2003). In Thailand, C. racemosa var. corynephora and var. macrophysa are eaten as a fresh salad, and C. lentillifera has been used in water treatment ponds in association with shrimp aquaculture (A. Chirapart, pers. comm.). On the other hand, C. taxifolia, commonly sold for use in home aquaria throughout the world, has escaped to become an obnoxious pest, most notably in the Mediterranean, around San Diego, California, and in Australia (Jousson et al 1998; Meinesz et al. 2001; Wiedenmann et al. 2001; Williams and Grosholz 2002).

Caulerpa in Vietnam

Dawson (1954) listed several species of *Caulerpa* from sites near Nha Trang, Vietnam: *C. ambigua (=Caulerpella ambigua), C. fastigiata, C. serrulata, C. verticillata, C. vickersiae (=Caulerpella ambigua),* and *C. racemosa* var. *macrophysa (=C. macrophysa)*. Pham (1969) listed 13 species of *Caulerpa* in the flora of Vietnam, adding the following to those reported by Dawson: *C. brachypus, C. lentillifera, C. mexicana* var. *vietnamica, C. microphysa, C. macrodisca* (*C. peltata* var. *macrodisca*), *C. racemosa* var. *peltata (=C. peltata), C. racemosa* var. *occidentalis, C. sertularioides,* and *C. taxifolia.* Specimens of *Caulerpa* are also reported in Nguyen et al. (1993). Pham (1996) listed new records for *C. cupressoides* var. *mamillosa, C. webbiana* f. *tomentella*, and *C. peltata* var. *typica*. Pham et al. (2000) listed *C. crassifolia (=C. mexicana)* from ConDao Island, and Pham et al. (2002) added two varieties of *C. cupressoides* and one of *C. serrulata.* In collections made in 1999 in the vicinity of Nha Trang, Vietnam, Abbott et al. (2002) found *C. racemosa* var. *macrophysa* (=*C. macrophysa*), *C. serrulata*, and *C. verticillata*. Fourteen species of *Caulerpa* and one of *Caulerpella* are currently recognized for the Vietnam flora.

Caulerpa in Thailand

The first record of *Caulerpa* from Thailand was made by Reinbold (1901), who reported 11 species from the islands on the east coast of the Gulf of Thailand: *C. fastigiata* f. *minor, C. filiformis, C. freycinetii (=C. serrulata)* var. *typica* and var. *pectinata, C. lentillifera* var. *longistipitata, C. racemosa* var. *peltata (=C. peltata), C. plumaris (=C. sertularioides)* f. *longipes, C. racemosa* var. *uvifera, C. scalpelliformis* var. *intermedia, C. sedoides* f. *crassicaulis, C. urvilliana (=C. cupressoides* var. *urvilleana)* var. *typica* f. *tristicha, and C. verticillata.* Egerod (1971, 1974, 1975) reported *C. ambigua (=Caulerpella ambigua), C. fastigiata, C. mexicana, C. racemosa* var. *macrophysa (=C. macrophysa), C. racemosa* var. *peltata (=C. peltata), C. microphysa,* and *C. sertularioides* from the Andaman Sea, off the west coast of Thailand. Lewmanomont and Ogawa (1995) listed 10 species, adding 2, *C. crassifolia (=C. mexicana)* and *C. taxifolia,* as well as one variety, *C. racemosa* var. *corynephora*. Fourteen species of *Caulerpa* and one of *Caulerpella* are reported from Thailand.

Caulerpa in the Hawaiian Islands

In the Hawaiian flora, Eubank (1946) and Egerod (1952) described *C. ambigua* (4 varieties) *(=Caulerpella ambigua), C. lentillifera, C. racemosa* var. *macrophysa (=C. macrophysa), C. racemosa* var. *microphysa (=C. microphysa), C. racemosa* var. *peltata (=C. peltata), C. racemosa* (3 varieties), *C. serrulata* (1 variety and 3 forms), *C. sertularioides, C. taxifolia,* and *C. webbiana*. Magruder and Hunt (1979) provided photographs of *C. racemosa, C. serrulata, C. sertularioides,* and *C. taxifolia*. Abbott (1989) listed *C. ambigua (=Caulerpella ambigua), C. racemosa* vars. *clavifera, imbricata, laetevirens,* and *turbinata, C. racemosa* var. *peltata (=C. peltata), C. serrulata, C. taxifolia,* and *C. webbiana* from the Northwestern Hawaiian Islands. Thus 9 species of *Caulerpa* and the single *Caulerpella* species were reported from the Hawaiian Islands prior to this study.

Materials and Methods

The authors examined 102 specimens brought to the Hilo workshop from Vietnam, Thailand, and the Hawaiian Islands. All but 2 were dried herbarium specimens; the exceptions were liquid-preserved specimens of *C. nummularia* and *C. macrophysa* collected on Oahu, Hawaiian Islands, by the first author. Specimens were examined, and consensus was reached on species identifications. In the interests of collegial harmony, designations of variety and form were kept as determined by the original collector if there was no change in the species name and no clear reason to doubt the variety or form names. Additional Hawaiian specimens were examined after the workshop.

Following other workers, notably Kraft (2000) and Littler and Littler (2000), we recognize *C. macrophysa, C. nummularia,* and *C. peltata* rather than treat them as varieties of *C. racemosa*. We do, however, recognize that the specific boundaries in this group will remain poorly understood, and that other authors may disagree, until genetic or culture experiments clarify the situation.

Results[1]

Specimens of 16 species of *Caulerpa* were examined at the Hilo workshop, including 63 specimens of 10 species and many varieties from Vietnam, 25 specimens of 13 species from Thailand, and 14 specimens of 8 species from the Hawaiian Islands. Recent collections (obtained since the Hilo workshop) from the Northwestern Hawaiian Islands have yielded 4 new records for the northern archipelago: *C. antoensis* from Necker Island and Gardner Pinnacles, *C. cupressoides* from French Frigate Shoals, *C. elongata* var. *disticha* from Lisianski Island, and *C. microphysa* from Midway Atoll. The first 3 are also new records for the Hawaiian Islands as a whole. In addition, the presence of *C. nummularia* in the Hawaiian Islands is confirmed in this paper.

Caulerpa antoensis Yamada, Kagaku Nanyo 3, pp. 100–101, fig. 8, 1940.

Type Locality: Ant Atoll, near Pohnpei, Caroline Islands, Federated States of Micronesia.

Specimens Examined: *NWHI:* Necker Island, IA 29071, June 29, 2002; Gardner Pinnacles, from 48–74 m deep, IA 29064, June 30, 2002.

Plants up to 2 cm tall. Uprights featherlike, with terete central axis. Branchlets cylindrical and opposite, with acute tips.

Remarks: This species looks like a small, delicate *C. taxifolia*, but its stolons and parts of the erect branches are characteristically sticky with adherent sand grains. The presense of *C. antoensis* is a new record for the Hawaiian Islands.

Caulerpa brachypus Harvey, Proc. Amer. Acad. Arts 4, p. 333, 1860.

var. *parvifolia* (Harvey) Cribb, Univ. Queensland Pap. Bot. 3, p. 209, 1958.

Type Locality: Tanega-shima, Kagoshima Prefecture, Japan.

Specimens Examined: *Vietnam:* Myhoa, Phanrang, southern Vietnam, TR 98510, May 16, 1998.

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[1] The following abbreviations are used in the Results section: HI, Hawaiian Islands; NWHI, Northwestern Hawaiian Islands. Specimens from Vietnam and the Spratlys (TR) were provided by Pham Huu Tri; specimens from Thailand (KL, VS) were provided by K. Lewmanomont; and specimens from the Hawaiian Islands (IA, KM) were provided by L. Hodgson, K. McDermid, and I. A. Abbott.

Plants small. Uprights leaflike with small marginal teeth, obtuse at apex, up to 50 mm long and 2–4 mm wide.

Caulerpa cupressoides (Vahl) C. Agardh, Syn. algarim Scandinaviae, p. XXIII, 1817.

Type Locality: St. Croix, Virgin Islands.

Specimens Examined: *Vietnam:* Van Phong Bay, Khanh Hoa, TR 74280, July 3, 1974; Lyson Island, Quangngai, central Vietnam, TR 21065, March 15, 2002. *Thailand:* Ao Makham, Phuket, KL 0913, Oct. 13, 1971; Ko Samui, Surat Thani, S 2801, April 13, 1985. *NWHI:* French Frigate Shoals, KM 5928, Sept. 12, 2002.

Uprights tough, highly variable, irregularly branched. Each branch covered with several rows of short, terete, spiniform, upwardly curved branchlets.

Remarks: This is a new record for the Hawaiian Islands. This species is highly variable, and several varieties have been described.

Caulerpa cupressoides var. ***cupressoides*** Weber-van Bosse, In: Gepp and Gepp, Trans. Linn. Soc. London, 2d ser., Bot. 7, pp. 171–173, 1908.

Specimens Examined: *Vietnam:* Lyson Island, central Vietnam, TR 02600, March 15, 2002.

Caulerpa cupressoides var. ***flabellata*** Børgesen, Kongel. Danske Vidensk. Selsk. Skrift. 7, p. 368, 1907.

Specimens Examined: *Vietnam:* Hon Thu Island, southern Vietnam, TR 81344a,b, April 1981; Myhiep, Phanrang, TR 96432, March 15, 1996; Condao Island, southern Vietnam, TR 98201, Oct. 20, 1998. *Spratly Archipelago:* TR 93469, April 16, 1993;

Caulerpa cupressoides var. ***lycopodium*** Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, p. 335, pl. XXVII, figs. 8–13, 1898.

Specimens Examined: *Vietnam:* Coto Island, northern Vietnam, TR 75075, June 15, 1975; Lyson Island, central Vietnam, TR 83442, March 24, 1983; Hon Thu Island, southern Vietnam, TR 97301–2, May 8, 1997; Lyson Island, central Vietnam, TR 01282, April 12, 2001.

Caulerpa cupressoides var. ***mamillosa*** (Montagne) Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, pp. 332–333, pl. XXVIII, 1898.

Specimens Examined: *Vietnam:* Lyson Island, central Vietnam, TR 01084, April 2001. *Spratly Archipelago:* TR 270303, 870302, 1981; TR 93107–8, May 1993; TR 93456, May 1, 1993.

Caulerpa cupressoides var. ***urvilleana*** Coppejans and Prud'homme van Reine, Bull. Seanc. Acad. r. Sci. Outre-Mer Meded. Zitt. K. Acad. overzeese Wet. 37, p. 686, 1992.

(=*C. urvilliana* Montagne, In: Hombron and Jacquinot, Voyage au Pole Sud et dans l'Oceanie... p. 21, 1845)

Specimens Examined: *Spratly Archipelago:* TR 81541–43, April 7, 1984; TR 94500, April 15, 1994.

Remarks: The twisted variety of *C. cupressoides* is distinguished as var. *urvilleana*. We were surprised at how difficult it was to distinguish *C. cupressoides* var. *urvilleana* from twisted specimens of *C. serrulata* in herbarium specimens. We also found that the *C. serrulata* "teeth" were often almost as large as *C. cupressoides* ramuli. Therefore, identification on a herbarium sheet required the soaking of a section of the thallus and examination under dissecting microscope. In life or in liquid-preserved material, these taxa should be easy to distinguish.

Caulerpa elongata Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, pp. 271–272, pl. XXI, 1898.

Paratype Localities: Macassar (Ujung Pandang), Celebes, Indonesia, and Tongatapu, Tonga.

Specimens Examined: *NWHI:* Lisianski Island, KM 7274, Oct. 2, 2002.

Uprights usually numerous, covered with whorls of stiff branchlets 3 or 4 times dichotomously branched in alternate planes, with acute tips. Stolons often covered with whorls of branchlets too.

Remarks: This represents a new record for the Hawaiian Islands.

Caulerpa fastigiata Montagne, Ann. Sci. Nat. Bot., ser. 2, 8, pp. 353–354, 1837.

Type Locality: Cuba.

Specimens Examined: *Vietnam:* Van Phong, Nhatrang,TR 81890, March 20, 1981; Songlo, Nhatrang Bay, TR 820305, March 2, 1982. *Thailand:* Palian, Trang, KL 1404, June 24, 1973; Suan Son, Rayong, KL 1750, April 29, 1974 (var. *confervoides*).

Plants filamentous, 0.15–0.2 mm in diameter, forming mats, with little or no morphological differentiation between stolon and erect parts, except that stolons bear rhizoids, branching irregular to alternate to opposite. Branchlets with blunt tips.

Caulerpa filiformis (Suhr) Hering, Ann. Mag. Nat. Hist. 8, p. 91, 1841.

Type Locality: Algoa Bay, Cape Province, South Africa.

Specimens Examined: none.

Uprights flattened, strap-shaped with rounded tips, branched dichotomously or unbranched. Branchlets absent.

Remarks: This species was reported from Thailand by Reinbold (1901).

Caulerpa lentillifera J. Agardh, Abhandl. gabrete nat., Vol. 2, p. 173, 1873.

Type Locality: coast of Eritrea, Africa.

Specimens Examined: *Thailand:* Ko Kradat, Trat, KL 7074, Jan. 26, 1991. *HI:* Hilton Waikaloa Dolphin Lagoon, Hawaii, KM NC43, Oct. 11, 2002.

Uprights irregularly branched, densely covered with several longitudinal rows of subspherical (1–2 mm in diameter) branchlets clearly constricted at the base where the pedicel meets the sphere.

Remarks: This species can be confused with *C. racemosa*. In the South Pacific islands, *C. lentillifera* is eaten raw with freshly grated coconut and chili peppers or pickled in salads (Littler and Littler 2003). *Caulerpa lentillifera* was reported from Vietnam by Pham (1969).

Caulerpa macrophysa (Sonder ex Kützing) G. Murray, Ann. Mag, Nat. Hist., ser. 5, 20, p. 38, 1887.

Type Locality: Central America.

Specimens Examined: *Vietnam:* Tre Island, near Nha Trang, IA 24083, April 1999. *Thailand:* Ban Phe, Rayong, VS 1901, Aug. 2, 1976 (specimen labeled *C. racemosa* var. *macrophysa*). *HI:* Hunakai St., Kahala, Oahu, May 22, 2002 (Specimens were collected for dissection at this meeting and not numbered or kept; many specimens exist in the collections of I. A. Abbott and in the Bishop Museum herbarium).

Uprights bear sessile, spherical, mushroom-shaped or discoid branchlets, 3–7 mm in diameter. Stolons coarse, up to 4 mm in diameter.

Remarks: This species can be confused with *C. racemosa*. Photographs of *C. racemosa* in Payri et al. (2000, pp. 89, 95) look like our specimens of *C. macrophysa.*

Caulerpa mexicana Sonder ex Kützing, Sp. algarum, p. 496, 1849.

Type Locality: Mexico.

Specimens Examined: *Vietnam:* Quangninh, northern Vietnam, TR 69453, April 24, 1969; Condao Island, TR 98681–86, southern Vietnam, Oct. 15, 1998. *Thailand:* Ko Samet, Rayong, VS 3501, Dec 27, 1992; Kao Pilai, Phangnga, KL 2131, Sept. 5, 1975.

Plants variable in size. Uprights flattened and featherlike. Branchlets opposite, flat, upcurved, slightly constricted at base, tips tapering to acute apices.

Remarks: Some of the specimens from Vietnam and Thailand were labeled by their collectors as *Caulerpa crassifolia* (C. Agardh) J. Agardh, which was placed in synonomy with *C. mexicana* by Papenfuss (1956). *Caulerpa mexicana* was reported from Vietnam by Pham (1969). *Caulerpa mexicana* and *C. taxifolia* are similar in overall structure. However, in photographs such as those in Littler and Littler (2000), and in some drawings in Coppejans and Prud'homme van Reine (1992), these two species seem fairly distinct. The drawings and photographs usually agree in showing *C. mexicana* to be the "flatter" of the two, and *C. taxifolia* to have a slight but distinctive narrowing at the base of each branchlet. *Caulerpa mexicana* in the Caribbean has a more obviously flattened erect axis, especially at its base, whereas *C.*

taxifolia is clearly terete at the base of the erect axis, and the axis itself is more terete along its length than in *C. mexicana* (J. Norris, pers. comm.). The flat nature of *C. mexicana* is evident in the photograph in Huisman (2000, p. 253). On pressed herbarium sheets it is sometimes difficult to see the terete nature, so it is best to check this character prior to pressing. In Pham Huang Ho's (1969) drawings, the branchlets of *C. mexicana* are shown as overlapping. The KL specimen from Thailand was clearly flattened at the base of the upright axis, and other characters of the ramuli were consistent with its designation as *C. mexicana.* We do, however, recognize that the flattening could be an artifact of pressing. In Hawaiian specimens labeled *C. mexicana* in the herbarium of I. A. Abbott (examined after the workshop), the erect axis looked quite terete, and a slight narrowing of the ramuli at the base was visible, which transfers these specimens to *C. taxifolia.* Therefore, we have no clear evidence that *C. mexicana* is present in the Hawaiian Islands.

Caulerpa microphysa (Weber-van Bosse) J. Feldmann, Rev. Generale de Bot. 62, p. 430, 1955.

Type Locality: : Macassar (Ujung Pandang), Celebes, Indonesia.

Specimens Examined: *Thailand:* Kao Bae Na,Trang, KL 7701, March 14, 1998. *NWHI:* Midway Atoll, KM 5551, Sept. 20, 2002.

Plants small, 1–2 mm tall. Uprights bear sparse to clustered, small spherical branchlets that are clearly constricted at the base where the pedicel meets the sphere.

Remarks: *Caulerpa microphysa* is much like a small *C. racemosa* with sparse spherical ramuli about 1–2 mm in diameter. It is, however, distinctive in that its chloroplasts contain pear-shaped pyrenoids, whereas the chloroplasts of *C. racemosa* have no pyrenoids. A small fragment of the specimen from Thailand was soaked overnight, then treated with a drop of IKI and observed. The chloroplasts could be seen to have pyrenoids that were somewhat oblong, although not as clearly pear-shaped as seen in Coppejans and Meinesz (1988: figs. 15–16; also, figs. 17–21 show that *C. opposita* has pyrenoids, but they are spherical and the plant has larger, regularly opposite ramuli). Recent Hawaiian specimens also clearly show oval (not spherical) pyrenoids. *Caulerpa microphysa* was reported from Vietnam by Pham (1969). This is a new record for the Northwestern Hawaiian Islands.

Caulerpa nummularia Harvey ex. J. Agardh, Till algernes syst., p. 38, 1873.

Type Locality: Tonga and Nukahiva, Marquesas Islands.

Specimens Examined: *HI:* Coconut Island, Oahu, in sea tables, IA 28326, April 20, 2001, and IA 28165, Feb. 9, 2001; Hunakai St., Kahala, Oahu, IA 28262, March 14, 2001.

Uprights bear solitary or clustered, flattened, peltate branchlets with crenate or scalloped margins. Stolons thin, 0.4–0.9 mm in diameter.

Remarks: *Caulerpa racemosa* var. *exigua* was reported by Egerod in 1952, but it has not been collected in the Hawaiian Islands since then and may be identical with what we have now identified as *C. nummularia*. However, Eubank (1946:422) described her specimens as having peltate discs with "irregular serrations and proliferations at the margins," a character not quite consistent with *C. nummularia*. That feature is also shown for *C. racemosa* var. *exigua* in Kraft (2000:600, fig. 33F) from Lord Howe Island in the southwestern Pacific. *Caulerpa nummularia* is often identified as *C. peltata* (or *C. racemosa* var. *peltata)*, but upon close examination the species can be easily distinguished by noting the "not-quite-round" shape of the peltate ramuli as well as the presence of at least some ramuli with clearly crenate margins. Occasionally a new disc arises from the edge of an older disc. This last character was described by Reinke (1900) but doubted by Svedelius (1906). Hawaiian specimens look exactly like the drawing in Svedelius (1906:133, fig. 36) from Ceylon and also like the photograph in Littler and Littler (2000) from the Caribbean and the photograph labeled *C. peltata* in Payri et al. (2000). Although this species has been recognized for some time in the Hawaiian Islands, this is the first published report.

Caulerpa peltata Lamouroux, Nouv. Bull. Sci., Soc. Philomath. Paris 1, p. 332, 1809.

Type Locality: Antilles, West Indies.

Specimens Examined: *Vietnam:* Nghiloc, Nghean, northern Vietnam, TR 650445, 650415, April 22, 1965; Lyson Island, southern Vietnam, TR 82651, March 26, 1982; Condao, southern Vietnam, TR 98010, Oct. 20, 1998. *Spratly Archipelago:* TR 4105a,b, April 13, 1991, and TR 93405, May, 1993. *Thailand:* Ko Chik, Chanthaburi, KL 0622, May 8, 1969; Khlong Chao Mai, Trang, KL 7717, March 22, 1998. *HI:* Maalaea, Maui, IA 28254, May 18, 2001; Coconut Island, Oahu, in sea tables, IA 28162, Feb, 9, 2001. *NWHI:* Midway Atoll, KM 5569, Sept. 20, 2002; Kure Atoll, KM 7359, Sept. 25, 2002; Laysan Island, KM 7539, Sept. 17, 2002.

Uprights are unbranched and terminate in a peltate disc.

Remarks: Some specimens from Vietnam and Thailand were labeled by their collectors as *Caulerpa racemosa* var. *peltata* (Lamouroux) Eubank. *Caulerpa peltata* seems distinctly different from very similar plants with branched (racemose) upright axes and peltate ramuli in the *C. racemosa* complex. Kraft (2000) maintained these as 2 distinct species, *C. peltata* and *C. racemosa* var. *peltata*. Although we agree that Kraft is probably correct, we have utilized only the name *C. peltata* in this paper for both racemose and non-racemose forms, following the treatment in Silva et al. (1996) until such time as genetic or molecular research clarifies the situation.

Caulerpa peltata var. ***macrodisca*** (Decaisne) Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, p. 376, pl. XXVIII, 1898.

Specimens Examined: *Vietnam:* Hatien, southern Vietnam, TR 79403, April 18, 1979.

Caulerpa racemosa (Forsskål) J. Agardh, Lunds Univ. Arsskrift. 9(8), p. 35, 1872.

Type Locality: Suez, Egypt.

Specimens Examined: *HI:* Kaalawai, Oahu, IA 28345, May 17, 2001; Kaaawa, Swanzy Beach Park, Oahu, IA 28240, May 12, 2001. *NWHI:* Midway Atoll, KM 5594, Sept. 21, 2002; Necker Island (intertidal), KM 5670, Sept. 10, 2002; La Perouse Pinnacle (intertidal), French Frigate Shoals, KM 5859, Sept. 11, 2002; Laysan Island, KM 5999, Sept. 17, 2002.

Uprights bear small, 2–4 mm in diameter, spherical, oval or clavate, inflated branchlets in clusters like bunches of grapes. Stolons usually thick, 2–3 mm in diameter.

Remarks: Specimens TR 68024 and KL 8303 were equivocal and may actually turn out to be *C. ashmeadii* Harvey (Nereis boreali-americana, Pt. III, Smithson. Contr. 10(2), p. 18, pl. XXXVIIIA, 1858). *Caulerpa racemosa* has variable morphology, and several varieties have been described. Ohba and Enomoto (1987) confirmed that light and temperature influence morphology of *C. racemosa* in culture. Coppejans and Beeckman (1989) suggested that light intensity is a factor in development of varietal characteristics.

Caulerpa racemosa is eaten as a salad in the Cook Islands and French Polynesia (Payri et al. 2000). This species is also consumed at subsistence or commercial levels in Fiji, Samoa, Tonga, and the Solomon Islands (Chamberlain 1998).

Caulerpa racemosa (Forsskål) J. Agardh var. ***corynephora*** (Montagne) Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, p. 364, pl. XXXIII, 1898.

Specimens Examined: *Vietnam:* Quangninh, northern Vietnam, TR 68024, April 20, 1968, and TR 57365, March 1969; Lyson Island, Quangngai, central Vietnam, TR 21057, 21017, April 12, 2001. *Thailand:* Khlong Chao Mai, Trang, KL 7716, March 22, 1998; Khura Buri, Phangnga, KL 8301, 8303, Dec. 4, 2001.

Caulerpa racemosa var. ***occidentalis*** (Montagne) Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, p. 364, pl. XXXIII, 1898.

Specimens Examined: *Vietnam:* Sonhai, Phanrang, TR 80580, March 20, 1980.

Caulerpa racemosa (Forsskål) J. Agardh var. ***racemosa*** Weber-van Bosse, Ann. Jar. Bot. Buitenzorg 15, p. 363, pl. XXXIII, fig. 7, 1898.

Specimens Examined: *Vietnam:* Honchong, Nhatrang,TR 21201, March 31, 2002.

Caulerpa scalpelliformis (R. Brown ex Turner) C. Agardh, Syn. algarum Scandinaviae, p. XXII, 1817.

Type Locality: southern coast of Australia.

Specimens Examined: none.

Uprights flattened, fernlike. Central axes of branches wide and flattened. Branchlets flattened, pinnate, arising at an acute angle, about as long as the width of the central axis, with mucronate tips and without constricted bases.

Remarks: Reinbold (1901) reported this species from Thailand.

Caulerpa sedoides C. Agardh, Syn. algarum Scandinaviae, p. XXIII, 1817.

Type Locality: Kent Islands, Bass Strait, Australia.

Specimens Examined: none.

Uprights simple or sparingly branched, with distichous branchlets. Branchlets globose or obovate, and succulent, like leaves of stonecrops or members of the Crassulaceae.

Remarks: Reinbold (1901) reported this species from Thailand.

Caulerpa serrulata (Forsskål) J. Agardh, Mus. Senckenbergianum 2, p. 174, 1837.

Type Locality: Mokha, Yemen.

Specimens Examined: *Vietnam:* Sonhai, Phanrang,TR 78231, Oct. 23, 1978; Lyson Island, Quangngai, central Vietnam, TR 01060, April 12, 2001; Hon Thu Island, southern Vietnam, TR 81067, April 1981. *Spratly Archipelago:* TR 81540, 81561, April 7, 1981. *Thailand:* Moo Ko Ang Thong, Surat Thani, KL 1904, April 11, 1975; Ko Similan, Phangnga, KL 6716, March 13, 1990; Ko Kradat, Trat, KL 7068, Jan. 26, 1991. *HI:* Kaalawai, Oahu, IA 28346, May 17, 2001; Malaekahana, Oahu, IA 28142, Dec. 2, 2000. *NWHI:* Midway Atoll, KM 5592, Sept. 21, 2002; French Frigate Shoals, KM 5983, Sept.12, 2002; Laysan Island, KM 6035, Sept. 17, 2002; Maro Reef, KM 7046, Sept. 16, 2002; Pearl and Hermes Atoll, KM 7344, Sept. 12, 2002; Kure Atoll, KM 7449, Sept. 26, 2002.

Uprights with narrow, flattened, foliar branches, rick-rack-shaped (a flat, zigzag trim for clothing), sometimes contorted or twisted. Branches stiff with serrate, toothed margins and no branchlets.

Remarks: When *C. serrulata* twists, it becomes difficult to see that the teeth are present only along the margins. The twisting action makes the teeth overlap the axes, especially when pressed to make a herbarium sheet. For additional comments, see the note on *C. cupressoides* var. *urvilleana,* above.

Caulerpa serrulata var. **serrulata** f. **lata** (Weber-van Bosse) Tseng, Chin. Mar. Biol. Bull. 1, p. 178, 1936.

Specimens Examined: *Vietnam:* Hon Thu Island, southern Vietnam, TR 81422, April 22, 1981; Condao Island, southern Vietnam, TR 98204, Oct. 20, 1998; Lyson Island, Quangngai, central Vietnam, TR 82125, March 25, 1982.

Caulerpa sertularioides (Gmel.) Howe, Bull. Torr. Bot. Club, 32, p. 576, 1905.

Type Locality: "in coralliis americanis" (possibly tropical Atlantic America).

Specimens Examined: *Vietnam:* Phanrang, Cana, TR 280021, 280024, April 15, 1978. *Thailand:* Khura Buri, Phangnga, KL 8304, Dec. 4, 2001. *HI:* Malaekahana, Oahu, IA 28141, Dec. 2, 2000. *NWHI:* Laysan Island, KM 5998, Sept. 17, 2002.

Uprights featherlike, sometimes branched, with terete central axes with pinnate, opposite branchlets. Branchlets terete, not constricted at base, upcurved with mucronate tips.

Remarks: *Caulerpa sertularioides* is eaten in salads in some parts of the Pacific (Littler and Littler 2003).

Caulerpa sertularioides f. **bevies** (J. Agardh) Svedelius, Ceylon Mar. Biol. Lab. 2, pp. 114–115, fig. 10, 1906. (=Ceylon Mar. Biol. Rep. 4).

Specimens Examined: *Thailand:* Kao Lak, Phangnga, KL 2161, Dec. 1, 1975.

Caulerpa sertularioides var. **longipes** (J. Agardh) Collins, Tufts Coll. St. (Sci.) 2, p. 415, 1909.

Specimens Examined: *Thailand:* Ko Samet, Rayong, VS 3502, Dec. 27, 1992.

Caulerpa sertularioides var. **longiseta** (Bory) Svedelius, Ceylon Mar. Biol. Lab. 2, pp. 114–115, fig. 10, 1906. (=Ceylon Mar. Biol Rep. 4).

Specimens Examined: *Vietnam:* Quangninh, northern Vietnam, TR68035, May 20, 1968; Condao Island, southern Vietnam, TR98202, Oct. 20, 1998. *Thailand:* Taka Pa, Phangnga, KL 2121, May 5, 1975; Khura Buri, Phangnga, KL 8305, Dec. 4, 2001.

Caulerpa taxifolia (Vahl) C. Agardh, Sp. algarum, p. 435, 1822.

Type Locality: St. Croix, Virgin Islands.

Specimens Examined: *Thailand:* Kao Bae Na, Trang, KL 7702, March 14, 1998. *HI:* Hunakai St., Kahala, Oahu, IA 25028, 25047, March 15, 2000. *NWHI:* French Frigate Shoals, KM 5895, Sept. 12, 2002; Maro Reef, KM 7146, Sept. 16, 2002; Lisianski Island, KM 7295, Oct. 2, 2002.

Uprights flattened and shaped like fern fronds, with compressed central axes. Branches with pinnate, flattened, sickle-shaped branchlets. Branchlets curved, usually not overlapping, tapering toward acuminate apices, constricted at base.

Remarks: Without careful examination, this species can be confused with *C. mexicana* or *C. sertularioides. Caulerpa taxifolia* was reported from Vietnam by Pham (1969). See note for on *C. mexicana,* above.

Caulerpa verticillata J. Agardh, Öfvers Förh. Kongl. Svenska Vetensk.-Akad. 4, p. 6, 1847.

Type Locality: West Indies.

Specimens Examined: *Vietnam:* Songlo, Nhatrang Bay, TR 820305, March 3, 1982; Hon Mieu Rocks, near Nha Trang, IA 24104, April 1999. *Thailand:* Khura Buri, Phangnga, KL 8303, Dec. 4, 2001. *HI:* Coconut Island, Oahu, in sea tables, IA 28164, 28327, Feb. 11, 2001.

Plants growing in dense, soft tufts 3–7 cm high, densely branched. Uprights with conspicuous, delicate, whorls of verticillate clusters of branchlets. Branchlets up to 0.25 mm in diameter, dichotomously branched 5–7 times.

Caulerpa webbiana Montagne, Ann. Sci. Nat, Bot, ser 2, 8, p. 354, 1837.

f. **tomentella** (Harvey ex J. Agardh) Weber-van-Bosse, Ann. Jar. Bot. Buitenzorg 15, pp. 270–271, pl. XXI, fig. 4, 1898.

Type Locality: Arrecife, Isla Lansarote, Islas Canarias.

Specimens Examined: *Spratly Archipelago:* TR93105–6, May 20, 1993. *HI:* Kaalawai, Oahu, IA 28348, May 17, 2001. *NWHI:* Kure Atoll, KM 5822, Sept. 25, 2002; French Frigate Shoals, KM 5949, Sept. 12, 2002; Laysan Island, KM 6034, Sept. 17, 2002; Maro Reef, KM 7067, Sept. 16, 2002; Necker Island, KM 7185, Sept. 10, 2002.

Plants small. Uprights covered with whorled or opposite branchlets. Branchlets less than 1 mm long, dichotomously branched, terete at base, flattened at tips.

Caulerpella ambigua (Okamura) Prud'homme van Reine and Lokhorst, Nova Hedwigia 54, p. 114, 1992.

Type Locality: Ogasawara-gunto (Bonin Islands), Japan.

Specimens Examined: *Vietnam:* Nhatrang Bay, central Vietnam, TR78050 *(=C. vickersiae),* May 16, 1978. *Thailand:* Samae Sarn, Chon Buri, KL 3543, Aug. 22, 1982. *HI:* Laie, Oahu, IA 11466, Aug. 29, 1973; Maalaea, Maui, IA 14503, Aug. 30, 1978.

Plants small, usually less than 2 cm tall, forming cushions often on rocks, irregularly branched. Each branch bears whorls of fine branchlets, giving furry appearance. Branchlets terete, distichous or irregularly radially arranged, simple or with forked tips, mostly near tips of branch. Fertile branchlets that bear compound whorls of zoosporangia are separated from main axis by transverse wall.

Remarks: Silva et al. (1996) retained this species in the genus *Caulerpa* based on the shared internal trabeculate structure. They thought that non-holocarpic reproduction, as reported by Prud'homme van Reine and Lokhorst (1992), should have infrageneric taxonomic value.

Conclusions

In summary, Vietnam has a total of 14 species of *Caulerpa*, Thailand has 15 species, and the Hawaiian Islands 14, with many shared species (Table 1). This diversity of *Caulerpa* species is well within the range reported from elsewhere in the central and south Pacific. For instance, 14 *Caulerpa* species are known from Papua New Guinea (Coppejans and Meinesz 1988; Coppejans 1992; Coppejans et al. 1994); 12 from Fiji (South and N'Yeurt 1993); 11 from Pohnpei and Ant in the Caroline Islands (Hodgson and McDermid 2000); 7 from Lord Howe Island (Kraft 2000); 11 from French Polynesia (Payri et al. 2000); and a total of 26 species reported from throughout the South Pacific (Littler and Littler 2003).

Table 1. Distribution of Species of *Caulerpa* and *Caulerpella* among Vietnam, Thailand, and the Hawaiian Islands, Based on Specimens Examined and Previous Literature Reports

	Vietnam	Thailand	Hawaiian Islands
Caulerpa antoensis	-	-	+
Caulerpa brachypus	+	-	-
Caulerpa cupressoides	+	+	+
Caulerpa elongata	-	-	+
Caulerpa fastigiata	+	+	-
Caulerpa filiformis	-	+	-
Caulerpa lentillifera	+	+	+
Caulerpa macrophysa	+	+	+
Caulerpa mexicana	+	+	-
Caulerpa microphysa	+	+	+
Caulerpa nummularia	-	-	+
Caulerpa peltata	+	+	+
Caulerpa racemosa	+	+	+
Caulerpa scalpelliformis	-	+	-
Caulerpa sedoides	-	+	-
Caulerpa serrulata	+	+	+
Caulerpa sertularioides	+	+	+
Caulerpa taxifolia	+	+	+
Caulerpa verticillata	+	+	+
Caulerpa webbiana	+	-	+
Caulerpella ambigua	+	+	+

Eleven species in this study were present in all three locales, Vietnam, Thailand, and the Hawaiian Islands: *Caulerpa cupressoides, C. lentillifera, C. macrophysa, C. microphysa, C. peltata, C. racemosa, C. serrulata, C. sertular-*

ioides, C. taxifolia, C. verticillata, and *Caulerpella ambigua.* Some species seemed to have more restricted distributions among the three locations: *C. brachypus, C. filiformis, C. scalpelliformis, C. sedoides, C. antoensis, C. elongata,* and *C. nummularia.* This similarity in species richness and composition was unexpected in light of the Hawaiian Islands' relative geographic isolation and the depauperate nature of some of its other marine populations (e.g., fish and coral). The recent four new records from the Northwestern Hawaiian Islands were particularly surprising. Three of them, *C. antoensis, C. cupressoides,* and *C. elongata,* have not been found in the more southerly, and hence more tropical, main Hawaiian islands. *Caulerpa nummularia* is newly reported from the main Hawaiian islands, although it may be the same entity formerly reported as *C. racemosa* var. *exigua.*

Caulerpa remains an enigmatic, ecologically variable genus that challenges the taxonomist. With upcoming DNA sequencing data to assist in clarifying relationships, we may soon have a better understanding of some of the morphological varieties. In the meantime, the economic and ecological importance of *Caulerpa* demands that we expand our efforts to understand this beautiful and speciose group of seaweeds.

Literature Cited

Abbott, I. A. 1989. Marine algae of the Northwest Hawaiian Islands. Pacific Sci. 43(3):223–233.

Abbott, I. A., Fisher, J., and McDermid, K. J. 2002. Newly reported and revised marine algae from the vicinity of Nha Trang, Vietnam. In: Tax. Econ. Seaweeds 8, pp. 291–321.

Agardh, J. G. 1872. Till algernes systematik. Nya bidgrag. Lunds Universitets Ars-Skrift. Afdelningen for Mathematik och Naturvetenskap 9. I. *Caulerpa.* 71 pp.

Børgesen, F. 1913. The marine algae of the Danish West Indies, Part 1. Chlorophyceae. Dansk. Bot. Ark. 1(4):1–158, 126 figs., map.

Børgesen, F. 1940–1953. Some marine algae from Mauritius. Kongel. Danske Vidensk. Selsk. Biol. Meddell. 14(4):1–81, 1940; 20(6):1–46, 1946; 21(9):1–62, 1953.

Carruthers, T. J. B., Walker, D. I., and Huisman, J. M. 1993. Culture studies on two morphological types of *Caulerpa* (Chlorophyta) from Perth, Western Australia, with a description of a new species. Bot. Mar. 36(6):589–596.

Chamberlain, T. 1998. Field study, proximate analysis, shelf-life extension experiments and culture experiments for the edible seaweed *Caulerpa racemosa.* Univ. South Pacific Tech. Rept. 98/1, 33 pp.

Coppejans, E. 1992. Marine algae of Papua New Guinea (Madang Prov.): 2. A revised and completed list of *Caulerpa* (Chlorophyta—Caulerpales). Blumea 36:383–410.

Coppejans, E., and Beeckman, T. 1989. *Caulerpa* section Sedoideae (Chlorophyta, Caulerpales) from the Kenyan coast. Nova Hedwigia 49(3–4):381–893.

Coppejans, E., and Beeckman, T. 1990. *Caulerpa* (Chlorophyta, Caulerpales) from the Kenyan coast. Nova Hedwigia 50(1–2):111–125.

Coppejans, E., DeClerck, O., and Van Den Heede, C. 1994. Annotated and illustrated survey of the marine macroalgae from Motupore Island and vicinity (Port Moresby, Papua New Guinea): I. Chlorophyta. Biol. Jaarb. Dodonaea 62:70–108.

Coppejans, E., and Meinesz, A. 1988. Marine algae of Papua New Guinea (Madang Prov.): 1. Caulerpaceae (Chlorophyta—Caulerpales). Blumea 33:181–196.

Coppejans, E., and Prud'homme van Reine, W. F. 1992. Seaweeds of the Snellius II Expedition (E. Indonesia): The genus *Caulerpa* (Chlorophyta—Caulerpales). Bull. Seanc. Acad. r. Sci. Outre-Mer Meded. Zitt. K. Acad. Overzeese Wet. 37 (1991–4):667–712.

Dawson, E. Y. 1954. Marine plants in the vicinity of the Institute Oceanographique de Nha Trang, Vietnam. Pacific Sci. 8:372–469, 63 figs., 1 map.

Egerod, L. E. 1952. An analysis of the siphonous Chlorophycophyta: With special reference to the Siphonocladales, Siphonales, and Dasycladales of Hawaii. Univ. Calif. Publ. Bot. 25(5):325–424.

Egerod, L. E. 1971. Some marine algae from Thailand. Phycologia 10:121–142.

Egerod, L. E. 1974. Report of the marine algae collected on the Fifth Thai–Danish expedition of 1966: Chlorophyceae and Phaeophyceae. Bot. Mar. 17:130–157.

Egerod, L. 1975. Marine algae of the Andaman Sea coast of Thailand: Chlorophyceae. Bot. Mar. 18:41–66.

Eubank, L. L. 1946. Hawaiian representatives of the genus Caulerpa. Univ. Calif. Publ. Bot. 18(18):409–432, 22 plates.

Fama, P., Wysor, B., Kooistra, W. H. C. F., and Zuccarello, G. 2002. Molecular phylogeny of the genus *Caulerpa* (Caulerpales, Chlorophyta) inferred from chloroplast *tuf*A gene. J. Phycol. 38:1040–1050.

Gilbert, W. J. 1942. Notes on *Caulerpa* from Java and the Philippines. Pap. Michigan Acad. Sci. 27:7–26.

Hodgson, L. M., and McDermid, K. J. 2000. Marine plants of Pohnpei and Ant Atoll: Chlorophyta, Phaeophyta and Magnoliophyta. Micronesica 32(2):289–307.

Huisman, J. M. 2000. Marine plants of Australia. University of Western Australia Press, Australian Biological Resources Study. Nedlands, Western Australia. 300 pp.

Jousson, O., Pawlowski, J., Zaninetti, L., Meinesz, A., and Boudouresque, C.- F. 1998. Molecular evidence for the aquarium origin of the green alga *Caulerpa taxifolia* introduced to the Mediterranean Sea. Mar. Ecol. Prog. Ser. 172:275–280.

Kraft, G. T. 2000. Marine and estuarine benthic green algae (Chlorophyta) of Lord Howe Island, south-western Pacific. Austral. Syst. Bot. 13:509–648.

Kützing, F. T. 1849 [1845–1871]. Species algarum. Leipzig. 922 pp.

Lamouroux, J. V. G. 1809. Memoire sur les Caulerpes. J. Bot. (Desvaux) 2:136–146, pls. 1–3.

Lewmanomont, K., and Ogawa, H. 1995. Common seaweeds and seagrasses of Thailand. Faculty of Fisheries, Kasetsart University. 164 pp.

Littler, D. S., and Littler, M. M. 2000. Caribbean reef plants. Offshore Graphics, Washington, D.C. 542 pp.

Littler, D. S., and Littler, M. M. 2003. South Pacific reef plants. Offshore Graphics, Washington, D.C. 331 pp.

Magruder, W. H., and Hunt, J. W. 1979. Seaweeds of Hawaii: A photographic identification guide. Oriental Publishing, Honolulu. 116 pp.

Meinesz, A., Belsher, T., Thibaut, T., Anatolic, B., Mustapha, K. B., Boudouresque, C.- F., Chiaverini, D., Cinelli, F., Cottalorada, J.- M., Djellouli, A., El Abed, A., Orestano, C., Grau, A. M., and Ivesa, L. 2001. The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. Biol. Invasions 3(2):201–210.

Meñez, E. G., and Calumpong, H. P. 1982. The Genus *Caulerpa* from central Visayas, Philippines. Smithsonian Contr. Mar. Sci. 17:1–21.

Nguyen Huu Dinh, Huynh Quang Nang, Tran Hgoc But, and Nguyen Van Tien. 1993. Marine algae of North Vietnam. Science and Technique Publishing House, Hanoi, Vietnam.

Ohba, H., and Enomoto, S. 1987. Culture studies on *Caulerpa* (Caulerpales, Chlorophyceae): II. Morphological variation of *C. racemosa* var. *laetevirens* under various culture conditions. Sorui Jpn. J. Phycol. 25:178–188.

Ohba, H., Nashima, H., and Enomoto, S. 1992. Culture studies on *Caulerpa* (Caulerpales, Chlorophyceae): 3. Reproduction, development and morphological variation of laboratory-cultured *C. racemosa* var. *peltata*. Bot. Mag. (Tokyo) 105(1080):589–600.

Papenfuss, G. F. 1956. Notes on South African marine algae: IV. J. S. African Bot. 22:65–77.

Payri, C., N'Yeurt, A. D. R., and Orempuller, J. 2000. Algues de Polynesie française. Au Vent Des Îles, Tahiti. 320 pp.

Pham Hoang Ho. 1969. Marine algae of South Vietnam. Ministry of Education and Youth. 558 pp.

Pham Huu Tri. 1996. Contribution to study on the seaweeds in Spratly Archipelago. In: Vo, V. L. (ed.), Collection of marine research works, Vol. 7, pp. 147–162. Science and Technique Publishing House, Hanoi.

Pham Huu Tri, Nguyen Huu Dai, and Nguyen Xuan Vy. 2000. New records of marine algae from Vietnam. In: Nguyen, T. A. (ed.), Collection of marine research works, Vol. 10, pp. 127–140. Science and Technique Publishing House, Hanoi.

Pham Huu Tri and Nguyen Huu Dai. 2002. Some new records of marine algae from Vietnam 1. In: Nguyen, T. A. (ed.), Collection of marine research works, Vol. 12, pp. 149–158. Science and Technique Publishing House, Hanoi.

Prud'homme van Reine, W. F., and Lokhorst, G. M. 1992. *Caulerpella* gen. nov., a non-holocarpic member of the Caulerpales (Chlorophyta). Nova Hedwigia 54:113–126.

Reinbold, T. 1901. Marine algae (Chlorophyceae, Phaeophyceae, Dictyotales, Rhodophyceae). In: Schmidt, J. [1900–1916], Flora of Koh Chang: Contributions to the knowledge of vegetation in the Gulf of Siam, Pt. 4, pp. 187–201. Bianco Luno, Copenhagen.

Reinke, J. 1900. Ueber *Caulerpa*. Ein Beitrag zur Biologie der Meeres-Organismen. Wissenschaftl. Meeresuntersuchungen herausgegeben von der Kom. zur wiss. Untyers. d. deutsche Meere in Kiel. N. Folge, Bd V., Heft I. Abt. Kiel. u. Leipzig (as cited and discussed in Svedilius,1906).

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. Univ. Calif. Publ. Bot. 79:1–1259.

South, G. R., and N'Yeurt, A. D. R. 1993. Contributions to a catalogue of benthic marine algae of Fiji: II. *Caulerpa* and *Caulerpella* (Chlorophyta—Caulerpales). Micronesica 26(2):109–138.

Svedelius, N. 1906. Ecological and systematic studies of the Ceylon species of *Caulerpa*. Ceylon Mar. Biol. Reports, Part II, June, 1906, 81–144.

Taylor, W. R. 1950. Plants of Bikini and other Northern Marshall Islands. University of Michigan Press, Ann Arbor. 227 pp.

Taylor, W. R. 1965. An interesting *Caulerpa* from the Andaman Sea. J. Phycol. 1:154–156.

Taylor, W. R. 1967. Species of *Caulerpa* (Chlorophyceae) collected on the International Indian Ocean Expedition. Blumea 15(1):45–53.

Weber-van Bosse, A. 1898. Monographie des *Caulerpa.* Ann. Jar. Buitenzorg 4(2):243–401, 15 pl.

Wiedenmann, J., Baumstark, A, Pillen T. L., Meinesz, A., and Vogel, W. 2001. DNA fingerprints of *Caulerpa taxifolia* provide evidence for the introduction of an aquarium strain into the Mediterranean Sea and its close relationship to an Australian population. Mar. Biol. 138(2):229–234.

Williams, S. L.,and Grosholz, E. D. 2002. Preliminary reports from the *Caulerpa taxifolia* invasion in southern California. Mar. Ecol. Prog. Ser. 233:307–310.

Yamada, Y. 1940. *Caulerpa* in Micronesia. Kagaku Nanyo 3(2):11–23.

Yamada, Y. 1944a. New *Caulerpas* and *Halimedas* from Micronesia. Sci. Pap. Inst. Algol. Res., Fac. Sci. Hokkaido Univ. 3:27–29.

Yamada, Y. 1944b. A list of the marine algae from the Atoll of Ant. Sci. Pap. Inst. Algol. Res., Fac. Sci. Hokkaido Univ. 3:31–45.

INTRODUCTION

Isabella A. Abbott

We have a "new" seaweed in this section, which is actually a very old one since *Dictyota* is a Lamouroux genus of 1809. Roy Tsuda has done those of us who occasionally work on floras from far-off places like Micronesia (which is where he is) the favor of bringing together various species that were misidentified or had misapplied names. Not only does he give them correct names, using the new and comprehensive monograph on *Dictyota* by De Clerck,[1] but he also gives a clearer description about where they are distributed in those myriad islands of the western central Pacific. *Dictyota* may not be an important economic genus, but it is so common in the tropics that we can use any help we can get to help identify the species.

The four papers on *Sargassum* represent three different ways to handle that genus (at least temporarily). The paper by Ajisaka and Lewmanomont shows a good way of using the interests of two phycologists from two different countries in a challenging ecological study on the stolon-like bases of *Sargassum stolonifolium*. They expanded the distribution of the species from

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[1] De Clerck, O. 2003. The genus *Dictyota* (Dictyotales, Phaeophyta) in the Indian Ocean. Opera Botanica Belgica, vol. 13. National Botanic Garden, Meise, Belgium. 205 pp., 54 figs.

Penang Island (the type locality) to other locations on the Andaman Sea coast of Thailand, indicating that the appearance of the stolons was dependent on where the plants were growing. Two papers on the taxonomy of *Sargassum,* one from China by Tseng and Lu and one from Vietnam by Nguyen Huu Dai, show that there are many new species to discover. Finally, morphological and molecular examinations of taxa in subgenus *Schizophycus* of *Sargassum* show that inconclusive or puzzling results mean, not only that much rearrangement is in store for the subgenus and the researchers, but without doubt when "the dust is settled" the systematics of that subgenus will be in better shape than it is now. There will be numerous impacts to the entire classification of the genus. We will be eagerly awaiting further results.

DICTYOTA (PHAEOPHYCEAE) FROM MICRONESIA

Roy T. Tsuda

Abstract

Of the 12 species of *Dictyota* and 1 species of *Dilophus* (Phaeophyceae, Dictyotales, Dictyotaceae) reported from Micronesian marine waters, 5 species of *Dictyota* which encompass 7 previously recorded species are recognized at this time in this region, namely, *D. bartayresiana* Lamouroux (=*D. bartayresii* Lamouroux, includes *D. cervicornis* Kützing as a misapplied name), *D. ceylanica* Kützing (previously recognized as *D. divaricata* Lamouroux a misapplied name), *D. friabilis* Setchell, *D. grossedentata* De Clerck et Coppejans (previously recognized as *D. patens* J. Agardh and *D. crenulata* J. Agardh as misapplied names), and *D. hamifera* Setchell. Two species, *D. acutiloba* J. Agardh and *D. pinnatifida* Kützing, were reported from Pohnpei and the Marshall Islands, respectively; however, these species identifications were based on fragmentary specimens. Collections of mature intact specimens should be made from the respective islands and atolls to substantiate the presence of these species in Micronesian waters. Further collections and studies are needed to determine the erect and broad species of *Dictyota* commonly lumped into the *D. dichotoma* (Hudson) Lamouroux (=*D. apiculata* J. Agardh) complex. *Dictyota alternifida* J. Agardh was mistakenly listed as previously reported in 1930 from Palau; the species has never been reported from Micronesia. *Dilophus radicans* Okamura, initially described as a new species from Pohnpei, is now considered to be the vaughaniella stage of *Padina boryana* Thivy and, thus, was not transferred to the genus *Dictyota*.

Introduction

Within the division Phaeophyta, the taxonomy of the genera *Sargassum* and *Dictyota* (Phaeophyceae, Dictyotales, Dictyotaceae) in Micronesian marine waters has been problematic. Tsuda (1988) reported the taxonomy of the common Micronesian *Sargassum* on the basis of field and microscopic observations of *Sargassum* from Guam and other Micronesian islands, with the collaboration of algal taxonomists from Hawaii and the neighboring Pacific countries during the 1986 Qingdao Workshop.

The present report on the Micronesian *Dictyota* is, likewise, mainly based on field observations of *Dictyota* in the inshore marine waters of Guam, Northern Marianas, Palau, Federated States of Micronesia, Marshall Islands, and Hawaii. Secondary metabolites such as diterpenes in *D. bartayresiana* Lamouroux and "*Dictyota cervicornis* Kützing," a misapplied name for the spirally twisted *D. bartayresiana,* have been the subject of feeding deterrent studies relative to tropical herbivores on Guam (Paul 1987; Wylie and Paul

1988; Meyer et al. 1994). Extracts of secondary metabolites of *"D. cervicornis"* served as an effective deterrent against predation by herbivores (Paul 1987); however, the live intact narrow spiral thalli were highly susceptible to grazing by herbivores in the field. Pachydictyol A has been isolated from Guam's *D. bartayresiana* (Wylie and Paul 1988), whereas 3 diterpenoid secondary metabolites—acutilol A acetate, acutilol A, and acutilol B—have been isolated (Cronin et al. 1997) from Hawaii's *D. acutiloba* J. Agardh.

Tsuda and Wray (1977) and Tsuda (1981a, 2002a,b,c, 2003) report a total of 10 species of *Dictyota* from publications applicable to Micronesia: *D. apiculata* J. Agardh, *D. bartayresiana* Lamouroux, *D. cervicornis* Kützing, *D. crenulata* J. Agardh, *D. dichotoma* (Hudson) Lamouroux, *D. divaricata* Lamouroux, *D. friabilis* Setchell, *D. hamifera* Setchell, *D. patens* J. Agardh, and *D. pinnatifida* Kützing. An eleventh species, *D. acutiloba* J. Agardh, was recently reported from Pohnpei and Ant Atoll by Hodgson and McDermid (2000).

Tokida (1939) listed *D. alternifida* J. Agardh in his compilation of Micronesian marine benthic algae and credited Yamada (1930) as reporting the species from Palau. There is, however, no mention of *D. alternifida* in the paper by Yamada (1930), which describes the new species *Udotea geppii* Yamada, from Palau. The type locality of *D. alternifida* is Port Phillips Head, Victoria, Australia.

Dilophus radicans Okamura was originally described from Pohnpei by Okamura (1916) and was also reported from Palau by Tokida (1939) and Kanda (1944). Fan (1953) studied specimens attributed to *D. radicans* and concluded that the specimens represented the vaughaniella stage of *Padina commersonii* Bory; *P. commersonii* is now considered a misapplied name for *P. boryana* Thivy. If *D. radicans* had remained a distinct species, the species would have to be transferred to the genus *Dictyota* with a different specific epithet. *Dictyota radicans* Harvey already exists, and its type locality is Rottnest Island, Fremantle, Western Australia.

In a study of the effects of different habitats on the morphological variation of 3 species of *Dictyota* on Guam, Potter (1986) concluded that *D. friabilis* and *D. cervicornis,* as reported by Tsuda (1972a) from Guam, were really ecomorphs (i.e., environmental growth forms) of *D. bartayresiana.* The transplantation and field observations of the growth of live thalli at three sites—leeward wave-washed rocky shore, quiet lagoonal environment, and windward reef flat—indicated that the intensity of water movement at a particular site appeared to be the primary causal factor for the development of the ecomorphs. Prostrate thalli resembling *D. friabilis* were dominant on the leeward wave-washed rocky shore of Luminao Reef, whereas long spiral thalli resembling *D. cervicornis* were conspicuous in the quiet lagoonal environment of Cocos Lagoon. The typical clumps of *D. bartayresiana* were dominant on the windward reef flat of Pago Bay.

Methods

The present taxonomic account is based on field observations of the morphological ranges within each of the species in different habitats and microscopic examinations in relation to the findings of previous investigators. The following political entities are covered in this study: Territory of Guam, Commonwealth of the Northern Mariana Islands, Republic of Palau, Federated States of Micronesia (Yap State, Chuuk State, Pohnpei State, and Kosrae State), Marshall Islands, Kiribati (Gilbert Islands), and Tuvalu (Ellice Islands). The latter two island groups are not normally considered political parts of Micronesia, but these southern atolls and islands are contiguous with the Marshall Islands.

Silva et al.'s (1996) catalogue on Indian Ocean algae and De Clerck's (1999) doctoral dissertation on Indian Ocean *Dictyota* served as the major literature on the nomenclature and taxonomy of the genus *Dictyota*.

Results

Of the remaining 11 species of *Dictyota* (i.e., excluding *D. alternifida* and *Dilophus radicans*) reported from Micronesia, 5 species appear morphologically distinct based on examinations of live, pickled, and dried specimens; these 5 species incorporate 4 misapplied names. The 5 species are *D. bartayresiana* Lamouroux (=*D. bartayresii* Lamouroux, includes *D. cervicornis* Kützing as a misapplied name), *D. ceylanica* Kützing (previously recognized by the misapplied name *D. divaricata* Lamouroux), *D. friabilis* Setchell, *D. grossedentata* De Clerck et Coppejans (previously recognized by the misapplied names *D. patens* J. Agardh and *D. crenulata* J. Agardh), and *D. hamifera* Setchell.

The identifications of *D. acutiloba* J. Agardh from Pohnpei and Ant Atoll (Hodgson and McDermid 2000) and *D. pinnatifida* Kützing (Taylor 1950) from the Marshall Islands were based on fragmentary specimens and represent the only records of these two species from Micronesia. I have not examined any specimens of *D. pinnatifida* from Micronesia. I have observed a 2-cm long fragment of *D. acutiloba* from Ant Atoll identified by Hodgson and McDermid (2000). I feel confident that further observations of these two species from the applicable islands and atolls will reinforce the presence of these species in Micronesian waters.

Micronesian specimens identified as *D. dichotoma* (Hudson) Lamouroux and *D. apiculata* J. Agardh must be revisited and studied. *Dictyota apiculata* J. Agardh is recognized as a synonym of *D. dichotoma* (Hudson) Lamouroux (Womersley 1987), and *D. dichotoma* is a species restricted to the North Atlantic (Schnetter et al. 1987).

Vegetative Key to 8 Species of Micronesian *Dictyota*

1\. Thallus procumbent. 2
1\. Thallus upright 4
  2. Apices acute, branches less than 2 mm wide, wide angled . . . .
  . . . . *D. ceylanica* Kützing
  [*D. divaricata* Lamouroux, misapplied name]
  2. Apices rounded, branches 2–4 mm wide, not wide angled 3
3\. Margins entire, iridescent bluish green. . . . . *D. friabilis* Setchell
3\. Margins with few triangular teeth, greenish brown . . . .
. . . . *D. grossedentata* De Clerck et Coppejans
[*D. patens* J. Agardh, misapplied name]
  4. Thallus not bushy or in clumps, narrow basal portion
  expanding terminally . . . . *D. dichotoma* (Hudson) Lamouroux
  [=*D. apiculata* (Hudson) Lamouroux]
  4. Thallus bushy or in clumps, margins entire 5
5\. Thallus upright, bushy, yellow brown to dark brown 6
5\. Thallus prostrate and upright, clumps, greenish brown 7
  6. Branches, dark brown, spirally twisted, dichotomous, apices acute . . . .
  . . . . *D. acutiloba* J. Agardh
  6. Branches, greenish brown, alternate to irregular, apices blunt
  . . . . *D. pinnatifida* Kützing
7\. Terminal branches occasionally hooklike, apices acute to rounded
. . . . *D. hamifera* Setchell
7\. Terminal branches slightly or extensively spirally twisted,
basal branches prostrate and not twisted, apices rounded
. . . . *D. bartayresiana* Lamouroux
[includes *D. cervicornis* Kützing]

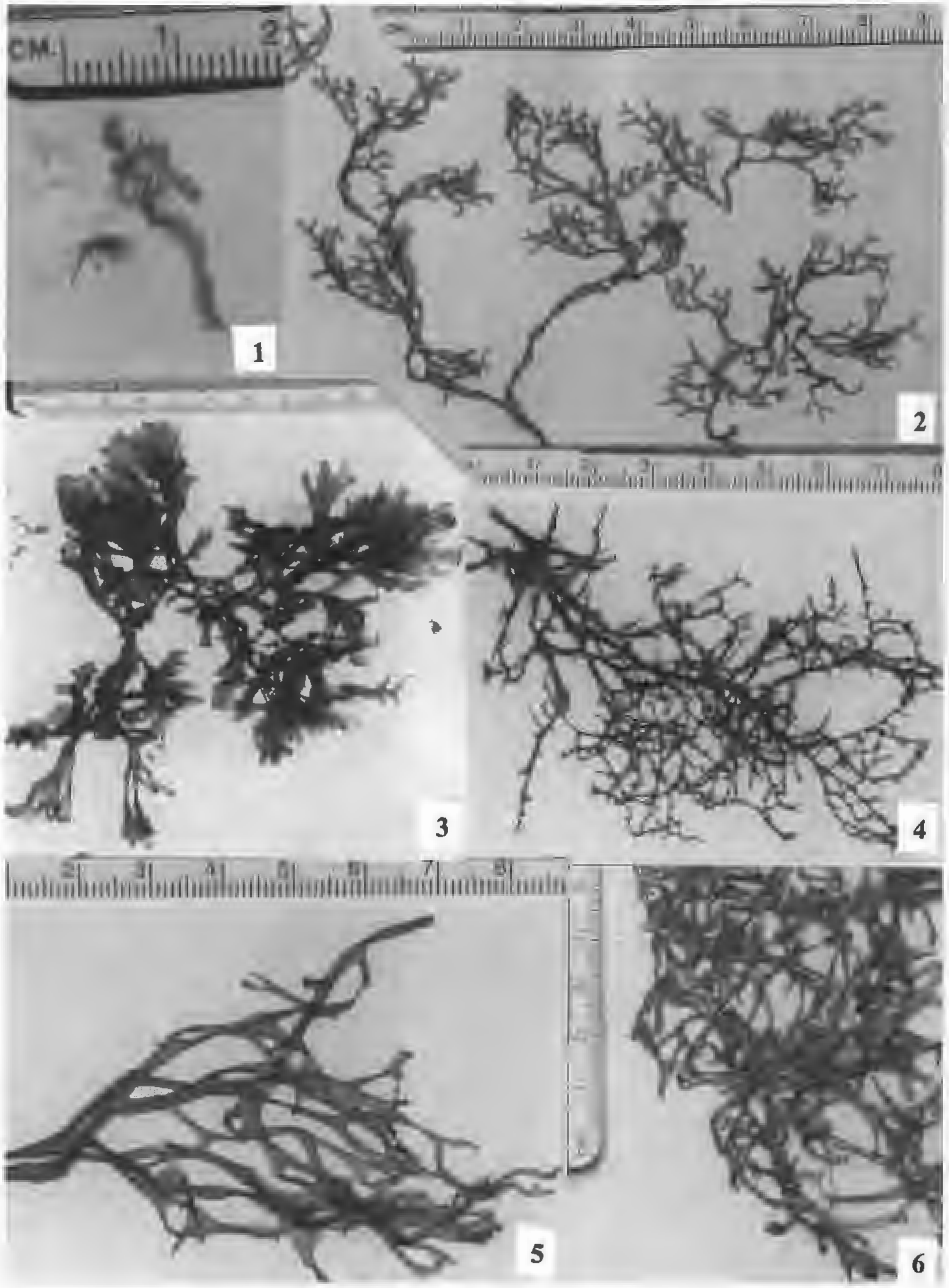
Descriptions and Distribution of the Micronesian *Dictyota*

Although 3 of the 8 species are still in need of further studies, it seems best to discuss all 8 species of *Dictyota*. The references and islands from which the specimens were previously reported are cited below under each species. Depth is in meters and relative to mean lower low water (MLLW).

Dictyota acutiloba J. Agardh, Spec. gen. ord. alg. 1, pp. 91–92, 1848. (Figs. 1–2)

Misapplied Name: *Dictyota cervicornis* Kützing, Tab. phycol. 9, p. 11, pl. 24, fig. 11, 1859 (for some Micronesian specimens).

Thallus upright, up to 15 cm long, light to dark brown, appearing bushy when several branches arise from basal sector, appearing straggly and twisted when few branches present. Branches dichotomous, 1–2 mm wide at base, approximately 1 mm wide at rounded apices. Tetrasporangia scattered on dorsal surface of thallus. (Description based on specimens collected by R. Tsuda, Waikiki Beach, Oahu, early 1960s.)



Figs. 1–6. Fig 1, ***Dictyota acutiloba,*** Ant Atoll (Hodgson 22291). Fig 2. ***Dictyota acutiloba,*** Oahu, Hawaii (RT 42). Fig 3, ***Dictyota bartayresiana,*** Palau (RT 4091b). Fig. 4, ***Dictyota bartayresiana,*** Guam (RT 2057). Fig. 5, ***Dictyota bartayresiana,*** Guam (RT 2599). Fig. 6, ***Dictyota bartayresiana,*** Yanagi I., Chuuk (RT 3385).

Past Records: *Caroline Islands:* Pohnpei and Ant Atoll (Hodgson and McDermid 2000).

Additional Records. None.

Notes: The specimens from Pohnpei and Ant Atoll reported by Hodgson and McDermid (2000) represent the first and only records of *D. acutiloba* from Micronesia. Hodgson No. 22291, which was given to the University of Guam Herbarium, is a 2-cm long thallus collected from a channel, 3–22 m deep, at Ant Atoll, Nov. 27, 1994. Other than the records from Pohnpei and Ant Atoll, *D. acutiloba* is known from Hawaii and Australia.

In my discussion of *D. cervicornis* in Tsuda (1972a), I stated that "a few of the specimens appear very much like *D. acutiloba* J. Ag. when the widened basal portion is absent." During the Ninth Algal Taxonomy Workshop, at the University of Hawaii–Hilo, the Micronesian *D. cervicornis* Kützing was thought to be instead *D. acutiloba*, not *D. bartayresiana*. What was called *D. cervicornis* in Micronesia clearly lacked surface proliferations, which are a characteristic feature of the Caribbean and Indian Ocean *D. cervicornis*. After my return to Guam, further observations showed the twisted branching pattern of the Hawaiian *D. acutiloba* to be morphologically different from the Micronesian specimens of *D. bartayresiana,* which were erroneously referred to as *D. cervicornis* for the past 35 years. Cronin et al. (1997) isolated acutiol A acetate, acutiol A, and acutilol B from Hawaiian *D. acutiloba*; these isolates have not been reported from Micronesian "*D. cervicornis*."

Dictyota bartayresiana Lamouroux, J. Bot. (Desvaux) 2, p. 43, 1809.
(Figs. 3–6)

Synonym: *Dictyota bartayresii* Lamouroux, Nov. Bull. Sci...1, p. 331.

Misapplied Name: *Dictyota cervicornis* Kützing, Tab. phycol. 9, p. 11, pl. 24, fig. 11, 1859 (for Micronesian specimens).

Branches prostrate and dichotomous, greenish brown, compact or loosely clumped, up to 10 cm long and 1–4 mm wide. Lower mature branches with or without marginal proliferations, terminal branches twisted or non-twisted with rounded or acute apices. Internodes varying 3–15 times width depending on depth of collection. In calm water, thalli appearing straggly and spirally twisted with short cervicorn-like branches.

Past Records: *Mariana Islands:* Guam (Tsuda 1972a, as *D. bartayresii* and *D. cervicornis*); Anatahan, Guguan, Alamagan, Pagan, Agrihan, Asuncion, Maug, and Uracas (Tsuda and Tobias 1977, as *D. bartayresii*). *Caroline Islands:* Palau (Kanda 1942, 1944; Ohba, 1996); Ngcheangel (Kayangel) Atoll (Tsuda 1981b, as *D. bartayresii*); Yap (Tsuda and Belk 1972, as *D. cervicornis*); Chuuk (Tsuda 1972b and Tsuda et al. 1977, as *D. bartayresii*); Pohnpei (Hodgson and McDermid 2000); Ant Atoll (Yamada 1944). *Marshall Islands:* Enewetak Atoll (Gilmartin 1960, as *D. cervicornis*). *Tuvalu:* Funafuti Atoll (Chapman 1955).

Additional Records: *Mariana Islands:* Rota, epiphytic on *Halimeda opuntia* (Linnaeus) Lamouroux, tidepool, 0.5 m deep in champignon area, Sasanlago Bay, RT 2738, March 14, 1969, leg. R. T. Tsuda; Tinian, Tinian Harbor, 1 m deep, RT 3713, Aug. 16, 1970, leg. R. T. Tsuda; Saipan, peppery-tasting specimens, 1 m deep, Papau Beach, RT 1973, Feb. 25, 1968, leg. R. T. Tsuda; Saipan, fringing reef on seaward side of Managaha Island, 0.6 m deep, RT 3165, May 18, 1970, leg. R. T. Tsuda; Saipan, sandy substratum in *Halodule uninervis* bed, 0.5 m deep, north of Pt. Agingan, San Antonio, RT 3214, May 18, 1970, leg. R. T. Tsuda. Saipan, sandy substratum in *Halodule uninervis* bed, 0.6–1 m deep, Marpi Beach, RT 3259, May 19, 1970, leg. R. T. Tsuda; Saipan, reef flat with surge channels, 0.5 m deep, Tank Beach, RT 3345, May 20 1970, leg. R. T. Tsuda. *Caroline Islands:* Palau, washed into shallow water along beach, Ngechelobel I., MVCF 1007, Nov. 20, 1968, leg. M. V. C. Falanruw; Palau, inner barrier reef, 1–2 m deep, west of Konrei, North Babeldaob, RT 4091a, Jan. 7, 1971, leg. R. T. Tsuda; Palau, inner barrier reef, 1–2 m deep, north Babeldaob, RT 4091b, Jan. 7, 1971, leg. R. T. Tsuda; Ulithi Atoll, Eoet, west of Asor, RT 2156a, June 15, 1968, leg. R. S. Jones.

Notes: Three growth forms are found in Micronesia. One form consists of compact prostrate clumps on the reef flat in water less than 1 m deep. A second form consists of loose prostrate mats with narrow branches and extremely long internodes (10–15 times the width); this form inhabits deeper turbid waters. The straggly and twisted thalli represent a third growth form.

In my discussion (1972a) of *D. cervicornis,* I stated that “other specimens which are narrow and conspicuously twisted appear like the terminal branches of *D. bartayresii*.” In their study of the Dictyotales and Cutleriales from Lord Howe Island, New South Wales, Allender and Kraft (1983) commented that the *D. cervicornis* from Guam reported in Tsuda (1972a) may represent their new variety of *D. bartayresiana,* var. *plectens. Dictyota cervicornis* was first described from Key West, Florida, in 1859.

Based on his field experiments in Guam waters, Potter (1986) indicated that the species erroneously referred to as *D. cervicornis* seemed to be a calm-water ecomorph of *D. bartayresiana.* Likewise, certain specimens that appeared to be *D. friabilis* Setchell were really juvenile *D. bartayresiana.* Allender and Kraft (1983) made similar observations at Lord Howe Island.

Silva et al. (1987, 1996) and De Clerck (1999) recognized *D. cervicornis* Kützing as a species present in the Indian and western Pacific Oceans. The Micronesian specimens possess cervicorn-like branching; however, all specimens clearly lack the surface proliferations that characterize *D. cervicornis* as found in the Atlantic (Taylor 1960; Littler and Littler 2000) and Indian Ocean (De Clerck 1999). Kapraun and Bowden (1978) and Ajisaka and Enomoto (1985) report *D. cervicornis* from Fiji.

Dictyota ceylanica Kützing, Tab. phycol. 9, p. 11, pl. 25, fig. 1, 1859. (Figs. 7–8)

Misapplied Name: *Dictyota divaricata* Lamouroux, J. Bot. (Desvaux) 2, p. 43, 1809 (for the Micronesian specimens).

Thallus erect or prostrate, often in loose mats, 3–4 cm high and 0.5–3 mm wide at basal portion, tapering to acute apical tips. Angles between dichotomy usually wide, up to 100° but in some cases narrower.

Past Records (all as *D. divaricata*): *Mariana Islands:* Guam (Tsuda 1972a). *Caroline Islands:* Yap (Okamura 1904; Tokida 1939; Trono 1969); Chuuk and Kosrae (Trono 1969); Pohnpei (Trono 1969); Pohnpei and Ant Atoll (Hodgson and McDermid 2000). *Marshall Islands:* Enewetak Atoll (Dawson 1957; Gilmartin 1960, 1966).

Additional Records: *Mariana Islands:* Guam, reef slope, 6 m deep, Gun Beach, RT 2507, Dec. 12, 1968, leg. R. T. Tsuda; Tinian, seaward terrace and slope, 7–40 m deep, between Lananibot Point and Adgidun Point, RT 3579, Aug. 11, 1970, leg. R. T. Tsuda; Saipan, epiphytic on *Halimeda opuntia,* patch reef, 2–3 m deep, Tanapag Lagoon, RT 3722, Oct. 17 1970, leg. R. T. Tsuda. *Caroline Islands:* Palau, shoreward of reef rubble zone, 1.4 m deep, Ngeruktubel (Urukthapel) Island, RDW 42d, July 4, 1968, leg. R. DeWreede; Yap, *Enhalus acoroides* (Linnaeus f.) Royle bed, inner reef, 1–2 m deep, Pelak, RT 3980, Nov. 25, 1970, leg. R. T. Tsuda.

Notes: Specimens of *Dictyota* with narrow branches, acute apices, and wide angles between dichotomies have been called *D. divaricata* Lamouroux for at least 35 years in Micronesia. Since *D. divaricata* Lamouroux is now considered a synonym of *D. dichotoma* (Hudson) Lamouroux var. *intricata* (C. Agardh) Greville (Hörnig et al. 1992a,b), it seems best to be consistent and follow the lead of Isabella A. Abbott and Mitchell D. Hoyl in the use of the name *D. ceylanica* Kützing for both the Hawaiian and Micronesian entities, which are similar in appearance. Silva et al. (1996) recognized *D. divaricata* as a pantropical species based on Allender and Kraft's (1983) study of what appeared to be the type from the Mediterranean coast of France.

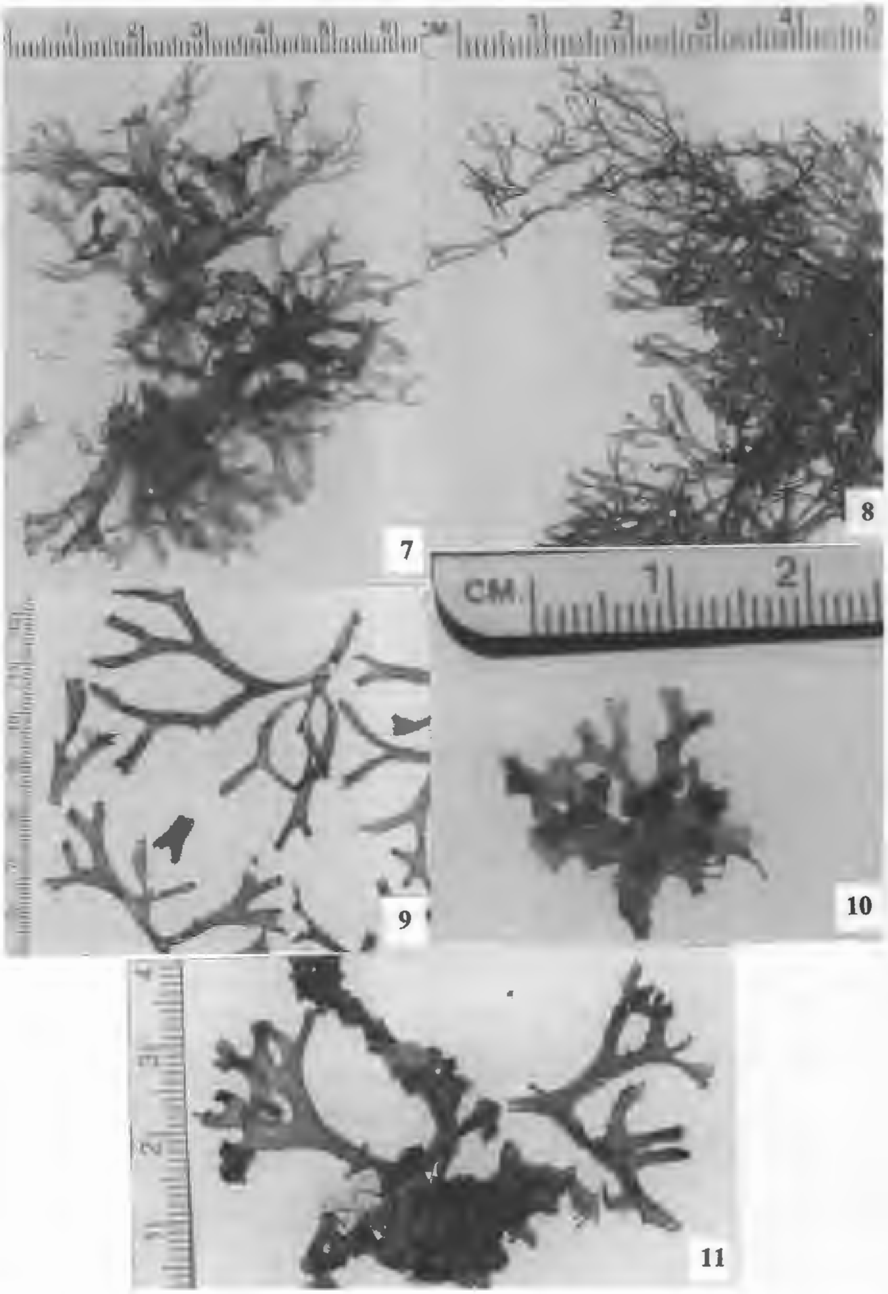
Dictyota dichotoma (Hudson) Lamouroux, J. Bot. (Desvaux) 2, p. 42, 1809. (Fig. 9)

Synonym: *Dictyota apiculata* J. Agardh, Lunds Univ.…Handl. 29, p. 67, 1894.

Thallus up to 10 cm tall; branches dichotomous, basal sector may become broader, up to 4 mm wide, toward rounded apices. Trono (1969) reports tetrasporangia scattered on both sides of thallus.

Past Records: *Caroline Islands:* Palau (Trono 1969; Ohba 1996), Yap (Tsuda and Belk 1972), Chuuk (Tsuda 1972b), all as *D. apiculata*. *Marshall Islands:* Enewetak Atoll (Gilmartin 1960). *Tuvalu:* Funafuti Atoll (Chapman 1955).

Additional Records. *Caroline Islands:* Palau, epiphytic on *Padina*, 1.5 m deep, Airai Channel, PA 68-7, April 25, 1968, leg. R. A. Marin; Yap, in



Figs. 7–11. Fig 7, ***Dictyota ceylanica***, Guam (RT 2507). Fig. 8, ***Dictyota ceylanica***, Yap (MSD 21610). Fig. 9, ***Dictyota dichotoma***, Yap (RT 5223). Fig. 10, ***Dictyota friabilis***, Yap (RT 4037). Fig. 11, ***Dictyota grossedentata***, Moen I., Chuuk (RT3500a).

Thalassia–Enhalus bed, 0.3 m deep, Yap Hospital, Colonia, RT 5223, March 4, 1977, leg. R. T. Tsuda.

Notes: Schnetter et al. (1987), Hörnig and Schnetter (1988), and De Clerck and Coppejans (1997) follow the premise that *D. dichotoma* is restricted to the North Atlantic; therefore, the Pacific species cited as *D. dichotoma* and *D. apiculata* should bear another name.

Dictyota friabilis Setchell, Univ. Calif. Publ. Bot. 12. pp. 91–92, pl. 13, figs. 4–7, pl. 20, fig. 1, 1926. (Fig. 10)

Thallus prostrate, iridescent bluish green in the field, often in compact clumps. Branches 3–4 cm long and 1–4 mm wide, with apices rounded or tapered. Sporangia scattered on dorsal side of thallus.

Past Records: *Mariana Islands:* Guam (Tsuda 1972a). *Caroline Islands:* Palau (Ohba 1996), Yap (Trono 1969), Chuuk (Trono 1969), Pohnpei and Ant Atoll (Hodgson and McDermid 2000); Kapingamarangi Atoll (Newhouse 1969); Kosrae (Trono 1969). *Kiribati:* Marakei Atoll, Nukunau Atoll, Tamana Atoll, and Tarawa Atoll (Tsuda 1964).

Additional Records: *Mariana Islands:* Rota, compact mats adjacent to freshwater spring, Tatachog Point, RT 2705, March 13, 1969, leg. R. T. Tsuda; Aguijan, seaward terrace, 3–33 m deep, cove on north side of island, RT 3613, Aug. 12, 1970, leg. R. T. Tsuda; Saipan, patch reef, 1 m deep, Muchot Point in Tanapag Harbor, RT 3103, May 17, 1970, leg. R. T. Tsuda. *Caroline Islands:* Yap, inner barrier reef, 1–2 m deep, Tamil Harbor, RT 4037, Nov. 30, 1970, leg. R. T. Tsuda; Ulithi Atoll, Eoet, west of Asor, RT 2160a, June 15, 1968, leg. R. S. Jones.

Notes: Potter (1986) reported that the prostrate, immature thalli of *D. bartayresiana* can appear similar to those of *D. friabilis* in the some habitats.

Dictyota grossedentata De Clerck et Coppejans, Phycologia 38, pp. 184–194, 1999. (Fig. 11)

Misapplied Name: *Dictyota patens* J. Agardh, Lunds Univ....Naturve. 17. p. 93, 1882 (for Micronesian specimens).

Thallus prostrate (decumbent) and crisp, up to 3 cm long and 2–4 mm wide, with dichotomous branches possessing few triangular dentitions along margins. Juveniles lacking dentitions. Internode length varying 2–4 times width, depending on availability of sunlight. Reproductive organs and rhizoids scattered throughout dorsal side of thallus.

Past Records: *Mariana Islands:* Guam (Tsuda 1972a, as *D. patens*). *Caroline Islands:* Palau (Kanda 1944 and Ohba 1996, as *D. patens*); Chuuk (Tsuda 1972b, as *D. patens*); Pohnpei (Okamura 1916, as *D. patens?;* Glassman 1952, as *D. patens*); Kapingamarangi Atoll (Newhouse 1969, as *D. patens*); *Marshall Islands:* Enewetak Atoll (Dawson 1957, as *D. patens*). *Kiribati:* Marakei Atoll and Tarawa Atoll (Tsuda 1964, as *D. crenulata* in publication; correction made by author, June 13, 1969, to herbarium specimen MSD 18880A/BISH 556203, as *D. patens*; other herbarium specimen, MSD 18919/BISH 556292, noted as too fragmentary).

Additional Records: *Caroline Islands:* Palau, on coral, 2–5 m deep, Aurashekaru Island, RT 4056, Jan. 1, 1971, leg. R. T. Tsuda.

Notes: De Clerck (1999) stated, "Tsuda (1972:96–97, pl. 4, fig. 3) reports *D. patens* J. Agardh from Guam, Mariana Islands, but the description and illustration clearly represent a *D. grossedentata* specimen and also the ecology, terraces beyond the reef margin, 3–20 m deep, corresponds very well with the ecology of the latter." De Clerck and Coppejans (1999) distinguished *D. grossedentata* from other species of *Dictyota* by its prostrate or decumbent habit, dentate margins, and triangular shape of the teeth. The Micronesian specimens have few teeth as compared to the specimen illustrated by De Clerck and Coppejans (1999). *Dictyota patens* is considered a synonym of *D. bartayresiana* Lamouroux (De Clerck and Coppejans 1997, 1999).

I reported *Dictyota crenulata* J. Agardh (Tsuda 1964) from Kiribati but later had second thoughts on that determination. Specimen MSD 18880A (BISH 556203) from Tarawa Atoll was reexamined 5 years later in June 1969, and the determination was changed to *D. patens* as indicated by my notes on the herbarium sheet and verified during my May 2002 visit to the Bishop Museum herbarium. My notation on the herbarium label of specimen MSD 18919 (BISH 556292) from Marakei Atoll stated that it was too fragmentary for redetermination.

Dictyota hamifera Setchell, Univ. Calif. Publ. Bot. 12. p. 92, pl. 14, figs. 1–6, 1926.

Thallus prostrate, 4 cm long with branches up to 2 mm wide. The presence of hamate or hooklike terminal branches on selected portion of the thallus is characteristic of this species. Few hamate branches are present on the Asuncion Island specimens; however, the hamate branches are distinctive when viewed under a dissecting microscope. The thallus could be mistaken for *D. friabilis* Setchell upon cursory observation with the naked eye.

Past Records: *Mariana Islands:* Asuncion (Tsuda and Tobias 1977).

Additional Records: None.

Notes: This species is rare in the Micronesian region and, thus far, is known only from Asuncion Island in the Northern Marianas.

Dictyota pinnatifida Kützing, Tab. phycol. 9, p. 16, pl. 39, fig. 1, 1859.

The only Micronesian records of *D. pinnatifida* are the rare or occasional fragments dredged in waters 46–57 m deep from the lagoons of Bikini and Enewetak Atolls in the Marshall Islands. No other species of *Dictyota* was reported from the Marshall Islands by Taylor (1950). Taylor (1950) described his specimens: "Plants sparsely bushy, exceedingly fragile, not adhering well to paper, about one decimeter tall, the branching irregularly dichotomous to alternate, without considerable tapering from base to apex, the branches flat, 2.5–3.5 mm. in width, the tips usually blunt."

Past Records: *Marshall Islands:* Bikini Atoll and Enewetak Atoll (Taylor, 1950).

Additional Records: None.

Discussion

The taxonomic study of the Micronesian *Dictyota* continues, especially in terms of *D. acutiloba, D. pinnatifida,* and *D. dichotoma.* Chromosome counts and reproductive compatibility (Weber-Peukert 1985) and further analyses of chemical compounds in secondary metabolites should provide a clearer delineation of the *Dictyota* species in the region.

The number of species in the genus *Dictyota* within Micronesia (Table 1) does not show an attenuation to either the east or to the west. Three species, *D. bartayresiana, D. ceylanica,* and *D. friabilis,* appear pantropical; these species are also present in Hawaii (I. A. Abbott, pers. comm., May 2002). Although it has not yet been reported from Yap, *D. grossedentata* can also be considered pantropical within the Micronesian region. Specimens belonging to the *D. dichotoma* complex seem excluded from the Marianas; however, the species complex is present in Palau, Yap, Chuuk, and Marshall Islands/Tuvalu. On the other hand, *D. hamifera, D. acutiloba,* and *D. pinnatifida* have each been reported from only one island group—Asuncion Island in the Northern Marianas Islands, Pohnpei and Ant Atoll, and Bikini Atoll and Enewetak Atoll in the Marshall Islands, respectively. *Dictyota hamifera* is easily recognized by its hamate terminal branches. More collections of *D. acutiloba* and *D. pinnatifida* must be made to reconfirm these two species in Micronesia.

Table 1. Distribution of *Dictyota* Species within Micronesia

	Marianas	Palau	Yap	Chuuk	Pohnpei/ Kosrae	Marshall/ Kiribati/Tuvalu
D. acutiloba	–	–	–	–	+	–
D. bartayresiana	+	+	+	+	+	+
D. ceylanica	+	+	+	+	+	+
D. dichotoma	–	+	+	+	–	+
D. friabilis	+	+	+	+	+	+
D. grossedentata	+	+	–	+	+	+
D. hamifera	+	–	–	–	–	
D. pinnatifida	–	–	–	–	–	+

Except for Marianas to the north, island groups arranged west to east.

Acknowledgments

I thank Drs. Isabella A. Abbott and Karla J. McDermid for inviting me to participate in the Workshop and acknowledge the University of California and University of Hawaii Sea Grant Programs for their continuous funding and support of the nine algal taxonomic workshops, which began in Guam in June 1984. I acknowledge Dr. Abbott for sharing her references on *Dictyota* and for providing me a preview of her manuscript on the Hawaiian Chlorophyta and Phaeophyta, which included her taxonomic treatment with Dr. Mitchell D. Hoyl of the genus *Dictyota*. I also acknowledge the discussions on *Dictyota* with Dr. Abbott and others while studying the Micronesian specimens at the University of Hawaii–Hilo. Contribution No. 546, University of Guam Marine Laboratory.

Literature Cited

Ajisaka, T., and Enomoto, S. 1985. *Dictyota* Lamouroux (Dictyotales, Phaeophyceae) of the Fiji and Solomon Islands. Kagoshima University Research Center for the South Pacific, Occas. Pap. 5:35–41.

Allender, B. A., and Kraft, G. T. 1983. The marine algae of Lord Howe Islands (New South Wales): The Dictyotales and Cutleriales (Phaeophyta). Brunonia 6:73–130.

Chapman, V. J. 1955. Algal collection from Funafuti Atoll. Pac. Sci. 9:354–356.

Cronin, G., Paul, V. J., Hay, M. E., and Fenical, W. 1997. Are tropical herbivores more resistant than temperate herbivores to seaweed chemical defenses? Diterpenoid metabolites from *Dictyota acutiloba* as feeding deterrents from tropical versus temperate fishes and urchins. J. Chemical Ecol. 23:289–302.

Dawson, E. Y. 1957. An annotated list of marine algae from Eniwetok Atoll, Marshall Islands. Pac. Sci. 11:92–132.

De Clerck, O. 1999. A revision of the genus *Dictyota* Lamouroux (Phaeophyta) in the Indian Ocean. Doctoral Dissertation, University of Gent. 354 pp. + Apps. I and II.

De Clerck, O., and Coppejans, E. 1997. The genus *Dictyota* (Dictyotaceae, Phaeophyta) from Indonesia in the Herbarium Weber-van Bosse, including the description of *Dictyota canaliculata* spec. nov. Blumea 42:407–420.

De Clerck, O., and Coppejans, E. 1999. Two new species of *Dictyota* (Dictyotales, Phaeophyta) from the Indo-Malayan region. Phycologia 38:184–194.

Fan, K. C. 1953. The identity of *Dilophus radicans* Okamura. Taiwan Fish. Res. Inst., Lab. Hydrobiol. Rept. 6:12–13.

Gilmartin, M. 1960. The ecological distribution of the deep water algae of Eniwetok Atoll. Ecology 41:210–221.

Gilmartin, M. 1966. Ecology and morphology of *Tydemania expeditionis,* a tropical deep water siphonous green alga. J. Phycol. 2:100–105.

Glassman, S. F. 1952. List of non-vascular plants from Ponape, Caroline Islands. Amer. Midl. Natur. 48:735–740.

Hodgson, L. M., and McDermid, K. J. 2000. Marine plants of Pohnpei and Ant Atoll: Chlorophyta, Phaeophyta and Magnoliophyta. Micronesica 32:289–307.

Hörnig, I., and Schnetter, R. 1988. Notes on *Dictyota dichotoma, D. menstrualis, D. indica and D. pulchella* spec. nova (Phaeophyta). Phyton (Austria) 28(2):277–291.

Hörnig, I., Schnetter, R., and Prud'homme van Reine, W. F. 1992a. The genus *Dictyota* (Phaeophyceae) in the North Atlantic. I. A new generic concept and new species. Nova Hedwigia 54(1–2):45–62.

Hörnig, I., Schnetter, R., and Prud'homme van Reine, W. F. 1992b. The genus *Dictyota* (Phaeophyceae) in the North Atlantic. II. Key to the species. Nova Hedwigia 54:397–402.

Kanda, C. 1942. The seaweeds in Garu-berugairu watercourse in Palao. Kagaku Nanyo 5:144–150.

Kanda, C. 1944. Ecological studies on the marine algae from Kororu and adjacent islands in the South Sea Islands. Palao Trop. Biol. Stat. Stud. 2:737–800.

Kapraun, D. F., and Bowden, W. A. 1978. Additions to the benthic marine algal flora of Fiji. Micronesica 14:199–207.

Littler, D. S., and Littler, M. M. 2000. Caribbean Reef Plants. Offshore Graphics, Washington, D.C. 542 pp.

Meyer, K. D., Paul, V. J., Sanger, H. R., and Nelson, S. G. 1994. Effects of seaweed extracts and secondary metabolites on feeding by the herbivorous surgeonfish *Naso lituratus*. Coral Reefs 13:105–112.

Newhouse, J. 1969. The algae of Kapingamarangi Atoll, Caroline Islands: Pt. 1. Checklist of the Cyanophyta, Chlorophyta and Phaeophyta. Atoll Res. Bull. (121):1–7.

Ohba, H. 1996. The benthic marine flora of the Palau Islands (WCI): New records, missing records and implications for biodiversity. In: Aoyama, T. (ed.), Progress report of the 1995 survey of the research project "Man and the Environment in Micronesia," pp. 45–54. Kagoshima Univ., Research Center for the South Pacific, Occas. Pap. 30.

Okamura, K. 1904. List of marine algae collected in Caroline Islands and Australia. Bot. Magazine (Tokyo) 18:77–96.

Okamura, K. 1916. List of marine algae collected in Caroline Islands and Mariana Islands, 1915. Bot. Magazine (Tokyo) 30:1–14.

Paul, V. J. 1987. Feeding deterrent effects of algal natural products. Bull. Marine Science 41: 514–522.

Potter, T. S. 1986. Effects of different habitats on morphological variation within natural populations of three reported species of *Dictyota* (Phaeophyta). University of Guam M.S. Thesis in Biology. 33 pp.

Schnetter, R., Hornig, I., and Weber-Peukert, G. 1987. Taxonomy of some North Atlantic *Dictyota* species (Phaeophyta). Hydrobiologia 151/152:193–197.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. Univ. of California Press, Berkeley. xiv + 1259 pp.

Silva, P. C., Menez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contrib. to the Mar. Sci. 27:1–179.

Taylor, W. R. 1950. Plants of Bikini and other northern Marshall Islands. University of Michigan Press, Ann Arbor. ix + 220 pp.

Taylor, W. R. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. Univ. of Michigan Press, Ann Arbor. ix + 870 pp.

Tokida, S. 1939. A list of marine algae from Micronesia. Kagaku Nanyo 2:16–26.

Trono, G. C., Jr. 1969. The marine benthic algae of the Caroline Islands: II. Phaeophyta and Rhodophyta. Micronesica 5:25–121.

Tsuda, R. T. 1964. Floristic report on marine benthic algae of selected islands in the Gilbert Group. Atoll Res. Bull (105):1–13.

Tsuda, R. T. 1972a. Marine benthic algae of Guam. I. Phaeophyta. Micronesica 8:87–115.

Tsuda, R. T. 1972b. Some marine benthic algae from Truk and Kuop, Caroline Islands. Atoll Res. Bull. (155):1–10.

Tsuda, R. T. 1981a. Bibliography of marine benthic algae of Micronesia: Addendum. Micronesica 17:213–218.

Tsuda, R. T. 1981b. Marine benthic algae of Kayangel Atoll, Palau. Atoll Res. Bull. (255):43–48.

Tsuda, R. T. 1988. *Sargassum* from Micronesia. In: Tax. Econ. Seaweeds 2, pp. 59–63.

Tsuda, R. T. 2002a. Checklist of the marine benthic algae from the Palau Archipelago based on past references. Palau International Coral Reef Center, PICRC Publ. 02-019. 21 pp.

Tsuda, R. T. 2002b. Checklist and bibliography of the marine benthic algae from islands and atolls within Yap State, Federated States of Micronesia. Univ. of Guam Marine Lab., Tech. Rept. No. 105. 21 pp.

Tsuda, R. T. 2002c. Checklist and bibliography of the marine benthic algae from the Marshall Islands. Univ. of Guam Marine Lab., Tech. Rept. No. 106. 33 pp.

Tsuda, R. T. 2003. Checklist and bibliography of the marine benthic algae from the Mariana Islands (Guam and CNMI). Univ. of Guam Marine Lab., Tech. Rept. 107. 49 pp.

Tsuda, R. T., Amesbury, S. S., and Moras, S. C. 1977. Preliminary observations on the algae, corals and fishes inhabiting the sunken ferry "Fujikawa Maru" in Truk Lagoon. Atoll Res. Bull. (212):1–6.

Tsuda, R. T., and Belk, M. S. 1972. Additional records of marine benthic algae from Yap, western Caroline Islands. Atoll Res. Bull. (156):1–5.

Tsuda, R. T., and Tobias, W. J. 1977. Marine benthic algae from the Northern Mariana Islands, Chlorophyta and Phaeophyta. Bull. Jpn. Soc. Phycol. 25:67–72.

Tsuda, R. T., and Wray, F. O. 1977. Bibliography of marine benthic algae in Micronesia. Micronesica 13:85–120.

Weber-Peukert, G. 1985. Ontogenetische, autokologische und taxonomische Untersuchungen an ausgewahlten Arten der Gattung *Dictyota* (Dictyotales, Phaeophyceae): I. Cytologische Daten als Differenzierungsmerkmale. Nova Hedwigia 42:123–149.

Womersley, H. B. S. 1987. The marine benthic flora of southern Australia: Part II. South Australian Government Printing Division, Adelaide. 484 pp., 169 figs., 8 pls.

Wylie, C. R., and Paul, V. J. 1988. Feeding preferences of the surgeonfish *Zebrasoma flavescens* in relation to chemical defenses of tropical algae. Mar. Ecol. Prog. Ser. 45: 23–32.

Yamada, Y. 1930. Une nouvelle espece d'*Udotea* du Pacifique: *Udotea geppii* sp. nov. Rev. Algol. 5:139–142.

Yamada, Y. 1944. List of marine algae from the Atoll of Ant. Sci. Pap. Inst. Algol. Res. Fac. Sci. Hokkaido Imp. Univ. 3:31–45.

VARIATIONS IN THE BASAL SYSTEM AND STOLONS OF *SARGASSUM STOLONIFOLIUM* IN THE ANDAMAN SEA

Tetsuro Ajisaka and Khanjanapaj Lewmanomont

Abstract

Dried and fertile specimens of *Sargassum stolonifolium* Phang et Yoshida from 7 populations along the coast of the Andaman Sea in Thailand were studied. The characteristic basal system with stolons, defined as cylindrical modified cauline leaves, was found in all populations. These structures were, however, sometimes absent from a few populations, not appearing during stages before fertilization. Juvenile plants collected from 3 populations in Thailand and the type locality (Penang Island, Malaysia) were also studied. We found two types of morphology in cauline leaves on the stem, elliptical cauline leaves from the upper portion and cylindrical stolons from the lower portion. In some juvenile plants, only stolons were present; perhaps the elliptical cauline leaves were never formed, or were lost. In two northern localities, stolons on some stems of juvenile and fertile plants were also absent. We suggest that the formation of stolons in *S. stolonifolium* is affected by wave action. Having found stolons lacking in some populations that otherwise show stolons, we believe that *S. grevillei* reported by Egerod (1974) could be identified as *S. stolonifolium.*

Introduction

Sargassum stolonifolium Phang et Yoshida (1997) is one of 6 species of the genus known from Thailand. This paper describes the stolons in this species as observed in a variety of habitats at 7 locations on the Andaman Sea.

Sargassum stolonifolium was described as a new species by Phang et Yoshida (1997) on the basis of stolons derived early from cauline leaves on the lower part of the short stem. Stolons are formed from the primary branches on the upper half of the stem in *S. polycystum* C. Agardh and *S. herporhizum* Setchell et Gardner.

In this study, some morphological characteristics of *S. stolonifolium* specimens were observed, and most were in agreement with the original descriptions of the species (Phang and Yoshida, 1997). Our collections were made from 7 locations on the Andaman Sea. Very few stolons on the holdfast were found in the northern Thailand populations. Descriptions of specimens in each population were prepared, and morphological characteristics compared among them. The original description and that of *S. grevillei* reported by Egerod (1974) were also compared with features shown by *S. stolonifolium.* Some observations on juvenile plants of 4 populations along the Andaman Sea and south into the Strait of Malacca were also made and are discussed.

Materials and Methods

Dried herbarium specimens of *S. stolonifolium* from 7 populations from the Andaman Sea in Thailand, collected by the second author and deposited in the herbarium of the Faculty of Fisheries, Kasetsart University, Thailand, were studied. Fresh material from 3 populations in the Andaman Sea was collected on May 9 and 10, 1998, for detailed study of juvenile basal systems, and this was compared to materal collected at the type locality, Penang Island, Malaysia. Collection sites of dried and fresh specimens are shown in Fig. 1.

Results

Dried Specimens

Description of dried specimens from Thailand are provided in tabular form (Table 1) for easy comparison. Items that are not easily tabulated are given below by collection site.

1) Ko Nui, Ranong (coll. April 4, 1997; Figs. 2–5), and

2) Ko Ra, Ranong (coll. Jan. 17, 1997; Figs. 6–8): Male receptacles cylindrical, warty on surface, up to 6 mm long, up to 0.5 mm in diameter, pseudozygocarpic (usually with pedicels on receptacles).

3) Phang-nga (coll. Feb. 4, 1975; Figs. 9–12): Female receptacles compressed to triquetrous, with clear dentations at margins or only at apex, up to 3 mm long, up to 1 mm wide, 1–3 times forked, pseudozygocarpic to holozygocarpic (pedicels on receptacles either present or absent).

4) Phang-nga (coll. Dec. 24, 1988; Figs. 13–16): Female receptacles pseudozygocarpic to holozygocarpic (with pedicels on receptacles present or absent); male receptacles, also pseudozygocarpic to holozygocarpic.

5) Ko Phuket (coll. Dec. 23, 1988; Figs. 17–20): Female receptacles compressed, with clear dentations at margins, up to 3 mm long, up to 1 mm wide, pseudozygocarpic to holozygocarpic; male receptacles with pedicels present on receptacles.

6) Laem Yong Ling, Trang (coll. March 17, 1988; Figs. 21–24): Both female and male receptacles with pedicels attached to receptacles.

7) Kao Bae Na, Trang (coll. March 15, 1988; Figs. 25–28): No observations were made on the relationships of pedicels to receptacles.

Basal System

A comparison of the basal systems (stolons) in fresh specimens from Thailand and Batu Ferringhi, Malaysia, the type locality of *S. stolonifolium*, are shown in Table 2.

1) Batu Ferringhi, Penang Island, Maylasia (coll. Jan. 1, 1998; Figs. 29–30)

Juvenile plants up to 12 cm tall; holdfast discoid, up to 6 mm in diameter, giving rise to short terete stem; from upper portion of stem, lanceolate or

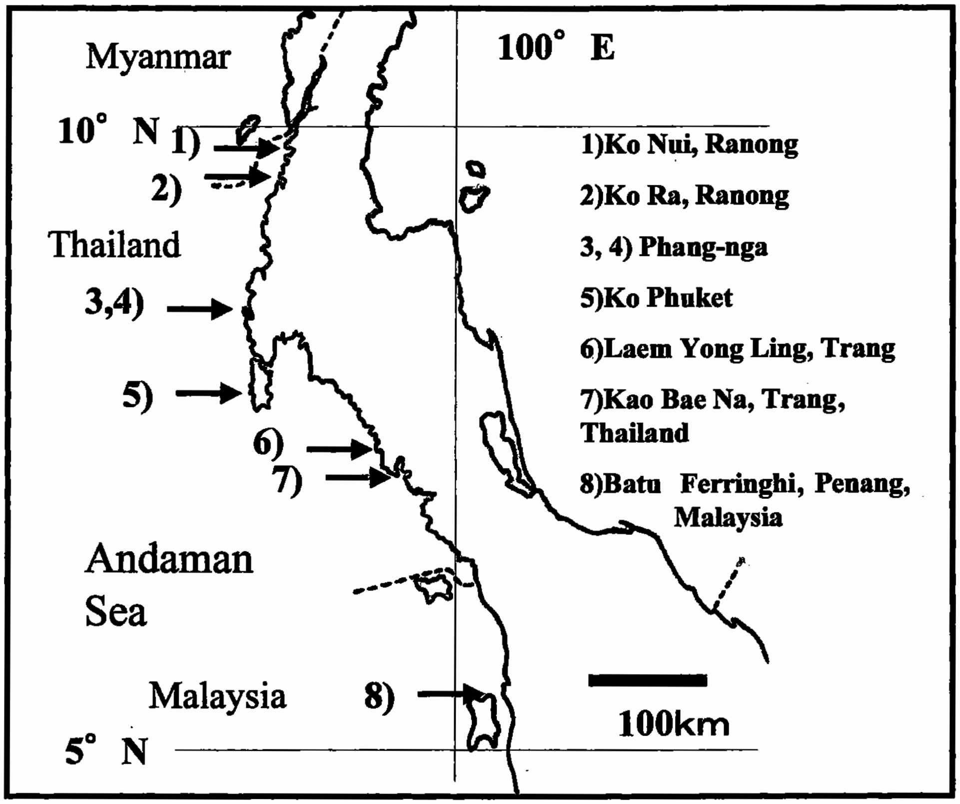


Fig. 1. Collection sites of dried and fresh specimens of *Sargassum stolonifolium* Phang et Yoshida.

slender-elliptical cauline leaves present, 5 cm long, up to 8 mm wide, with percurrent midrib and entire margins; lower cauline leaves cylindrical, up to 6 cm long, up to 1 mm in diameter, branching at their tips, producing some haptera, from which new plantlets arise.

2) Phang-nga (coll. May 10, 1998; Figs. 31–32)

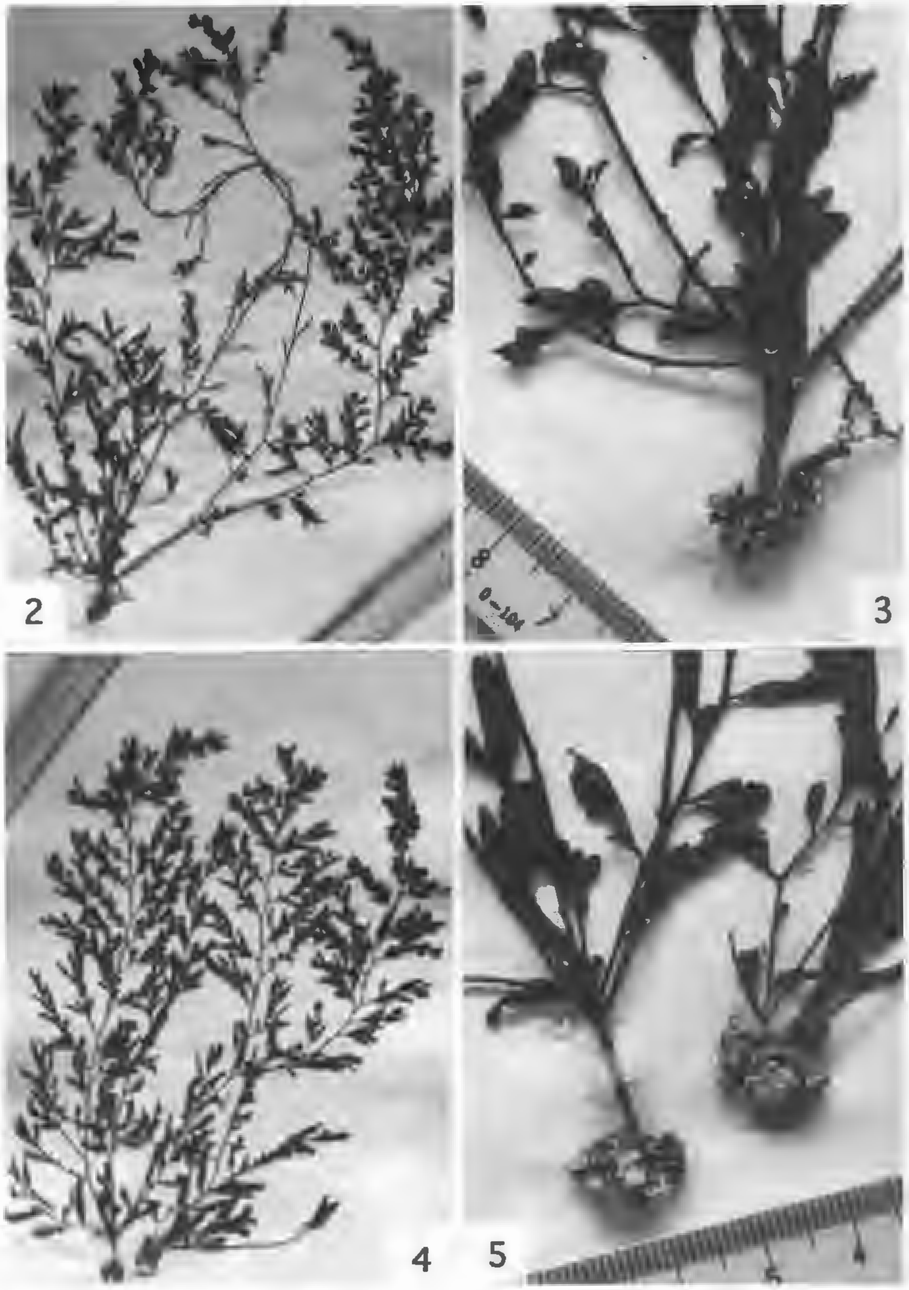
Plants yellowish brown when fresh; juvenile plants up to 10 cm tall; holdfast discoid, up to 12 mm in diameter, giving rise to short terete stem. From upper portion of stem, elliptical cauline leaves formed, up to 3 cm long, up to 6 mm wide, with percurrent midrib and entire margins (Fig. 26); these cauline leaves lost during developmental stage (Fig. 27). Lower cauline leaves cylindrical, up to 3 cm long, up to 1 mm in diameter, branching at their tips, producing some haptera, from which new plantlets arise (Figs. 31, 32).


6

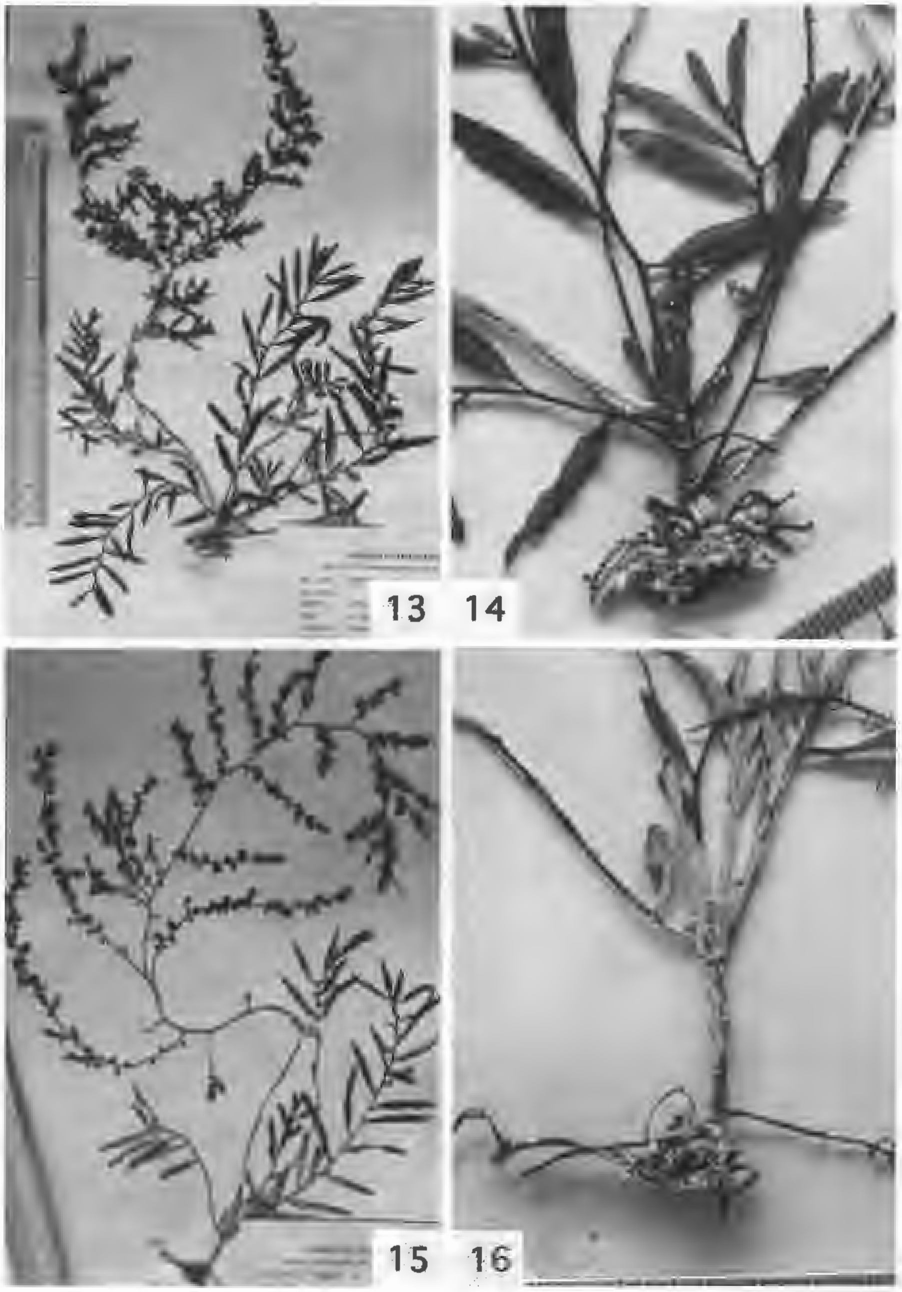

7


8

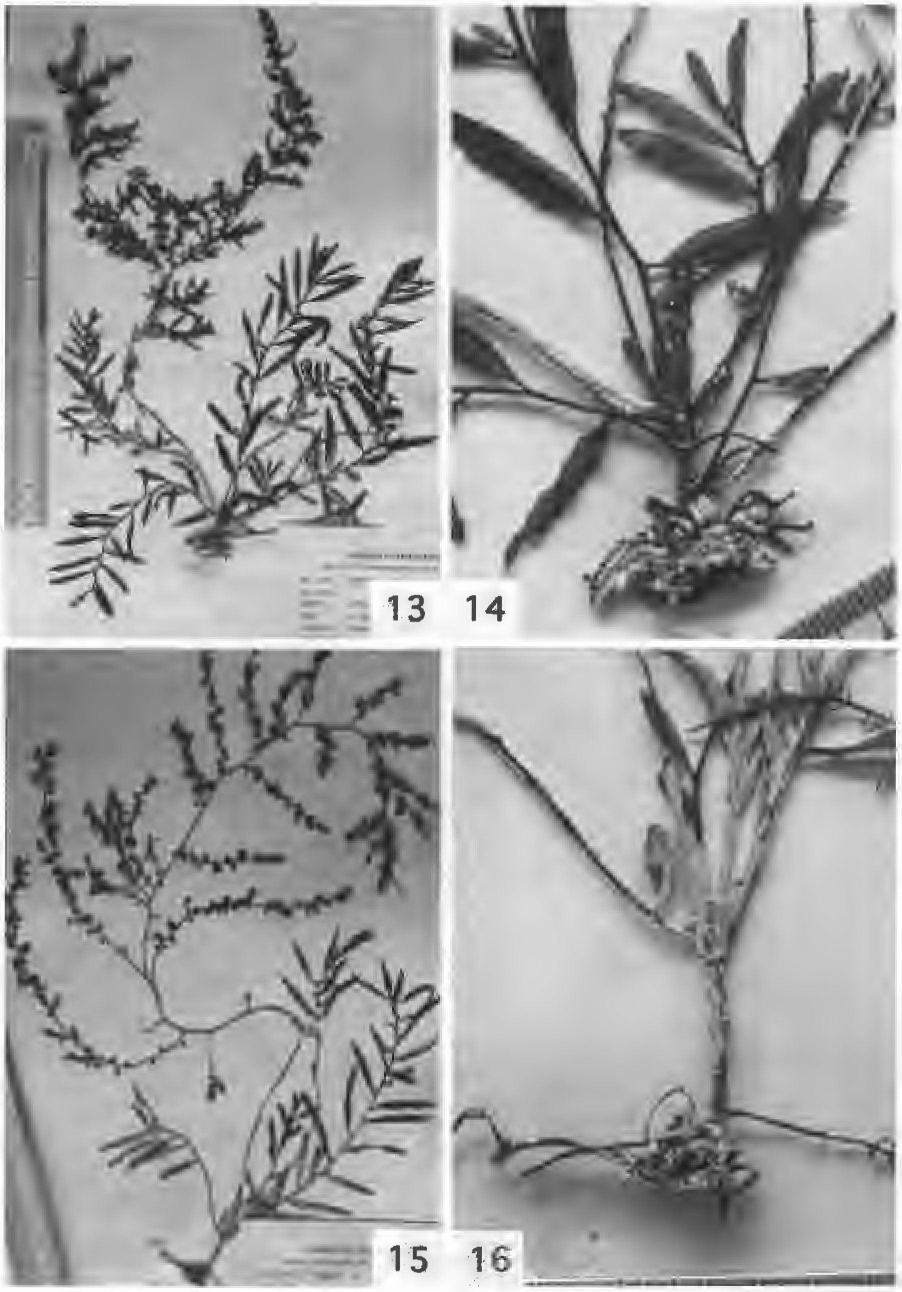
Figs. 6–8. Dried specimens of *S. stolonifolium* from Ko Ra, Ranong, collected Jan. 17, 1997.
Figs. 6, 7, Habit of male plant, and its upper portion, showing small leaves and cylindrical male receptacles. Fig. 8, Habit of male plant. Scale graduation = 1 mm.



Figs. 2–5. Dried specimens of *S. stolonifolium* from Ko Nui, Ranong, collected April 4, 1997. Figs. 2, 3, Habit of female plant, and its basal system. Figs. 4, 5, Habit of male plants, and their basal systems. Scale graduation = 1 mm.

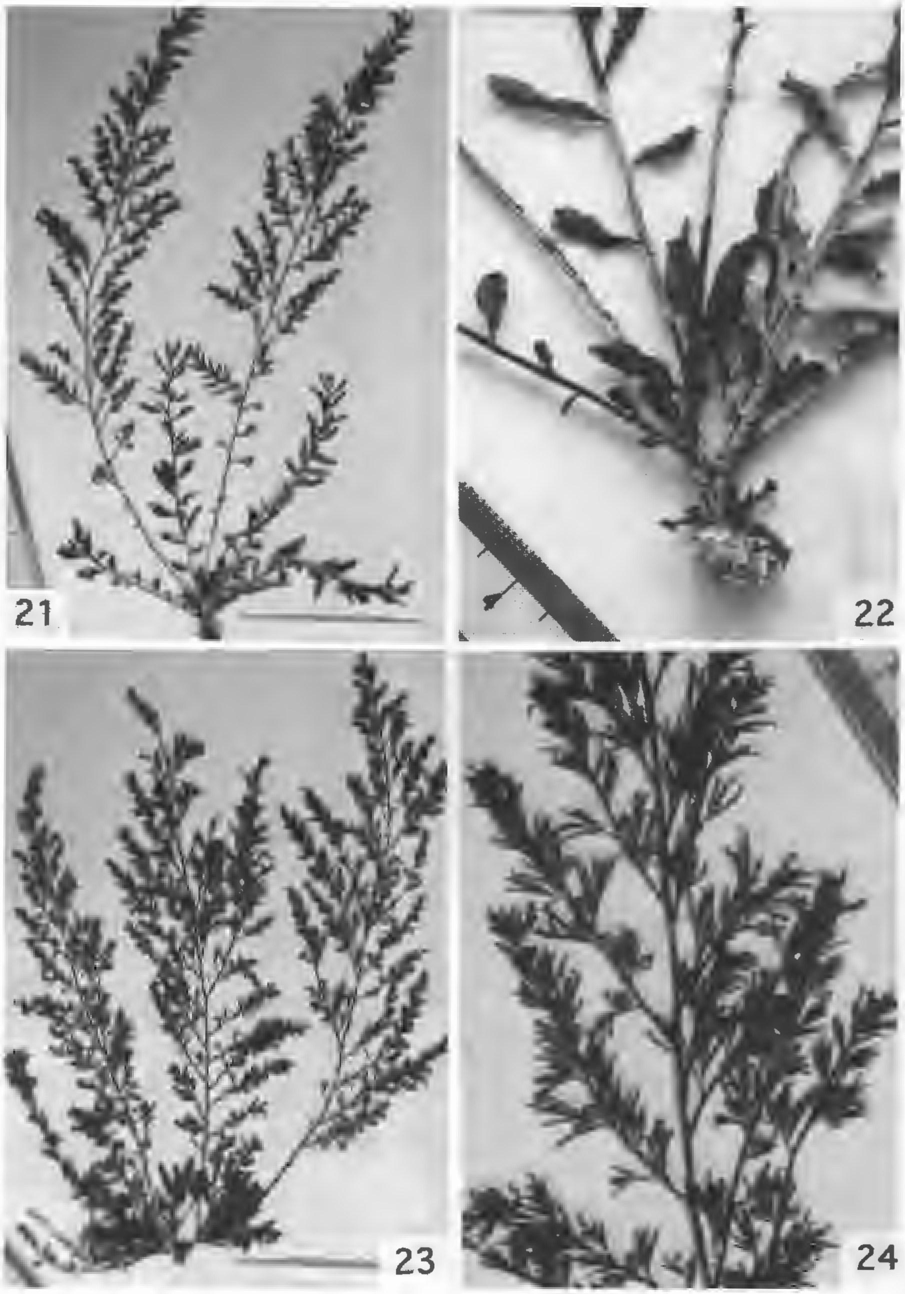


Figs. 13–16. Dried specimens of *S. stolonifolium* from Phang-nga, collected Dec. 24, 1988. Figs. 13, 14, Habit of female plant, and its basal system. Figs. 15, 16, Habit of male plant, and its basal system. Scale graduation = 1 mm.



Figs. 13–16. Dried specimens of *S. stolonifolium* from Phang-nga, collected Dec. 24, 1988. Figs. 13, 14, Habit of female plant, and its basal system. Figs. 15, 16, Habit of male plant, and its basal system. Scale graduation = 1 mm.

Figs. 17–20. Dried specimens of *S. stolonifolium* from Ko Phuket, collected Dec. 23, 1988. Figs. 17, 18, Habit of female plant, and its upper portion, showing small leaves, vesicles, and female receptacles. Figs. 19, 20, Habit of male plant, and its basal system. Scale graduation = 1 mm.



Figs. 21–24. Dried specimens of *S. stolonifolium* from Laom Yong Ling, Trang, collected March 17, 1988. Figs. 21, 22, Habit of female plant, and its basal system. Figs. 23, 24, Habit of male plant, and its upper portion, showing small leaves, vesicles, and male receptacles. Scale graduation = 1 mm.

Figs. 25–28. Dried specimens of *S. stolonifolium* from Kao Bae Na, Trang, collected March 15, 1988. Figs. 25, 26, Habit of female plant, and its basal system. Figs. 27, 28, Habit of male plant, and its basal system. Scale graduation = 1 mm.

Figs. 29–32. Basal systems in fresh specimens of *S. stolonifolium* in Thailand and Malaysia. Figs. 29, 30, Juvenile plants from Batu Ferringh, Penag Island (Malaysia), collected Jan. 1, 1988. Figs. 31, 32, Juvenile plants from Phang-nga, collected May 10, 1988. Scale graduation = 1 mm.

Figs. 33–36. Basal systems in fresh specimens of *S. stolonifolium* in Thailand. Figs. 33, 34, Juvenile plants from Ko Ra, Ranong, collected May 9, 1998. Figs. 35, 36, Juvenile plants from Ko Nui, Ranong, collected May 9, 1998. Scale graduation = 1 mm.

Table 1. Morphological Characteristics of Mature Plants Shown by *Sargassum stolonifolium* Phang et Yoshida in the Andaman Sea Localities (Thailand)

Coll. location	Ranong	Ranong	Phang-nga	Phang-nga	Phuket	Trang	Trang
	Ko Nui	Ko Ra				L-Y-Ling	K-B-Na
Coll. date	Apr. 4, 1997	Jun. 17, 1997	Feb. 4, 1975	Dec. 24, 1988	Dec. 23, 1988	Mar. 17, 1988	Mar. 15, 1988
Holdfast	discoid	discoid	discoid	discoid	discoid	discoid	discoid
stolon	few	few	common	common	few/common	few	few/common
1st leaves							
morphology	ellipt./lance.	ellipt./lance.	ellipt.	ellipt.	ellipt.	ellipt.	ellipt.
length(max)	3 cm	2 cm	2.5 cm	4 cm	4 cm	2.5 cm	3 cm
width(max)	5 mm	4 mm	3 mm	4 mm	4 mm	5 mm	9 mm
margins	entire/sm. dent.	entire/sm. dent.	entire/sm. dent.	entire	entire/sm. dent.	entire/sm. dent.	entire/sm. dent.
2nd leaves							
morphology	ellipt.	ellipt.	ellipt.	ellipt.	ellipt.	ellipt.	ellipt.
length(max)	1.5 cm	1.5 cm	1.0 cm	1.5 cm	1.5 cm	1.5 cm	1.5 cm
width(max)	3 mm	2 mm	1.5 mm	2 mm	4 mm	3 mm	6 mm
margins	entire/sm. dent.	entire/sm. dent.	entire/sm. dent.	entire	entire/sm. dent.	entire/sm. dent.	entire/sm. dent.
vesicles							
morphology	spher./obovoid	spher./obovoid	spher.	spher.	spher.	spher.	spher.
apex	round/pointed	round/pointed	round/pointed	round/pointed	round/pointed	round/pointed	round
receptacles	dioecious	dioecious	dioecious	dioecious	dioecious	dioecious	dioecious
female							
morphology	compr.	-	compr./triquetrous	compr.	compr.	compr.	compr.
surfaces	dent.	-	dent.	dent.	dent.	dent.	dent.
length(max)	2 mm	-	3 mm	3 mm	3 mm	5 mm	3 mm
width(max)	0.5 mm	-	1 mm	1 mm	1 mm	1 mm	1 mm
male							
morphology	fusiform/cylind.	cylind.	-	cylind.	cylind.	cylind.	cylind.
surfaces	warty	warty	-	warty	warty	warty	dent./warty
length(max)	5 mm	6 mm	-	5 mm	5 mm	7 mm	5 mm
width(max)	0.5 mm	0.5 mm	-	0.5 mm	0.5 mm	0.5 mm	0.5 mm
width(max)	0.5 mm	0.5 mm	-	0.5 mm	0.5 mm	0.5 mm	0.5 mm

cylind. = cylindrical, compr. = compressed, dent. = dentations, ellipt. = elliptical,
lance. = lanceolate, sm. dent. = small dentations, spher. = spherical

3) Ko Ra, Ranong (coll. May 9, 1998; Figs. 33–34)

Plants yellowish brown when fresh; juvenile plants up to 8 cm tall; holdfast discoid, up to 6 mm in diameter, giving rise to short terete stem; from upper portion of stem, elliptical cauline leaves formed, up to 3 cm long, up to 6 mm wide, with percurrent midrib and entire margins; stolons from lower portion cylindrical, up to 3 cm long, up to 1 mm in diameter, branching at their tips, producing some haptera, from which new plantlets arise (Fig. 33); some plants lacking elliptical leaves and stolons (Fig. 34).

4) Ko Nui, Ranong (coll. May 9, 1998; Figs. 35–36)

Juvenile plants up to 12 cm tall; holdfast discoid, up to 15 mm in diameter, giving rise to terete stem; few stolons from lower portion of stem cylindrical, up to 2 cm long, up to 1 mm in diameter, branching at their tips, producing some haptera, from which new plantlets arise (Fig. 35); some plants completely lacking stolons and elliptical cauline leaves (Fig. 36).

Table 2. Morphological Characteristics of Juvenile Plants Shown by *Sargassum stolonifolium* Phang et Yoshida in the Andaman Sea Localities

	Malaysia	**Thailand**	**Thailand**	**Thailand**
Coll. location	Penang Batu Ferringhi	Phang-nga	Ranong Ko Ra	Ranong Ko Nui
Coll. date	Jan. 1, 1988	May 10, 1998	May 9, 1998	May 9, 1998
plant height	to 1 cm	to 10 cm	to 8 cm	to 12 cm
holdfast	discoid	discoid	discoid	discoid
diam.	to 6 mm	to 12 mm	to 6 mm	to 15 mm
upper cauline leaves	lance./ellipt.	ellipt.	ellipt.	-
length(max)	5 cm	3 cm	3 cm	-
width(max)	8 mm	6 mm	6 mm	-
lower cauline leaves	cylind.	cylind.	cylind.	cylind.
length(max)	6 cm	3 cm	3 cm	2 cm
diam.(max)	1 mm	1 mm	1 mm	1 mm
branching	present	present	present	present
haptera	present	present	present	present

cylind. = cylindrical, ellipt. = elliptical, lance. = lanceolate

Discussion

Stolons modified from cauline leaves were observed to be common in some populations (Phang-nga, Phuket, and Trang) but uncommon in other populations (Ko Nui, Ko Ra (Ranong), Phuket, and Trang). These specimens were all fertile, with receptacles; the stolons may have been lost during the early developmental stage, with few surviving to the fertile stage.

Stolons of juvenile plants collected from 4 populations along the Andaman Sea and south to the type locality were also studied. The cauline leaves exhibited two types of morphology. Lanceolate to elliptical flattened cauline leaves were produced from upper portions of the stems, and cylindrical cauline leaves were produced from lower portions of the stems and later modified into stolons.

The cylindrical cauline leaves disappeared during developmental stages, and we were unable to find stolons from juvenile plants collected from Ko Ra and Ko Nui, Ranong. A specimen of *S. stolonifolium* collected from Ko Thalibong, Trang on Oct. 25, 2002 (made available by Dr. Hiroshi Kawai, Kobe University) is a young plant without receptacles and lacking stolons on the stem. From this material we surmise that the formation of stolons is not necessary for plants in stable environmental conditions on calm coasts or when protected by rocks from strong waves, whereas stolons may be necessary on rough coasts.

Phang and Yoshida (1997) proposed that the evolution of a proliferating system from the cauline leaves could be attributed to unstable environmental conditions in which the species had colonized. They suggested that "as soon as a plant was established on the slippery rock surface, it produced cauline leaves, which quickly branched out and produced haptera to attach at as many points as possible to the rock surface."

The northern coast of the Andaman Sea in Thailand is famous for large, strong waves in the monsoon season. However, at Ko Nui and Ko Ra we found *S. stolonifolium* in some habitats protected from strong waves, where the plants could grow in stable conditions. These plants would have no need to develop stolons from cauline leaves in response to rough seas. Furthermore, until the plants produce reproductive organs (receptacles), stolons may be lost from the basal stem in rough conditions.

Morphological characteristics of *S. stolonifolium* from Thailand are summarized as follows: slender elliptical primary and secondary leaves, 2–4 cm long, 3–9 mm wide, with entire or small dentations at margins; vesicles spherical, with round to pointed apex, with short terete stem; female receptacles compressed, with small dentations at margins, 2–5 mm long, 0.5–1 mm wide; male receptacles cylindrical, with warty to smooth surface, 5–7 mm long, 0.5 mm in diameter.

Egerod (1974) reported *Sargassum* plants from Ko Ra, in northern Thailand, and described them as follows: "a compact holdfast below and a cluster of closely placed primary branches above without appreciable intervening internodes; leaves irregularly ovate-lanceolate, 1.5-2.5 cm long and 4–7 mm wide, with apex varying from irregularly obtuse to somewhat tapered or truncated, margins entire and slightly undulate toward base of plant, becoming finely dentate above; inflorescences up to 1 cm long, mixed, bearing leaves, vesicles and receptacles, leaves reduced in size and number, particularly in male plants. Plants are dioecious. Male receptacles are cylindrical, 4–5 mm long, simple or forked. Female receptacles are compressed, 1–2 mm long, with dentate margins." Egerod (1974) listed these plants as *S. grevillei,* a species previously reported from the Solomon Islands by Womersley and Bailey (1970) based on a specimen originally described as *S. oligocystum* by Setchell (1935). The flattened primary branches characteristic of *S. grevillei* were not taken into account in Egerod's comparison, because the clusters of primary branches mentioned and illustrated by Egerod (1974, fig. 93) show terete primary branches which are characteristic of *S. stolonifolium* (Phang and Yoshida 1997). Our specimens from the Penang type locality show terete primary branches measuring 1–1.5 mm in diameter. We think that Egerod's materials were specimens of *S. stolonifolium* lacking stolons on the stem. Unfortunately, these specimens, which Egerod deposited in the National Museum of Phuket, have been lost (pers. comm., 2002), so we are unable to study its details.

Acknowledgments

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Literature Cited

Egerod, L. 1974. Report of the marine algae collected on the Fifth Thai–Danish Expedition of 1966. Chlorophyceae and Phaeophyceae. Bot. Mar. 17:130–157.

Lewmanomont, K., and Ogawa, H. 1995. Common seaweeds and seagrasses of Thailand. Faculty of Fisheries, Kasetsart University, Bangkok. 163 pp.

Phang, S. M., and Yoshida, T. 1997. *Sargassum stolonifolium* Phang et Yoshida sp. nov. from Penang Island, Peninsular Malaysia. Tax. Econ. Seaweeds 6, pp. 61–73.

Schmidt, J. 1900–1916. Flora of Koh Chang. Contributions to the knowledge of the vegetation in the Gulf of Siam. Bianco Luno, Copenhagen. 444 pp.

Setchell, W. A. 1935. Some marine plants of southeastern Melanesia. The Templeton Crocker Expedition to Western Polynesia and Melanesian Islands, 1933. Proc. Calif. Acad. Sci., ser. 4, 21:259–276, pls. 11–15.

Womersley, H. B. S., and Bailey, A. 1970. Marine algae of the Solomon Islands. Phil. Trans. Roy. Soc. London, B. Biol. Sci. 259 (830):257–352, figs. 1–10, pls. 24–27.

TWO NEW SPECIES OF THE SUBGENUS *SARGASSUM* (FUCALES, SARGASSACEAE) FROM VIETNAM

Nguyen Huu Dai

Abstract

Two new species of the subgenus *Sargassum* are described; both have dioecious receptacles. *Sargassum namoense* has lanceolate leaves with entire margins that may be finely dentate, and obovoid to subspherical, smooth, mucronate or apiculate vesicles. *Sargassum serratum* is characterized by small leaves with serrate to dentate margins and apiculate vesicles.

Introduction

The genus *Sargassum* in Vietnam is diverse, but knowledge of the taxonomy of its species is still limited. A great number of herbarium specimens collected throughout various localities of Vietnam beginning in 1960 are deposited in the Herbarium of the Institute of Oceanography in Nha Trang. Some of them are not yet identified or are misidentified. The plan is to reexamine these specimens, as well as to collect more samples, to contribute to the studies of *Sargassum* in Vietnam and the western Pacific.

Materials and Methods

In this study, specimens of *Sargassum namoense* sp. nov. were collected by Nguyen Huu Dai in Nam O village, Da Nang City, central Vietnam (Fig. 1) in 2002. For *S. serratum* sp. nov., a number of specimens collected by Nguyen Huu Dai in Binh Dinh, Khanh Hoa, and Ninh Thuan provinces of southern central Vietnam (in 1977, 1978, 1980, 1981, 1986) and by Pham Hoang Ho and Luong Cong Kinh in Khanh Hoa province (in 1960–1962) were examined. Most of the herbarium specimens from Pham Hoang Ho and Luong Cong Kinh are nonfertile.

Description of the Species

Sargassum namoense Nguyen Huu Dai, sp. nov. (Figs. 2–3)

Holotype: Female 02175 (Fig. 2), leg. Nguyen Huu Dai, Nam O village, Da Nang City, May 12, 2002. Deposited in the Herbarium of the Institute of Oceanography, Nhatrang, Vietnam.

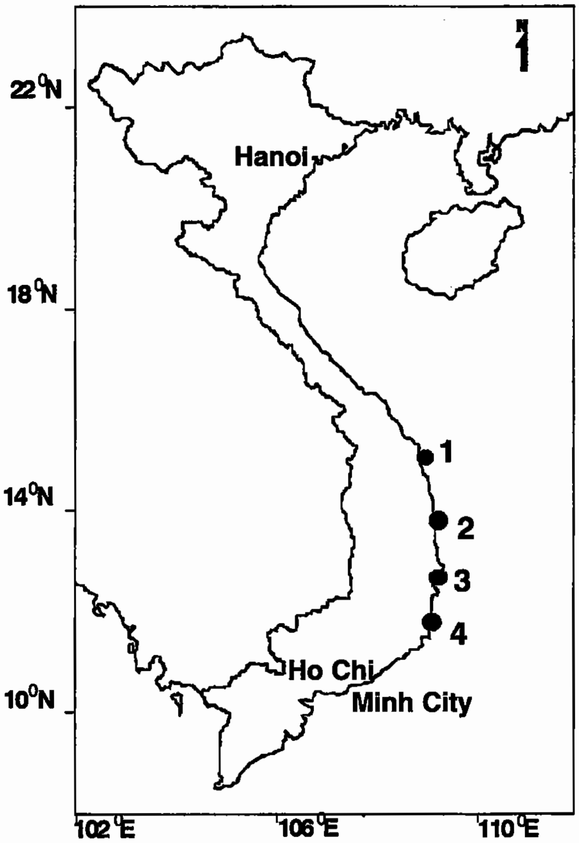

Fig. 1. Map of collection sites in Vietnam, 1, Da Nang (Nam O village); 2, Binh Dinh; 3, Khanh Hoa; 4, Ninh Thuan Province.

Frons lutea, brunnea, 80 cm alta, discus conicus circa 1 cm latus. Axis principalis cylindricus, brevis, circa 0.5–1 cm longus, 2–4 ramos primarios emittens, cylindricos, filiformes, laeves, circa 0.5–1 mm in diametro; rami secundarii ab folii axe, cylindrici, circa 20–30 cm longi, spatio 2–4 cm lato separati. Foliis lanceolatis, ad apicem plerumque obtusa, ad marginem leviter dentata vel quasi integra; costis percurrentibus vel infra apices evanida, cryptomatibus conspicuous; foliis in ramis primariis circa 3–4 cm longis, 3–6 mm latis; foliis in ramis secundariis et ramulis 2–2.5 cm longis, 2–4 mm latis. Vesiculae sphaericae, obovoideae vel oblongae, circa 2–4 mm in diametro, laeves, vel ad apicem cum spinas parvas nonnullas, vel apiculatae; stipi tereti, vesiculis breviore.

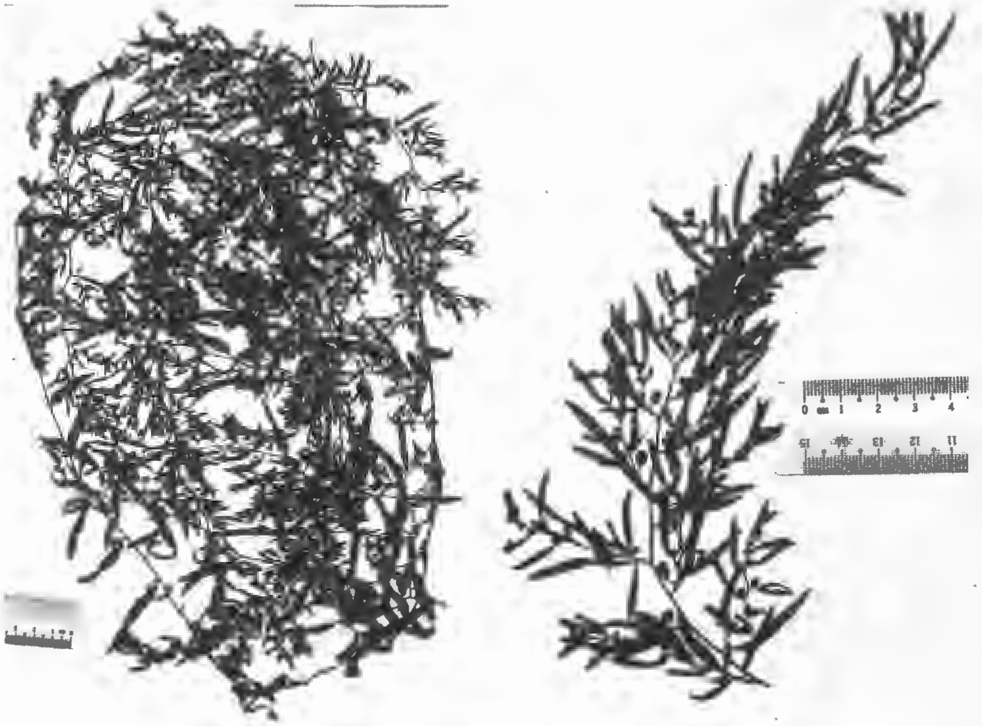

Fig. 2. *Sargassum namoense* sp. nov. left, Holotype specimen. right, Female branch.

Plantae dioeciae. Receptaculum masculinum teres, circa 0.4–1 cm longum, interdum cum spinam simplicem vel 1-furcatam. Receptaculum femineum triquetrum, circa 4–5 mm longum, ad marginem dentatum, simplex vel furcatum.

Frond dark brown, up to 80 cm tall. Holdfast discoid, about 1 cm in diameter. Main axis cylindrical and short, about 0.5–1 cm tall, giving rise to 2–4 primary branches cylindrical, filiform and smooth, about 0.5–1 mm in diameter. Secondary branches from leaf axil, cylindrical, about 20–30 cm long, generally at intervals of 2–4 cm between branches. Leaves (Fig. 3a) lanceolate, about 3–4 cm long and 3–6 mm wide in primary branches, about 2–2.5 cm long and 2–4 mm wide in secondary branches and branchlets; mostly obtuse at apices, slightly dentate at margins or nearly entire; with conspicuous midrib percurrent or disappearing below apices, and slightly raised cryptostomata irregularly scattered on both sides of midrib. Vesicles (Fig. 3b) obovoid to subspherical or elliptical oblong, about 2–4 mm in diameter, smooth or with some small spines or apiculate at apex; stipe terete, shorter than vesicles.

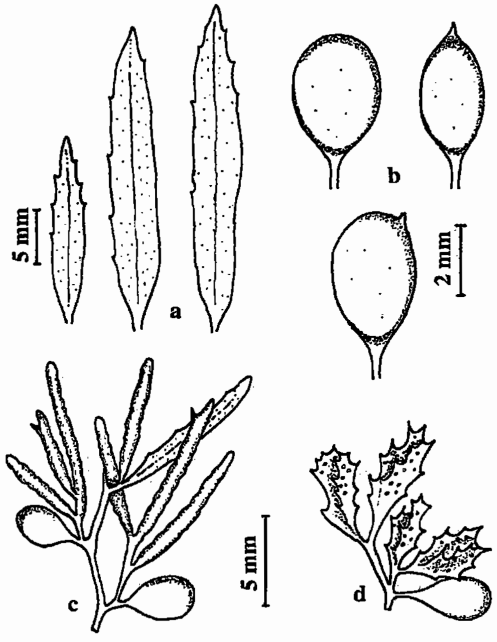

Fig. 3. ***Sargassum namoense*** **sp. nov.**
(a) leaf shapes; (b) vesicles;
(c) terete male receptacles;
(d) triquetrous female receptacles.

Plants dioecious. Male receptacle (Fig. 3c) terete, about 0.4–1 cm long, sometimes with a spine, simple or branched furcately. Female receptacle (Fig. 3d) triquetrous, about 4–5 mm long with a dentate margin, simple or furcately divided.

Other Specimens Examined: Female 02163, 02173, 02177, 02178, 02180; Male 02160, 02169, 02170, 02169, 02174, 02185, leg. Nguyen Huu Dai.

Etymology: Named for its type locality, Nam O village.

Habitat: Growing on subtidal rocks in dense stands.

Remarks: Endemic to Vietnam. This species belongs to the subgenus *Sargassum,* section *Acanthocarpicae* J. Agardh. It is characterized by lanceolate leaves with entire or finely dentate margins, and obovoid to subspherical, smooth, mucronate or apiculate vesicles. It is different from *S. plagiophyllum* C. Agardh and *S. fuscifolium* Tseng et Lu in the shape of leaves and vesicles.

Sargassum serratum Nguyen Huu Dai, sp. nov. (Figs. 4–5)

Holotype: Male 86086 (Fig. 5a), leg. Nguyen Huu Dai, Nhatrang, Khanh Hoa Province, May 15, 1986. Deposited in the Herbarium of the Institute of Oceanography, Nhatrang, Vietnam.

Plantae ochraceae, usque 40–80 cm altae, haptero discoideo 5–6 mm diam., axem principalem, laevem, cylindricum, brevissimum usque 1–3 mm longum procreante, 2–4 ramis primaries parte supera exorientibus; rami primarii teretes, leaves, 0.5–1 mm diam. Folia ramorum primariorum parva, oblonga, saepe 0.7–1.5 cm longa, 3–6 mm lata, irregulariter et grosse dentata, costa non percurrente, cryptostomatibus conspicuis; folia ramorum secundariorum et ramulorum parviora, 0.5–1 cm longa, 3 mm lata, similaria forma foliis ramorum primariorum. Vesiculae numerosae, parvae, 1–3 mm diam., ellipticae-oblongae, apice apiculato, interdum spinis vel ala dentata.

Plantae dioeciae. Receptacula mascula teretia, torulosa, usque 0.5–2 cm longa, racemosa. Receptacula feminea parviora, teretia vel fusiformia, interdum compressa, usque 2–5 mm longa, spinis paucis.

Plants yellow brown, attaining a height of 40–80 cm, discoid holdfast 5–6 mm in diameter, giving rise to smooth and cylindrical short main axes, up to 1–3 mm long; 2–4 primary branches arising from upper part. Primary branches terete, smooth, 0.5–1 mm in diameter. Leaves (Fig. 5b) small, oblong, on primary branches usually 0.7–1.5 cm long, 3–6 mm wide, irregularly and coarsely dentate. Midrib not percurrent, cryptostomata conspicuous. Leaves on secondary branches and branchlets smaller, 0.5–1 cm long, 1.5–3 mm

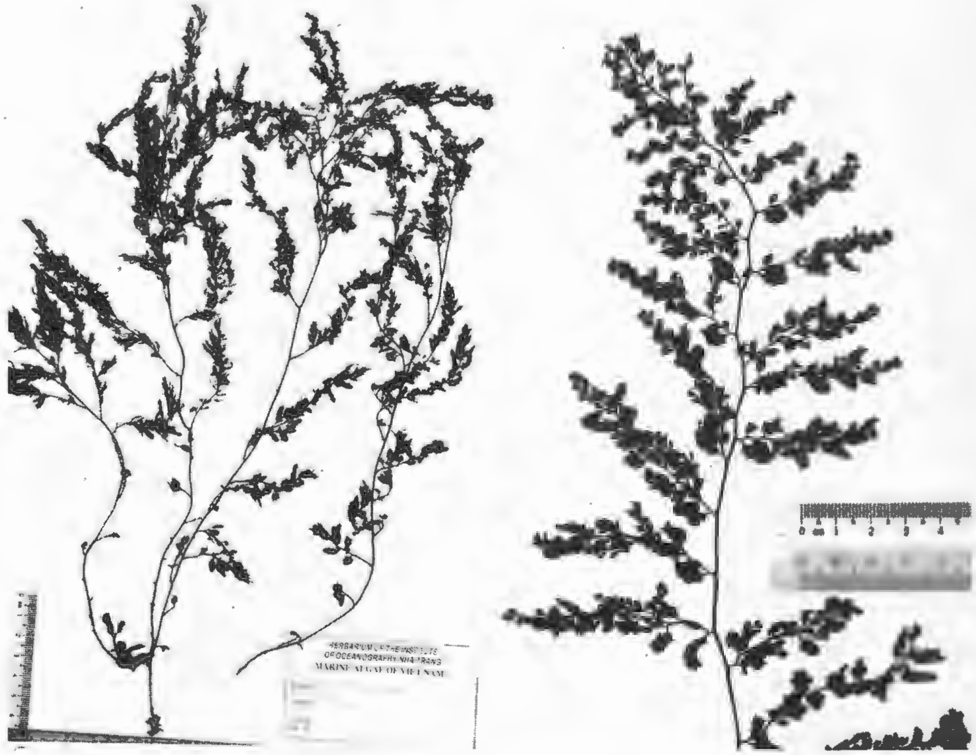

Fig. 4. ***Sargassum serratum*** **sp. nov. left, Holotype specimen. right, Habit of young branch.**

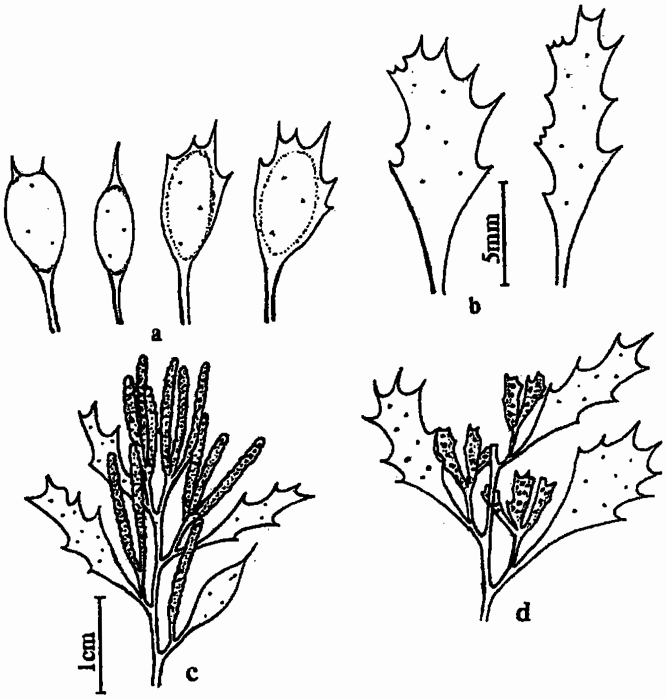

Fig. 5. ***Sargassum serratum*** **sp. nov. (a) vesicles; (b) leaf shapes; (c) terete male receptacles; (d) terete or compressed female receptacles.**

wide, very similar to those on primary branches in form. Vesicles (Fig. 5a) numerous, small, elliptical oblong, 1–3 mm, apiculate apex, sometimes with some spines or a dentate wing.

Plants dioecious. Male receptacles (Fig. 5c) terete, torulose, up to 0.5–2 cm long, racemosely arranged. Female receptacles (Fig. 5d) shorter than male receptacles, terete or fusiform, sometimes compressed with a few spines, up to 2–5 mm long.

Other specimens examined: Female 77163, 77164, 80156, 80157, 80159, 81123, 81126, 81127 (in March); Male 78248, 80153, 80154, 80155, 80156 (in March); nonfertile plants 78020, 78023, 81125, 81152 (in February).

Habitat: Growing on lower intertidal and subtidal rocks or dead coral; forming dense populations on rocks.

Local distribution: Binh Dinh, Khanh Hoa, and Ninh Thuan provinces.

Remarks: Endemic to Vietnam. This species belongs to the subgenus *Sargassum,* section *Zygocarpicae* (J. Agardh) Setchell, subsection *Pseudo-*

zygocarpicae Setchell as discussed by Ajisaka et al.(1995). It is characterized by small, serrate-dentate leaves and dioecious receptacles. It is different from *S. hemiphyllum* (Turner) C. Agardh in the holdfast and receptacles. We compared our specimens to the lectotype of *S. hemiphyllum* f. *serrata* Pham Hoang (PH 3242, nonfertile) and two other specimens (PH 3247, 3248, male; Pham Hoang Ho 1967:278). The holdfast, leaves, and vesicles are the same as in *S. serratum* sp. nov. We conclude that the lectotype PH 3242 and specimens PH 3247 and 3248 are not *S. hemiphyllum* because of their conical holdfast. We also examined specimen PH 3034 (nonfertile) of *S. kjellmanianum* sensu Pham Hoang Ho (Pham Hoang Ho 1967:278) and specimens 80150–155 and 80042–46 of *S. kjellmanianum* sensu Nguyen Huu Dai (Nguyen Huu Dai 1997:57). These specimens were misidentified (Yoshida et al. 2002: 98) and belong to *S. serratum* sp. nov. In summary, in Vietnam the names *S. hemiphyllum* f. *serrata* Pham Hoang (1967:276) and *S. kjelmanianum* sensu Pham Hoang Ho and sensu Nguyen Huu Dai should be deleted; all specimens previously assigned to these species deposited in the Institute of Oceanography Herbarium, Nha Trang, are *S. serratum* sp. nov.

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Literature Cited

Ajisaka, T., Noro, T., and Yoshida, T. 1995. Zygocarpic *Sargassum* species (Subgenus *Sargassum*) from Japan. In: Tax. Econ. Seaweeds 5, pp. 11–44.

Nguyen Huu Dai. 1997. Sargassaceae in Vietnam: Resources and utility. Agriculture Publishing House, Ho Chi Minh City. 199 pp.

Pham Hoang Ho. 1967. Contribution a l'etude des Algues littorales du Vietnam I: Le genre *Sargassum*. Ann. Fac. Sci. Saigon, pp. 259–332.

Yoshida, T., Nguyen Huu Dai, Ajisaka, T., and Noro, T. 2002. Verification of *Sargassum* species identified with subgenera *Bactrophycus, Phyllotrichia,* and *Schizophycus* in Vietnam. In: Tax. Econ. Seaweeds 8, pp. 95–102.

SOME NEW SPECIES OF THE HOLOZYGOCARPIC *SARGASSUM* FROM THE SOUTH CHINA SEA

C. K.Tseng and Lu Baoren

Abstract

In studies on Chinese species of section *Zygocarpicae* of subgenus *Sargassum*, we found 4 new species: *Sargassum angustifolioides* Tseng et Lu sp. nov. from Weizhou Island; *S. longicarpum* Tseng et Lu sp. nov. from Hong Kong; and *S. minimum* Tseng et Lu sp. nov. and *S. parvulum* Tseng et Lu sp. nov. from near Fangcheng City, Guangxi Province. All 4 species belong to subsection *Holozygocarpicae*.

Introduction

In their treatment of the Chinese Fucales, Tseng and Lu (2000) reported 22 species of holozygocarpic *Sargassum* in China from the South China Sea region; half of these species were first described from China, indicating the great abundance of this subsection of *Sargassum* in China. A search of the *Sargassum* specimens in our herbarium revealed 4 more new species, making a total of 26 species of *Holozygocarpicae* from China. The holotypes and specimens examined are deposited at the Herbarium of the Institute of Oceanology, Chinese Academy of Sciences, Qingdao (AST).

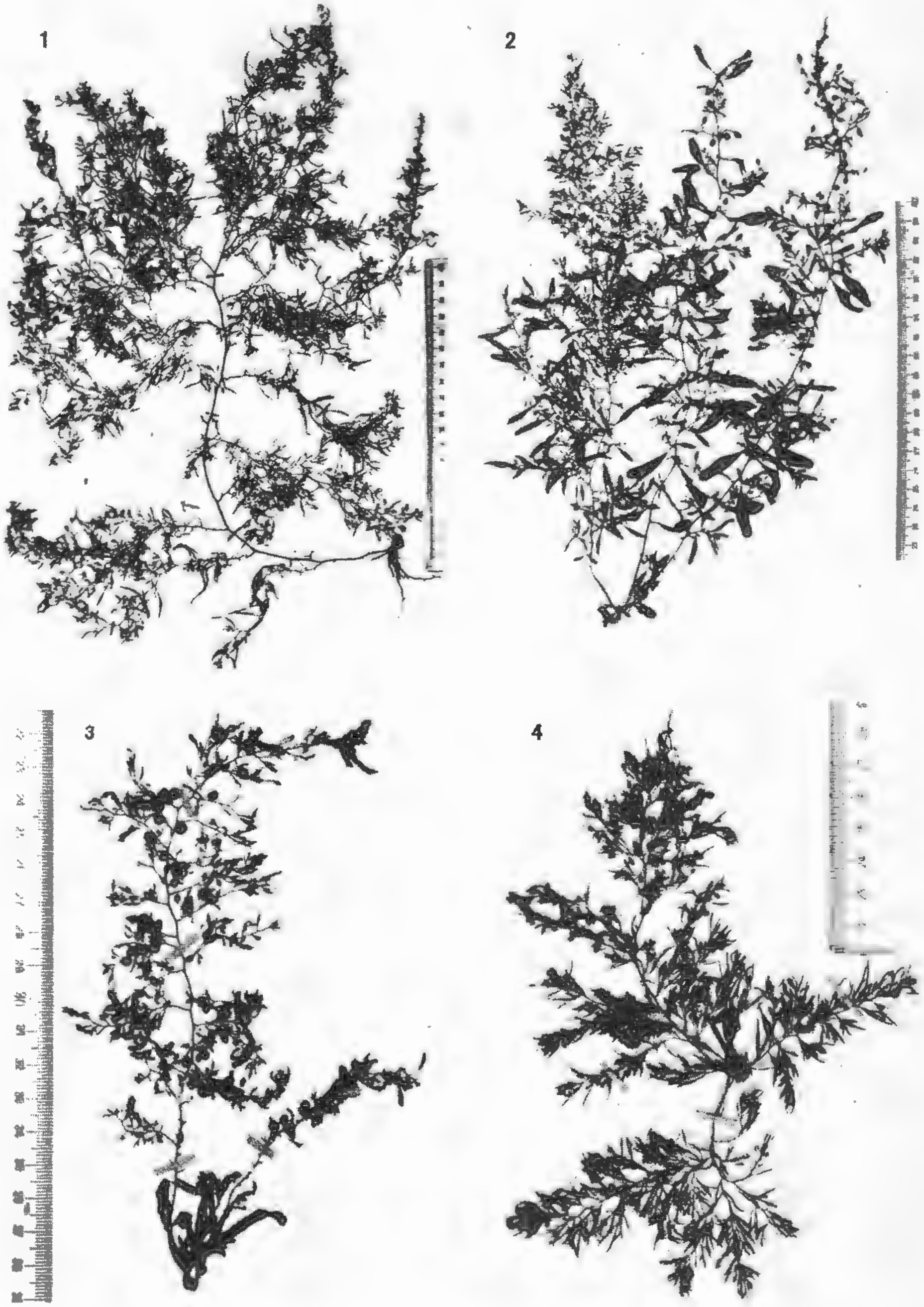
Description of the Species

Sargassum angustifolioides Tseng et Lu, sp. nov. (Figs. 1, 5)

Holotype: AST 55–1882, Zheng Shudong, April 27, 1955, on Weizhou I., Guangxi Province, South China Sea.

Frons lutea brunnea, 45 cm ultra alta. Haptero disciformi. Caule brevis, 5.0 mm longis, 2.0 mm in diametro. Ramis primariis et secundariis cylindricis, laevis, ramis ultimis glandibus. Foliis lanceolatis anguste, 2.5–3.0 cm longis, 1.5–2.0 mm latis, acutis ad extremum, cuneatis vel oblique at basim,margibus dentatibus, costis percurrenibus, cryptostomatibus dispersis ad utrinque costalis. Vesiculis sphaeris, 1.5–2.0 mm in diametro. Plantae androgynae. Receptaculis compressis vel subcylindricis, spinibus, 3.0–4.0 mm longis, 1.0–1.5 mm in diametro. Holozygocarpicae.

Frond yellow brown, about 45 cm high, slender with many irregular branches. Holdfast discoid, up to 5.0 mm in diameter. Main axes cylindrical, smooth, about 5.0 mm tall, 2.0 mm in diameter, giving rise to several primary branches



Figs. 1–4. **Fig. 1,** ***Sargassum angustifolioides*** **Tseng et Lu. sp. nov.** **Fig. 2,** ***Sargassum longicarpum*** **Tseng et Lu, sp. nov. Fig. 3,** ***Sargassum minimum*** **Tseng et Lu, sp. nov. Fig. 4,** ***Sargassum parvulum*** **Tseng et Lu, sp. nov.**

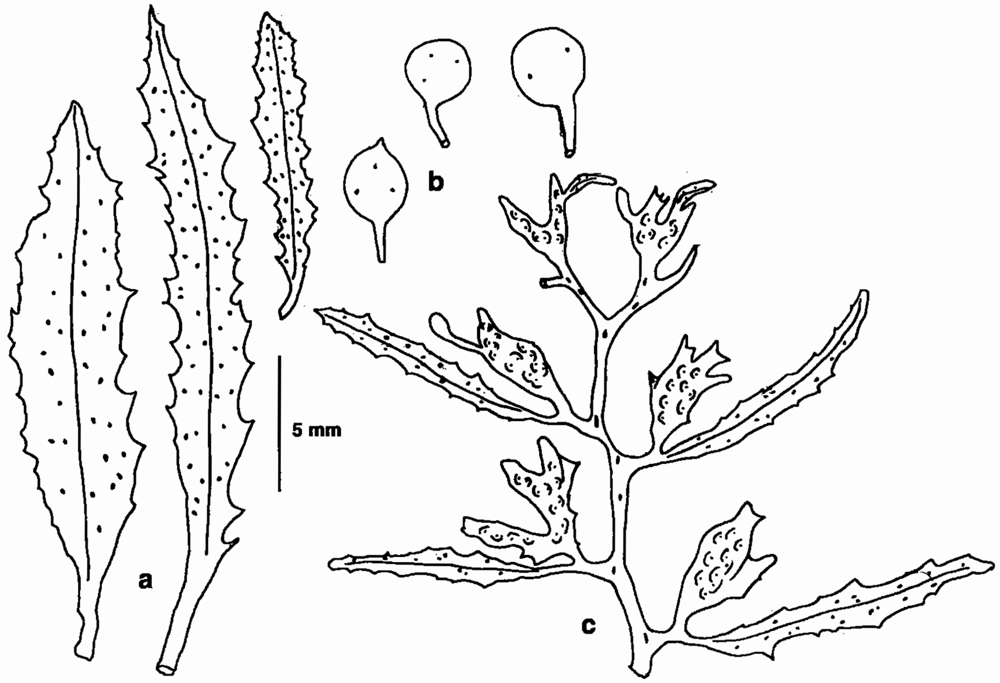


Fig. 5. ***Sargassum angustifolioides*** **Tseng et Lu, sp. nov. a, leaves; b, vesicles; c, receptacles with leaf.**

from its upper part. Primary branches cylindrical, smooth, about 44.5 cm tall, 1.5 mm in diameter. Secondary branches arising from leaf axils of primary branches, terete, glabrous, slender, short, about 18–20 cm long, 1.0 mm in diameter, alternate at intervals of 2.0–3.0 cm. Ultimate branchlets terete, slender and shorter, with some non-elevated glandular dots on surface, 3.0–4.0 cm long, less than 1.0 mm in diameter, beset with leaves, vesicles, and receptacles. Leaves on primary branches early deciduous. Leaves on secondary branches narrowly lanceolate, about 2.5–3.0 cm long, 1.5–2.0 mm wide, acute at apices, slightly and obliquely cuneate at base, conspicuously dentate at margins, with distinct percurrent midrib; cryptostomata irregularly scattered on both sides of midrib. Leaves on ultimate branchlets very similar to those on secondary branches in shape, but shorter and slenderer, about 1.5–2.0 cm long, 1.0–1.5 mm wide, dentate at margins, with percurrent midrib; cryptostomata arranged on both sides of midrib. Vesicles spherical, mostly on cylindrical stalks, sometimes acute at apices, about 1.5 –2.0 mm in diameter, with a few raised cryptostomata on surface, without earlike structure on both sides of vesicles, sometimes compressed above, cylindrical below.

Plants androgynous. Receptacles compressed or subcylindrical, usually forked, scarcely spinulose on surface, usually furcate at apices, about 3–4 mm long, 1.0 –1.5 in diameter, sometimes with small leaf or vesicle directly arising from its surface.

Other Materials Examined: Weizhou Island, AST 55-1818, -1832, -1833, -1871, -1881, -1895, -1905, 87-1193.

Etymology: This species is named for its narrow leaves, similar to those of *S. angustifolium* (Turner) C. Agardh (Agardh 1820).

Remarks: This new species is mainly characterized by its compressed or subcylindrical receptacles, sometimes spinulose on the surface; ultimate branches with non-elevated glandular dots; and narrowly lanceolate leaves, reminding one of *S. angustifolium* (Turner) C. Agardh. It is a member of the species group *Tenerrima* Setchell, near *S. parvivesiculosum* Tseng et Lu (Tseng and Lu 1979).

Sargassum longicarpum Tseng et Lu, sp. nov. (Figs. 2, 6)

Holotype: A115, Y. W. Taam, May 11, 1941, at Wongmakok, Kowloon, Hong Kong.

Isotype: A116, Y. W. Taam, May, 11, 1941, at Wongmakok, Kowloon, Hong Kong.

Frons lutea brunnea, 50 cm ultra alta. Haptero scutiformi. Caule cylindricis, 7.0 mm longis, 2.0 mm in diametro. Ramis primariis et secundariis cylindris, laevis, ramis ultimis glandibus. Foliis oblongis, 3.0–3.5 cm longis, 8.0–9.0 mm latis, rotundatis, obtuse ad extremum, cuneatis oblique ad basim, marginibus undulatis, denticulatis aliquando supra, costis obscures, vulgo sub mediis evanidis, cryptostomatibus dispersis ad utrinque, foliis supra pusillis et angustis. Vesiculis ellipsoidalis, apicibus acuminatis, 5.0 mm longis, 4.0 mm in diametro. Plantae dioeciae. Receptaculis femineis cylindricis, spinibus, 6.0–7.0 mm longis, 1.5–2.0 mm in diametro, receptaculis maribus cylindricis, spinibus, 24–25 mm longis, 1.0–1.2 mm in diametro. Holozygocarpicae.

Frond yellow brown, up to 50 cm high. Holdfast with rhizoidal filaments, up to 15 mm in diameter. Main axis cylindrical, glabrous, up to 7.0 mm tall, 2.0 mm in diameter. Several primary branches arising from upper part of axis, cylindrical , glabrous, about 49 cm long, 1.2 mm in diameter. Secondary branches arising from leaf axils of primary branches, cylindrical, alternate, at intervals of 1.0–1.5 cm, secondary branches of female plant shorter than those of male plant, about 4.0–10 cm long, 1.0 mm in diameter, with some raised gladular dots on surface. Secondary branches of male plant longer, 15 cm long, less than 1.0 mm in diameter. Ultimate branchlets shorter and slenderer, 3.0–4.0 cm long, less than 1.0 mm in diameter, with raised glandular dots on surface. Leaves on primary branches oblong, with short, compressed leafstalk, about 3.0–3.5 cm long, 8.0–9.0 mm wide, obtuse or rounded at apex, obliquely asymmetrically cuneate at base, usually broader outside than

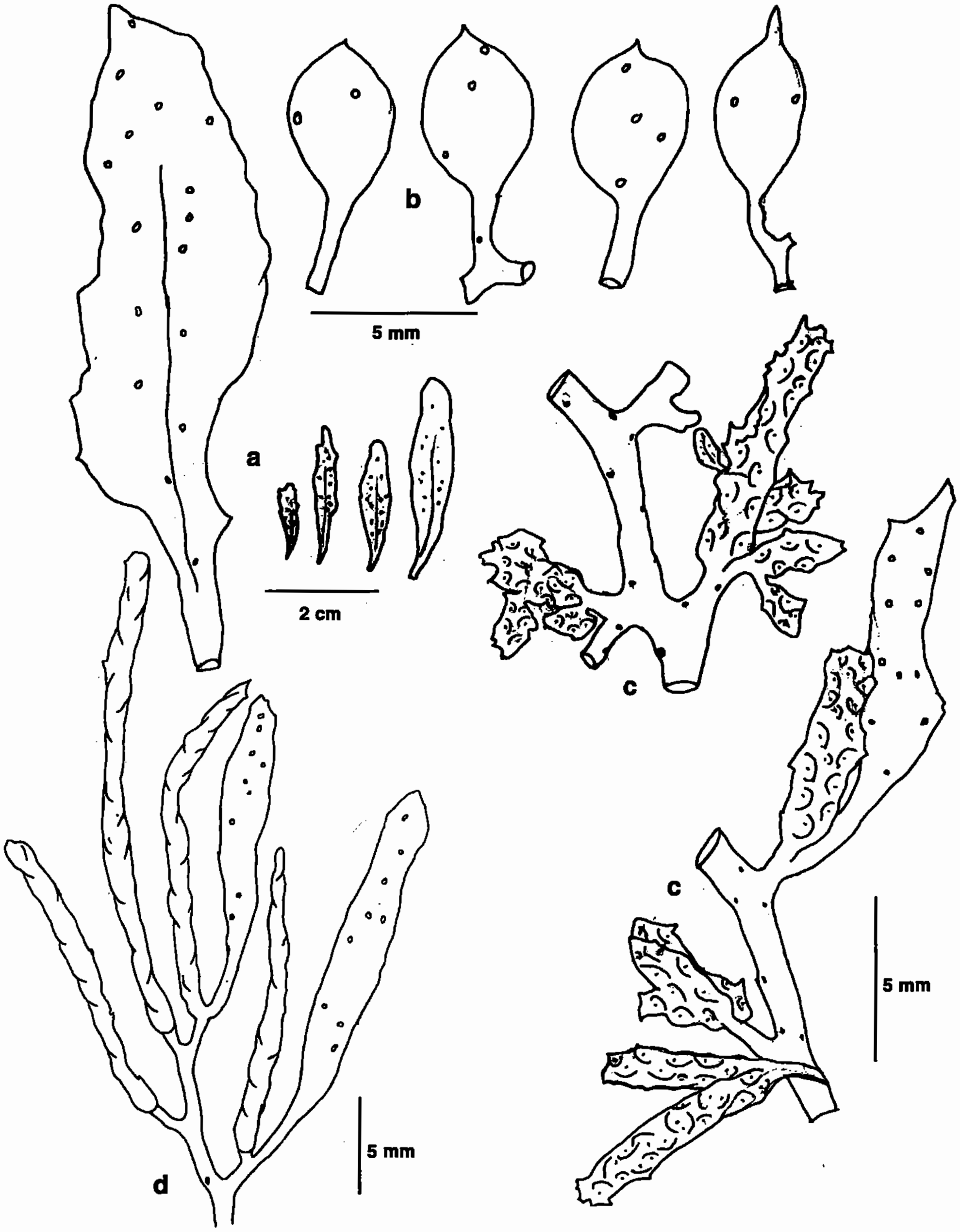


Fig. 6. ***Sargassum longicarpum*** **Tseng et Lu, sp. nov. a, leaves; b, vesicles; c. female receptacles; d. male receptacles.**

inside, some wavy or denticulate on upper part of leaves at margins, with midrib obscure, vanishing below 2/3 of apices, with slightly raised conspicuous cryptostomata irregularly arranged on both sides of midrib, leaves on secondary branches narrowly oblong, about 2.0–2.5 cm long, 4.0 mm wide, mostly obtuse, other acuminate at apices; obliquely cuneate at base, obscure midrib, with raised cryptostomata irregularly arranged on both sides of midrib, leaves on ultimate branches shorter and slenderer than those of secondary branches, about 4–6 mm long, 2.0 –3.0 mm wide, without midrib, slightly raised cryptostomata irregularly arranged on surface of leaves, with short cylindrical stalk, 2.0 mm long. Vesicles ellipsoidal, acuminate at apices, about 5.0 mm long, 4.0 mm in diameter, with several cryptostomata, cylindrical stalks, 4.0 mm long, less than 1.0 mm in diameter.

Plants dioecious. Female receptacles cylindrical, sometimes with a few spinules, 6.0–7.0 mm long, 1.5–2.0 mm in diameter, usually forked, male receptacles usually slender and longer than female receptacles, cylindrical, mostly wavy, occasionally with 1–2 spinules on surface, about 24–25 mm long, 1.0–1.2 mm in diameter, sometimes with small leaf or vesicle directly arising from receptacle surface.

Etymology: This species name reflects the morphological features of the receptacles: male receptacles are longer than female receptacles and lack the forks of the female receptacles.

Other Materials Examined: 214, leg. C .K. Tseng, Hong Kong and vicinity, May 26, 1940; 2810, leg. C . K. Tseng, Repulse Bay Beach, Hong Kong, May 26, 1940.

Habitat: Growing on lower littoral rocks.

Remarks: This new species is mainly characterized by its large, cylindrical branches; dioecious receptacles with short cylindrical spinous female receptacles and much longer and slenderer cylindrical and slightly spinulose male receptacles; and entire, wavy, oblong leaves, occasionally a few acuminate at the apices. It is a member of the species group *Vietnamensa* proposed by Ajisaka et al. (1995) near *S. myriocystum* J. Agardh (Agardh 1848).

Sargassum minimum Tseng et Lu, sp. nov. (Figs. 3, 7)

Holotype: AST 55-2108, Zheng Shudong, May 11, 1955, at Qisha Fangcheng, Guangxi Province, South China Sea.

Frons atrofusca, parvula, 20 cm ultra alta. Haptero disciformi. Caule brevis, 4 mm longis, 2.0 mm in diametro. Ramis primariis cylindricis, laevis, ramis secundariis similitudo ramis primariis, glandibus. Foliis lanceolelis, foliis basalis 4.0 cm longis, 3.0–3.5 mm latis, foliis supera 1.0–2.0 cm longis, 1.0–2.0 mm latis. Vesiculis ellipsoidalis vel subsphaericis, 3.5–4.5 mm longis, 3.0–3.5 mm in diametro. Plantae androgynae. Receptaculis compressis, aliquando triquetris supra, 4.5–5.5 mm longis, 1.0–1.5 mm latis, spinibus. Holozygocarpicae.

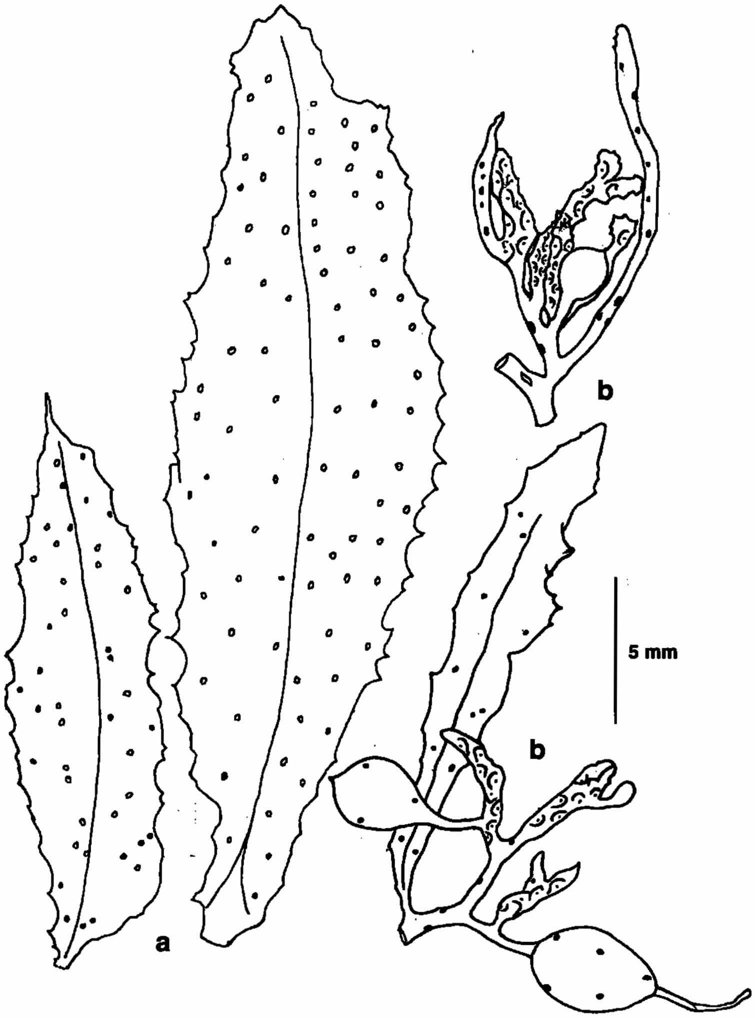


Fig. 7. ***Sargassum minimum*** **Tseng et Lu, sp. nov. a, leaves; b, receptacles with leaves and vesicles.**

Frond dark brown, small, up to 20 cm tall. Holdfast discoid, about 4.0 mm in diameter. Main axis cylindrical, short, glabrous, about 4 mm tall, 2.0 mm in diameter. Several primary branches arising from upper part of axis, cylindrical, slender, up to 19.6 cm long, 1.0 mm in diameter. Secondary branches arising from leaf axils of primary branches, very similar to primary branches, but small and short, about 4.0–5.0 cm long, less than 1.0 mm in diameter, alternate, with raised glandular dots, beset with leaves, vesicles, and receptacles at intervals of 3.0–5.0 cm. Leaves lanceolate, acute at apices, slightly oblique-cuneate at base, mostly percurrent midrib, with raised cryptostomata on both sides of midrib, basal leaves longer, about 3.5–4.0 cm long, 3.0–3.5 mm wide, upper leaves small and short, 1.0–2.0 cm long, 1.0–2.0 mm wide. Vesicles ellipsoidal, sometimes subspherical, 3.5–4.5 mm long, 3.0–3.5 mm in diameter, acute at apices, without earlike structures on vesicles, with several raised cryptosomata on surface and with cylindrical stalks, about 2.0–2.5 mm long, 0.5 mm in diameter.

Plants androgynous. Receptacles mostly compressed, sometimes triquetrous at upper part of receptacles, compressed below, 4.5–5.5 mm long, 1.0–1.5 mm wide, spinulose on surface, small leaf or vesicle usually arising directly from surface of receptacles.

Other Materials Examined: AST 55-2114a, -2117.

Etymology: This species is named for the small size of the mature fronds.

Habitat: Growing on subtidal rocks.

Remarks: This new species is mainly characterized by its compressed and conspicuously spiny receptacles, sometimes triquetrous in the upper parts; small fronds with secondary branches with glandular dots; and ellipsoidal vesicles, sometimes subspherical, acute at apices. It is a member of the species group *Tenerrima* Setchell, closely related to *S. subtilissimum* Tseng et Lu (Tseng and Lu 1978).

Sargassum parvulum Tseng et Lu, sp. nov. (Figs. 4, 8)

Holotypus: AST55-2116, Zheng Shudong, May 11,1955, at Qisha, Fangcheng, Guangxi Province, South China Sea.

Frons atrofusca, parvula, 13 cm altra. Haptero disciformi. Caule brevis, 3 mm longis, 1.0 mm in diametro. Ramis cylindricis, laevis. Foliis lanceolatis, filamenois, foliis basalis 1.5–2.3 cm longis, 1.0–1.5 mm latis, foliis supera 1.0–1.3 mm longis, 1.0 mm in diametro. Vesiculis obovatis vel ellipsoidalis, 1.5–2.0 mm longis, 1.0 –1.5 mm in diametro. Plantae dioeciae. Receptaculis feminis cylindricis, laevis, 3.0–5.0 mm longis, 1.0–1.2 mm in diametro, receptaculis maribus 6.0–8.0 mm longis, 1.0 mm in diametro. Holozygocarpicae.

Frond dark brown, small and slender, 13 cm tall; holdfast small discoid, about 5.0 mm in diameter. Axis short, cylindrical, glabrous, 3.0 mm tall, about 1.0 mm in diameter. Several primary branches arising from upper part of axis, about 10–12.7 cm long, less than 1.0 mm in diameter, cylindrical, glabrous. Secondary branches arising from leaf axils of primary branches, very similar to primary branches in shape, but small and slender, about 5.0–7.0 cm long, 0.5 mm or more in diameter, alternate. Intervals of 0.5–1.0 cm. Ultimate branchlets shorter, about 2.0–3.0 mm long, less than 0.5 mm in diameter, with leaves, vesicles, and receptacles. Leaves fleshy, linear or filamentous, about 1.5–2.5 cm long, 1.0–1.5 mm in diameter, acute at apices, cuneate at bases, without midrib, with cryptostomata, basal leaves usually very similar to

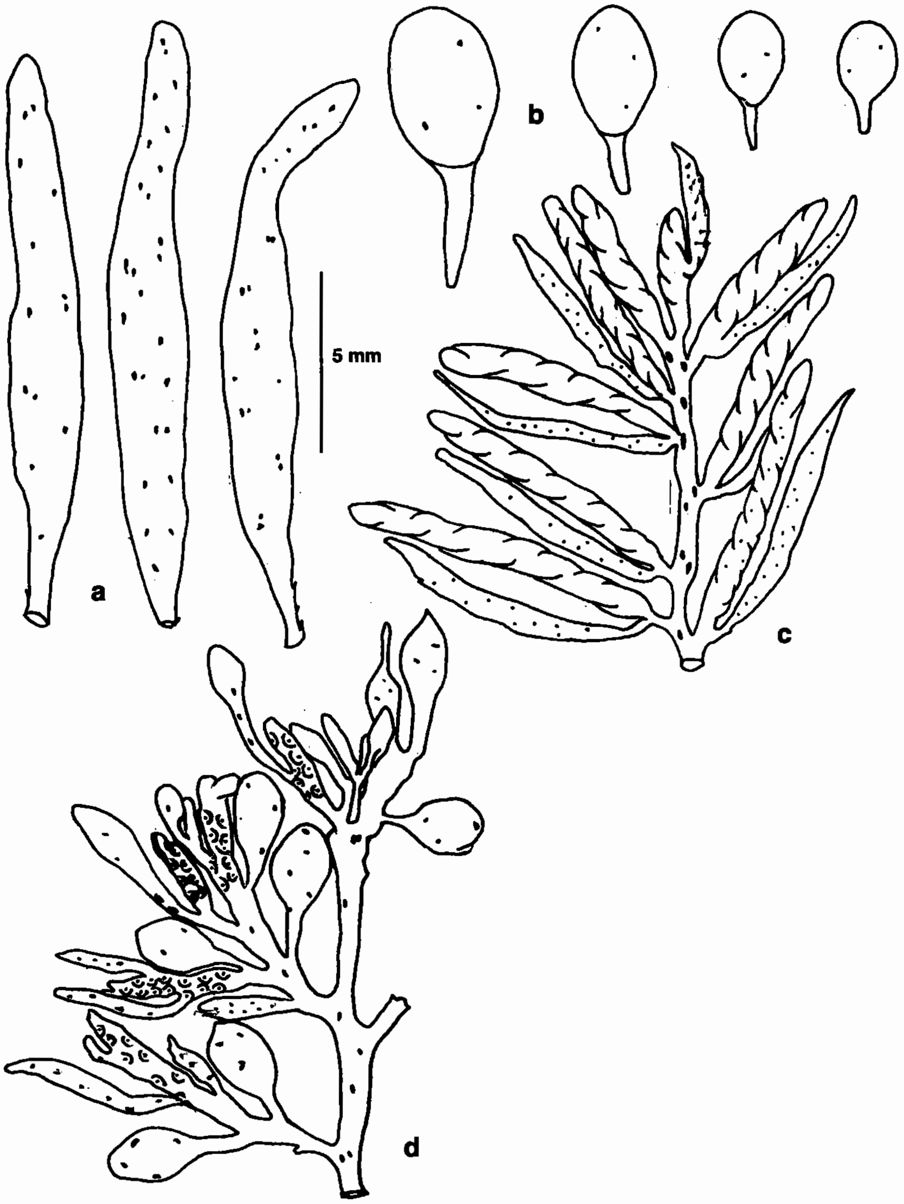


Fig. 8. *Sargassum parvulum* Tseng et Lu, sp. nov. a, leaves; b, vesicles; c, female receptacles arising directly from vesicles or leaves; d, male receptacles and leaves.

upper leaves in shape, longer than upper ones in size, 1.0–1.3 cm long, less than 1 mm in diameter, with short stalks. Vesicles ellipsoidal or obovate, mostly rounded, sometimes mucronate at apices, about 3.5–4.0 mm long, 1.5–2.5 mm in diameter, with cryptostomata and terete stalks.

Plants dioecious. Receptacles cylindrical, glabrous; female receptacles mostly simple, sometimes furcate, usually forked at apex, 3.0–5.0 mm long, 1.0–1.2 in diameter; male receptacles longer and slenderer than female receptacles, simple, 6.0–8.0 mm long, less than 1.0 mm in diameter, sometimes giving rise directly to small leaf or vesicle from surfaces.

Other Materials Examined: Sandun Beach, Qinzhou Bay, AST 55-2036, -2039; Qisha Beach, Fangcheng City, Guangxi Province, AST 55-2150, -2153a.

Etymology: This species is named for the small size of its mature fronds.

Remarks: This new species is mainly characterized by its small fleshy fronds with linear or filamentous ecostate leaves and secondary branches with glandular dots; and mostly compressed and spinulose receptacles, from which small leaves or vesicles usually arise directly. It is a member of the species group *Zhangia* Tseng et Lu and is near *S. baorenii* Nguyen et Huynh (Nguyen et Huynh 2001).

Conclusions

In this paper, 4 new species of holozygocarpic *Sargassum* collected from the South China Sea are reported and added to the Chinese algal flora, making a total of 26 species of holozygocarpic *Sargassum* in China. Until recently (Tseng and Lu 2000), 130 species of the genus *Sargassum* had been reported from China. Recently, Dr. Yoshida informed us that the genus *Hizikia* established by Okamura (1932) is genetically close to subgenus *Bactrophycus* J. Agardh (Agardh 1848). Perhaps *H. fusiformis* should be returned to *Sargassum fusiforme* (Harv.) Setchell (Setchell 1931). With the present increase of 4 species, the total species of the genus *Sargassum* in China should be corrected to 135. The presence of 135 species of *Sargassum* in China is indeed very significant.

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Literature Cited

Agardh, C. A. 1820. Species algarum, Vol. 1. Lund. 168 pp.
Agardh, J. G. 1848. Species genera et ordines algarum, Vol. 1. Lund. 363 pp.
Ajisaka, T., Noro, T., and Yoshida, T. 1995. Zygocarpic *Sargassum* species (subgenus *Sargassum*) from Japan. In: Tax. Econ. Seaweeds 5, pp. 11–44.

Nguyen Huu Dinh. and Huynh Quang Nang. 2001. Five new species of the genus *Sargassum* from Vietnam. National Centre for Natural Science and Technology of Vietnam, J. Biol. 23(1):1–10, figs. 1–5.
Okamura, K. 1931. *Hizikia* gen. nov. Icon. Jpn. Algae 6(10):89–90.
Setchell, W. A. 1931. Hong Kong seaweeds: I. Hong Kong Naturalist 2(1):39–60.
Tseng, C. K., and Lu Baoren. 1978. Studies on the Sargassaceae of the Xisha Islands, Guangdong Province, China. I. Stud. Mar. Sin. 12:1–11, pls. 1–5.
Tseng, C. K., and Lu Baoren. 1979. Studies on the Sargassaceae of the Xisha Islands, Guangdong Province, China. II. Stud. Mar. Sin. 15:1–20, pls. 1–7.
Tseng, C. K., and Lu Baoren. 2000. Fucales [of China]. In: Tseng, C. K. (ed.), Flora algarum marinarum sinicarum, 3(2). Science Press, Beijing. 238 pp., 31 pls.

SPECIES OF THE GENUS *SARGASSUM* SUBGENUS *SCHIZOPHYCUS*

Tadao Yoshida, Tetsuro Ajisaka, Tadahide Noro, and Takeo Horiguchi

Abstract

Five species are currently assigned to subgenus *Schizophycus,* characterized by the formation of main branches progressively from a foliar expansion, leaves extending in the same plane as the main branch, and vesicles with coronal leaf. Descriptions of the species are given on the basis of newly collected materials. Molecular phylogenetic analysis using ITS-2 nrDNA shows that *Sargassum patens* and *S. kushimotense* are positioned near *S. crassifolium* and *S. binderi* of subgenus *Sargassum.* The subgenus *Schizophycus* must be merged within subgenus *Sargassum.*

Introduction

The subdivision of the genus *Sargassum* was first proposed by C. Agardh (1820), who recognized several groups on the basis of receptacle position and leaf characters. Later, J. Agardh (1848) recognized 3 sections for the genus: *Pterophycus, Arthrophycus,* and *Eusargassum.* Section *Arthrophycus* was composed of 3 tribes: *Schizophylla, Holophylla,* and *Heterophylla.*[1] In 1889, J. Agardh again revised and divided the genus, now into 5 subgenera: *Phyllotrichia, Schizophycus, Bactrophycus, Arthrophycus,* and *Sargassum (=Eusargassum).* The tribe *Schizophylla* of section *Arthrophycus* nearly corresponded to subgenus *Schizophycus,* which was characterized by the development of main branches gradually transformed from foliar expansion with leaves expanded in the same plane as branches and vesicles crowned by coronal leaf. Phycologists treating this genus such as Yendo (1907), Reinbold (1913), Grunow (1915, 1916), and Setchell (1933) proposed minor correc-

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[1] Editors' note: These 3 tribes of section *Arthrophycus* are invalidly published because of misplaced ranks, under Article 4.1 of the St. Louis Code (Greuter et al. 2000), which states that "the secondary ranks of taxa in descending sequence are tribe (tribus) between family and genus, section (sectio) and series (series) between genus and species." A tribe, according to this article, cannot be part of a section. This situation is emphasized by Article 33.7: "A name given to a taxon of which the rank is at the same time...denoted by a misplaced term is not validly published." A somewhat similar situation was corrected by Abbott et al. (1988) for ranks between genus and species of *Sargassum.* Researchers should make every effort to establish correct ranks within this genus, so that future phylogenetic revisions do not incorporate incorrect nomenclature.

tions to Agardh's scheme. Womersley (1954) concluded that the distinction between *Phyllotrichia* and *Schizophycus,* on the basis of presence or absence of coronal leaf, could not be maintained, and he merged these two subgenera. Tseng and Lu (2000) agreed with this merger.

Subgenus *Schizophycus* included only *Sargassum patens* C. Agardh when J. Agardh (1889) proposed the subgenus, and *S. pinnatifidum* Harvey was tentatively appended. Yendo (1907) added *S. kashiwajimanum* Yendo and *S. tosaense* Yendo to the subgenus while relegating *S. rodgersianum* Harvey and *Halochloa schizophylla* Kützing as varieties of *S. patens.* Yendo (1907) described *S. kushimotense* Yendo from central Japan and attributed this species tentatively to subgenus *Arthrophycus.* Okamura (1936) followed this treatment. But Grunow (1915) listed this species in subgenus *Schizophycus,* and Yoshida (1998) agreed with Grunow's opinion. Species attributed to subgenus *Schizophycus* are distributed along the coasts of east Asia from Japan to southern China.

Recent molecular systematic analysis using ITS-2 nrDNA allows a consideration of phylogenetic relations among subdivisions of the genus *Sargassum* (Stiger et al. 2000, 2003). Such an analysis is presented here.

Description of Species

Sargassum patens C. Agardh, Spec. alg. 1(1), p. 27, 1820. (Figs. 1–5)

Type locality: "in mari Japonico" (probably around Nagasaki port).

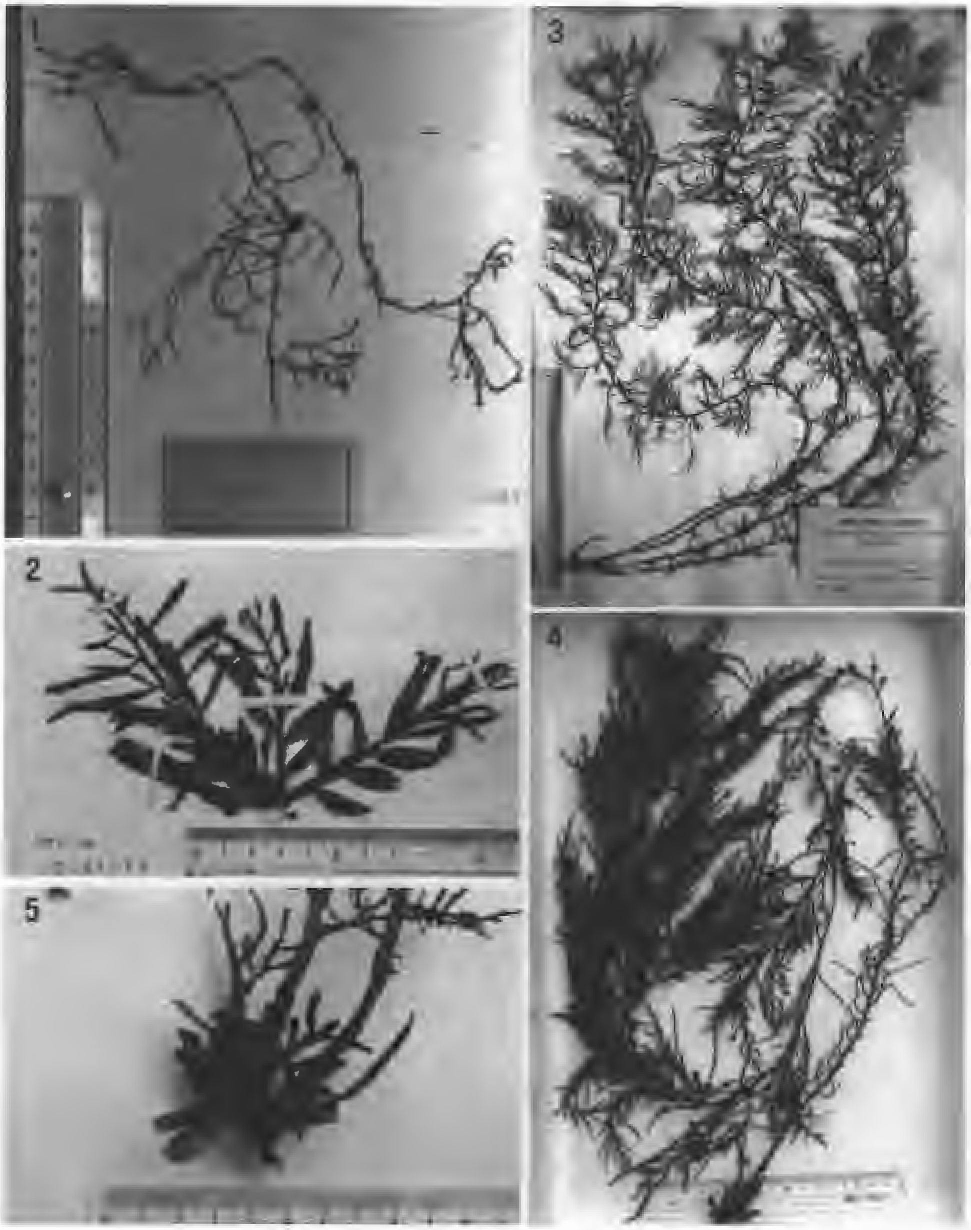
Lectotype: LD herb Agardh 2838. Collected by Tilesius, 1804–5. Botaniska Museum, Lund (Fig. 1).

Distribution: Japan, Korea, China.

Holdfast flat discoid. Stem upright, one to several from central part of holdfast, terete, 1–2 cm high, without branching. First-formed cauline leaves simple, linear-lanceolate, then gradually issuing lateral lobes, pinnately arranged (Fig. 2). Later, these branches transforming to main branches issuing spirally from upper end of stem. Lateral lobes of basal part of main branches simple, expanding in same plane as flattened main branch. Upper leaves on main branch becoming gradually narrower and finally filiform, branching several times alternate-pinnately, with inconspicuous midrib, margin entire. Lateral branches issuing from axil of leaves. Vesicles formed on lateral branches, elliptical to subspherical, with complanate stalk, longer than vesicle, crowned with a simple or divided filiform coronal leaf, similar to leaves on branch. Cryptostomata inconspicuous, scattered on plant.

Species dioecious, receptacles linear, compressed, often furcate, with smooth margin, without spinous process, arranged alternate-distichously on terminal branches. Maturation period from late spring to early summer.

The lectotype specimen of this species (Fig. 1) is a fragment collected by Tilesius from an unknown locality around "archipelago Japonica." Tilesius stayed at Nagasaki port from October 1804 to April 1805, and it is likely that



Figs. 1–5. ***Sargassum patens*** **C. Agardh. Fig. 1, Lectotype, "in mari Japonico," 1804–1805. Fig. 2, Young individual with 4 main branches, Tomioka, Kumamoto Pref., Mar. 22, 1959. Fig. 3, Immature specimen from Sado, Niigata Pref., Oct. 6, 1987. Fig. 4, Fertile specimen from Tsuyazaki, Fukuoka Pref., Mar. 28, 2002. Fig. 5, Basal part of specimen in Fig. 4.**

this material was picked up there or after the ship left the port for the Sea of Japan. This specimen has narrow leaves once or twice furcated, without reproductive structures.

Morphological variation among local populations is also conspicuous. Plants from coasts of the Sea of Japan are slenderer with much furcated leaves (Figs. 3–5), whereas those from Pacific coasts are stouter and larger with fewer furcated leaves.

Several varieties have been recognized: var. *schizophyllum* (Kützing) Yendo (1907, p. 67), var. *complanatum* Grunow (1915, p. 339), var. *rodgersianum* (Harvey) Grunow (1915, p. 339), and var. *simplicifolium* Grunow (1915, p. 339).

Var. *schizophyllum (=Halochloa schizophylla,* Fig. 7) was based on a specimen from "Japan." This is an old plant partly covered by coralline algae, with linear leaves once or twice furcated and with spherical vesicles.

Var. *rodgersianum (=Sargassum rodgersianum,* Fig. 6), based on a specimen from the "east coast of Japan," is characterized by simple linear leaves. The specimen shown in Fig. 8 has similar leaf morphology. This morphological feature is close to *Sargassum tosaense* Yendo.

We have not yet examined the type specimens of taxa described by Grunow. From his description, var. *complanatum* seems to be near var. *schizophyllum,* and var. *simplicifolium* is similar to var. *rodgersianum.*

Sargassum kashiwajimanum Yendo, J. Coll. Sci. Imp. Univ. Tokyo 21(12), p. 71. pl. 7, fig. 4, 1907. (Fig. 9)

Type locality: Kashiwajima Island, Kochi Prefecture, Japan.

Holotype: TI herb. Yendo (now in SAP). Collected by T. Makino, no date (Fig. 9).

Distribution: Shikoku, Japan.

"Lower portions of the frond are not known. The stem is compressed with rounded edges, alternately pinnately ramose. The leaves on the principal branches grow patently from the edges of the complanated stem, with a very short petiole: they are decompoundly pinnately or subdichotomously divided. An immersed rib traverses the whole length of the leaf running into the segments almost to the tip of each. Vesicles are spherical, with complanated stipe nearly as long as the diameter, coronate with one or two or often three pinnately divided leaflets. They are axillary and solitary. A lateral branch starts from the axil formed by a vesicle and the principal stem....Receptacles unknown" (Yendo 1907, p. 72).

***(right)* Figs. 6–9. Fig. 6, Holotype of *Sargassum rodgersianum* Harvey, "East coast of Japan," 1853–1856. Fig. 7, Holotype of *Halochloa schizophylla* Kützing, "Japan." Fig. 8, Specimen of *Sargassum patens,* Hirado, Nagasaki Pref., similar to *S. rodgersianum.* Fig. 9, Holotype of *Sargassum kashiwajimanum* Yendo, Kashiwajima, Kochi Pref.**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Yendo (1907) described this species based on only one specimen—the distal part of a branch about 20 cm long. We need further collections to ascertain whether this is recognizable as a distinct species or merely the range of variation of other species. We have no other reliable specimen.

Sargassum kushimotense Yendo, J. Coll. Sci. Imp. Univ. Tokyo 21(12), p. 72. pl. 16, fig. 20, 1907. (Figs. 10–14)

Type locality: Kushimoto, Wakayama Prefecture, Japan.

Lectotype: TI herb. Yendo (now in SAP). Anon., March 1902 (Fig. 10).

Distribution: Pacific coast of Honshu, Shikoku, Kyushu, Japan.

Holdfast flat discoid. Stem upright, terete, 1–3 cm high, without branching. Several main branches issuing spirally on stem, compressed, sharp spinal processes on margins of lower part of main branch. Leaves on lower part of main branch simple, linear-lanceolate, up to 10 cm long and 1.5 cm wide, base asymmetrical, with midrib diminishing near apex, margin serrulate, expanding in same plane as branch. Lateral branches originating from axil of leaves. Leaves becoming narrower on upper parts of branch, once furcate alternately, with midrib disappearing near apex. Vesicles obovoid to elliptical, with flattened stipe nearly same length as vesicle itself, crowned with coronal leaf, simple or once furcate, similar to leaves on branches. Cryptostomata scattered on leaves and vesicles. A young immature specimen is shown in Fig. 11; nearly all leaves are simple.

Species dioecious (Fig. 12). Receptacles linear, compressed, often furcate, usually with large, sharp spines on margins (Fig. 13), arranged alternate-distichously on branchlets. Male receptacles (Fig. 14) slenderer and spines fewer than on females. Maturation in late autumn to early spring.

Yendo (1907) described this species based on only two sterile fragments from Kushimoto, Wakayama Prefecture, and Shibushi, Kagoshima Prefecture. The lectotype specimen is the distal part of an immature plant about 24 cm in length. Leaves are linear-lanceolate, simple or once furcate, with serrulate margin. Elliptical vesicles have coronal leaf. Broad leaves with serrulate margin and spines on receptacles are main characteristics of this species.

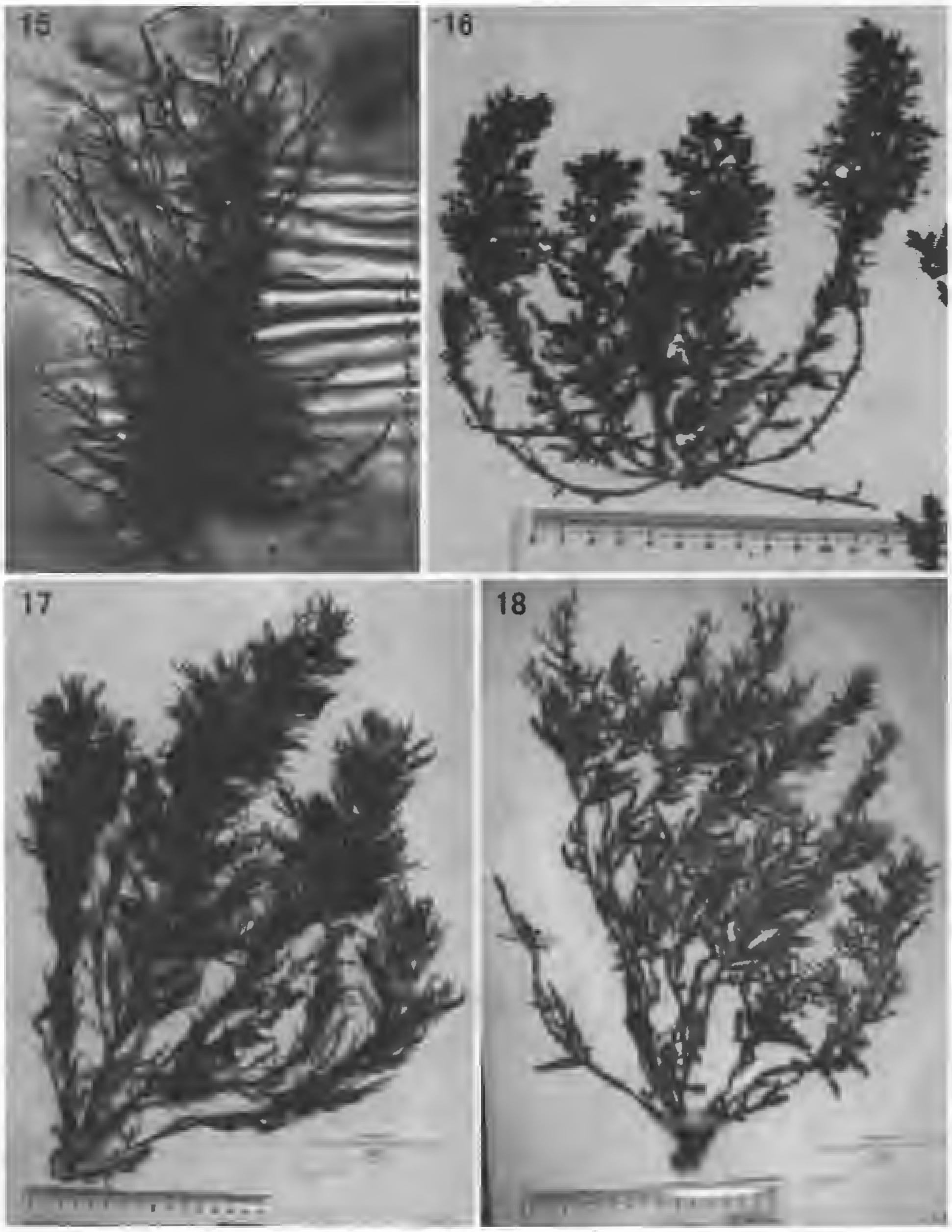
Sargassum pinnatifidum Harvey, Proc. Amer. Acad. Arts 4, p. 327, 1859. (Figs. 15–18)

Type locality: "Loo Choo Island," Okinawa Prefecture, Japan.

Holotype: TCD herb. Harvey. Trinity College, Dublin. Collected by C. Wright, 1853–1856 (Fig. 15).

Distribution: Okinawa.

***(left)* Figs. 10–14. *Sargassum kushimotense* Yendo. Fig. 10, Lectotype, Kushimoto, Wakayama Pref. Fig. 11, Young individual from Oita Pref., June 6, 1996. Fig. 12, Fertile specimen from Oita Pref. Fig. 13, Female receptacles with spinous processes. Fig. 14, Male receptacles, spines rare.**



Figs. 15–18. *Sargassum pinnatifidum* Harvey. Fig. 15, Holotype, "Loo Choo Island," Okinawa Pref., 1853–1856. Fig. 16, Young individual from Okinawa Pref., June 7, 1991. Fig. 17, Female plant from Okinawa Pref., Nov. 29, 1991. Fig. 18, Male plant from Okinawa Pref., Nov. 27, 1992.

"Branches compressed, distichously branched from the margin; leaves linear, deeply pinnatified, with midrib, sharply serrulate or upper leaves entire; vesicles ellipsoid, coronal leaf often furcated with serrulate margin; receptacles long remotely divided, cylindrical and without spines."

The above description is translated from Harvey (1859). Dawson (1959) added the unpublished comment of Harvey: "two very imperfect specimens of a distinctly marked species. The phyllodia are 1.5–2 inches long, a line wide, nerved, and distantly pinnatified, each furnished with 3–4 laciniae an inch in length. The upper leaves are much narrower and quite entire. The racemes of receptacles are as long as the leaves. The vesicles are 2–3 lines long, tipped with a leaf, which is generally bipartite."

Yendo (1907, p. 62) emended the original description of Harvey on the basis of specimens collected at Misaki, Kanagawa Prefecture, central Honshu. Our collections attributable to this species are confined to Okinawa (Ryukyu Islands).

Description of Specimens from Okinawa: Holdfast conical discoid, one to several stems arising from central part of disc. Stem cylindrical, up to 2 cm high. Several main branches originating spirally from apical part of stem. Main branches compressed, 3–5 mm wide, midrib thickened, marginal part thin, margin smooth or often with short spines. Leaves expanded in same plane as branch. Leaves on basal part of main branch simple or pinnately branched, with midrib evanescent near apex, margin often with sharp teeth, cryptostomata scattered on leaf surface. On certain parts of branch, leaves very narrow with smooth margins, apices acutely pointed. Vesicles elliptical, with flat stipe, shorter than vesicle, coronated with leaf simple or divided, with cryptostomata.

Species dioecious. Receptacles linear, slightly compressed, alternately branched, racemosely arranged in one plane, without spines on margin. Maturation period mainly in winter months.

Variation of leaf morphology is conspicuous depending on position on branch and growing season (Figs. 16–18).

According to Tseng and Lu (2000), the Chinese specimens are monoecious, male and female conceptacles on the same receptacle.

Sargassum tosaense Yendo, J. Coll. Sci. Imp. Univ. Tokyo 21(12), p. 69, pl. 9, figs. 1–4, 1907. (Figs. 19–21)

Type locality: Kochi Prefecture, Japan.

Lectotype: TI herb. Yendo (now in SAP). Anonymous, no date (Fig. 19).

Distribution: Pacific coasts of Honshu and Shikoku, Japan.

Holdfast small, discoid, one to several stems from holdfast. Stem erect, with several main branches spirally arranged from apex. Main branches complanate, with smooth margins. Leaves of lower part of main branch distantly formed, linear-lanceolate, up to 20 cm long and 1.5 cm at widest part, margin entire or slightly dentate. Midrib reaching apex. Leaves becoming narrower on upper part of main branch, rarely divided, midrib hardly discernible. Vesicles

Figs. 19–21. ***Sargassum tosaense*** **Yendo. Fig. 19, Lectotype, Kochi Pref. Fig. 20, Young individual from Wakayama Pref., Feb. 5, 1957. Fig. 21, Specimen from Shizuoka Pref., April 1, 1960.**

spherical to ovate, elliptical up to 15 mm long, with flattened stalk not longer than vesicle and a long simple or once furcate linear coronal leaf. Cryptostomata very few, scattered on branches, leaves, and vesicles.

Receptacles linear, slightly compressed, paniculately disposed on lateral branches.

This species is characterized by long leaves infrequently branched (Figs. 20, 21). Although Setchell (1933) listed this name from Hong Kong, Tseng and Lu (2000) could not obtain the Chinese specimen attributed to this species.

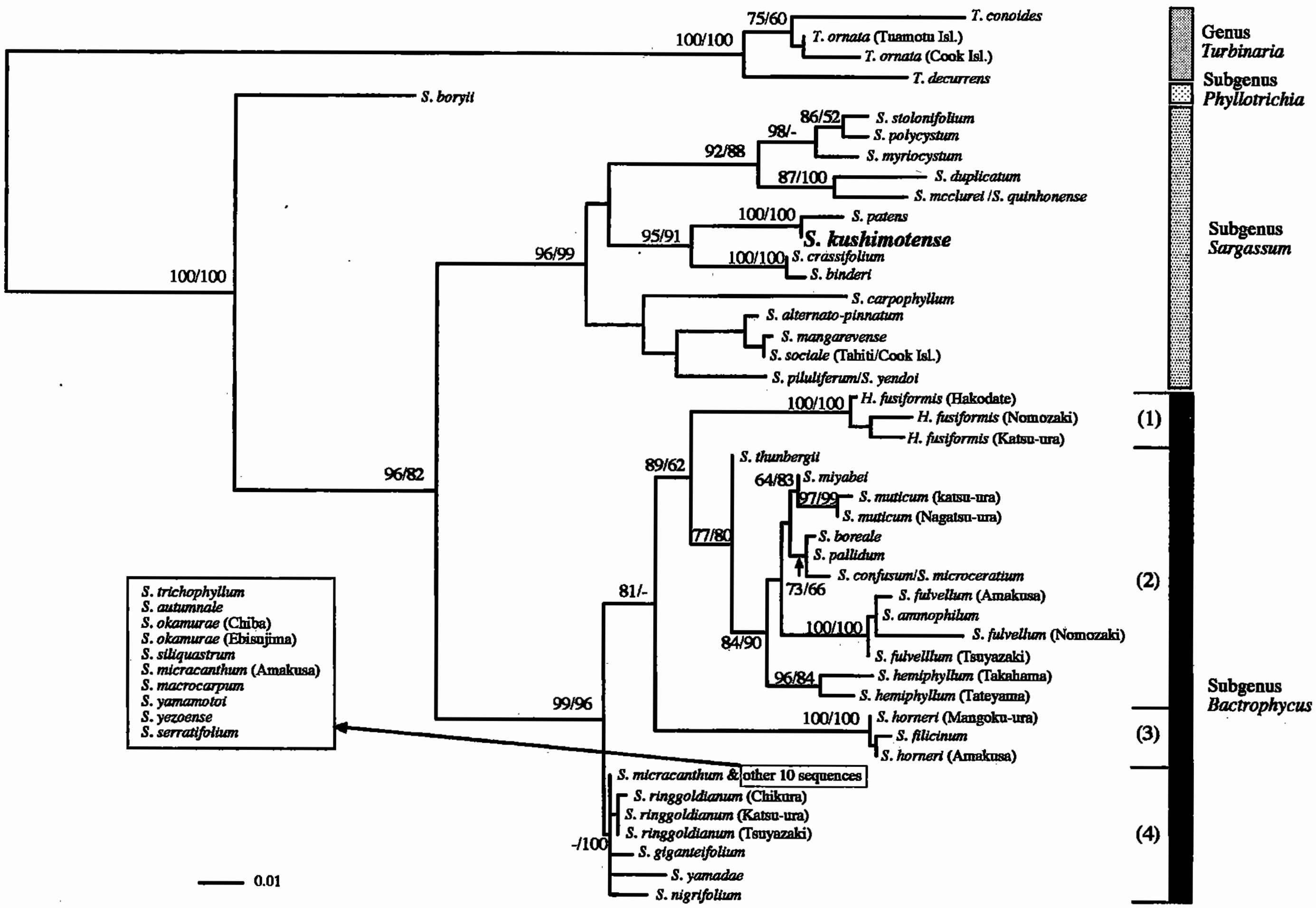
Molecular Systematic Analysis

We followed the procedure of DNA extraction and analysis of Stiger et al. (2000, 2003). A phylogenetic tree using the maximum likelihood method is shown in Fig. 22. *Sargassum kushimotense* forms a clade with *S. patens,* supported by a high bootstrap value (100% by NJ and MP methods) within the subgenus *Sargassum;* this clade is in a sister position to a *S. crassifolium/S. binderi* clade. Note that *S. piluliferum,* which was originally thought to be a member of subgenus *Phyllotrichia,* is also included in subgenus *Sargassum.*

Discussion

The type specimens of the 5 species (recorded above) in *Sargassum* subgenus *Schizophycus* are all very old and imperfect fragments. For example, the type materials of *Sargassum patens* and *Halochloa schizophylla* apparently were collected in the early 19th century during a Russian voyage in the vicinity of Nagasaki. These types give us little information about the morphological range of each species. Many specimens at hand intergrade among them and thus are difficult to place. *Sargassum tosaense* and *S. rodgersianum (=S. patens* var. *rodgersianum)* both have simple leaves. Heavily furcated leaves are a character of *S. kashiwajimanum* and *Halochloa schizophylla (=S. patens* var. *schizophyllum).*

Molecular systematic analyses using ITS-2 nrDNA (Stiger et al. 2000, 2003) and the *rbc*LS region (Phillips and Fredericq 2000) provides insight into relations within the genus *Sargassum.* Using ITS-2 nrDNA analysis, Stiger et al. (2000, 2003) showed that *S. patens* is positioned in a clade with *S. crassifolium* and *S. binderi* of subgenus *Sargassum.* The addition of *S. kushimotense* confirms this conclusion. Nearly the same result was obtained by *rbc*LS sequence analysis (Phillips and Fredericq 2000), and we conclude that subgenus *Schizophycus* should be merged with subgenus *Sargassum.* In spite of a supposed similarity, subgenus *Schizophycus* is in a position remote from subgenus *Phyllotrichia (S. boryi* from New Caledonia). Because the species in *Phyllotrichia* have a wide range of morphology, molecular systematic information on other species is urgently needed for further consideration of phylogeny within the genus *Sargassum.* In addition, the scheme of classifi-


75/60
T. conoides
100/100
T. ornata (Tuamotu Isl.)
T. ornata (Cook Isl.)
T. decurrens
S. boryii
86/52
S. stolonifolium
98/-
S. polycystum
S. myriocystum
92/88
87/100
S. duplicatum
S. mcclurei /S. quinhonense
100/100
S. patens
S. kushimotense
95/91
100/100
S. crassifolium
S. binderi
96/99
100/100
S. carpophyllum
S. alternato-pinnatum
S. mangarevense
S. sociale (Tahiti/Cook Isl.)
S. piluliferum/S. yendoi
100/100
H. fusiformis (Hakodate)
H. fusiformis (Nomozaki)
H. fusiformis (Katsu-ura)
S. thunbergii
89/62
64/83
S. miyabei
97/99
S. muticum (katsu-ura)
S. muticum (Nagatsu-ura)
77/80
S. boreale
S. pallidum
S. confusum/S. microceratium
73/66
S. fulvellum (Amakusa)
S. ammophilum
100/100
S. fulvellum (Nomozaki)
84/90
S. fulvelllum (Tsuyazaki)
96/84
S. hemiphyllum (Takahama)
S. hemiphyllum (Tateyama)
96/82
81/-
99/96
100/100
S. horneri (Mangoku-ura)
S. filicinum
S. horneri (Amakusa)
S. trichophyllum
S. autumnale
S. okamurae (Chiba)
S. okamurae (Ebisujima)
S. siliquastrum
S. micracanthum (Amakusa)
S. macrocarpum
S. yamamotoi
S. yezoense
S. serratifolium
S. micracanthum & other 10 sequences
S. ringgoldianum (Chikura)
S. ringgoldianum (Katsu-ura)
S. ringgoldianum (Tsuyazaki)
-/100
S. giganteifolium
S. yamadae
S. nigrifolium
0.01
Genus
Turbinaria
Subgenus
Phyllotrichia
Subgenus
Sargassum
(1)
(2)
(3)
(4)
Subgenus
Bactrophycus

***(left)* Fig. 22. Maximum likelihood (ML) phylogenentic tree inferred from ITS-2. Four species of *Turbinaria* used as an outgroup. Parameters and methods for ML analysis as described in Stiger et al. (2002). Bootstrap values of maximum parsimony (MP) and neighbor joining (NJ) methods are indicated (MP/NJ). The topologies of the latter two analyses were the same as that of the ML method. Scale bar = 0.01 substitution/site.**

cation within subgenus *Sargassum* must be reconsidered, because revision of tribe *Phyllocystae* (Stiger et al. 2000), merging of subgenus *Schizophycus,* and realignment of *S. piluliferum* into subgenus *Sargassum* cause an inconsistency of characters used for the sorting of subgenus *Sargassum* into lower taxa.

Literature Cited

Abbott, I. A., Tseng, C. K., and Lu Baoren. 1988. Clarification of some subgeneric nomenclature in *Sargassum* subgenus *Sargassum.* In: Tax Econ. Seaweeds 2, pp. 55–57.

Agardh, C. A. 1820. Species algarum. Vol. 1(1). Berling, Lund.

Agardh, J. G. 1848. Species genera et ordines Ficoidearum. Gleerup, Lund.

Agardh, J. G. 1889. Species Sargassorum Australiae descriptae et dispositae. Kgl. Svenska Vet-Akad. Handl. 23(3):1–133. pls. 1–31.

Dawson, E. Y. 1959. William H. Harvey's report on the marine algae of the United States North Pacific Exploring Expedition of 1853–1856. Pacific Naturalist 1(5):1–40.

Greuter, W. G. et al. (eds.). 2000. International Code of Botanical Nomenclature (Saint Louis Code). Koeltz, Königstein, Germany. [Regnum Vegetabile 138]

Grunow, A. 1915, 1916. Additamenta ad cognitionem *Sargassorum.* Verh. Zool.-Bot. Ges. Wien 65:329–448; 66:1–48, 136–185.

Harvey, W. H. 1859. Characters of new algae, chiefly from Japan and adjacent regions collected by Charles Wright in the North Pacific Exploring Expedition under Capt. John Rodgers. Proc. Amer. Acad. Arts 4:327–334.

Okamura, K. 1936. Nippon Kaisoshi. Uchida Rokakuho, Tokyo. (In Japanese)

Phillips, N., and Fredericq, S. 2000. Biogeographic and phylogenetic investigation of the pantropical genus *Sargassum* (Fucales, Phaeophyceae) with respect to Gulf of Mexico species. Gulf of Mexico Science 2000(2):77–87.

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

Setchell, W. A. 1933. Hong Kong seaweeds III. Hong Kong Naturalist, suppl. 2:33–49.

Stiger, V., Horiguchi, T., Yoshida, T., Coleman, A. W., and Masuda, M. 2000. Phylogenentic relationships of *Sargassum* (Sargassaceae, Phaeophyceae) with reference to a taxonomic revision of the section *Phyllocystae* based on ITS-2 NrDNA sequences. Phycol. Res. 48:251–260.

Stiger, V., Horiguchi, T., Yoshida, T., Coleman, A. W., and Masuda, M. 2003. Phylogenetic relationships within the genus *Sargassum* (Fucales, Phaeophyceae), inferred from ITS-2 nrDNA, with an emphasis on taxonomic subdivision of the genus. Phycol. Res. 51:1–10.

Tseng, C. K., and Lu Baoren. 2000. Fucales. Flora algarum marinarum sinicarum 3(2):1:238, pls. 1–31. (In Chinese)

Womersley, H. B. S. 1954. Australian species of *Sargassum,* subgenus *Phyllotrichia.* Aust. J. Bot. 2:337–354.

Yendo, K. 1907. The Fucaceae of Japan. J. Coll. Sci. Imp. Univ. Tokyo 21(12):1–174, pls. 1–18.

Yoshida, T. 1998. Marine algae of Japan. Uchida-Rokakuho, Tokyo. (In Japanese)

Section IV. Gelidiales

INTRODUCTION

Isabella A. Abbott

In Volume 7 of this series, using Malaysian material Bernabé Santelices described for the first time spermatangia of *Gelidiella acerosa*. This was a breakthrough since the status of *Gelidiella* has had researchers wondering for many years with respect to sexual structures—were they similar or different from those of other genera of Gelidiales? In Hawaii all year round, for example, the plants of the 5 available *Gelidiella* species are plentiful, but they are rarely fertile, and males and females have never been seen. In this volume, Santelices and Flores continue the saga of males, the only sexual plants known for the genus, this time from a plant described as *Gelidiella acerosa* from Haiti. Though the development of the spermatangia is similar to that of the Malaysian plant, there are differences, and more material would be necessary to assess what the variations are and how many of them are taxonomically acceptable for the genus and species.

The second paper in this section, by Santelices, Skelton, and South, investigates *Gelidium samoense* Reinbold from Samoa, Tahiti, and Fiji. Being unable to find the type material of *G. samoense,* these researchers had to rely on fresh and herbarium material from Fiji and UC herbarium specimens collected by Setchell in Samoa and Tahiti. They found that the Setchell material from Upolu, Samoa, matched Reinbold's description well, but material from Tutuila, Samoa, was not *G. samoense* but another species. Their new description of *G. samoense* is based on some of the Samoan material and on plants from Tahiti and Fiji, thus contributing to our knowledge of a previously little known, geographically remote species.

ADDITIONAL OBSERVATIONS ON SPERMATANGIAL SORI IN *GELIDIELLA ACEROSA* (GELIDIELLACEAE, GELIDIALES)

Bernabé Santelices and Verónica Flores

Abstract

Fertile male plants of *Gelidiella acerosa* were unknown until 1997, when male sori were found in a single individual collected in a shallow reef in Johore, Malaysia. Additional observations of fertile male plants are reported here from materials collected on the north coast of Haiti. A close comparison between the fertile male thalli from Malaysia and Haiti indicates similarities in the shape, pattern of division, and size of the cortical and spermatangial parent cells; the proliferation of internal cortical cells and external medullary cells during sori formation; and the resulting protrusion of the sorus over the thallus surface. Some differences also exist in the two groups of plants, especially in the size and degree of branching, the position of the soral tissues along the axes, the degree of proliferations of medullary cells, and the depth and size of the hemispheric cavities formed after spermatangial release. The taxonomic meaning of these differences is unknown, but perhaps they suggest that two taxonomic entities, one in the Pacific and the other in the Caribbean, are being confused under the name of the geographically widespread *G. acerosa.*

Introduction

Fertile spermatangial sori of specimens of *Gelidiella acerosa* were described (Santelices 1997) based on a single fertile individual collected in a shallow reef on Johore, Malaysia. The shapes, sizes, and patterns of division of the fertile cells were found to be similar to those described for male sori in other members of the Gelidiales, such as *Porphyroglossum (=Beckerella) subcostatum.* However, the male sorus found in *G. acerosa* exhibited a significant proliferation of internal cortical cells and external medullary cells. Thus, the fertile sori appeared as rounded, hemispheric swellings along the axes.

Besides adding information on the morphology and life history of this genus, the above observation allowed a reevaluation of the generic position of *Gelidiella* and the validity of the family in which it is placed. *Gelidiella* is a monotypic genus of the family Gelidiellaceae of the order Gelidiales, but the generic definition and the validity of the family have been under discussion for some time (see Santelices 1997, for a review). The family Gelidiellaceae was distinguished from the Gelidiaceae by the former's lack of sexual generation and lack of thick-walled, delicate fibers (rhizines) in the cortex or medulla. The detection of male gemetophytes contradicts one of the two characters (lack of sexual generation) used (Fan 1961) to distinguish the family. On the other hand, the morphological structure of the sorus in *G. acerosa,* with evident proliferation of internal cortical and external medullary cells, appeared as unique among equivalent structures described for other members of the order, supporting the family status of the Gelidiellaceae (Santelices 1997).

The new distinction was, however, based on only a single specimen. An additional search for fertile specimens among the *G. acerosa* specimens deposited in the herbarium of Bernice P. Bishop Museum in Honolulu, Hawaii, was made. This study reports additional observations on fertile male plants among these materials and describes the soral structures found.

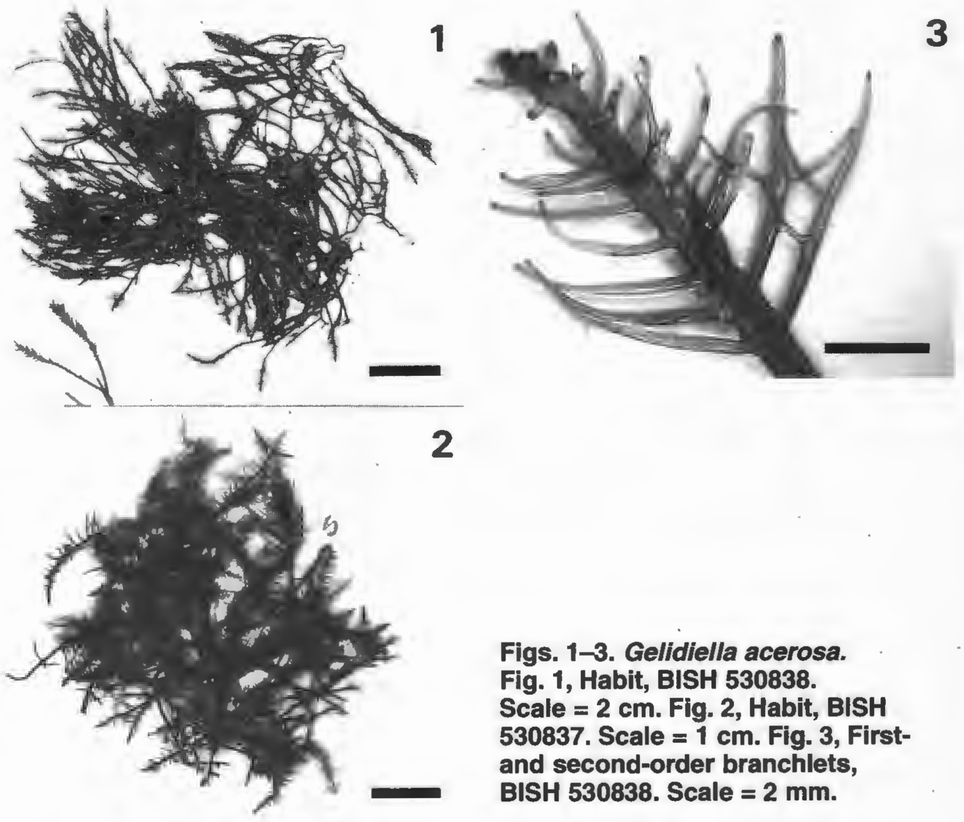
Materials and Methods

Our search for fertile materials included all the specimens (some 50 herbarium sheets) preserved in the herbarium collection of Bishop Museum (BISH). These have been collected by different persons in various localities of Southeast Asia, the South and Central Pacific, and the Caribbean. Specimens were first examined under a stereomicroscope, and the portions selected were hydrated, fixed in 4% formaldehyde solution, cut in 15–20 µm thick sections using a Leitz freezing microtome, and stained with aniline blue. Photomicrographs were taken with a Nikon Optiphot-2 microscope. Herbarium specimens and slides with sections of fertile materials are deposited at the Bishop Museum herbarium. Duplicate slides with fertile sori are being deposited in the Algal Collection of the Sala de Sistemática, Pontificia Universidad Católica de Chile (SS/UC).

Results

Two of the herbarium specimens examined contained fertile males. One such collection is BISH 530838 (Fig. 1), collected by H. H. Bartlett on May 6, 1941, at Jérémie, north coast of the southern peninsula of Haiti; specimens were collected in shallow but very rough water, on eroded reefs of limestone, exposed to heavy seas. The second collection is BISH 530837 (Fig. 2), also collected by H. H. Bartlett, on June 23, 1941, from a small islet offshore near the town of Bayeux, Anse à Margot, on the north coast of Haiti between Cap Haitien and Le Borgne; specimens were gathered from a narrow reef of (mostly dead) sand-covered or wave-worn corals on the landward side of the island covered with shallow water when the sea was rough and at high tides, enclosing deeper *Turbinaria* pools in which the water become hot when isolated at low tide.

The external morphology of both plants conforms well with descriptions of representatives of the species (Feldmann and Hamel 1934; Santelices 1977, 1997; Melo 1992). Specimens of BISH 530838 are up to 10 cm tall, and those of BISH 530837 are up to 5 cm tall. Both groups of plants are formed by several tufted, entangled, cylindrical, somewhat arcuate erect axes arising from



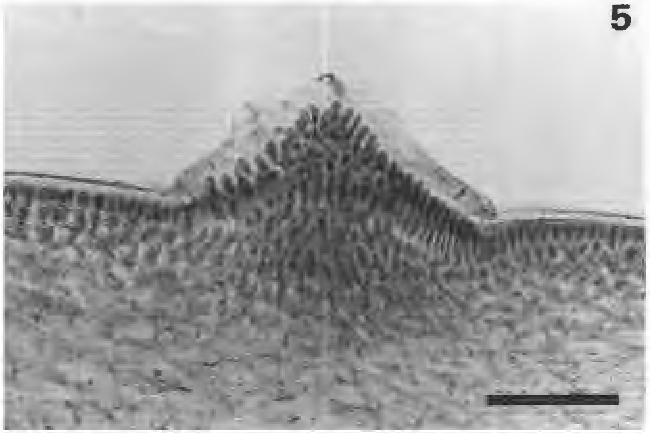
Figs. 1–3. *Gelidiella acerosa.* Fig. 1, Habit, BISH 530838. Scale = 2 cm. Fig. 2, Habit, BISH 530837. Scale = 1 cm. Fig. 3, First- and second-order branchlets, BISH 530838. Scale = 2 mm.

prostrate creeping axes attached to the substratum by clusters of unicellular rhizoids. Erect and prostate axes in both plants are up to 650 µm in diameter, with rounded but more frequently narrowed tips. Erect axes are invested by 2, 3, and even 4 rows of elongated branchlets (especially BISH 530837) disposed pinnately, subpinnately, or irregularly alternate. Terminal branchlets are filiform and slightly tapered at the tips, up to 8 mm long, the longest one with occasional second-order branchlets (Fig. 3). Compared to other specimens of *G. acerosa* described in the literature (see Santelices 1977, 1997; Melo 1992, for reviews) and to the male plants found in Malaysia (Santelices 1997), these specimens are considerably more branched, branches are longer, and, in turn, they may exhibit pinnately or subpinnately arranged branchlets.

A cross section through a vegetative erect axis shows the typical structure of the genus. External cortical cells are ovoid or anticlinally elongated, 3–6 µm in diameter, 6–9 µm long, followed by 2–3 layers of smaller (3 by 5 µm) rounded or slightly ovoid, inner cortical cells that later grade into larger medullary cells.

In these specimens, spermatangial sori appear at the middle and apical part of cylindrical branchlets. Two or more of these branches may emerge from a single point of the axis, appearing as a small cluster (Fig. 4). The tip of the branches may be rounded and slightly swollen, 0.8–1.0 mm in diameter.

Along the axes, spermatangial sori first appear as slight elevations of the most external cortical cells, 75–150 µm in diameter and comprising fewer than



Figs. 4–5. *Gelidiella acerosa.* Fig. 4, Cluster of branchlets and proliferations emerging from an erect axis; the cylindrical branchlet with rounded tip is a fertile branch. Scale = 2 mm. Fig. 5, Longitudinal section through a spermatangial sorus at early stage of development; note the slight proliferation of inner cortical and external medullary cells and the thick cuticle completely covering the sorus. Scale = 50 µm.

50 cells in longitudinal extent (Fig. 5). External cortical cells first elongate up to 7–10 μm and remain narrow (about 4 μm wide). By transverse divisions they cut off several spermatangial parent cells, which later produce spermatangia and spermatia. A raised, thickened cuticle (Fig. 5) covers all of the sorus.

More advanced stages of soral development (Fig. 6) show proliferation of the spermatangial mother cells, forming elongated rows of up to 5 sperma tangial parent cells, liberation of a few spermatia, and a thick cuticle with a honeycomb-like surface (Fig. 7). The most advanced stages of development (Figs. 7, 8) show the nemathecial sorus clearly elevated on the blade surface and rows of up to 5 spermatangial parent cells topped by ovoid or slightly clavate spermatia of 7–10 by 5–7 μm. The medullary tissue immediately beneath the sorus exhibits lateral connections, forming a cellular network, slight increase in the number of cell layers in the subcortex, and anticlinal alignment of medullary and cortical cells in the central part of the sorus.

After spermatangial discharge, the cortical cells and most external rows of medullary cells deliquesce and are lost. A slight cavity is formed (Fig. 9) lined by several rows of small, rounded, loosely arranged, cortical cells. At this time, some of the branchlets may become extensively infected, modifying their external appearance and resembling more a "wartlike proliferation" than a typical branchlet (Figs. 10, 11). Longitudinal sections through some of these proliferations show no evidence of spermatangia formation but the presence of heavy infection by various kinds of endophytes.

Discussion

The observation of male sori in the specimens from Haiti confirms the presence of a sexual generation in the genus, a characteristic supposed to be lacking in the family and used by Fan (1961) to provide family status for this genus. Cultivation and genetic studies (Sreenivasa Rao 1971; Kapraun et al. 1994) have anticipated the occurrence of this generation, and the presence of a single male plant in Malaysia (Santelices 1997) was the first evidence. The fertile male plants from Haiti described in this study are additional support. However, cystocarpic plants of *Gelidiella* have not been found. We are therefore still ignorant of the complete life history in the field. It seems clear, however, that the genus as represented by its type species, *G. acerosa,* is not heteromorphic.

The structure of the male sorus of the specimens from Haiti agrees in many respects with the respective description of the Malaysian males (Santelices 1997). The shape, pattern of division, and size of the cortical and spermatangial parent cells are similar. Although less pronounced than in the Malaysian specimens, the proliferation of internal cortical cells and external medullary cells and the protrusion of the sorus over the thallus surface also appear in the Haitian specimens. Proliferation of cortical and medullary cells

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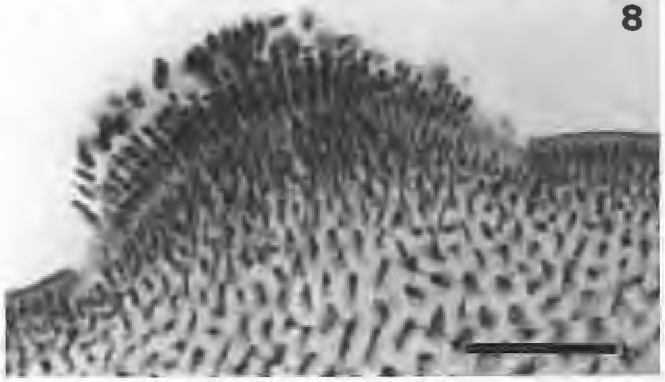
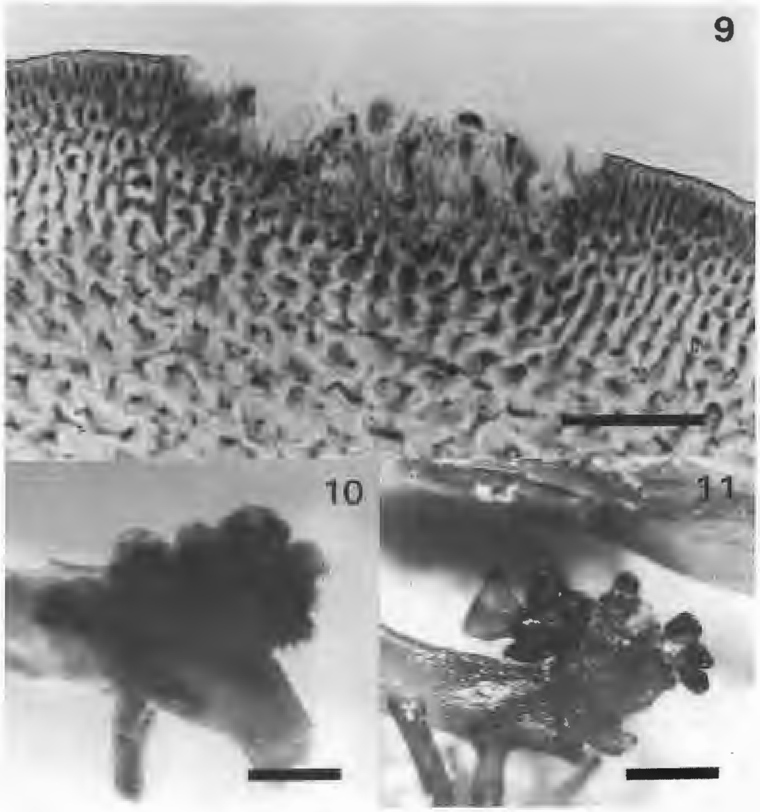


Figs. 6–8. *Gelidiella acerosa.* Fig. 6, Longitudinal section through an advanced stage of maturation of a fertile male sorus; note the proliferation of the mother cells, forming elongated rows of spermatangial cells, a few free spermatia, and a raised and thick cuticle. Scale = 50 µm. Fig. 7, Detail of thick cuticle with honeycomb-like surface. Scale = 20 µm. Fig. 8, Longitudinal section through a fertile spermatangial sorus; note the ovoid or slightly clavate spermatia being liberated and the rows of spermatangial parent cells. Scale = 50 µm.



Figs. 9–11. ***Gelidiella acerosa.*** **Fig. 9, Shallow hemispheric cavity along the axis with spermatangial sori, interpreted as remnants of old, discharged sorus. Scale = 50 µm. Figs. 10–11, Proliferations close to the tip of spermatangial thalli produced by endophyte infectations. Scale = 1 mm.**

and differentiation of a protruding sorus were described (Santelices 1997) as unique among equivalent structures so far described for other species in the order, suggesting that they constitute additional support to maintain the Gelidiellaceae as a separate family in the Gelidiales. Observation of these characters in the specimens from Haiti is consistent with this suggestion.

A close comparison between the fertile male thalli from Malaysia and Haiti also indicates some conspicuous differences. The most obvious is the size and degree of branching between the two groups of plants. The plants from Malaysia are small and sparsely branched, whereas the individuals from Haiti are twice the size of the Malaysian plants and profusely branched. The second important difference is the position and formation pattern of the male sorus. Whereas in the Malaysian specimens the male sori appear as rounded, hemispheric swellings along erect, unbranched, apically rounded low axes, the male sori in the specimens from Haiti appear at the tip and medium parts of branchlets, arising from large, highly branched, erect axes. A third difference relates to the relative importance of medullary cell proliferation during soral formation. Although in specimens from both populations the medullary cells proliferate, that of the Malaysian specimen was much more pronounced, exhibiting anticlinal arrangement and contributing to the protrusion of the sorus. A fourth difference relates to the fate of the male sorus after spermatangial release. In the Malaysian specimens, the inner cortical and external medullary cells that proliferated during spermatangial formation are lost after spermatangial release; hemispheric cavities are formed, lined internally by 6–10 rows of small, nearly cuboidal, loosely arranged cortical cells that eventually proliferate, filling the cavity. In the specimens from Haiti, the cavities are shallow, probably as a result of the slight proliferation of the medullary cells. In addition, the specimens from Haiti exhibit deformed, wartlike proliferations in some of the fertile branchlets, suggesting heavy pathogen infestation perhaps through the cavities after spermatangial release. At more advanced states of infestation, presumably the whole branch is lost.

The taxonomic meaning of the above differences is as yet unknown. *Gelidiella acerosa* has a widespread geographic distribution in tropical, subtropical, and warm-temperate waters (Santelices 1997), and phenotypic variation occurs even within local populations. Therefore, differences in size and branching patterns are of doubtful taxonomic value. However, other differences such as the position and formation pattern of the male sori, the amount of proliferation of the medullary cells, and the size of the resulting cavity after spermatangial release may suggest that two taxonomic entities are being confused under the name of the geographically widespread *G. acerosa,* one in the Pacific and the other in the Caribbean. In a comparative study, Melo (1992) found size differences in mature tetrasporangia between specimens from Caribbean Panama and those from localities in the Pacific (Hainan Island, China, and Gulf of California, Pacific Mexico). Future comparative population studies, including additional fertile material and a search for vegetative differences, should help to solve this problem.

Rico et al. (2002) obtained fertile male thalli of *Gelidiella tenuissima* under controlled laboratory conditions. The male structure of that species is similar to that described for other species of the Gelidiaceae (see Santelices 1997, for a review) and structurally different from that found in *G. acerosa.* Rico et al. (2002) suggested that two genera may be confused in *Gelidiella,* supporting a similar conclusion earlier reached by Santelices (2002) after the morphological comparison of *G. acerosa* and *G. adnata.*

Acknowledgments

My gratitude to Drs. I. A. Abbott and K. McDermid for the invitation to participate in the workshop, their hospitality while in Hawaii, and their reviews and editing of the manuscript. My appreciation also to I. A. Abbott and Jack Fisher for the loan of materials of *G. acerosa* from Bernice P. Bishop Museum. I acknowledge with pleasure cofunding by FONDECYT (Grant 1020855) and the California and the Hawaii Sea Grant College Programs, which enabled me to participate in the workshop in Hilo and to complete the work in Santiago.

Literature Cited

Fan, K. C. 1961. Morphological studies of the Gelidiales. Univ. Calif. Publ. Bot. 32:315–368.

Feldmann, J., and Hamel, G. 1934. Observations sur quelques Gelidiacées. Rev. Gén. Bot. 46:528–549.

Kapraun, D. F., Ganzon-Fortes, E., Bird, K. T., Trono, G., and Breden, C. 1994. Karyology and agar analysis of the agarophyte *Gelidiella acerosa* (Forsskäl) Feldmann et Hamel from the Philippines. J. Appl. Phycol. 6:545–550.

Melo, R. A. 1992. A note on the absence of hyphae (rhizines) in the thallus of *Gelidiella acerosa* (Forsskäl) Feldman et Hamel (Rhodophyta). In: Tax. Econ. Seaweeds 3, pp. 173–181.

Rico, J. M., Freshwater, D. W., Norwood, K. G., and Guiry, M. D. 2002. *Gelidiella tenuissima* (Gelidiales, Rhodophyta) from Gran Canaria (Canary Islands, Spain). Phycologia 41:463–469.

Santelices, B. 1977. A taxonomic review of Hawaiian Gelidiales (Rhodophyta). Pacific Sci. 31:61–84.

Santelices, B. 1997. The spermatangial sorus of *Gelidiella acerosa* (Gelidiellaceae, Gelidiales). In: Tax. Econ. Seaweeds 6, pp. 77–87.

Santelices, B. 2002. The taxonomic status of *Gelidiella adnata* (Gelidiales, Rhodophyta)). In: Tax. Econ. Seaweeds 8, pp. 151–166.

Sreenivasa Rao, P. 1971. Studies on *Gelidiella acerosa* (Forsskäl) Feldman et Hamel. V. Germination of tetraspores and nuclear changes of the germinating spores. Bull. Jpn. Soc. Phycol. 19:65–72.

OBSERVATIONS ON *GELIDIUM SAMOENSE* FROM THE FIJI ISLANDS

Bernabé Santelices, Posa A. Skelton, and G. Robin South

Abstract

Gelidium samoense Reinbold has been found among materials collected from Namada, island of Viti Levu, Fiji Islands. This study describes the Fijian specimens and other material from Samoa and Tahiti collected by W. A. Setchell. Forma *lineare* Setchell described from Tahiti is found to fit within the variation of the natural population of this species and is therefore not recognized.

Introduction

The Fiji Islands are an archipelagic state that spans the 180th meridian between 177°E and 180°W, and between latitudes 16°S and 20°S. The land area of some 18,276 km^2 is scattered over 332 islands. There are four main island groups within the archipelago: Viti Levu, Vanua Levu, Taveuni, and Kadavu, and three smaller groups, the Yasawas, the Lomaiviti Group, and the Lau Group. Most of the high islands are of volcanic origin, although there are some low atolls in the Lau Group. The islands are surrounded by some of the most extensive reef systems in the Southern Hemisphere. The most significant barrier reefs are the Great Astrolabe reef, around Kadavu, and the Great Sea Reef, to the north of Vanua Levu. The islands are tropical, with sea surface temperatures ranging from 25° to 30°C (occasionally to 31.5°).

A detailed account of earlier work on the benthic marine algae of Fiji has been provided by South and Kasahara (1992), documenting the collecting sites known up to that time. This was updated in N'Yeurt et al. (1996). In recent years, extensive exploration of the Fijian flora has continued; the most studied sites are the island of Rotuma, some 450 km north of Viti Levu (N'Yeurt 1996), the Suva Lagoon (N'Yeurt 2001), and the Great Astrolabe reef (M. and D. Littler, unpublished). Large areas of Fiji have yet to be visited by a phycologist. Of the 332 islands, collections have been made from only 10. Huge and important areas such as most of Vanua Levu, all of the Great Sea Reef, and most of the Lau islands are largely unexplored.

A total of 448 species of benthic marine macroalgae are currently known from the Fiji Islands, including 136 Chlorophyta, 46 Phaeophyta, and 266 Rhodophyta (South and Skelton, in press).

Some of the most important areas yielding new records of benthic macroalgae are reef fronts and slopes, often hazardous to access at most times of the year. Perhaps one of the most significant sites so far studied on the island of Viti Levu is Namada on the Coral Coast. Here, instead of the usual barrier reef and lagoon typical of most of Fiji, there is a fringing reef directly accessible from the shore, featuring a steep drop-off, many large bommies (large domed coral heads or isolated patch reefs) close to shore, and reefs that are directly in contact with bedrock. The Namada site is exposed to more or less continuous strong wave action and is also influenced by a small river that flows into the bay adjacent to the fringing reef. On the few occasions that it has been possible to snorkel or dive at this site, many interesting algae have been found. Among these is a diminutive species of *Gelidium,* described in this report.

The Gelidiaceae of Fiji are poorly known. The most abundant is *Gelidiella acerosa* (Forsskal) J. Feldmann et Hamel, whereas only 2 species of *Gelidium* have been recorded: *G. crinale* (Turner) Gaillon and *G. pusillum* (Stackhouse) Le Jolis (N'Yeurt et al. 1996). Neither has been studied in any detail. In this study we report the presence of *Gelidium samoense* Reinbold, a new record for these islands. Although this species was described in 1907, its description is rather incomplete and the type materials seemingly are lost. For all those reasons, we have prepared a detailed description of this species as found in the Fiji Islands.

Materials and Methods

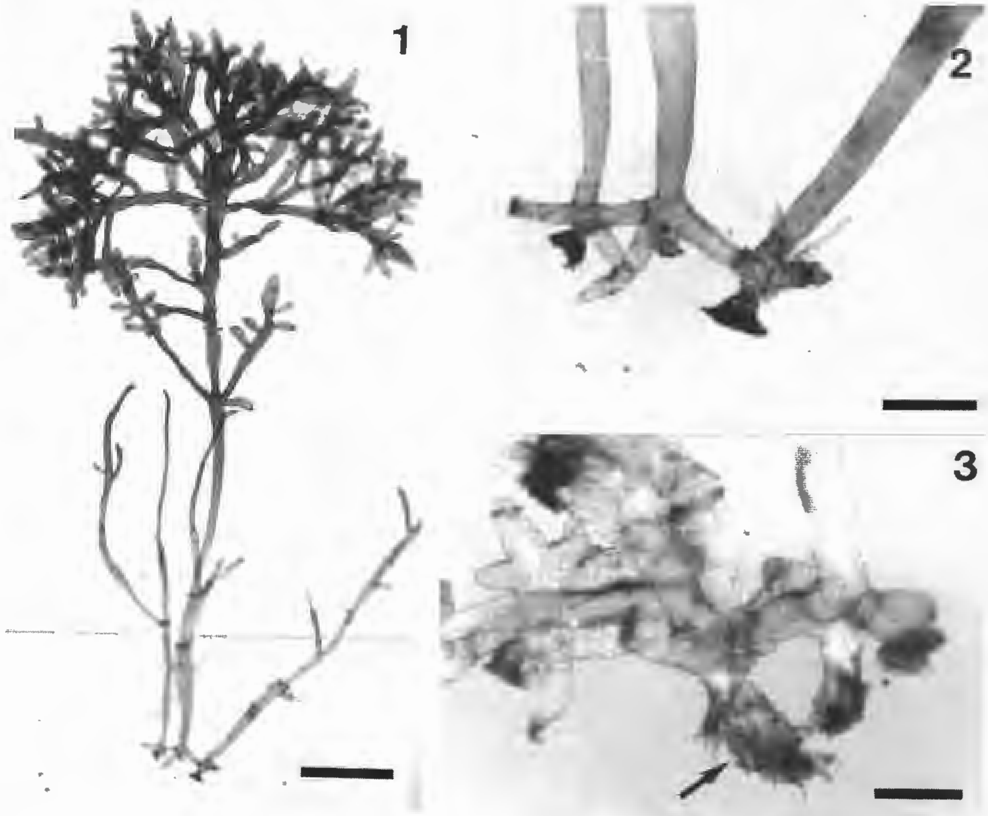
The materials were collected in Namada, on the island of Viti Levu (18°11'S, 177°36'E). There, *G. samoense* is present on rocks, among other turf species of Rhodophyta, under overhangs at or just below the low tide level in exposed sites subject to strong wave action for most of the year.

The specimens collected were preserved in 5–10% formalin/seawater. As in previous studies (e.g., Santelices 2002) transverse, longitudinal, and periclinal sections of the plants were made using a Leitz freezing microtome. Sections were stained with 1% aqueous aniline blue and mounted in dilute corn syrup. Photomicrographs were taken with a Nikon Optiphot-2 microscope. Slides and specimens are deposited at the Marine Reference Centre, University of the South Pacific (SUVA-A), and at the Algal Collection of the Sala de Sistemática, P. Universidad Católica de Chile (SS/UC).

Observations

The specimens of *G. samoense* Reinbold (1907) from Fiji are turfy, pale red or dark red, and up to 2 cm tall. They have a system of prostrate axes that originate erect axes. The creeping axes of several plants may grow intertwined among themselves, giving rise to dozens of erect axes that produce short, reddish cushions covering the substratum. The erect axes (Fig. 1) generally lack branching in their basalmost two-thirds, which contrasts with the abundant branching at the uppermost third of the axes. This arboriform pattern of branching is perhaps the most distinctive character of the fertile specimens of this species as observed under low resolution.

The creeping axes are cylindrical, 90–110 µm in diameter, giving rise on opposite sides to peglike haptera and erect axes (Fig. 2). Haptera are formed by bundles of colorless rhizoidal filaments sticking together, although they may be brushy (sensu Perrone 1994), especially when contacting and penetrating irregular substratum (Fig. 3). The interhapteral distance along the creeping axis is 75–100 µm. Often several haptera attach closely, forming a holdfast-like network of tightly packed creeping axes.



Figs. 1–3. *Gelidium samoense.* Fig. 1, External habit of the Fijian specimen. Scale = 2 mm. Fig. 2, Creeping axes, giving rise to peglike haptera and erect axes; note the rhizoidal hapteral filaments sticking together. Scale = 500 µm. Fig. 3, Apically brushy attachment structures (arrow). Scale = 250 µm.

Erect axes are basally cylindrical (Figs. 1, 2), then distally expanded and compressed. Normally a single erect axis is formed opposite a hapteron, but occasionally 2–3 erect axes may arise from the same point in the creeping axis. Erect axes are up to 100 µm diameter in the basalmost parts and up to 400 µm broad in the flat, bladelike parts. Their basalmost parts often are truncate (Fig. 4), with new axis regrowing from the medial and lateral part of the axes. The longest erect axes may have several truncations along their extent.

Branching may be of up to 4 orders. In sparsely branched axes (1–2 orders of branching), branching is distichous and the base of the branches is slightly narrower and more cylindrical than the corresponding parts of erect axis. Apically they are expanded and flat. In more highly branched specimens, primary branches are flat, broad, similar to the axis bearing them and resembling proliferations. In highly branched specimens, branches may also be produced from the blade surface (Fig. 5).

Very characteristically, the shape of the terminal branch and the position of the apical cell change with age and fertility of the branch. Young pinnules are cylindrical, with acute tips and the apical initial clearly projecting itself beyond or at the level of the cortical cells (Fig. 6). Older branches are rounded and flat, with the apical cell slightly projecting above the level of the cortical cells. In these branches the rapid cell division and proliferation of the pericentrals and derivatives (second-order filaments) give the image of an apical cell surrounded by a semihemispheric row of second-order filaments (Fig. 7). The largest branches (Figs. 8, 9) and the fertile branchlets are compressed, sometimes lobed, generally with an apical cell and lateral initials in close proximity.

A transection through the creeping axes (Fig. 10) shows 3–4 rows of rounded or slightly ovate pigmented cells, 6–8 µm in diameter, which increase in size inwardly, followed by 2–3 rows of medullary cells, of up to 10 µm in diameter with thick cell walls. Longitudinal sections show that the internal (medullary) cells are subcuboidal or rectangular (Fig. 11), up to 8 µm in diameter and 60 um long, while the cortical cells are rounded, almost isodiametric, up to 8 µm in diameter. The rhizoidal extensions forming the peglike haptera are produced by several rows of external cortical cells (Fig. 12). Internal rhizoids (rhizines) are common, especially around the medullary cells (Fig. 10).

A transection through the basal (cylindrical) part of erect axes (Fig. 13) shows a cortex formed by 2–4 rows of rounded, subcuboidal cortical cells, 7–10 µm in diameter, followed inwardly by 3–4 rows of thick-walled, rounded, medullary cells, up to 10 µm in diameter and often surrounded by internal rhizoids. Among the medullary cells, the cell line formed by the axial and periaxial cells is most evident at the median zone of the blade. In longitudinal view, the medullary cells are rectangular, up to 75 µm long and 12–15 µm in diameter, surrounded by 2–3 layers of rounded or slightly ovate cortical cells, up to 12 µm in diameter, the smaller the most external. In surface view of the thallus, these external cortical cells are polygonal, 7–9 µm wide, up to 18 µm long, disposed without order (Fig. 14).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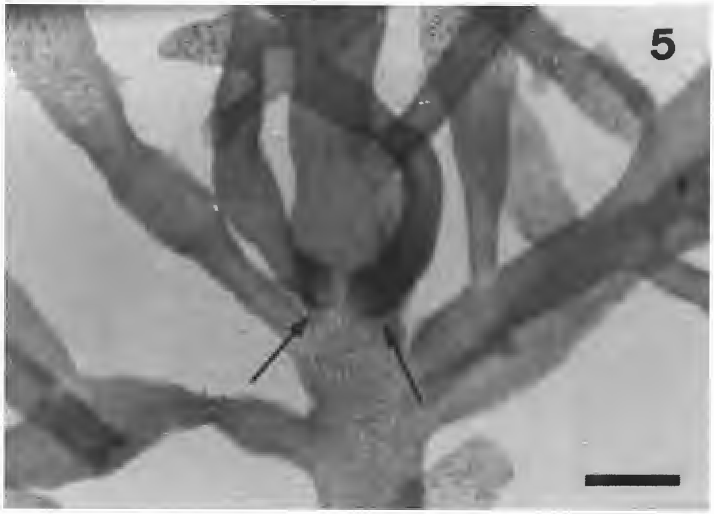
Figs. 4–5. ***Gelidium samoense.*** **Fig. 4, New axis (arrows) regrowing from medial and lateral parts of erect axes. Scale = 500 µm. Fig. 5, Highly branched specimen with branches produced from blade surfaces (arrows). Scale = 100 µm.**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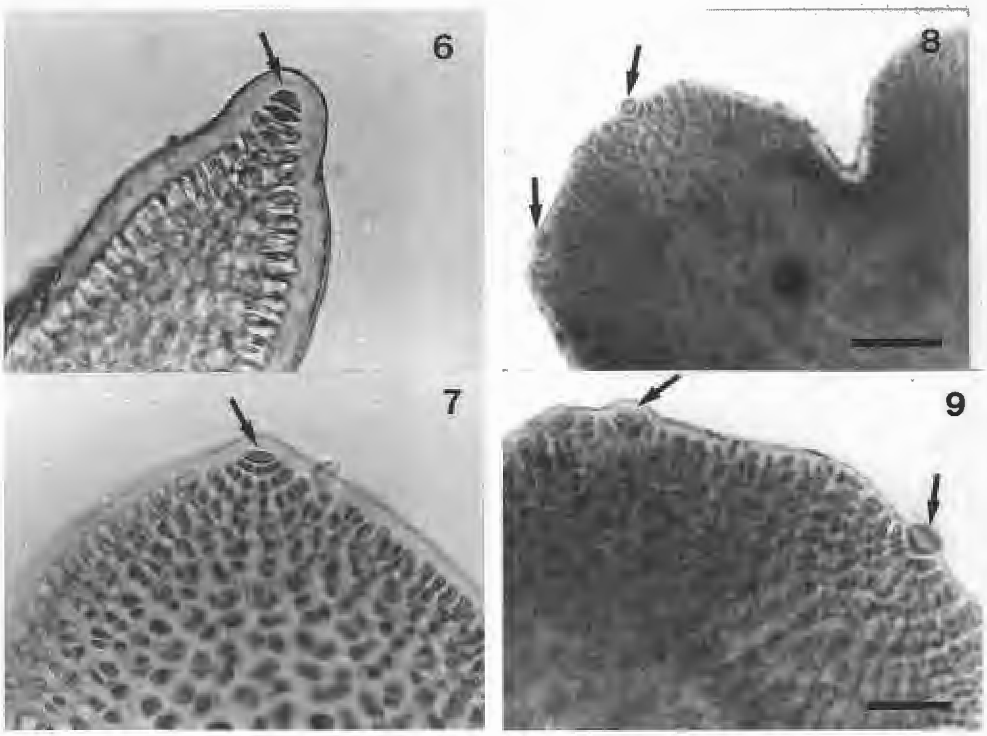
Medullary cells progressively increase in size (up to 90 µm long) and in number of rows toward the uppermost parts of the blade (Fig. 16). Transections through the flat parts of the blades (Fig. 15) show 3–4 layers of internally enlarging cortical cells and 1–3 layers of medullary cells. The middle row of axial and periaxial cells is very evident in young blades, but it can

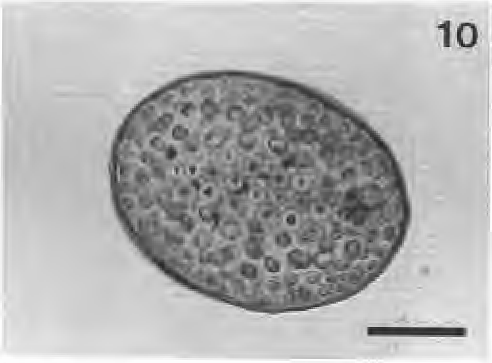


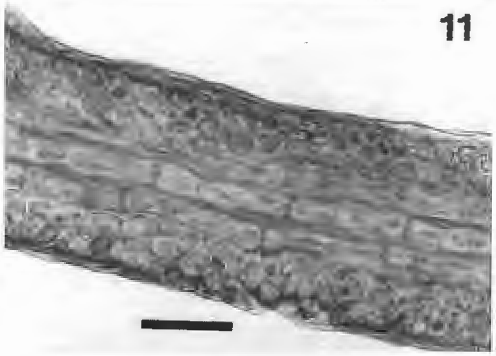
Figs. 6–9. *Gelidium samoense.* Fig. 6, Young pinnule with a prominent apical cell (arrow). Scale = 25 µm. Fig. 7, Older, more rounded branchlet; note the rows of pericentral cells and derivatives immediately below the apical cell (arrow). Scale = 25 µm. Fig. 8, Broad branch; note the apical initial and the lateral initial in close proximity (arrows). Scale = 50 µm. Fig. 9. Enlargment of a rounded, broad branch with apical and lateral initial in close proximity (arrows). Scale = 25 µm.

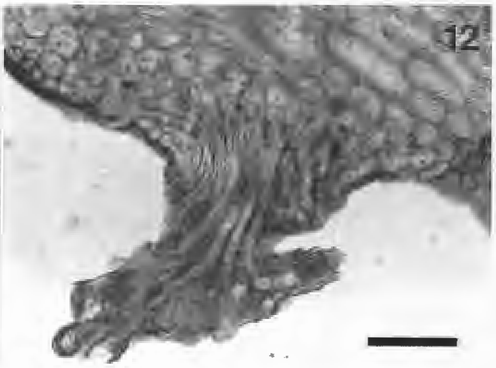
be darkened by the abundance of internal rhizoids in the thicker and older parts of blades. The axial and periaxial cells along the middle of the blade often show pit connections between them.

Tetrasporangia are irregularly disposed in branches and branchlets at the uppermost third of the plant (Figs. 17, 18). Tetrasporangia are rounded, cruciately divided, 20–25 µm in diameter or slightly ovoid, up to 30 µm long and 25 µm broad. As in other Gelidiales, a tetrasporangial initial is cut off laterally from the apical cell of a cortical filament. The apical cell continues to divide and branch, forming a cortical branch (Fig. 19), while the tetrasporangium enlarges and elongates. In *G. samoense,* however, tetrasporangial initials are also formed by cells higher up in the cortical branch (Fig. 20).

Cystocarps not seen.





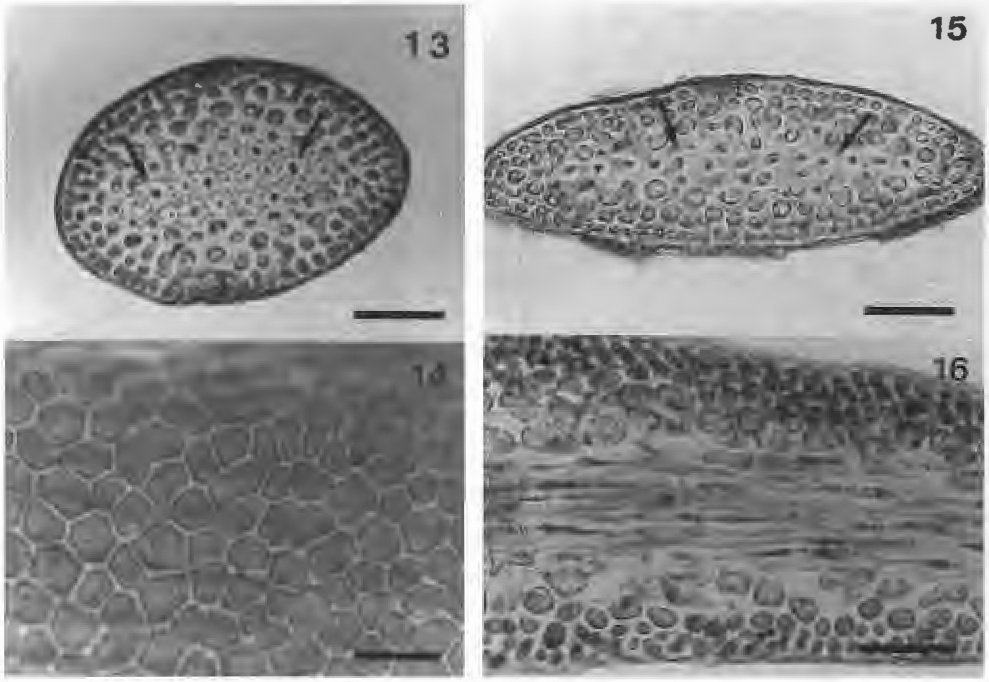


Figs. 10–12. *Gelidium samoense.* Fig. 10, Transection through the creeping axis. Scale = 50 µm. Fig. 11, Longitudinal section of creeping axis. Scale = 50 µm. Fig. 12. Longitudinal section of creeping axis showing internal rhizoidal extensions forming peglike structures. Scale = 50 µm.

Discussion

Gelidium samoense was described by Reinbold (1907:8–9) from materials collected by K. Rechinger in August 1905 at a coral reef near Apia, Upolu Island, Samoa. The type materials of the species were not available for this study, but the Fijian materials exhibit several characteristics already underlined by Reinbold in his original description. His materials were up to 3 cm tall, forming a turfy cover difficult to take apart; the erect axes were cylindrical at the base, flattened above and up to 2 mm broad. Branching was abundant and restricted to the uppermost part of the plant. Branching was variable and irregular; it could be pinnate, but according to Reinbold's description it was not rare to see proliferations coming off the margins, the tip, and even the surfaces of the blade. Furthermore, the intertwining of the lower part of the plant, together with the attachment to the substratum of neighboring creeping axes in close proximity, made Reinbold comment that this algal cover formed a compact mass, such that it was difficult to dissect a single axis without damaging the plants.

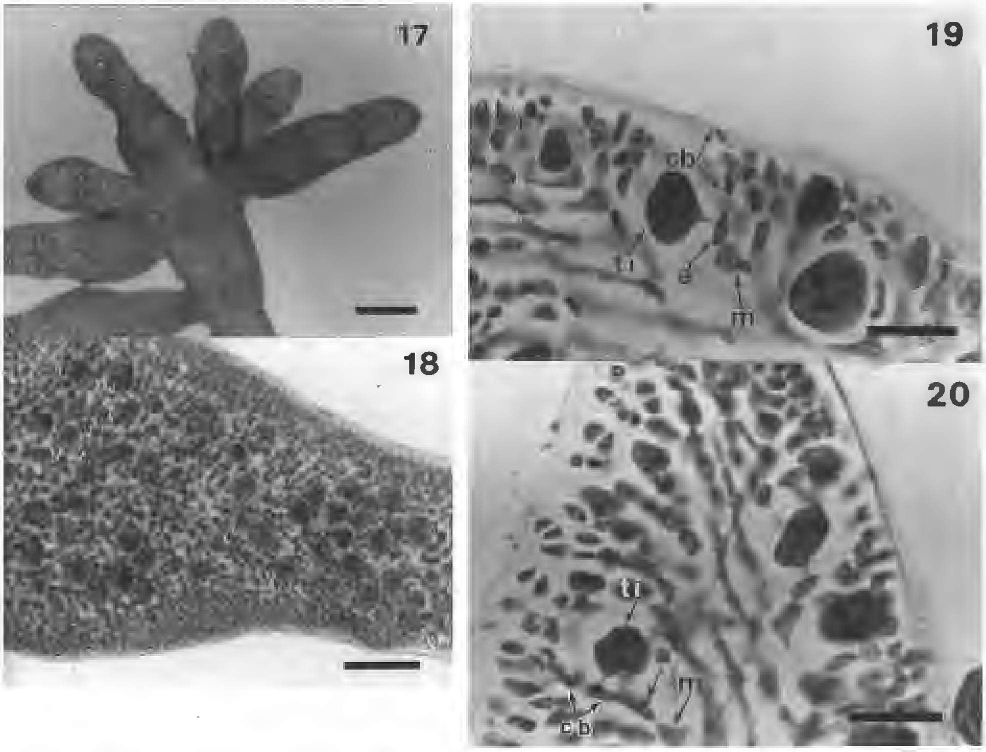
Gelidium samoense was later reported by Setchell (1924) from Ava Reef off Latone and from Laulii Reef, Tutuila Island, American Samoa. Setchell



Figs. 13–16. *Gelidium samoense.* Fig. 13, Transection through the basal part of erect axis; note the middle cell line formed by the axial and periaxial cells (arrows). Scale = 50 µm. Fig. 14, Surface view of external cortical cells. Scale = 25 µm. Fig. 15, Transection of flattened branch; note the median line of axial and periaxial cells (arrows) and the inwardly larger cortical cells. Scale = 50 µm. Fig. 16, Longitudinal section of compressed branch. Scale = 50 µm.

(1924:163) concluded that the compressed branches and tufted habit, together with the methods of branching and dimensions, indicated that his plants were the same as those described by Reinbold (1907). Setchell also noted that many *Gelidium*-like red algae living on crustose coralline algae were similar to *G. samoense,* although they were minute and seemingly simpler in structure. He designated these materials under a different form, f. *minus.*

We examined Setchell's materials (Setchell 1061) from Tutuila (UC 237044), and they lack several of the specific characters shown by *G. samoense* from Fiji. None of the branches studied shows an apical cell surrounded by a row of cortical cells. In surface view, the cortical cells are rounded, irregularly arranged, and lacking the polygonal shape of equivalent cells in *G. samoense.* A transection through the flat parts of the blades shows medullary and cortical cells of approximately similar size and does not show a medial line of medullary cells formed by the axial and periaxial cells. In addition, in transections the total number of cortical and medullary cell rows is



Figs. 17–20. *Gelidium samoense.* Fig. 17, Pattern of branching, shape, and tetrasporangial disposition in fertile branchlets. Scale = 250 µm. Fig. 18, Surface view of tetraspores in the fertile sporophylls. Scale = 100 µm. Fig. 19, Tetrasporangia formation; tetrasporangium initial (ti) formed from the apical cell (a) of a cortical filament: m = medullary cell, cb = cortical branch. Scale = 25 µm. Fig. 20, Tetrasporangium formed from cells higher up in the cortical branch; abbreviations as in Fig. 19. Scale = 25 µm.

about twice the number of rows in *G. samoense.* We conclude, therefore, that the materials from Tutuila identified by Setchell (1924) as *G. samoense* do not belong to this species. Representative specimens of f. *minus* were not available for study, so no conclusion can be reached at this time on the status of that form.

In 1926, Setchell reported again on *G. samoense*, now forming a dark red turf, collected on reefs between Papenu and Huau in Tahiti, French Polynesia (Setchell 5109a). Setchell distinguished and illustrated two forms among the materials collected, a form clearly resembling Reinbold's description (Setchell 1926: pl. 17, figs. 1, 2) and a narrow flattened form (1926: pl. 17, figs. 3–6) that he distinguished as f. *lineare.* We examined the specimens identified by Setchell (1926; UC 261322), which we found to be in agreement with the

Fijian materials. In both cases there is abundant branching near the apex of erect blades; the creeping axes show stolons and erect axes emerging from the same point along the creeping axes; and the terminal pinnules are rounded and may sometimes appear as proliferations. Transections through the flat parts of the blade show the medial line of axial and periaxial cells, similarly to Setchell's illustrations; and the apical cell may appear surrounded by a semihemispheric row of second-order filaments. Similar to Setchell (1926), we have also found among the Fijian materials narrow flattened forms intermixed with the more typical broad form. These correspond to the natural population variation of this species and thus do not need to be recognized as forms.

Gelidium samoense has been so far found in Samoa, Fiji, and Tahiti only. Specimens of this species are, however, of low stature and could have been easily overlooked or confused with *G. pusillum*. The frequency of truncate erect axes shown by *G. samoense,* the absence of branches in the lower parts of the plants, the abundant presence of tetraspores in axes and branches of the fertile plants, and the tissue decay exhibited by empty branchlets after spore release all suggest that the lower parts of the plants are perennial while the apical parts are seasonal. After spore release, the fertile branchlets probably die and new flat branches may be produced again from the truncate axis during the next growing season. If this is true, the lower parts of this plant could be easily misidentified with other small-sized species of *Gelidium* and *Pterocladiella.* Therefore, this species probably has a broader geographic distribution than presently known.

Acknowledgments

The authors thank Dr. I. A. Abbott for the invitation to participate in the workshop and for reviewing and editing the manuscript. B. S. acknowledges with pleasure cofunding by FONDECYT (Grant 1020855) and the California Sea Grant College Program, which enabled him to participate in the workshop in Hawaii and to complete part of the work in Santiago. P. S. and G. R. S. thank the International Ocean Institute and Oceania Research and Development Associates, Inc., for financial assistance, as well as the California Sea Grant College Program for our costs at the University of Hawaii–Hilo. The histological and photographic work of Ms. Verónica Flores is acknowledged with gratitude. The specimens in the Herbarium at the University of California, Berkeley, were kindly supplied by Dr. Paul Silva.

Literature Cited

N'Yeurt, A. D. R. 2001. Marine algae from the Suva Lagoon and Reef, Fiji. Austral. Syst. Bot. 14:689–869.

N'Yeurt, A. D. R., South, G. R., and Keats, D. W. 1996. A revised checklist of the benthic marine algae of Fiji (including the island of Rotuma). Micronesica 29:49–96.

Perrone, C. 1994. Diagnostic and taxonomic value of rhizoids in the Gelidiales: Some considerations. Giornale Botanico Italiano 128:1088–1091.

Reinbold, T. 1907. Meersalgen (Forschungsreise nach den Samoa-Inseln, dem Neu-Guinea-Archipel und den Salomons-Inseln). In: Botanische und Zoologisch Ergebnisse einer wissenschaftl. Denkschriften Akademiens Wien 81, pp. 200–208.

Santelices, B. 2002. The taxonomic status of *Gelidiella adnata* (Gelidiales, Rhodophyta). In: Tax. Econ. Seaweeds 8, pp. 151–166.
Setchell, W. A. 1924. American Samoa, Pt. I: Vegetation of Tutuila Island; Pt III: Vegetation of Rose Atoll. Publ. Carnegie Inst. Wash. 341. 275 pp., 57 figs., 37 pls.
Setchell, W. A. 1926. Tahitian algae and Tahitian spermatophytes collected by W. A. Setchell, C. B. Setchell and H. E. Parks. Univ. Calif. Publ. Bot. 12:61–240.
South, G. R., and Kasahara, H. 1992. A preliminary checklist of the benthic marine algae of Fiji. Micronesica 25:41–70.
South, G. R., and Skelton, P. A. in press. Catalog of the marine benthic macroalgae of the Fiji Islands, South Pacific. Austral. Syst. Bot. 17.

Section V. *Hypnea* Species

INTRODUCTION

Isabella A. Abbott

A common species of *Hypnea* has been known for some years in Fiji under a variety of names that have been checked with authentic material from elsewhere. All names previously applied have been found to be incorrect. Morphological investigations have not helped to determine which might be the correct species name, and preliminary molecular studies were inconclusive. Robin South therefore is publishing this unnamed taxon, partly hoping that someone might be "in the same boat"—having the same species but not knowing what name to give it—and could offer some help.

I refer new readers of this section to the five papers on *Hypnea* that appeared earlier in this series: Taxonomy of Economic Seaweeds, Vol. 6, 1997. These papers make a good start at trying to sort out *Hypnea* species in the Pacific.

HYPNEA sp. (GIGARTINALES, RHODOPHYTA) FROM FIJI, SOUTH PACIFIC, AND A LIST OF *HYPNEA* SPECIES PRESENT IN THE FIJI ISLANDS

G. Robin South

Abstract

The common edible *Hypnea* from the Fiji Islands appears to be an undescribed species, morphologically close to *H. charoides* Lamouroux, and genetically close to *H. cornuta* (Lamouroux) J. Agardh, but fitting neither sufficiently closely to allow identification. It is recommended that a formal description be made following further DNA sequencing, since this appears to be the most reliable method of separating these morphologically variable entities; this entity is left unnamed until more data are available. A total of 8 species of *Hypnea* have been reported from Fiji. Of these only 5 are listed here: 3 have been substantiated (*Hypnea* sp., *H. esperi* Grunow, and *H. pannosa* J. Agardh); 2 others require reexamination of single collections from Fiji (*H. cornuta* and *H. spinella* [C. Agardh] Kützing). The remainder are placed in synonymy.

Introduction

The 8 species of *Hypnea* Lamouroux reported from the Fiji Islands have been listed in South and Kasahara (1992) and N'Yeurt et al. (1996). Current work on the Fijian flora is concentrating on verification of earlier published records. One species reported as a principal food item in the diet of Fijians was tentatively identified as *H. pannosa* J. Agardh (South 1993, p. 342, figs. 7–9), but this is now known to be incorrect.

A reexamination of Fijian *Hypnea* collections at the South Pacific Regional Herbarium (SUVA-A) as well as collections at the University of California at Berkeley (UC) and Bernice P. Bishop Museum (BISH) suggested that this edible species belonged to the *H. charoides-valentiae* complex as recently revised by Yamagishi and Masuda (1997, 2000). Plants are widely distributed in Fiji, from Viti Levu, the Yasawa Islands, and the Lau Islands.

Some preliminary DNA sequencing was carried out by Y. Yamagishi to assist in identifying the Fijian plants, and comparisons among Fijian, Japanese, and Malaysian *Hypnea* were made using *rbc*L sequencing at Hokkaido University. The detailed results of this work will be published elsewhere (Yamagishi, in prep.). The current report deals with the preliminary identification of the Fijian plants and provides a revised list of *Hypnea* species for the Fiji Islands.

Materials and Methods

Images of whole specimens were preserved using Nikon Coolpix 990 and 995 digital cameras. Specimens housed in the South Pacific Regional Herbarium (SUVA) are designated as SUVA-A, to distinguish the algal collections from the vascular plants.

Results

The genus *Hypnea* (Hypneaceae, Gigartinales) was erected by Lamouroux (1813) and is lectotypified by *H. musciformis* (Wulfen) Lamouroux (Masuda et al. 1997). The taxonomy and nomenclature of the genus are confused, thus making it difficult to identify specimens with certainty. In their overview of the genus, Masuda et al. (1997) provided a revised circumscription of the genus and outlined the morphological characteristics of possible taxonomic value. The genus is widely dispersed in the warmer waters of the world, and a number of species are used as food or for production of phycocolloids (Hoppe 1969). The species under discussion here, misidentified as *H. pannosa,* is an important commercial species in Fiji, where it is a favored food item of indigenous Fijians (South 1993).

A reexamination of Fijian collections in the light of the work of Yamagishi and Masuda (1997, 2000) and Womersley (1994), as well as a study of representative collections housed in UC and BISH, has revealed that the Fijian plants morphologically resemble members of the *H. charoides–valentiae* complex (Fig. 1). The possibility that the plants also superficially resemble *H. flexicaulis* Yamagishi and Masuda was considered, and material was sent to Yamagishi for his examination and comment.

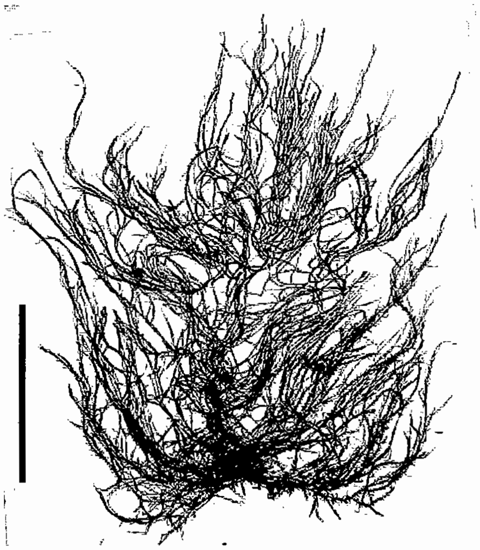


Fig. 1. Herbarium specimen of typical *Hypnea* sp., Suva Point, Fiji, Nov. 1990. Scale = 50 mm.

The *Hypnea charoides–valentiae* Complex

The proposal to recognize the *H. charoides–valentiae* complex was made at the Kuala Lumpur workshop convened by Abbott (1997), and the representative taxa were reviewed by Yamagishi and Masuda (1997). Other participants at the Kuala Lumpur workshop also discussed the complex (Lewmanomont 1997; Chiang 1997). In a later work, Yamagishi and Masuda (2000) revised their concept of the complex, concluding that it comprised 2 species, *H. charoides* Lamouroux and *H. flexicaulis. Hypnea charoides* (including *H. valentiae*) is widely distributed in the Indian (Silva et al. 1996) and Pacific Oceans and is described in detail in Womersley (1994, as *H. charoides* and *H. valentiae*). *Hypnea flexicaulis* appears to be restricted to Japan (Yamagishi and Masuda 2000).

Identity of *Hypnea* sp. from Fiji

The Fijian plants were described and illustrated in detail in South (1993; see also Fig. 1). The habit is lax and the plants are often entangled and loose-lying, attached to coral rubble, shell fragments, or sand by a simple, disclike holdfast (South 1993, fig. 7), with the medulla composed of isodiametric cells, their length equal to or slightly exceeding the diameter. Hyphae are lacking, and the outer layer is composed of 1 or 2 layers of small cells. Tetrasporangia are abundant from September to December and are borne in saddle-shaped nemathecia (South 1993, figs. 8–9), usually confined to the lower side of the ultimate branchlets as described by Dawson (1956) and Kasahara (1985). Tetrasporangia are zonately divided and are interspersed with sterile paraphyses. Sexual stages have not been seen.

From an examination of extensive herbarium collections it was initially concluded that morphologically the Fijian plants most closely resemble *H. charoides* or *H. flexicaulis*. Formalin- and alcohol-preserved material was sent to Y. Yamagishi of Hokkaido University for his examination. Yamagishi (pers. comm.) concluded that the Fijian plants do not resemble *H. flexicaulis*, since the upper branching pattern is different. In *H. flexicaulis* the upper portions exhibit pseudodichotomous branching, with the two sides being symmetrical. This opinion was confirmed by Xia Bangmei, who examined images of the Fijian plants during the Sea Grant workshop in Hilo. Xia considered the Fijian material to be morphologically closest to *H. charoides* (Fig. 2).

Preliminary DNA sequencing of the Fijian plants has been carried out by Y. Yamagishi (Yamagishi, pers. comm.). Partial *rbc*L sequencing (1000 bases) indicates that they are most closely related to *H. cornuta* (Lamouroux) J. Agardh (separated by only 4 bases), that they are very distant from *H. flexicaulis* (by 52 bases), and that they differ from other Japanese species by 30–55 bases. The stellate branches with constricted bases characteristic of *H. cornuta* are completely absent from the Fijian plants. The absence of stellate processes does not necessarily rule out *H. cornuta;* in some Thai and Malaysian populations, some thalli have many basally constricted stellate

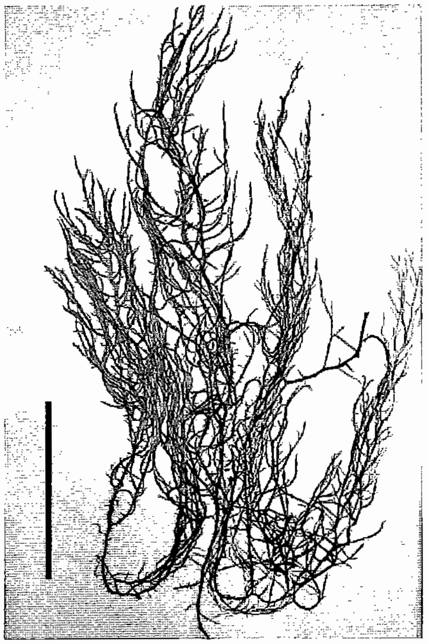


Fig. 2. *Hypnea charoides,* Asamushi, Japan, Aug. 1940. Scale = 50 mm.

branchlets, whereas others in the same population lack them (I. Abbott, pers. comm., and Y. Yamagishi, pers. comm.).

The Fijian plants are thus morphologically similar to *H. charoides* but genetically close to *H. cornuta*. It is recommended that further DNA sequencing be completed before deciding on the identity of the Fijian plants. The evidence at hand strongly suggests that it is an undescribed species, and it is thus referred to here as *Hypnea* sp. inedit.

Revised List of *Hypnea* Species from Fiji

The author has examined all Fijian and Pacific Island collections of *Hypnea* housed in SUVA-A, BISH, and UC. Of the species previously reported from Fiji in N'Yeurt et al. (1996), only 3 (*Hypnea* sp., *H. esperi,* and *H. pannosa*) can be listed with any certainty. The records of *H. cornuta* and *H. spinella* have yet to be confirmed, and the remaining taxa are placed in synonymy.

Hypnea sp.

Misapplied names: *Hypnea pannosa* sensu pro parte South and Kasahara, Micronesica, 1992; South, Bot. Mar. 36, p. 342, figs. 7–9, 1993; N'Yeurt et al., Micronesica 29, p. 79, 1996; N'Yeurt, Austral. Syst. Bot. 14, p.780, 2001 [non *Hypnea pannosa* J. Agardh, Öfvers. Kongl. Svenska Vetens.-Akad. Förhandl. 4, p. 14, 1847]. *Hypnea divaricata* sensu Grunow in Fenzl, Reise der österreichenischen Fregatte Novara..., p. 79, 1867; Chapman, Rev. Algol. 2, pp. 164–171, 1971; N'Yeurt et al., Micronesica 29, p. 79, 1996 [non *Hypnea divaricata* (C. Agardh) Greville, Algae britannicae..., p. lix, 1830].

Representative specimens at SUVA-A: Suva Point, leg. G. R. South, Nov. 18, 1990 (SUVA-A630); Nasese, Suva Lagoon, leg. P. A. Skelton, Jan. 22, 1998 (SUVA-A1224); Beqa Lagoon, leg. G. R. South, Nov. 26, 1992 (SUVA-A422); Rakiraki, H. Kasahara 20763, Oct. 11, 1985 (SUVA-A1024, 1035); Tavua, H. Kasahara 20799, Oct. 11, 1985 (SUVA-A1034); Nukulau I., Suva Lagoon, leg. G. R. South, Sept. 9, 1991 (SUVA-A435); Suva Point (Drift), leg. G. R. South, July 7, 1990 (SUVA-A458, 459); Rakiraki, H. Kasahara 20790, Oct. 24, 1985; Kaba, leg. A. D. R. N'Yeurt, Aug. 18, 1997 (SUVA-1238); Tavua, H. Kasahara 20796, Oct. 11, 1985 (SUVA-A1031); Yasawa Is. (ex Nadi Market), leg. G. R. South, Feb. 11, 1991 (SUVA-A571); Suva Lagoon, leg. G. R. South, Nov. 2, 1991 (SUVA-A572); Nasese, Suva Lagoon, leg. G. R. South, Sept. 22, 1991 (SUVA-A654); Yasawa Is. (ex Nadi Market), leg. G. R. South, Sept. 11, 1991 (SUVA-A573); Suva Lagoon (ex Suva Market), leg. G. R. South, Nov. 2, 1991 (SUVA-A926; 927); Nukulau I., leg. G. R. South, Dec. 19, 1990 (SUVA-A658); ex Suva Market, leg. G. R. South, Oct. 26, 1991 (SVA-A921); Nasese, Suva Lagoon, leg. T. D. Pickering, April 27, 1995 (SUVA-A907).

Other Material Examined (and showing close morphological resemblance to *Hypnea* sp.): Asamishi, Mutsu Province, Japan, Aug. 1940 (UC 794256); Ono-i-Lau, Fiji, leg. Y. Kondo, Sept. 1968 (BISH 534342); Pulau Tanjung Sau, Indonesia, leg. J. R. Fisher, March 14, 1989 (BISH 189442); Aldinza, South Australia, leg. E. M. Gordon (BISH 5346920); Kipukai, Kauai, Hawaii, W. H. Magruder, Sept. 21, 1979 (BISH 519278, as *H. valentiae*).

Note: The collection from the Suva Lagoon (SUVA-A 572) cited in N'Yeurt (2001) is incorrectly assigned to *H. pannosa*. N'Yeurt (2001) makes no reference to the entity described here as *Hypnea* sp., even though it is one of the most common benthic algae in the Suva Lagoon. Previous studies have misidentified this entity as *H. pannosa* or *H. divaricata*.

Hypnea cornuta (Kützing) J. Agardh, Spec. gen. ord. algarum, 2(2), pp. 449–450, 1852

Basionym: *Chondroclonium cornutum* Kützing, Spec. algarum, p. 741, 1849 (type locality: Guinea Coast, Atlantic Ocean).

Note: The single record in Kapraun and Bowden (1978) requires confirmation, as the author has been unable to locate any Fijian specimens fitting the description of this species.

Hypnea esperi Grunow, in Fenzl, Reise der österreichischen Fregatte Novara..., p. 79, 1867.

Intended synonym: *Hypnea musciformis* (Wulfen) Lamouroux var. *esperi* J. Agardh, Spec. gen. ord. algarum, 2(1), pp. 442–443, 1851 (type locality: Mauritius).

Note: Askenasy (1888), Chapman (1971), Kasahara (1985), and South (1991) have reported *H. esperi* from Fiji. However, the name *H. esperi* has been called into question (Silva et al. 1996) because it was erroneously substituted for *Fucus nootkanus* Esper by Bory de Saint-Vincent (1828). *Hypnea musciformis* var. *esperi* is a valid but illegitimate name based on a group of collections, including those misidentified by Bory de Saint-Vincent. The entity currently referred to as *H. esperi* needs a new species name, if it is to be recognized as the species level (Silva et al. 1996; Yamagishi and Masuda 1997).

Hypnea pannosa J. Agardh, Öfvers. Kongl. Svenska Vetensk.-Akad. Förhandl. 4, p. 14, 1847 (type locality: San Agustín, Oaxaca, México).

Synonym: *Hypnea nidulans* Setchell, Publ. Carnegie Inst. Wash. 341, pp. 161–163, fig. 30, 1924 (type locality: Tutuila I., American Samoa).

Note: *Hypnea pannosa* has been reported from Fiji as *H. nidulans* by Grunow (1874), Chapman (1971), Kasahara (1985), South (1991), and N'Yeurt et al. (1996). South (1993) misapplied *H. pannosa* for specimens of the *Hypnea* sp.

Hypnea spinella (C. Agardh) Kützing, Bot. Zeit. 5, p. 23, 1847.

Basionym: *Sphaerococcus spinellus* C. Agardh, Sp. algarum 1(2), p. 323, 1822 (type locality: West Indies).

Synonym: *Hypnea cervicornis* J. Agardh, Sp. gen. ord. algarum 2(2), p. 451,1852 (paratype localities: West Indies, Brazil, Mauritius, Mexico).

Note: The single record of this species in Kapraun and Bowden (1978) and its subsequent listing in N'Yeurt et al. (1996) requires confirmation, as no other Fijian material referable to this species has been found.

Acknowledgments

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Literature Cited

Abbott, I. A. (ed.). 1997. Taxonomy of economic seaweeds, Vol. 6. California Sea Grant College System. Report No. T-040. La Jolla, CA. xviii + 212 pp.

Askenasy, E. 1888. Algen. In: Forschungsreise S.M.S. "Gazelle." IV. Theil Botanik. [Fasc. 2] Berlin. 58 pp., 12 pls.

Bory de Saint-Vincent, J. B. G. M. 1828. Cryptogamie. In: Duperrey, L. I., Voyage autour du monde, exécuté par ordre du Roi, sur la corvette de sa majesté, La Coquille, pendant les années 1822, 1823, 1824 et 1825. Paris, pp.97–200.

Chapman, V. J. 1971. The marine algae of Fiji. Rev. Algol. 2:164–171.

Chiang, Y. -M. 1997. Species of *Hypnea* Lamouroux (Gigartinales, Rhodophyta) from Taiwan. In: Tax. Econ. Seaweeds 6:163–177.

Dawson, E. Y. 1956. Some marine algae of the southern Marshall Islands. Pacific Sci. 10:25–66.

Grunow, A. 1874. Algen der Fisdschi-, Tonga- und Samoa-Inseln, gesammelt von Dr E. Graeffe. Journal des Museums Godeffroy [Hamburg] 3:23–50.

Hoppe, H. A. 1969. Marine algae as raw materials. In: Levring, T., et al. (eds.), Marine algae: A survey of research and utilization, pp. 126–187. Cram de Gruyter, Hamburg.

Kapraun, D. F., and Bowden, W. A. 1978. Additions to the benthic marine algal flora of Fiji. *Micronesica* 14:199–207.

Kasahara, H. 1985. Marine green and red algae collected at Viti Levu and Ndravuni Islands of Fiji. M. Ag. Thesis, Kyoto University. 83 pp.

Lamouroux, J. V. F. 1813. Essai sur les genres de la famille des thalassiophytes non articulées. Annales du Muséum d'Histoire Naturelle [Paris] 20:21–47, 115–139, 267–293, pls 7–13.

Lewmanomont, K. 1997. Species of *Hypnea* from Thailand. In: Tax. Econ. Seaweeds 6:179–191.

Masuda, M., Yamagishi, Y., Chiang, Y.-M., Lewmanomont, K. and Xia B. 1997. Overview of *Hypnea* (Rhodophyta, Hypneaceae). In: Tax. Econ. Seaweeds 6:127–133.

N'Yeurt, A. D. R. 2001. Marine algae from the Suva Lagoon and reef, Fiji. Austral. Syst. Bot. 14(5):689–869.

N'Yeurt, A. D. R., South, G. R., and Keats, D. W. 1996. A revised checklist of the benthic marine algae of the Fiji Islands, South Pacific (including the Island of Rotuma). Micronesica 29(1): 49–98.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. University of California Press, Berkeley. 1259 pp.

South, G. R. 1991. Benthic marine algae from Dravuni Island, Astrolabe Islands, Kadavu. University of the South Pacific Marine Studies Programme Technical Report 1991(5):1–13.

South, G. R. 1993. Edible seaweeds of Fiji: An ethnobotanical study. Bot. Mar. 36:335–349.

South, G. R., and Kasahara, H. 1992. A preliminary checklist of the benthic marine algae of the Indian Ocean. Micronesica 25(1):41–70.

Womersley, H. B. S. 1994. The marine benthic flora of Southern Australia, Part IIIA. Bangiophyceae and Florideophyceae (Acrochaetiales, Nemaliales, Gelidiales, Hildenbrandiales and Gigartinales *sensu lato*). Australian Biological Resources Study, Canberra. 508 pp.

Yamagishi, Y., and Masuda. M. 1997. Species of *Hypnea* from Japan. In: Tax. Econ. Seaweeds 6:135–162.

Yamagishi, Y., and Masuda, M. 2000. A taxonomic revision of a *Hypnea charoides-valentiae* complex (Rhodophyta, Gigartinales) in Japan, with a description of *Hypnea flexicaulis* sp. nov. *Phycol. Res.* 48:27–35.

Section VI. *Halymenia floresia*—Generitype

INTRODUCTION

Isabella A. Abbott

Halymenia is a genus with many species, many of which have been underdescribed in that development of the carposporophyte is usually lacking. Yet these characters are necessary for generic placement as well as species distinction. As with most red algae that have been described in the eight previous volumes of this series, one or two specimens is not a sufficient number to establish a new species or to unravel all the necessary elements to maintain an old species. I admire the methodical way in which Shigeo Kawaguchi has attacked the widely distributed or important species of *Halymenia;* when specimens cross the paths of Workshop participants, they will be armed with the absolutely necessary piece of literature necessary to help identify these attractive plants.

The anatomical examination of the type specimen of *Halymenia floresia* in this volume is of great importance, for this species is the type of the genus. Any old or new species must, in the end, be examined in terms of the critical details shown in this study. Because the type specimen and other materials from the type locality (Cadiz, Spain) have been critically compared with specimens from the French Mediterranean coast, India, and Malaysia and found to be in accord, we are reassured that, variable as the specimens may appear to be externally, they are very stable in their internal details.

MORPHOLOGICAL OBSERVATIONS OF THE TYPE AND SOME AUTHENTIC MATERIAL OF *HALYMENIA FLORESIA* (CLEMENTE y RUBIO) C. AGARDH, WITH NOTES ON PREVIOUS REPORTS OF THIS ALGA

Shigeo Kawaguchi

Abstract

The morphology of the lectotype and other authentic specimens of *Halymenia floresia* is described. The features of this alga are as follows: blades irregularly branched for 3 or 4 orders; no maculation and no proliferations on the surface; blades of thin cortex (4 or 5 cells) and sparse medulla (vertical filaments conspicuous); gametophytes monoecious; auxiliary cell ampullae branched to the third order and wide across the top; tetrasporangia broadly ellipsoidal and embedded in the outer cortex. These features are compared with those in previous reports of this alga. Both French Mediterranean and Indian material described by Codomier (1974) and Balakrishnan (1961), respectively, are in good accordance with the Spanish material. So is the Malaysian material described in the present study. The Japanese material described by Yoshida and Kawaguchi (in Yoshida 1998) is, however, different from the Spanish material in having surface maculation, and its status remains to be clarified.

Introduction

The red algal genus *Halymenia* (Halymeniaceae, Rhodophyta) currently includes some 50 species (Guiry and Dhonncha 2003). *Halymenia floresia*, the generitype, was originally described by Clemente (1807) as *Fucus floresius* on material from Andalucia, southern Spain. Carl Agardh (1817) established the genus *Halymenia* on this alga and several other species, most of which were removed from the genus later. Schmitz (1889) chose *H. floresia* as lectotype of the genus.

Halymenia floresia has been reported worldwide from tropical seas. Around the northwestern Pacific, this alga has been reported from Japan (Yoshida and Kawaguchi in Yoshida 1998), Indonesia (Weber van Bosse 1921), and Malaysia (Phang and Wee 1991). However, probably due to its morphological plasticity, the specific discrimination of *H. floresia* from other species, such as *H. durvillei* Bory de Saint-Vincent, is sometimes very difficult and confusing. De Smedt et al. (2001), who made a comprehensive study of *Halymenia* species from the Philippines, questioned the presence of *H. floresia* in the Indo-Pacific. To avoid possible confusion, a careful comparison with the type material would be most important. In the present study, detailed observations of the lectotype and other authentic material of *H. floresia* are made, and the results are compared with previous studies of this alga. The presence of a Malaysian alga with a very similar morphology and without a doubt assignable to genuine *H. floresia* is also reported here.

Materials and Methods

The lectotype and other authentic specimens of *H. floresia,* on loan from the herbarium of Real Jardin Botanico in Madrid, Spain (MA-1829, -1830, -1832, -1833, -1834, -1835, -1836, -1837), were used. These specimens were all formerly housed in the herbarium of S. de R. Clemente.

Spanish Material: The lectotype (MA-1832), a tetrasporophyte, was collected at "Playa de Sanlucar de Barrameda," Cadiz, Spain, at the end of August, no year given (but probably prior to 1807, when it was described). Specimen MA-1835 is a monoecious gametophyte collected at the same place as the lectotype in August. Of the other 6 specimens, MA-1829 and -1833 are small and very fragmentary specimens that were not used in the anatomical study. The remaining 4 specimens, MA-1830 (tetrasporophyte), -1834 (gametophyte), -1836 (gametophyte), and -1837 (gametophyte), all from the type locality or Cadiz, were dried without spreading over the paper and may be fragmentary, since I could not find the holdfasts. The present study is, therefore, based mainly on specimens MA-1832 and -1835, with specimens MA-1830, -1834, -1836, and -1837 used supplementarily. The collector and the exact collection dates of these specimens are all unkown.

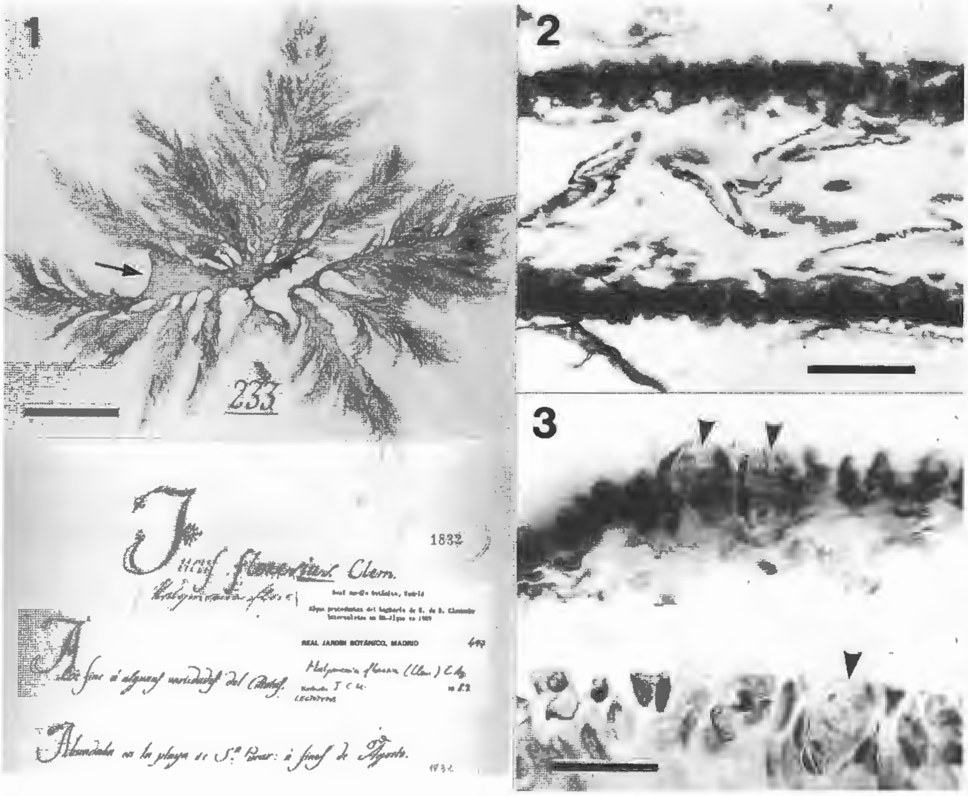
Malaysian Material: gametophyte, tetrasporophyte, May 14, 1998, Pulau Tikus, Sandakan, leg. S. Kawaguchi (Kawaguchi 1167, 1168, 1171, 1172); sterile, May 18, 1998, Nunuyan Laut, Sandakan, leg. S. Kawaguchi (Kawaguchi 1170, 1173).

Hand sections were made on resoaked small fragments that had been carefully dissected from the specimens under the dissecting microscope. The sections were then mounted onto glass slides with a 50% seawater/glycerol mixture and stained with 0.5% (w/v) cotton-blue in a water/glycerol/lactic acid/phenol (1:1:1:1) solution. The slides are kept in the Laboratory of Fishery Sciences, Faculty of Agriculture, Kyushu University.

Results

Morphological Observations of Spanish Specimens

MA-1832 (lectotype, Fig. 1): The plant has a short cylindrical stipe, 3–5 mm long, then expanding into a foliose blade with a wide cuneate base. The blade is complanately and irregularly branched for 3 orders, up to 15 cm high. The exact length of this plant is, however, uncertain because one of the axes with the maximum width (2.3 cm) is apparently cut off near the base (Fig. 1). Each axis, 0.8–2.3 cm wide, produces irregularly pinnate laterals with round axils, which in turn produce lesser laterals of the same type. The ultimate laterals are beset with short, spinelike processes. The margins of the axes and major laterals are mostly entire, with occasional spinelike processes. The color is pinkish light brown or partly light yellow without any sign of maculation on the surface. The original color is uncertain, but judging from the pre-



Figs. 1–3. ***Halymenia floresia*. Fig. 1, Lectotype specimen MA-1832; arrow shows the portion where the axis is cut off. Scale = 5 cm. Fig. 2, Transverse section of the blade showing vegetative construction. Scale = 50 μm.**
Fig. 3, Tetrasporangia (arrowheads) embedded in the cortex. Scale = 25 μm.

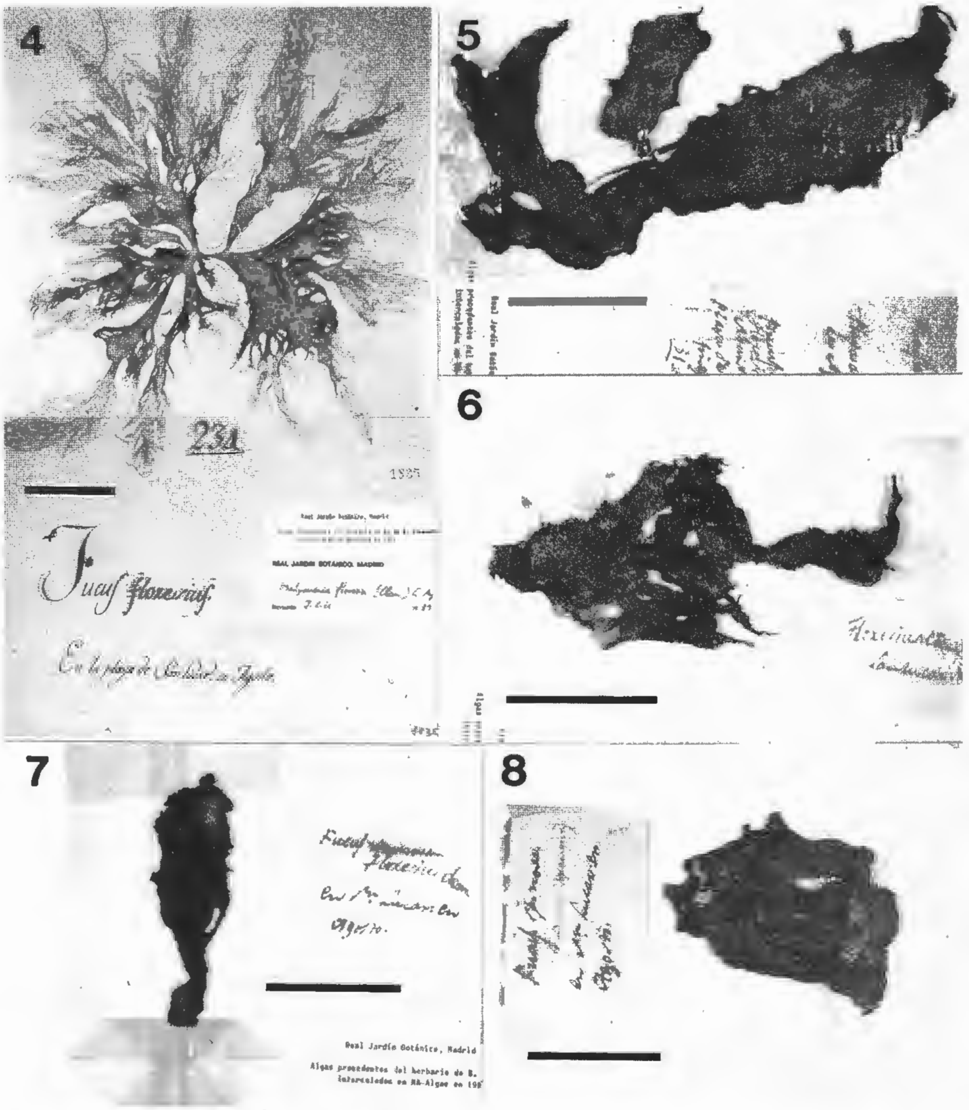
served color, it could not be dark red. Surface proliferations were not produced. Internally the blade consists of a thin cortex and a loose filamentous medulla (Fig. 2). The cortex consists of 4 or 5 cells, with the inner 2 or 3 cells larger and irregularly shaped. The outer 2 or 3 cells are smaller and rounded. The outermost cells are slightly elongated and tapering. The medulla consists of sparsely distributed filaments, which seem to run obliquely from cortex to cortex. This is, however, apparently the result of imperfect restoration to the original condition when resoaked, and the direction of these filaments is considered to be mostly vertical. For the same reason, the blade thickness is difficult to measure accurately. Tetrasporangia are broadly ellipsoidal and embedded in the outer cortex (Fig. 3).

MA-1835 (Fig. 4): The plant has a short stipe, 3–4 mm long, and expands into a foliose blade with a cuneate base. The blade is complanately and irregularly branched for 3 or 4 orders, up to 15 cm high. The axes, up to 4 cm wide, irregularly produce laterals with round axils. The laterals again irregularly produce lesser laterals with tapering apices and roughly toothed margins. The margins of the axes and major laterals are mostly entire, with occasional spinelike processes. The color is light brown without maculation or proliferations on the surface. Internally, the blade consists of a thin cortex and a loose filamentous medulla (Fig. 9). The cortex consists of 5 or 6 cells in the central portion of the blade, the inner 3 or 4 cells being larger and irregularly shaped. The outer 2 or 3 cells are smaller and rounded. The outermost cells are slightly elongated and tapering. The medulla consists of sparsely distributed filaments. The medullary filaments mostly run vertically from cortex to cortex (Fig. 11).

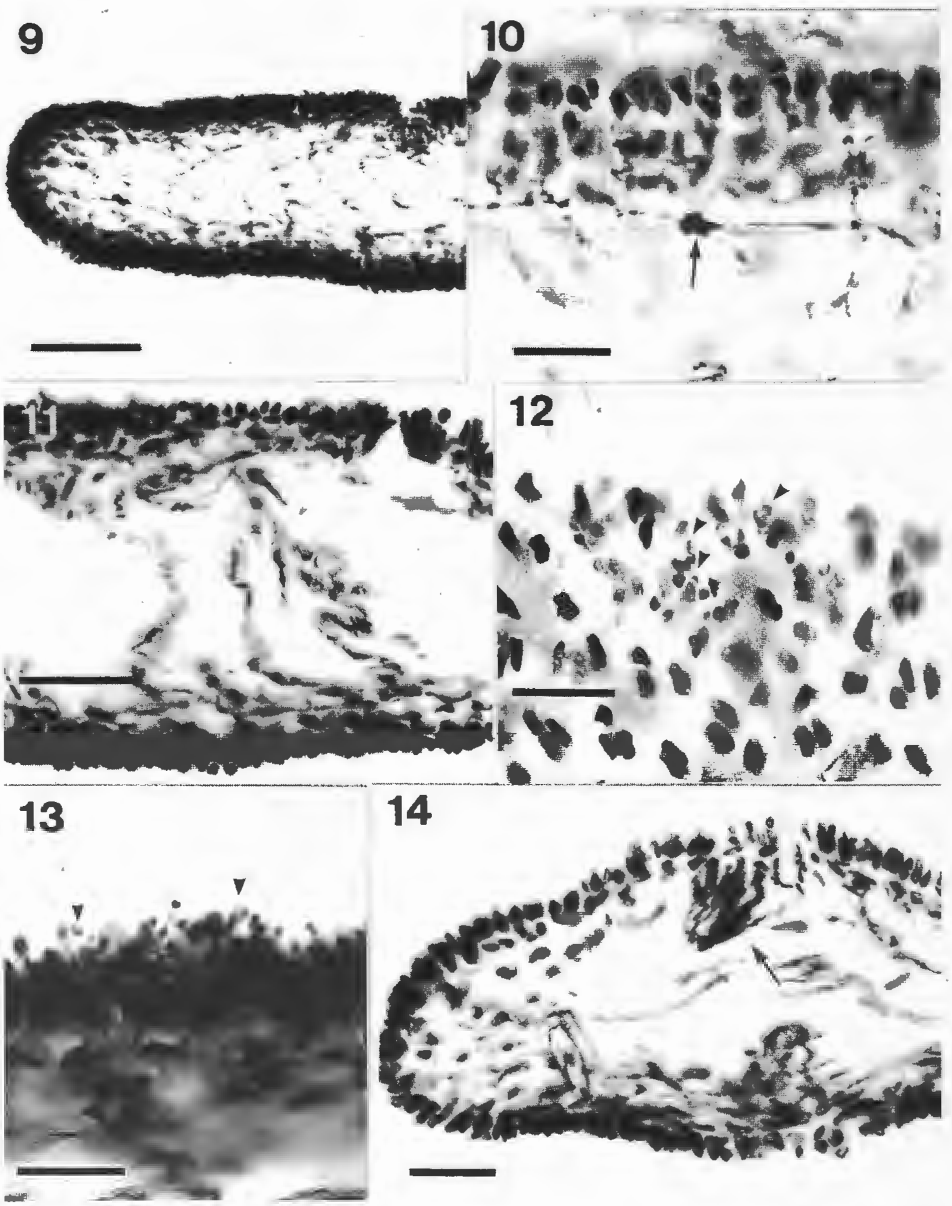
This specimen is a monoecious gametophyte. Spermatangia are irregularly gathered in patches over the blade and are cut off from the outermost cortical cells (Fig. 13); carpogonial branches were not found; auxiliary cells are formed in ampullae (Figs. 14, 15); the auxiliary cell ampullae are branched at least to the third order and wide across the top (Fig. 16). The process of gonimoblast development was not followed in this specimen.

MA-1834, -1836, -1837 (Figs. 5–7): All these specimens are monoecious gametophytes. Because they are folded, the exact sizes and gross morphologies cannot be clarified. Internally, these plants have a vegetative construction very similar to that of MA-1835: the blades consist of thin cortex and a very loose medulla; the cortex consists of 5 or 6 cells in the central portion of the blade; the inner 2 or 3 cells are larger and irregularly shaped; the outer 3 or 4 cells are smaller and rounded except for the outermost cells, which are slightly elongated and tapering; the medulla consists of sparsely distributed filaments mostly running vertically from cortex to cortex. Large stellate cells with deep staining substance are occasionally found in the periphery of the medulla (Fig. 10). Spermatangia are formed from the outermost cortical cells in patches over the blade (Fig. 12). Carpogonial branches and early post-fertilization events were not observed. Gonimoblasts were developed deep inside the medulla and are surrounded by a loose network of sterile filaments (Fig. 17). Mature carposporophytes measure 120–140 µm in diameter in surface view (Fig. 18).

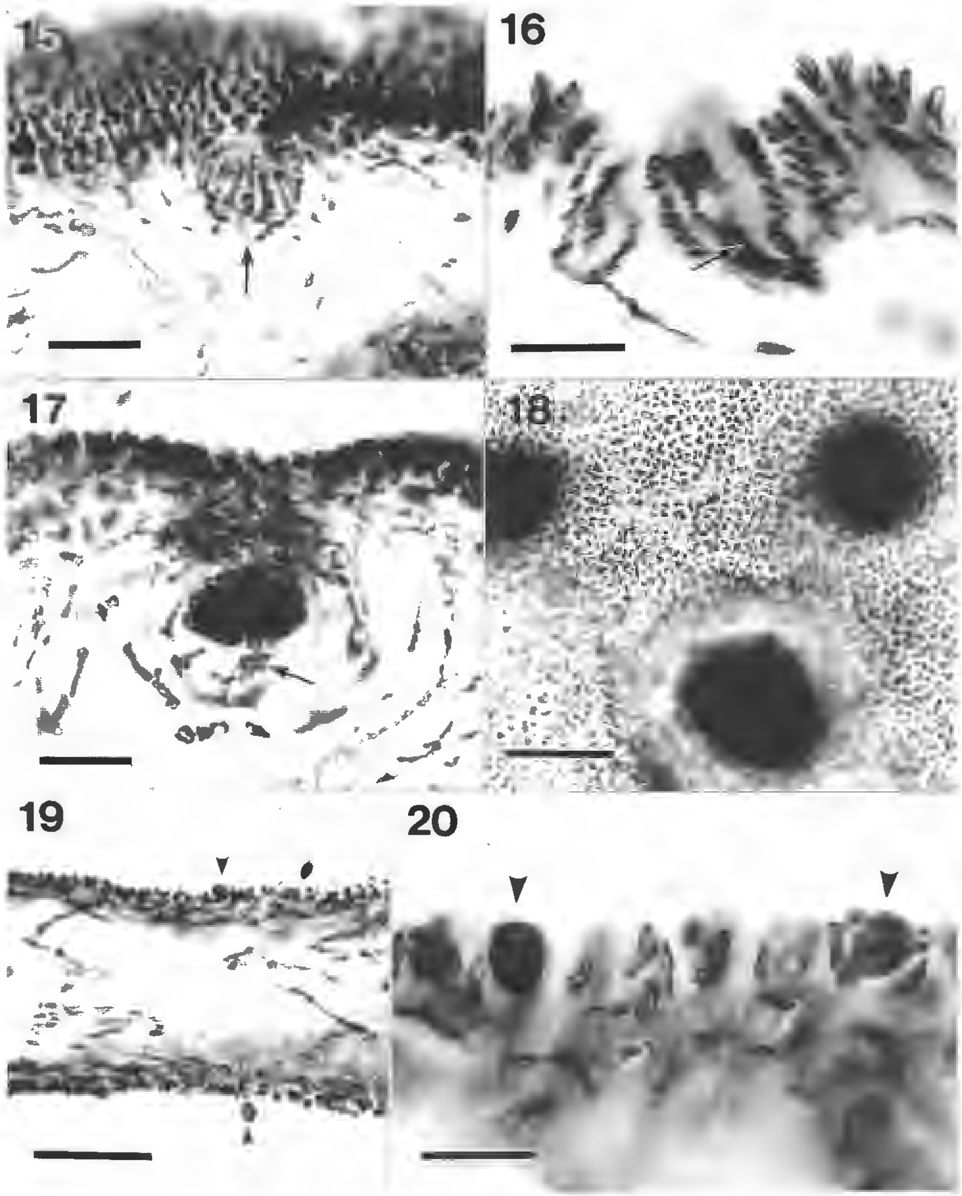
MA-1830 (Fig. 8): This plant is tetrasporangial. The vegetative construction is very similar to that of MA-1832 (Fig. 19). Tetrasporangia are broadly ellipsoidal, 13–17 µm wide by 20–25 µm long, usually isolated and embedded in the cortex (Fig. 20).



Figs. 4–8. ***Halymenia floresia*****. Fig. 4, Gametophytic specimen MA-1835. Fig. 5, Gametophytic specimen MA-1834. Fig. 6, Gametophytic specimen MA-1836. Fig. 7, Gametophytic specimen MA-1837. Fig. 8, Tetrasporophytic specimen MA-1830. All scales = 5 cm.**



Figs. 9–14. *Halymenia floresia.* Transverse sections of MA-1835, unless otherwise indicated. Fig. 9, Vegetative construction. Scale = 100 µm. Fig. 10, Cortical construction and large stellate cell with dark staining substance (arrow) (MA-1837). Scale = 50 µm. Fig. 11, Medullary filaments running vertically from cortex to cortex. Scale = 50 µm. Fig. 12, Surface view of blade forming spermatangia (arrowsheads) (MA-1837). Scale = 25 µm. Fig. 13, Spermatangia (arrowheads) produced from the outermost cortical cells. Scale = 25 µm. Fig. 14, Auxiliary cell ampulla (arrow). Scale = 50 µm.



Figs. 15–20. *Halymenia floresia.* Transverse sections, unless otherwise indicated. Fig. 15, Auxiliary cell ampulla (arrow) (MA-1835). Scale = 50 µm. Fig. 16, Auxiliary cell ampulla; arrow shows an auxiliary cell (MA-1835). Scale = 25 µm. Fig. 17, Gonimoblasts developed from an auxiliary cell (arrow) (MA-1837). Scale = 50 µm. Fig. 18, Surface view of cystocarps (MA-1834). Scale = 100 µm. Fig. 19, Vegetative construction of blade forming tetrasporangia (arrowheads) (MA-1830). Scale = 100 µm. Fig. 20, Tetrasporangia (arrowheads) embedded in the cortex (MA-1830). Scale = 25 µm.

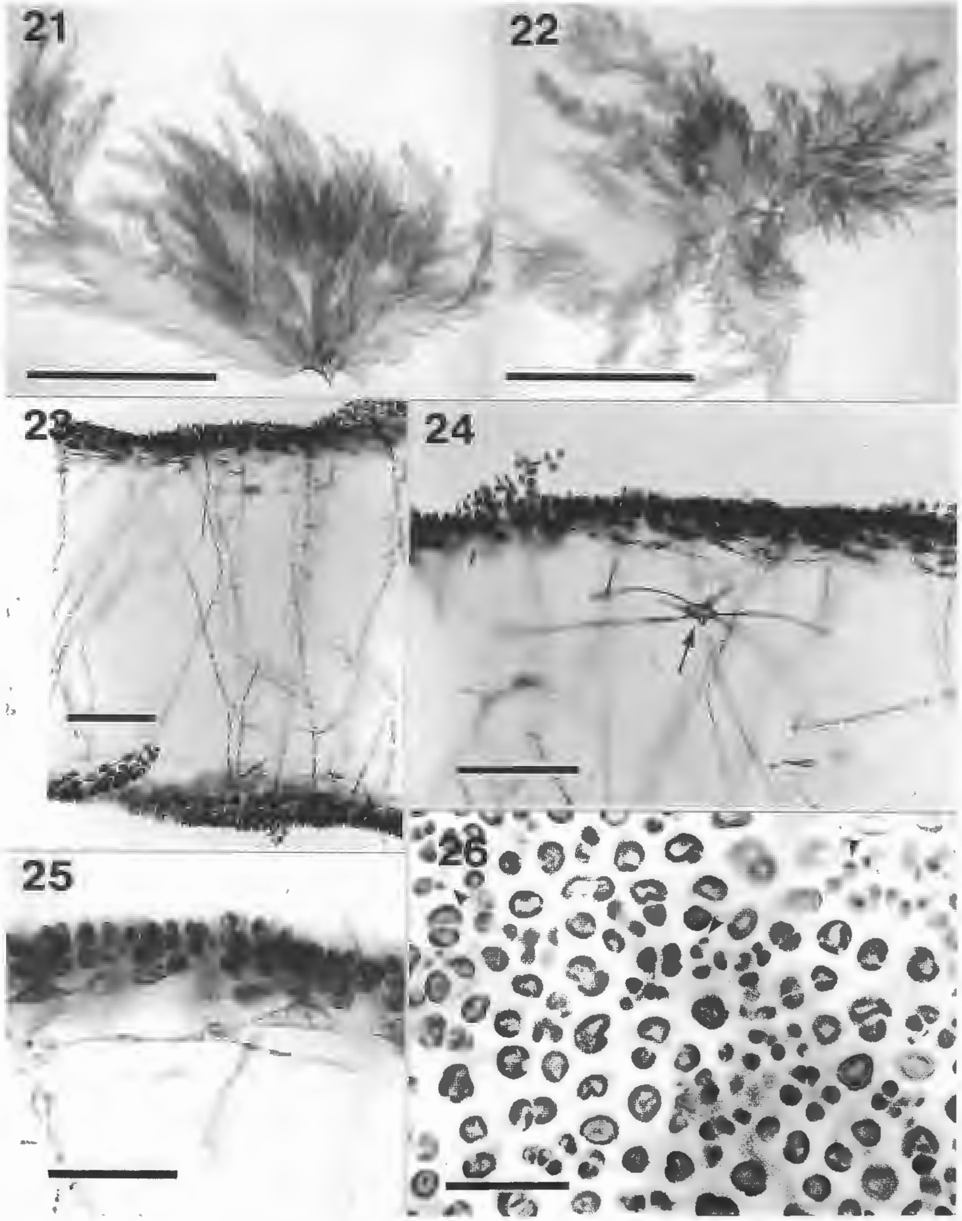
Morphological Observations of Malaysian Specimens

The plants are rose red in color, soft and very gelatinous in consistency. The plants are shortly stipitate, up to 5 mm long, and attached to the substratum with a small discoid holdfast. The dissected blades are complanately and irregularly branched for 3–5 orders, up to 32 cm high. The axes, up to 7 cm wide, up to 600 µm thick in the middle portion of blades, irregularly produce laterals, which again produce lesser laterals with a similar morphology. The ultimate laterals are tapering to acute apices and have roughly toothed margins (Figs. 21, 22). Internally, the blade consists of a thin cortex and a loose filamentous medulla (Fig. 23). The cortex consists of 4 or 5 cells; the inner 2 or 3 cells are larger and irregular or stellate; the outer 2 or 3 cells are smaller and rounded, with the outermost cells being slightly elongated and tapering (Fig. 25). The medulla consists of sparsely distributed filaments that run mainly vertically from cortex to cortex (Fig. 23). Large stellate cells with dark staining substance are occasionally present in the periphery of the medulla (Fig. 24). The diameter of vertical filaments is 10–13 µm.

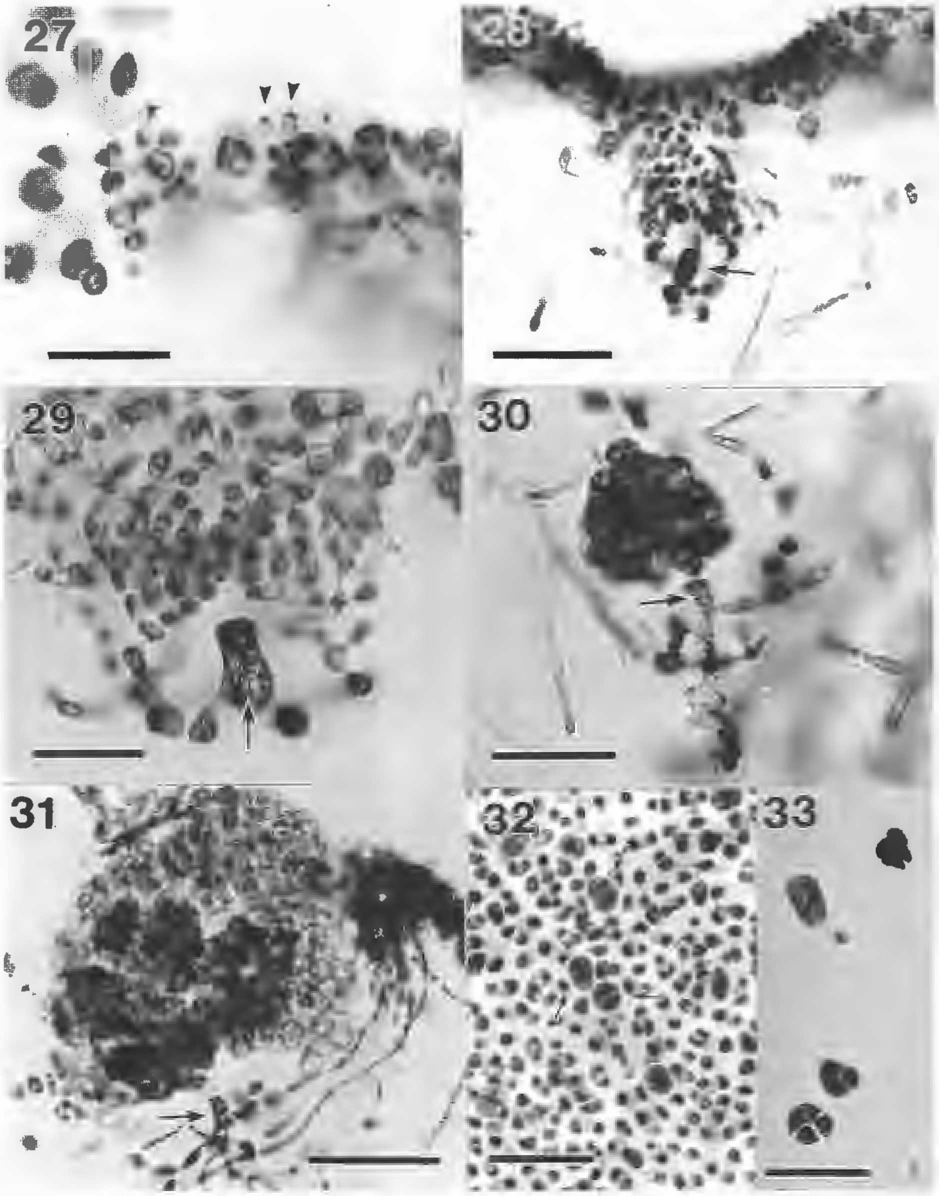
The sexual plants are monoecious. Spermatangia are irregularly gathered in patches over the blade (Fig. 26) and are cut off from the outermost cortical cells (Fig. 27). Carpogonial branches were not found. Auxiliary cells are formed in ampullae (Fig. 28). The auxiliary cell ampullae are branched to at least the third order, more or less wide across the top (Fig. 29). Auxiliary cells are conspicuously larger than ampullary cells and narrowly ellipsoidal in shape, 20–22 µm long by 10–12 µm wide (Fig. 29). Early post-fertilization events were not observed. Gonimoblasts were produced from the auxiliary cells presumably in contact with a connecting filament (Fig. 30). In some instances, several outgoing connecting filaments were produced from a cell that is directly connected to the lower side of the auxiliary cell. Mature cystocarps are deeply embedded in the blade interior with a loose network of enveloping sterile filaments and carposporangia in several gonimolobes (Fig. 31). Tetrasporangia are broadly ellipsoidal, 15–20 µm wide by 18–28 µm long, embedded in the outer cortex, cruciately or decussately divided (Figs. 32, 33).

Discussion

From this study, the morphological features of *H. floresia* are summarized as follows: blade complanately and irregularly branched with 3 or 4 orders of laterals; no maculation and no proliferations on the surface; cortex thin, consisting of the inner 2 or 3 larger and irregularly shaped cells and the outer 2 or 3 smaller and rounded cells, with the outermost cells slightly elongated and tapering; medulla of sparsely distributed filaments running mainly vertically from cortex to cortex; large stellate cells with dark staining substance occasionally present in the periphery of medulla; gametophytes monoecious, spermatangia irregularly gathered in patches over the blade, auxiliary cell ampullae branched at least to the third order and wide across the top; tetrasporangia broadly ellipsoidal, embedded in the cortex.



Figs. 21–26. *Halymenia floresia*. Material from Pulau Tikus, Sandakan, Malaysia. Transverse sections unless otherwise indicated. Fig. 21, Gametophytic specimen (Kawaguchi 1167). Scale = 10 cm. Fig. 22, Tetrasporophytic specimen (Kawaguchi 1168). Scale = 10 cm. Fig. 23, Vegetative construction showing vertical medullary filaments. Scale = 100 µm. Fig. 24, Large stellate cell (arrow) with dark staining substance. Scale = 100 µm. Fig. 25, Cortical construction. Scale = 50 µm. Fig. 26, Surface view of blade forming spermatangia (arrowheads). Scale = 25 µm.



Figs. 27–33. *Halymenia floresia*. Material from Pulau Tikus, Sandakan, Malaysia. Transverse sections unless otherwise indicated. Fig. 27, Spermatangia (arrowheads). Scale = 25 µm. Fig. 28, Auxiliary cell ampulla with large auxiliary cell (arrow). Scale = 50 µm. Fig. 29, Auxiliary cell ampulla with large auxiliary cell (arrow). Scale = 25 µm. Fig. 30, Gonimoblast development from an auxiliary cell (arrow). Scale = 50 µm. Fig. 31, Mature cystocarp; arrow shows an auxiliary cell. Scale = 100 µm. Fig. 32, Surface view of blade forming tetrasporangia (arrows). Scale = 50 µm. Fig. 33, Cruciately divided tetrasporangia. Scale = 50 µm.

Of the previous studies of *H. floresia,* the features of the French Mediterranean material described by Codomier (1974) are summarized as follows: blades up to 25 cm high by up to 12 cm wide, basal part tubular 1 cm from the holdfast, expanding into flat blades; branches 1–10 cm long with again pinnate branchlets with pointed apices; cortex consisting of 4 cells, outwardly in a row of stellate cells with refractive content, smaller stellate cells, oval cells 30–35 µm in diameter and small ellipsoidal cells (12–13 µm long by 8–10 µm wide); medulla, up to 800 µm thick, occupying 3/4 of blade thickness; medullary filaments running transversely from cortex to cortex, 18–22 µm wide; rhizoids 10–12 µm wide issuing from the ovoid cortical cells; tetrasporangia cruciate, in the second cortical layer. These features are almost all in good accordance with those of the type and other material from Spain.

Balakrishnan (1961) made a detailed morphological study of this species based on material from India, with features as follows: blade rose red in color, soft and gelatinous in consistency; basal portion almost stipitate, expanding into a much divided leaflike blade, ramification tri- or quadripinnate, often irregular; margin entire without proliferations; blade 200–250 µm thick, of loose medulla and comparatively thin cortex; cortex 3–5-layered, the innermost cells irregular to substellate; middle cortical layer with more rounded cells; surface layer (outermost cortical layer) almost isodiametric; medullary filaments 10–12 µm wide, simple or branched, running transversely from cortex to cortex; intermingled with medullary filaments, slender rhizoids (3–5 µm thick) and large stellate cells with arms to 100 µm long containing deep staining substance. Overall features of the Indian material are also in good accordance with those of the Spanish and French specimens, except for the diameter of vertical medullary filaments (10–12 µm in India vs. 18–22 µm in France) and the blade thickness (200–250 µm in India vs. up to 800 µm in France). Although De Smedt et al. (2001) questioned the presence of *H. floresia* in the Indo-Pacific, the features of the Indian material strongly suggest that it is conspecific with genuine *H. floresia.*

The Malaysian material described here also shows a close resemblance to *H. floresia* from Spain. In the Malaysian alga, blade thickness is up to 600 µm thick, similar to that of the material from France, and the diameter of vertical medullary filaments is 10–13 µm, close to that of the material from India. These differences between French Mediterranean and Indian material remain to be reassessed.

Halymenia floresia described from Japan (Yoshida and Kawaguchi in Yoshida 1998) is similar to the Spanish and French material in its soft-gelatinous texture, irregularly branched foliose thalli, thin cortex of 5 or 6 cells, medulla of sparsely distributed filaments mainly vertically directed, and also in reproductive details. However, the material from Japan is different from the Spanish and French *H. floresia* in having surface maculation, which is totally absent in the latter. De Smedt et al. (2001) doubted the presence of *H. floresia* in the Indo-Pacific because the specimens assigned to *H. floresia* from this region have a spotted surface and more profusely branched blades.

Meanwhile, *H. porphyraeformis* Parkinson (formerly known as *H. porphyroides* Børgesen) is considered to include plants both with and without surface spots (De Smedt et al. 2001). The taxonomic importance of surface maculation (or spots) as a specific character in *Halymenia* is therefore still debatable and needs to be verified. The exact status of Japanese *H. floresia* must remain uncertain until such an investigation is made.

Recent molecular studies (Wang et al. 2001; Kawaguchi et al. 2002; Gavio and Fredericq 2002) have shown that DNA sequence analysis, particularly of chloroplast-encoded *rbc*L gene, is useful for the elucidation of intergeneric and interspecific relationships among the members of the Halymeniaceae. To establish a sounder and more natural classification system of *Halymenia,* the need for further comprehensive study on molecular grounds as well as morphological is quite apparent.

Acknowledgments

I thank Dr. Francisco Pando, curator of the Herbario, Real Jardin Botanico, for loan of the valuable herbarium specimens of *Halymenia floresia*. This study was partly supported by a Grant-in-Aid for Scientific Research (No. 14540640) from the Japan Society for the Promotion of Science.

Literature Cited

Agardh, C. A. 1817. Synopsis algarum Scandinaviae. Berlin, Lund. xl + 135 pp.

Balakrishnan, M. S. 1961. Studies on Indian Cryptonemiales, III. *Halymenia* C. A. Ag. J. Madras Univ., B. 31:183–217.

Clemente y Rubio, S. de R. 1807. Ensayo sobre las variedadas de la vid commun que vegetan en Andalucia con un indice etimologico y tres listas de plantas. Madrid, xviii + 324 pp.

Codomier, L. 1974. Recherches sur la structure et la development des *Halymenia* C. Ag. Vie Millieu 24:1–42.

De Smedt, G., De Clerck, O., Leiliaert, F., Coppejans, E., and Liao, L. M. 2001. Morphology and systematics of the genus *Halymenia* C. Agardh (Halymeniales, Rhodophyta) in the Philippines. Nova Hedwigia 73:293–322.

Gavio, B., and Fredericq, S. 2002. *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. Eur. J. Phycol. 37:349–359.

Guiry, M. D., and Dhonncha, N. E. 2003. AlgaeBase. World-wide Web electronic publication. [http://www.Algaebase.org]

Kawaguchi, S., Wang, H. W., Horiguchi, T., Lewis, J. A., and Masuda, M. 2002. Rejection of *Sinkoraena* and transfer of some species of *Carpopeltis* and *Sinkoraena* to *Polyopes* (Rhodophyta, Halymeniaceae). Phycologia 41:619–635.

Phang, S. M., and Wee, Y. C. 1991. Benthic marine algae. In: Kiew, R. (ed.), The state of nature conservation in Malaysia, pp. 51–61. Malayan Nature Society, Kuala Lumpur.

Schmitz, F. 1889. Systematische Uebersicht der bisher bekannten Gattungen der Florideen. Flora, Jena 72:435–456.

Wang, H. W., Kawaguchi, S., Horiguchi, T., and Masuda, M. 2001. A morphological and molecular assessment of the genus *Prionitis* J. Agardh (Halymeniaceae, Rhodophyta). Phycol. Res. 49:251–261.

Weber van Bosse, A. 1921. Liste des Algues du Siboga. II. Rhodophyceae. Part I. Protofloriddae, Nemalionales, Cryptonemiales. Siboga-Expeditae, Monogr. 59b, pp. 187–310, pls. 6–8.

Yoshida, T. 1998. Marine algae of Japan. Uchida-Rokakuho, Tokyo. 1222 pp. (in Japanese)

Section VII. *Gracilaria* Species

INTRODUCTION

Isabella A. Abbott

The papers included in the *Gracilaria* section this time are six, of rather different points of view, although five of them are taxonomic. To demonstrate that *Gracilaria* is still a genus in need of close systematic examination, there are new species described from Thailand, China, Australia, and Samoa and a new record of *G. yamamotoi* that was originally named by Zhang and Xia from southern China but has now been found in southern Japan, Dr. Yamamoto's home base.

The nutritional analyses of *Gracilaria* species found in the Hawaiian Islands (cultured as well as wild) will be welcomed by all who eat seaweeds, whether as fresh vegetables or dried. This is a new field for Karla McDermid and her student Brooke Stuercke, and they should be congratulated for this very useful contribution. I will be happy to emphasize the good minerals and the amount of fiber and protein that might be found in different species when I am "selling" seaweeds.

MOLECULAR SYSTEMATICS AND TAXONOMY OF FLATTENED SPECIES OF *GRACILARIA* GREVILLE (GRACILARIACEAE, GRACILARIALES, RHODOPHYTA) FROM THE WESTERN ATLANTIC

Carlos Frederico D. Gurgel, Suzanne Fredericq, and James N. Norris

Abstract

There has been much taxonomic and nomenclatural confusion with the previously reported flattened species of *Gracilaria* from the western Atlantic. Most records are poorly known, inadequately characterized, or misidentified. Based on phylogenetic analysis of chloroplast-encoded *rbc*L sequences and comparative morphological studies of flattened species of western Atlantic *Gracilaria*, two major lineages are identified: the "*Gracilaria venezuelensis* clade," comprising *G. venezuelensis* W. Taylor, *G. intermedia* J. Agardh subsp. *intermedia, G. intermedia* subsp. *ganesana* subsp. nov., and *G. yoneshigueana* sp. nov.; and the "*Gracilaria mammillaris* clade," comprising *G. mammillaris* (Montagne) Howe, *G. galetensis* sp. nov., *G. hayi* sp. nov., *G. oliveirarum* sp. nov., and *G. smithsoniensis* sp. nov. Of the flattened taxa included in these two clades, 5 new species and 1 subspecies are described, and the other flattened species are clarified and characterized. Our findings show that the number of compressed to flat *Gracilaria* taxa in the western Atlantic has been underestimated and includes previously overlooked or inadequately described taxa with validly published names.

Introduction

Our taxonomic knowledge of the economically important agarophyte *Gracilaria* Greville (1830, pp. liv, 121) nom. cons.[1] (Gracilariaceae, Rhodophyta) is based primarily on comparative morphological studies (e.g., Sjöstedt 1926; Kylin 1930, 1932, 1956; Dawson 1949, 1961; Ohmi 1958; Taylor 1960; Bodard 1967; Chang and Xia 1976; Yamamoto 1978, 1984; Bird and McLachlan 1982, 1984; Oliveira et al. 1983; Oliveira 1984; Abbott 1985; Fredericq and Norris 1985, 1992; Norris 1985; Bird and Oliveira 1986; Bird et al. 1986a,b; Meneses and Abbott 1987; Xia and Abbott 1987; Fredericq and Hommersand 1989a,b, 1990; Abbott et al. 1985, 1991; Gargiulo et al. 1992; Withell et al. 1994; Abbott 1995, 1999; Womersley 1996; Millar 1997a,b; Dreckmann 2002). One driving force to understand the species of *Gracilaria* is the commercial uses and demands for the colloid agars produced within its cell walls. Despite the progress made, questions still abound within the

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[1] The conserved generic type, *Gracilaria compressa* (C. Agardh) Greville [basionym: *Sphaerococcus compressus* C. Agardh; type locality: Cadiz, Spain], is a taxonomic synonym of *G. bursa-pastoris* (Gmelin) Silva (Steentoft et al. 1991; Silva et al. 1996; Greuter et al. 2000).

Gracilariaceae, especially concerning the inter- and intrageneric relationships with regard to *Gracilaria* sensu lato (Abbott et al. 1991; Abbott 1995, including *Hydropuntia* Montagne). Taylor (1960:438–439) suggested that identification of *Gracilaria* based on habit shape alone should not be attempted. These ambiguities are primarily the result of a high morphological plasticity, which generates high levels of homoplasies among many species. While clarification and understanding of species concepts for many taxa has been successful, others continue to be elusive. Different types of molecular biological techniques have been successfully used to resolve systematic issues of some taxa of *Gracilaria* sensu lato. These studies have provided insight into the evolutionary relationships of some species and related nonparasitic genera (e.g., Goff and Coleman 1988; Bhattacharya et al. 1990; Scholfield et al. 1991; Bird et al. 1990, 1992, 1994; Rice and Bird 1990; Intasuwan et al. 1993; Kapraun 1993; Kapraun et al. 1993, 1996; Goff et al. 1994; Bird 1995; Candia et al. 1999; Bellorin et al. 2002).

Phylogenies inferred from chloroplast-encoded *rbc*L have shown at least 9 distinct evolutionary lineages and strong patterns of character evolution within the genus *Gracilaria* sensu lato (Gurgel and Fredericq 2003). Two of these lineages, composed solely of poorly understood or undescribed compressed or flattened western Atlantic species, are the focus of this study. Five new species and 1 new subspecies of flattened *Gracilaria* are herein described.

Materials and Methods

Morphological analysis. Specimens studied, including vouchers, were fixed and liquid-preserved in buffered 5% formalin/seawater and/or pressed and air-dried on herbarium sheets and deposited in US Alg. Coll., LAF, MICH, and UC (herbaria abbreviations follow Holmgren et al. 1990). Specimens were photographed on a Zeiss Stemi 2000-C dissection scope attached to a Minolta 35mm camera. Some were scanned into the computer either as "wet" (liquid-preserved) specimens or directly from a herbarium sheet using a Microtek ScanMaker III scanner. Transverse sections (25–70 µm thick) for morphological studies were hand-made using double-edged stainless steel razor blades and then stained in a 3% aniline blue solution (Tsuda and Abbott 1985) for 10–15 minutes. The stained specimens were fixed with 1 drop of 3% acetic acid, rinsed with distilled water, and then mounted in a 50% Karo clear corn syrup/distilled water solution with phenol added as a preservative. Photomicrographs were taken with a Polaroid DMC Ie digital camera attached to an Olympus BX60. Images were edited and assembled into plates using Adobe Photoshop v.5.0.

Molecular analysis. Silica gel-dried specimens and extracted DNA samples were deposited in the Seaweed Laboratory (University of Louisiana at Lafayette) and stored at –20° C. DNA samples were prepared using the DNeasy Plant Mini Kit or were submitted to a CTAB-cesium chloride DNA procedure (Freshwater and Rueness 1994). Plastid-encoded *rbc*L was selected to infer a phylogeny for *Gracilaria*. PCR and sequencing primers used in this study were *Frbc*L start, F7, F57, F492, F577, F753, F993, R753, and R1381, and *Rrbc*S start (as listed in Freshwater and Rueness 1994; Hommersand et al. 1994; Gavio and Fredericq 2002). Protocols for gene amplification, automated sequencing, and alignment are identical to those given in Lin et al. (2001) and Gurgel et al. (2003a,b).

Partial *rbc*L sequences were produced from 26 recently collected samples of *Gracilaria*. Their collection information includes species analyzed, specimen locality, collection date and collector, percentage of *rbc*L gene sequenced, and GenBank accession numbers (Table 1). *Gracilaria gracilis, G. pacifica,* and *G. arcuata* were chosen as the outgroup based on their close phylogenetic relationship with the ingroup (Gurgel 2001).

Phylogenetic analysis was performed with PAUP* v.4.0 beta 10 (Swofford 2002) for the Macintosh. Maximum parsimony (MP) trees were inferred using unordered and unweighted characters, heuristic search of 5000 random replications that allowed holding of 30 trees at each step, Trees Bisection Reconnection (TBR) swapping algorithm, saving multiple trees (MULTREES), and STEEPEST DESCENT options. Support for nodes was assessed by calculating bootstrap proportions (BP) values (Felsenstein 1985) based on 5000 resamplings of heuristic searches, TBR algorithm, MULTREES, and STEEPEST DESCENT option with SIMPLE sequence additional options in effect.

Results

Among the 24 tested taxa in the dataset (Fig. 1), 76.1% (1042 base pairs, or bp) are identical, 23.8% (326 bp) vary at least once, and 15.0% (206 bp) vary and are phylogenetically informative. No insertion or deletion mutations were found in the *rbc*L sequences produced in this study, allowing for unambiguous alignment of all sequences. Tree lengths of 100,000 randomly generated trees for these data had a skewed distribution ($g_1 = -0.817$, $p < 0.01$), indicating the presence of nonrandom structures and the presence of a phylogenetic signal in the dataset (Hillis and Huelsenbeck 1992; Hillis et al. 1993). The MP analysis produced one single most parsimonious tree (Fig. 1) with a length of 554 evolutionary steps, CI = 0.48 and RI = 0.656, and Informative Characters = 554.

For the 9 taxa of the two lineages of *Gracilaria* sensu lato focused on in this study, all branches are fully resolved, mostly with high bootstrap support. The positions of *G. textorii* from Japan and *G. multipartita* from Atlantic France are unresolved, often lacking bootstrap support, and are frequently placed in different branches in more complex and larger phylogenetic analyses using other phylogenetic methods (Gurgel 2001). Regardless of their precise phylogenetic delineation, the latter are members of the most derived group in the *Gracilaria* sensu lato major clade (Gurgel and Fredericq 2003).

Table 1: List of Species Studied, Collection Information, Accession Numbers, and *rbcL* Fraction Sequenced (%)

Species Studied	Collection Data*	GenBank no.	%
G. apiculata J. Agardh	La Encrucijada, Peninsula Paraguana, Falcón, Venezuela; leg. Gurgel, Carmona, and Conde, FG-20, July 13,1999	ay049333	98.1
G. arcuata Zanardini	Hilutangdu, Cebu, Philippines; leg. S.-M. Lin, April 19,1998	ay049383	98.6
G. beckeri (J. Agardh) Papenfuss	Sharks Bay, Port Alfred, South Africa; leg. M. H. Hommersand, July 19,1993	ay049377	96.3
G. capensis Schimtz ex Mazza	Sharks Bay, Port Alfred, South Africa; leg. M. H. Hommersand, July 19, 1993	ay049378	96.5
G. curtissiae J. Agardh	Mangue Lloroso, Peninsula Paraguana, Venezuela; leg. Gurgel, Conde, and Carmona, July 13, 1999	ay049327	98.4
G. flabelliforme (P.et H. Crouan in Schramm et Mazé) Gurgel	Buchuaco, Peninsula Paraguana, Falcón, Venezuela; leg. Gurgel, Carmona, and Conde, July 13, 1999	ay049334	96.4
**G. galetensis* n. sp.	Galeta Point, Caribbean Panama, BW-715	ay049320	97.3
G. gracilis (Stackhouse) Irvine, Steentoft et Farnham	W. Angle Bay, Wales, UK; leg. M. H. and F. Hommersand, July 22, 1997	ay049400	98.0
**G. hayi* n. sp.	South Hutchinson Is., Atlantic Florida	ay049319	95.6
**G. hayi* n. sp.	Galeta Point, Caribbean Panama, BW-737	ay049315	98.1
**G. intermedia* J. Ag. subsp. *intermedia*	Buchuaco, Venezuela, FG-28	ay049335	88.5
**G. intermedia* subsp. *ganesana* n. subsp.	Puerto Escondido, Venezuela, FG-24	ay049336	97.6
G. lacinulata (Vahl) Howe	La Encrucijada, Peninsula Paraguana, Falcón, Venezuela; leg. Gurgel, Carmona, and Conde, FG-19, July 13, 1999	ay049332	98.0
**G. mammillaris* (Montagne) Howe	offshore Louisiana, Gulf of Mexico	ay049323	97.1
G. multipartita (Clement) Harvey	Carantec, Brittany, France; leg. J. Cabioch, June 22, 1993	ay049317	87.2
G. occidentalis (Børgesen) Bodard	offshore Louisiana, Gulf of Mexico; leg. S. Fredericq, June 26, 2000	ay049322	98.6
**G. oliveirarum* n. sp.	La Vela de Coro, Venezuela, FG-12	ay049330	91.8
G. ornata Areschoug	Ft. Randolph, Caribbean Panama; leg. B. Wysor, Feb. 26, 1999	ay049318	92.9
G. pacifica Abbott	Indian Is., Washington; leg. M. H. Hommersand, s.n.	ay049397	97.7
**G. smithsoniensis* n. sp.	Galeta Point, Caribbean Panama, BW-737	ay049321	97.3
G. spinulosa (Okamura) Chang et Xia	Taiwan; leg. S.-M. Lin, May 11, 1998	ay049395	93.3
G. textorii (Suringar) De Toni	Gobogahana, Japan; July 10, 1994	ay049325	97.5
**G. venezuelensis* Taylor	Indian River Lagoon, Atlantic Florida		95.0
**G. venezuelensis*	Cockroach Bay, west coast of Florida		97.8
G. vieillardii Silva	Taiwan; leg. S.-M. Lin, April 22, 1998	ay049394	95.5
**G. yoneshigueana* n. sp.	Prainha, Estado do Rio de Janeiro, Brazil	ay049372	93.4

*See text for additional collection data.

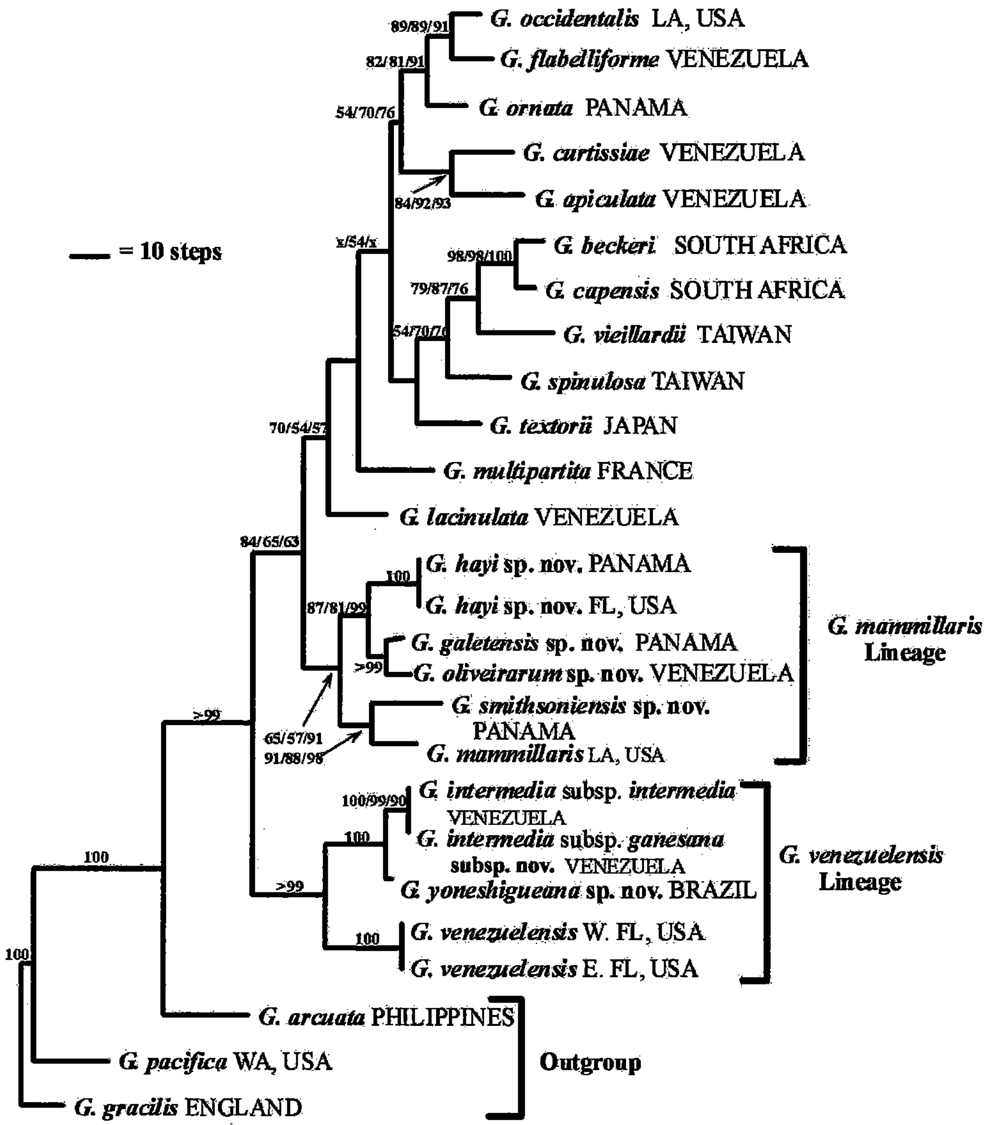

Fig. 1. Single most parismonious *rbc*L tree of the flattened species of *Gracilaria*. Tree length = 554, CI = 0.481, RI = 0.656. Outgroup composed of *Gracilaria arcuata, G. gracilis,* and *G. pacifica*. Support for nodes based on 5000 bootstrap resamplings.

The *Gracilaria venezuelensis* Clade

This well-supported clade (BP = 99) comprises 3 species, including 1 new species and 1 new subspecies. Although compressed, *G. venezuelensis* is the least flattened and the most morphologically stable species in this lineage, with *G. intermedia* subsp. *intermedia, G. intermedia* subsp. *ganesana* subsp. nov., and *G. yoneshigueana* sp. nov. all showing wider phenotypic variation.

Gracilaria venezuelensis W. Taylor, Allan Hancock Atlantic Exped. Rep. 2, p. 110, pl. 3, fig. 10, pl. 15, figs. 1–2, 1942. (Fig. 2A–E)

Type Locality: dredged off coarse black-sand bottom, 3.5–9.0 m depth, off SW end of Cubagua I., S of Isla Margarita, Venezuela (10°47'55" N, 64°13'53" W)

Holotype: MICH (W. R. Taylor-39-482).

Isotype: US Alg. Coll.-56501 (W. R. Taylor-39-482).

Paratype: MICH (W. R. Taylor-39-479a); dredged off sand bottom, 3.5–9.0 m depth, off SW end of Cubagua I., S of Isla Margarita, Venezuela.

Misapplied Name: *Gracilaria tikvahiae* sensu Schneider and Searles, Seaweeds Southeastern U.S., p. 325, figs. 377–380, 1991; Littler and Littler, Carib. reef plants, p. 116, 2000 [non *G. tikvahiae* McLachlan, Phycologia 18, p 19, fig. 1, 1979].

Habit bushy, up to 15 cm tall; axes and branches compressed to flattened, (1–)2–5(–7) mm wide, thin (300–)400–470(–500) µm, and fragile (sometimes extremely brittle). Branching up to 6 orders, mostly proliferous, alternate to irregularly dichotomous to polychotomous; upper portions mostly subdichotomous and branching at wide angles (>45°); branches narrowing upward; often with numerous short, subsimple branchlets along margins, and acute, often bifucated tips. Thin cortex of 1–2(–3) small pigmented cells; abrupt transition to the medulla of 5–6 large, thick-walled cells.

Cystocarps prominent, scattered on branch surfaces and margins, 750–1500 µm in diameter; thick pericarp with tubular filaments; carpospores surrounding gonimoblast. Spermatangia and tetrasporangia not observed in this study.

Distribution: Atlantic: Florida, Venezuela, Belize. Gulf of Mexico: Florida, Veracruz, Mexico.

Habitat: Unattached, often as drifting mats; or attached on coral rubble and rocks; mid-intertidal to shallow subtidal.

Specimens Studied: *West Coast of Florida:* from large drifting mat, close to mouth of Cockroach Bay, Tampa Bay, Oct. 26, 1999, leg. C. J. Dawes, FG-96 (US Alg. Coll.-204368). *Atlantic Florida:* from dense drift, off Link Port jetty, Indian River Lagoon, Link Port (vicinity of Fort Pierce), Oct. 20, 1998, leg. C. F. D. Gurgel, H-4 (US Alg. Coll.-204365). *Belize:* Tony's Lagoon, on coral rubble, 0.3–1.5 m depth, Manatee Cay, Pelican Cays, May 20, 2001, leg. R. H. Sims, RHS-9641 (US Alg. Coll.-204319).

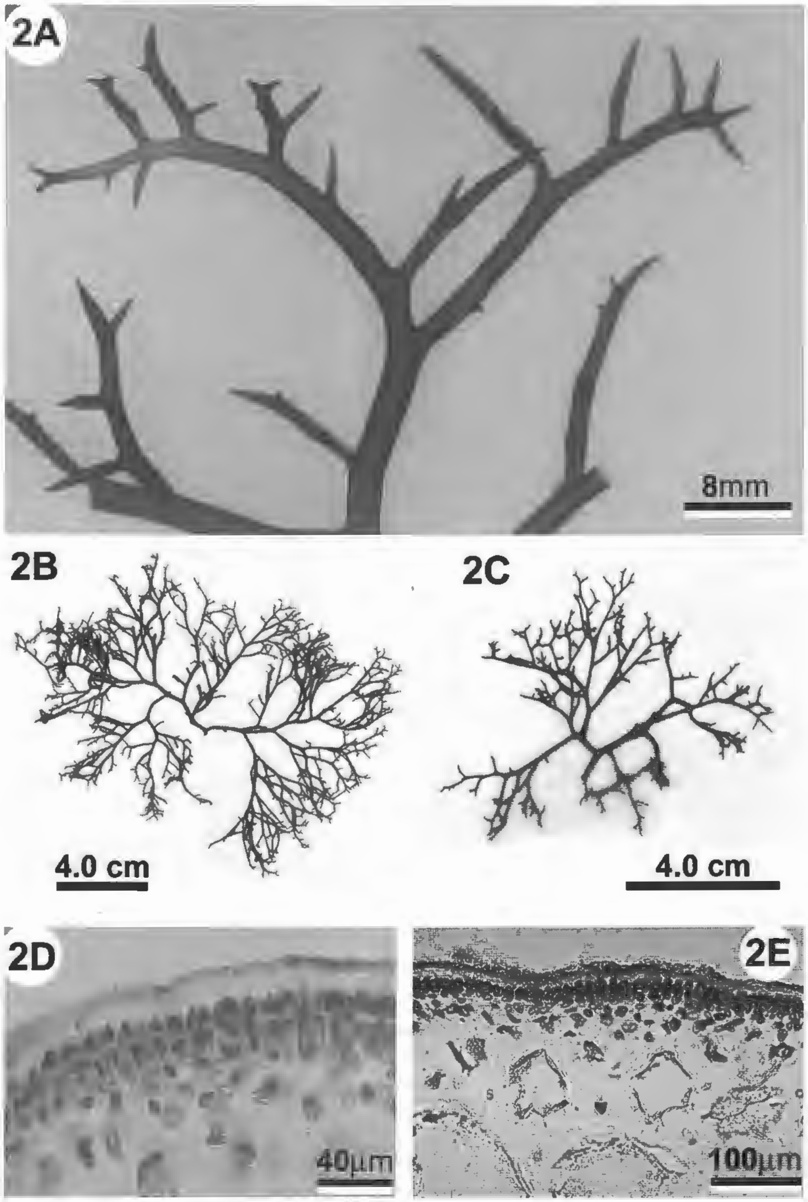

Fig. 2. *Gracilaria venezuelensis* W. Taylor. 2A, Habit of liquid-preserved drift specimen from Fort Pierce, Florida. 2B–C, Habits of herbarium specimens (US Alg. Coll.-204368), from Tampa Bay, Florida. 2D, Transection showing cortex. 2E, Transection showing cortex–medulla transition.

Remarks: Based on the original description (Taylor 1942), *G. venezuelensis* has vegetative and cystocarpic anatomy typical of the Gracilariaceae. Small specimens of *G. venezuelensis* can be confused with cylindrical to slightly compressed species such as *G. tikvahiae* and the little known western Atlantic species *G. secunda* P. et H. Crouan in Schramm et Mazé. When found in drifting algal mats, these 3 species apparently lose their reproductive capacity and exhibit a high degree of convergence in habit.

Even though *G. venezuelensis* can sometimes be hard to identify, some of its characters are distinct, such as its bushy habit and usually proliferous dichotomous branching pattern with wide angles (>45°), and numerous short sub-simple branchlets, with acute, often bifurcated tips. Taylor (1942) mentioned that *G. venezuelensis* has a thin and fragile texture and is extremely brittle. Specimens that had long been drifting in protected bays (e.g., those from Tampa Bay) are thinner (up to 2 mm wide) and more fragile than attached older specimens (3–4 mm wide).

Gracilaria venezuelensis has also been reported from Veracruz, Mexico, in the Gulf of Mexico (Dreckmann and Pérez-Herández 1994), and from the Philippines (Westernhagen 1974). This latter record should be reexamined because it is very unlikely that southeastern Asia and the Caribbean share species of *Gracilaria* that have not been artificially introduced.

Gracilaria intermedia J. Agardh, Sp. gen. alg, pp. 95–96, 1901, subsp. ***intermedia*** (Fig. 3A–B)

Type Locality: "St. Augustine Indiae occidentalis."

Lectotype: Herein designated to be LD 29649 (=Bot. Mus. 89704-0014). Lectotype specimen has hand-written on it only "St. Augustine." The locale surely is St. Augustine, Atlantic coast of Florida, and the alga was probably collected and sent to J. G. Agardh by Mrs. G. A. Hall of Florida.

Misapplied Name: *Gracilaria foliifera* sensu Taylor, Mar. algae east.... Americas, p. 447, 1960, pro parte [non *Gracilaria foliifera* (Forsskål) Børgesen, Dansk. Bot. Arch. 8, p. 7, 1932].

Algae completely flattened, usually up to 18(–20) cm tall; main axes straplike, dichotomously to subdichotomously branched in the same plane, 3–4 cm wide, 685–884 (mean = 778) µm thick, arising from small disclike holdfast. Orders of branching variable on different portions of same thallus. Main axes with strongly compressed branches, distributed irregularly, opposite to alternate along margins. Young branchlets slightly constricted at base; old branches with broad insertions. Terminal branchlets of long branches dichotomously or subdichotomously to polychotomously branched, with expanded rounded or obtuse apices. Cortex composed of 2(–3) cell layers of pigmented, variously shaped cortical cells; cuticle 8 mm thick. Cortical cells in surface view, rounded, 5.0–7.5 (mean = 6.3) µm in diameter; in transverse sections, variable, mostly isodiametric, 5.0–8.8 (mean = 6.3) µm by (5.0–)6.25 µm, or anticlinally elongated cells, (7.5–)8.8 µm in diameter. Hair cells, conspicuous, radially elongated, up to 13.8 µm long by 6.3(–8.8) µm wide. Gland cells, occasional, 10.0–11.3 (mean = 10.4) µm in diameter, interspersed among cortical cells. Outer medulla of several, smaller, thick-walled cells with gradual transition toward cortex, i.e., microcystidiate condition (=Microcystideae sensu Agardh 1901); medullary cells close to cortex with refringent properties. Central medullary cells, larger and compressed, 224.6–274.5 (mean = 246.5) µm by 109.8–144.7 (mean = 116.2) µm. In upper portions of thallus, outer medullary cells adjacent to cortex composed of 1–2 layers of small pigmented, refringent rounded cells widely interspersed by thick-walled cells, 49.4–61.8 (mean = 54.0) µm. Lower portions of thallus, 1–2 cm above base, with wider cortex of 3–4(–7) cortical cell layers; medullary cells with somewhat thinner cell walls.

Cystocarps protruding on upper surfaces and margins, dome-shaped, sometimes slightly constricted at base where protruding from thallus, (750–) 900–1700 µm in diameter, with ostiole. Spermatangia formed in verrucosa-type cavities.

Distribution. Atlantic: Florida, Venezuela.

Habitat: On rocks, sometimes within crevices; low intertidal to shallow subtidal, 1.0–4.5 m depths.

Specimens Studied: *Atlantic Florida:* Riomar reef (N of Riomar Beach), 2.5–4.5 m depths, Aug. 19, 1982, leg. J. N. Norris, S. M. Blair, R. H. Sims, and M. E. Hay, JN-1154, -11757, -11760♀, and -11762♂ (US Alg. Coll.-204375 to -79); Walton Rocks State Park, rock reef, 1.0–4.0 m depths, Dec. 6, 1984, leg. J. N. Norris and K. E. Bucher, JN-12097 (US Alg. Coll.-204380). *Venezuela:* Puerto Escondido, on intertidal rocky shore among beds of *Gracilaria cornea,* Paraguana Peninsula, Estado Falcon, July 13, 1999, leg. C. F. D. Gurgel, C. Carmona, and J. E. Conde, FG-28 (US Alg. Coll.-204366) (Fig. 3B).

Remarks: Based on new molecular and morphological evidence, we propose that the name *G. intermedia* be applied to specimens in agreement with its description and type specimen. *Gracilaria intermedia* is one of several ignored or overlooked, validly published, but poorly characterized western Atlantic *Gracilaria* taxa that needed to be studied. In Venezuela, *G. intermedia* is apparently a common member of the shallow subtidal, often growing inside dense beds of *Gracilaria cornea,* and within deep, shaded crevices of moderately exposed rocky shores and coral fringes.

Some specimens of *G. intermedia* may resemble 3 other similar looking species, none of which is found in the western Atlantic. *Gracilaria foliifera* has not been found in the Atlantic Ocean (Guiry and Freamhainn 1986), *G. multipartita* is apparently confined to the eastern Atlantic (Guiry and Freamhainn 1986), and *G. tikvahiae* is probably restricted to the northeastern Atlantic (McLachlan 1979).

Two very distinct morphological phenotypes of *G. intermedia* were found in the Venezuelan material. Although their *rbc*L sequences are 100% identical, no intermediate or overlapping morphologies were found between the two. Specimens (Fig. 3B) matching the lectotype (Fig. 3A) of *G. intermedia*

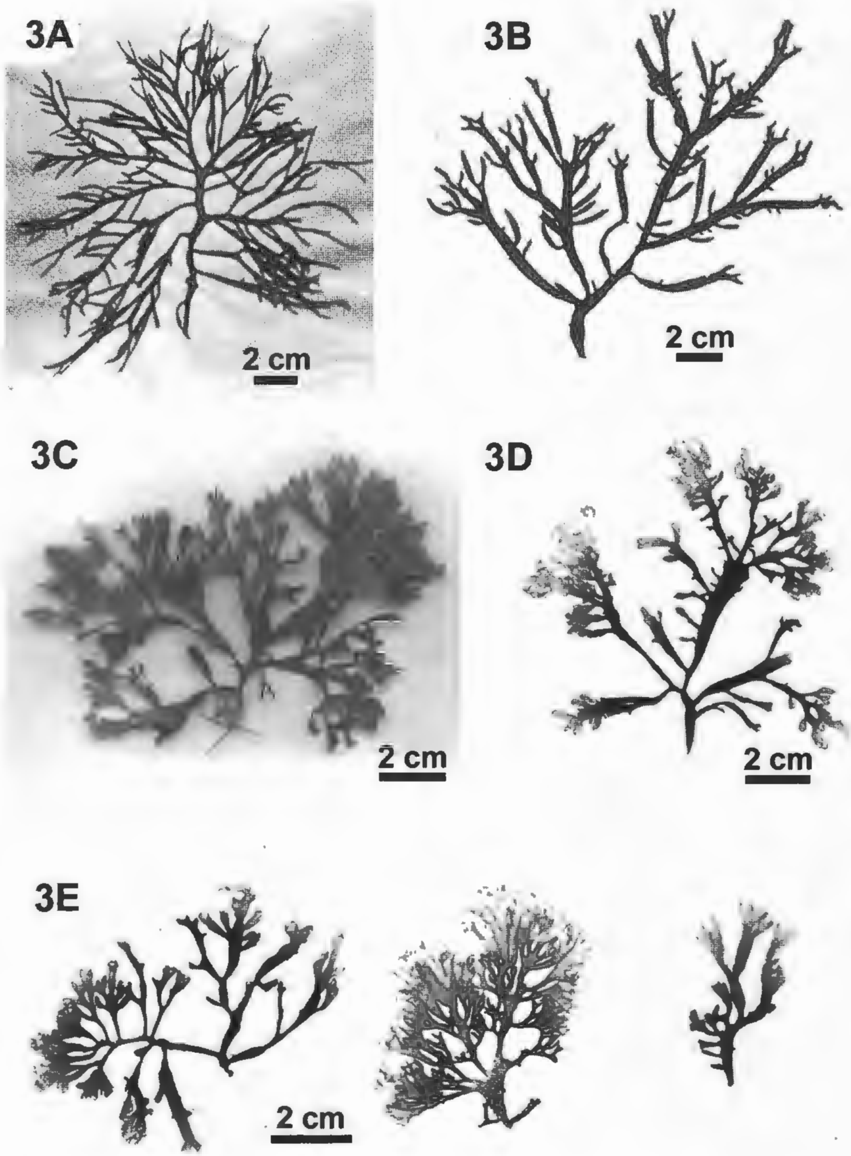

Fig. 3. *Gracilaria intermedia* J. Agardh. 3A, Specimen selected as lectotype (Agardh Herbarium, LD!). 3B, *G. intermedia* subsp. *intermedia*, habit of liquid-preserved specimen (US Alg. Coll.-204366), from Venezuela.
3C–E: *G. intermedia* subsp. *ganesana* Gurgel, Fredericq et J. Norris, subsp. nov., from Venezuela. 3C, Liquid-preserved isotype specimen (LAF). 3D, Holotype (US Alg. Coll.-204335). 3E, Isotype specimens (LAF; US Alg. Coll.), showing habit variation.

subsp. *intermedia* grow in the shallow subtidal (0.5–1.6 m depths) or in the drift and are larger and thicker, whereas the second distinct morphs, growing on exposed intertidal rocky shores, are smaller and thinner. In view of the new molecular and morphological evidence, we propose *G. intermedia* subsp. *ganesana* subsp. nov. for the second phenotype.

Gracilaria intermedia subsp. ***ganesana*** Gurgel, Fredericq et J. Norris, subsp. nov. (Figs. 3C–E, 4A–F)

Type Locality: Venezuela: Buchuaco [11°59.21' N, 69°49.16' W], Peninsula Paraguana, Estado Falcon.

Holotype: US Alg. Coll.-204335 (Fig. 3D), July 13, 1999, leg. C. F. D. Gurgel, C. Carmona, and J. E. Conde, FG-24.

Isotypes: LAF; US Alg. Coll.-204367 (Fig. 3E).

Misapplied Name: *Gracilaria lacinulata* sensu Ganesan, Bol. Inst.... Cumaná 28, p.85, 1989 [non *Gracilaria lacinulata* (Vahl) Howe, Bahama flora, p. 19, 1920].

Thallus idem est ac in *G. intermedia,* sed magis parvus gracilisque, subdichotoma ramificiatione partibus medi-infernis ad superas sine axe distincto, constrictiones absentes ad basem ramorum.

Algae (5–)6–9(–13) cm tall and 3–4(–6) mm wide, pinkish to pale red. Main axis branched in same plane, subdichotomously at basal and middle portions, becoming irregular to polychotomous closer to apices, especially at regenerating tips. Axes narrow at base, becoming wider at middle portions. Branchlets abundant, concentrated around upper portion of thallus, opposite to irregularly distributed along margins. Branchlets constricted at base, becoming wider at middle and terminal portions, or sometimes dichotomously to subdichotomously branched with smooth margins. Apices mostly cylindrical with acute tips. Cortex of up to 6 layers of predominately transversely divided cells near base, with 1–2 layers of concavo-convex divided cells in upper portions.

Cystocarps scattered irregularly on both surfaces of upper portion of branches, 1.0–1.5 mm in diameter, conspicuous, constricted at base, sometimes slightly rostrated (mammillate), with ostioles. Pericarp composed of 8–9 rows of small-spaced cells of irregular and variable shape, cell wall material among inner pericarp cells abundant, 10–15 µm thick in transverse sections. Gonimoblasts composed of large, thick-walled isodiametric cells. Four to six rows of small isodiametric cells present at base of cystocarp. Long and narrow tubular nutritive cells abundant. Spermatangia not observed in this study, but textorii-type spermatangial conceptacles are reported (Ganesan 1989, as *G. lacinulata*). Tetrasporangia not found.

Etymology: This species is named to honor Dr. E. K. Ganesan (Professor, Universidad de Oriente, Cumaná) in recognition of his contributions to our understanding of the marine algae of Venezuela.

Distribution: Venezuela.

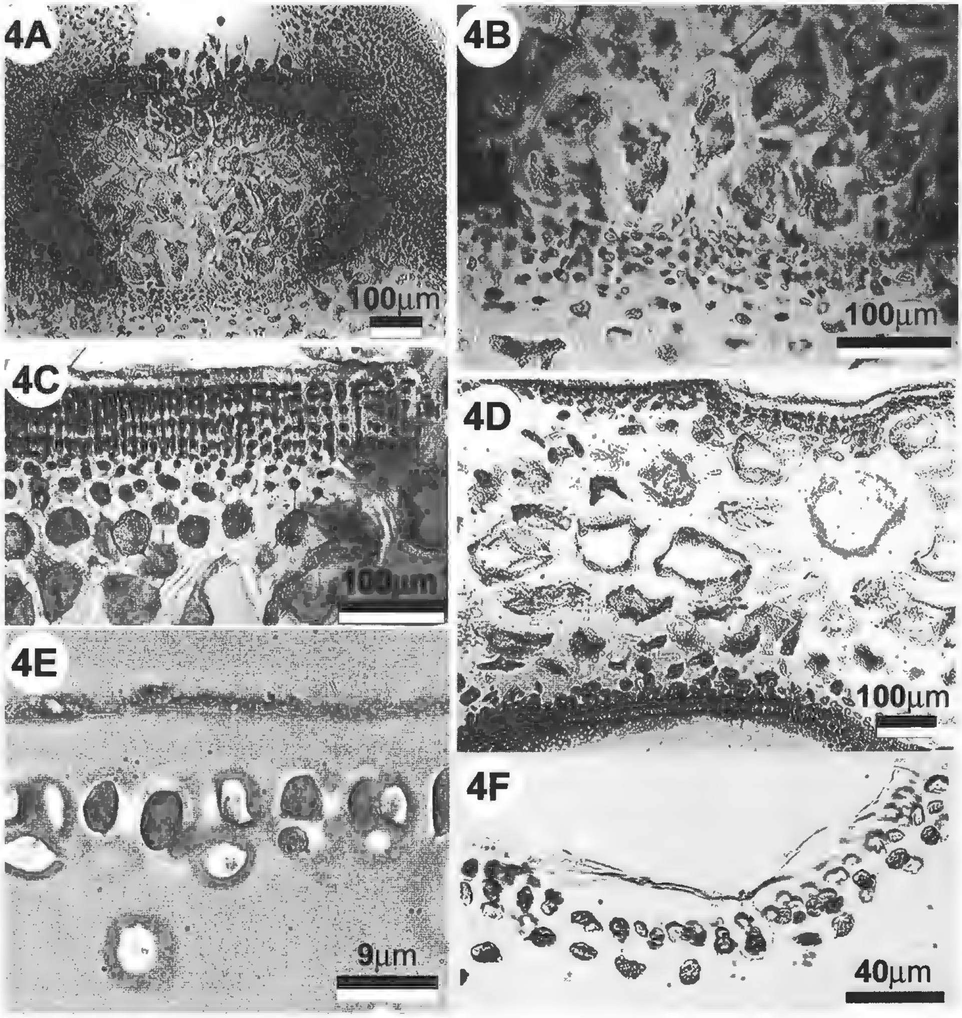

Fig. 4. *Gracilaria intermedia* subsp. *ganesana* Gurgel, Fredericq et J. Norris, subsp. nov., transections. 4A, Mature cystocarp. 4B, Detail of cystocarp showing 6–7 layers of small cells at base of cystocarp. 4C, Cortical region close to base. 4D, Cortex–medulla transition. 4E–F, Detail showing outer cortex.

Habitat: Mid- to low intertidal rocky shores; collected in clear shallow water of tidal pools among *Thalassia testudinum* beds.

Specimens Studied: Holotype (US Alg. Coll.-204335). Paratypes: *Venezuela:* Buchuaco [11°59.21' N, 69°49.16' W], Peninsula Paraguana, Estado Falcon, July 13, 1999, leg. C. F. D. Gurgel, C. Carmona, and J.E. Conde, s.n.

Remarks: *Gracilaria intermedia* subsp. *ganesana* differs from *G. intermedia* subsp. *intermedia* by its bifurcated, straplike, subdichotomous to irregular branched thallus, which has proliferous short marginal and broad lateral branches that arise from the mid to upper portions of the thallus. It further differs in usually being shorter, in lacking the more evenly dichotomous branching and distinct main axis in the lower middle to upper portions, and in having branches with basal constrictions, long nutritive tubular cells in the cystocarp, cortical hair cells, and distinct branch tips.

Similar morphs noted by Ganesan (1989, fig. 6, as *G. lacinulata*) match *G. intermedia* subsp. *ganesana.* Though not mentioned by Ganesan (1989, fig. 19), critical details seen in his photomicrographs include the presence of 4–6 rows of small cells at the cystocarp base, a character unique to *G. intermedia* subsp. *ganesana*. Other diagnostic characters seen in our specimens and those of Ganesan are gonimoblasts composed of large, thick-walled polygonal cells, small darkly staining carposporangia, and abundant tubular nutritive cells deeply inserted within the cystocarp. A single picture (Ganesan 1989, fig. 21) reveals a sharp transition between the medulla and cortex and relatively thin medullary cell walls, whereas our material displays a gradual medulla–cortex transition and thick medullary cell walls. However, the degree of transition between the cortex and medulla depends on where the sections are made in *G. intermedia* subsp. *ganesana*. Apical regions and young thalli tend to display a more pronounced transition, whereas older thalli or basal portions of the thallus reveal a more gradual transition.

Gracilaria lacinulata is in need of a more precise taxonomic delineation. Although Ganesan (1989) recognized the need for more critical studies on morphological variation and spermatangial and cystocarp formation, for now it remains poorly known. In the western Atlantic, *G. lacinulata* was previously considered by Taylor (1928, 1960) to be a synonym of *G. foliifera,* a species from the Red Sea. On several occasions names of taxa from the Red Sea have been misapplied to species from the tropical Atlantic (e.g., Børgesen 1932; Taylor 1960; Edwards 1970; Bird et al. 1986b). For example, *G. foliifera* and *G. debilis* (Forsskål) Børgesen were names incorrectly used to identify the eastern North American *G. tikvahiae* and the western Atlantic *G. cornea* (Bird et al. 1986b), respectively. Guiry and Freamhainn (1986) presented evidence that *G. foliifera* is restricted to the Red Sea and does not occur in the western Atlantic. They also noted that what was known as *G. foliifera* in the eastern Atlantic is actually *G. multipartita.*

Gracilaria yoneshigueana Gurgel, Fredericq et J. Norris, sp. nov. (Fig. 5A–G)

Type Locality: Brazil: intertidal on rocks, Praia Rasa, Município de Búzios, Estado do Rio de Janeiro.

Holotype: US Alg. Coll.-204329 (Fig. 5B), Jan. 5, 2002, leg. C. F. D. Gurgel, s.n.

Isotypes: LAF.

Thalli complanati omnino, normaliter 2.0–3.5(–5.0) cm alt., axibus principalibus ramisque ligulatis, 0.7–1.0(–3.0) mm lat., exorientes haptero parvo circularis. Axes principales ramosi infra usque ad 3 ordines, sparsim didichotomos-subdichotomos; ordines magis altae ramificationum subdichotomae ad polychotomas, interdum irregulares; ramificatio normaliter abunde apices. Rami veteribus axibus non constricti ad basem. Partes supernae saepe formantes aut parvam flabelliformem laminam pluribus ramellis linearibus variabilibus palmata-digitatascentibus aut elongatas lineares laminas ferentes parva initia ramorum irregulariter distributa circa margines. Cortex 1–2(–3)-stromaticus, medulla 6–7(–9)-stromatica transitione gradatim versus corticem.

Thallus flattened throughout, usually 2.0–3.5(–5.0) cm tall, with straplike main axes and branches, 0.7–1.0(–3.0) mm wide, and 548–585 µm thick, arising from small round holdfast. Lower portion of main axes branched up to 3 orders, sparsely dichotomous to subdichotomous; branching in upper portions of main axes usually subdichotomous to polychotomous, or sometimes irregular; branching usually abundant at tips. Branches off old main axes not constricted at base. Upper parts of frond usually becoming wider, forming small foliose flabelliform blade from which several linear branchlets of variable lengths arise, giving palmate-digitate shape to terminal blades, or of long linear blades bearing several small branch initials irregularly distributed around margins. Ultimate branchlets minute, mostly around margins but sometimes arising from surface and apical portions of frond; slightly to sharply constricted at base. Cortex (in transverse section) composed of 1–2(–3) layers of pigmented cells of variable shape and size, but mostly radially elongated, 5–12 (mean = 6) µm by 2–5 (mean = 3) µm in upper blade, and 6.25–8.75 (mean = 7.0) µm by 3.75–7.5 (mean = 5.8) µm basally. Hair cells common, ampulliform, 18.75 by 6.25 µm. Gland cells mostly round, sometimes quadrate, abundant, immersed in cortex, 10.0–11.25 µm by 5–7.5 µm. Medulla composed of 6–7(–9) cell layers with gradual transition toward cortex. Central medullary cells rounded to isodiametric at basal portion of thallus, 86–125 (mean = 100) µm by 56–94 (mean = 71) µm. At middle and upper portions and in younger branches, central medullary cells usually compressed, 185–284 (mean = 214) µm by 111.15–136.0 (mean = 125) µm.

Tetrasporangia scattered over upper blades, cruciate, 32.5 µm by 22.5 µm. Cystocarps and spermatangial reproductive structures not seen.

Etymology: In naming this species, we honor our friend and colleague Dr. Yocie Yoneshigue (Professor, Universidade Federal do Rio de Janeiro, Brazil) for her contributions to the taxonomy of Brazilian marine algae.

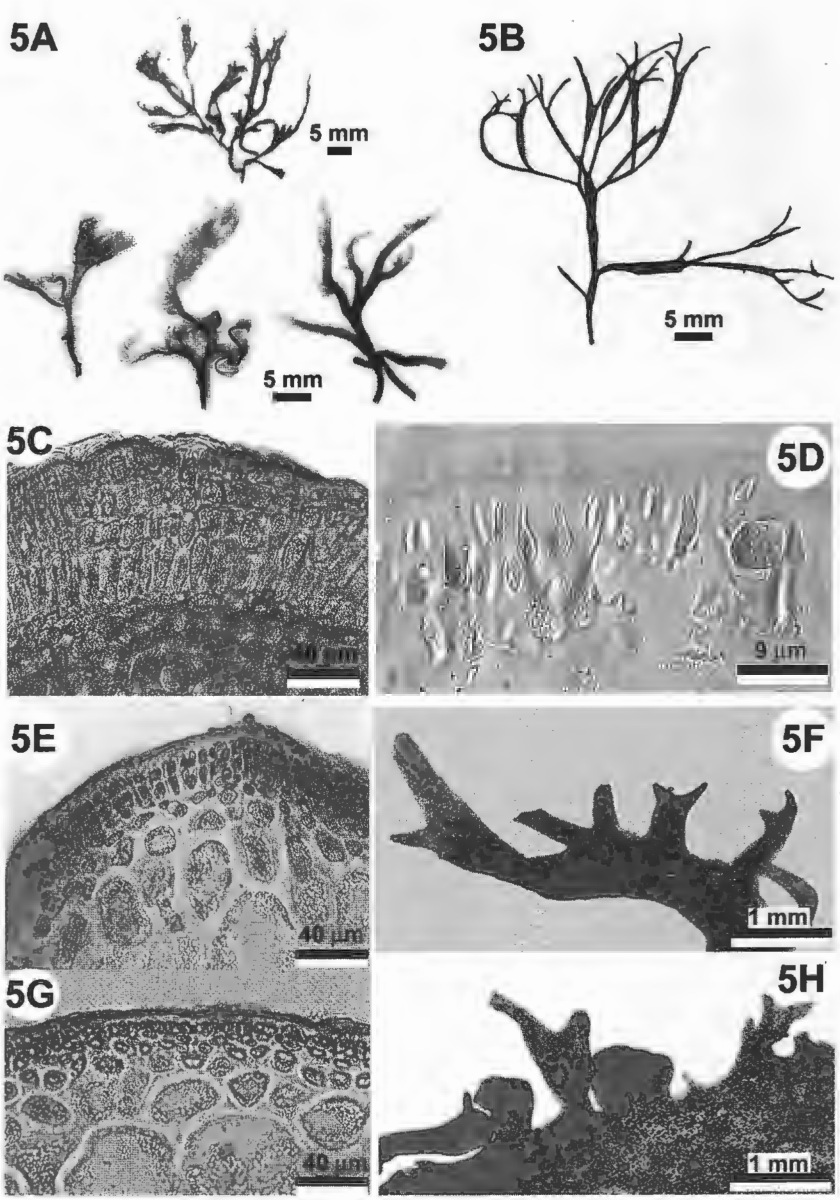

Fig. 5. *Gracilaria yoneshigueana* Gurgel, Fredericq et J. Norris, sp. nov. 5A, Habit variation of four paratypes from Prainha, Arraial do Cabo, Estado do Rio de Janeiro, Brazil. 5B, Holotype (US Alg. Coll-204329), from Praia Rasa, Município de Búzios, Estado do Rio de Janeiro, Brazil. 5C and 5E, Transection of cortex close to base. 5D, Transection of cortex in apical region of main axis. 5F, Detail of apical tips of lateral branchlets. 5G, Transection of cortex in middle part of main axis. 5H, Short, lateral branchlets along axis and branch margins.

Distribution: Brazil.

Habitat: Intertidal; rocky shores.

Specimens Studied: Holotype (US Alg. Coll.-204329) and isotype. Paratypes: *Brazil:* Arraial do Cabo Prainha, Estado do Rio de Janeiro, March 13, 1998, leg. André Taouil, FG-187 (Fig. 5B); Praia das Conchas, Cabo Frio, SE coast of Estado do Rio de Janeiro, Oct. 23, 2002, leg. Y. Yoneshigue-Valentin, s.n.

Remarks: Most morphological aspects, especially its small, delicate habit, show *G. yoneshigueana* to be distinct from any other known western Atlantic species of *Gracilaria*. The discovery of reproductive structures in *G. yoneshigueana* will be helpful to better characterize this proposed new species.

The *Gracilaria mammillaris* Clade

The *G. mammillaris* clade (Fig. 1) is composed solely of flattened species that have apparently long been confused with or misidentified as *G. mammillaris*. There is a high degree of phenotypic variation exhibited by many of the flat *Gracilaria* species within this lineage.

Five of the molecularly distinct species in the *G. mammillaris* clade exhibit similar habits. The discovery of 4 distinct flattened *Gracilaria* species in the Caribbean in addition to the known species, *G. cuneata, G. ornata,* and *G. curtissiae,* reveals that the actual number of compressed, straplike, dichotomously branched species of *Gracilaria* is much larger than previously recognized (e.g., Taylor 1960; Wynne 1998).

The *G. mammillaris* clade is likely an endemic lineage restricted to the subtidal environments of the Caribbean and the southeastern coast of the United States. Within this clade, two distinct subgroups can be observed (Fig. 1): one, formed by an earlier divergence, is composed of *G. mammillaris* and *G. smithsoniensis* sp. nov.; the other comprises *G. hayi* sp. nov., *G. galetensis* sp. nov., and *G. oliveirarum* sp. nov. Characters of these taxa and other similar flattened taxa are listed in Table 2.

Gracilaria mammillaris (Montagne) Howe, Bahama flora, p. 515, 1920. (Figs. 6A–C, 12E–G, Tab. 2)

Basionym: *Rhodymenia mammillaris* Montagne, Hist. phys.... Cuba, p. 252, 1842.

Epitype: US Alg. Coll.-204336 (Fig. 6B); *NW Gulf of Mexico:* offshore Louisiana, dredged from ca 75 m depth, R/V *Pelican* station 3.2 [27°56.358' N, 92°00.540' W], July 1, 2001, leg. S. Fredericq.

Holotype: PC!

Type Locality: Martinique, French West Indies, Windward Is., Lesser Antilles.

Algae 7–9(–10) cm tall, 5–8 mm wide, 250–330 µm thick, flat throughout, with fleshy, membranous to leathery texture, pinkish to bright red. Thalli attached to substratum by small tough holdfast of irregular shape from which

Table 2. Comparison of Species of the *Gracilaria mammillaris* Clade with Other Similar Flattened Species from the Tropical Western Atlantic

Character	*G. galetensis*	*G. oliveirarum*	*G. smithsoniensis*	*G. mammillaris*	*G. hayi*	*G. curtissiae*	*G. occidentalis*
Thallus thickness (µm)	254–275	500(–750)	to 300	(250–)330	Thin; to 100	(620–)670–1000	810 (at margins)
Cortical cell layers	1–2(–3)	1(–2)	1–2	(1–)2	1–2	1–2	1–2
Shape of cortical cells	Isodiametric, mostly slightly compressed	Variable; inconspicous subcortical cells mostly radially elongated	Variable; mostly perclinally elongated	Mostly isodiametric; sometimes anticlinally elongated	Periclinally compressed	Isodiametric	Compressed
Cortical cell sizes (µm)	3.7–5.2(–10) by 5.0–8.5(–12.5)	(3–)4–5(–9)	3.7–5.6(–6.2) by 5.0–6.5(–7.5)	(3.7–)5.8–7.5 by 6.2–8.6(–11.8)	(6–)8–10 by (2.5–)5.0–6.5	(3.75–)5.6–6.25	(5–)7.0–10 by (8.75–)13.7–16.2
Glandular cells	Yes	Rare	No	No	Small	Conspicuous but uncommon	Small
Cortex–medulla transition	Gradual	Sharp	Sharp	Sharp	Sharp	Sharp	Sharp
Medullary cell rows	4–5	4–5; inner medulla usually 2 large compressed cells	5–6; smaller and isodiametric	4(–5); rounded to slightly compressed	3–4(–5)	3–4	3–4
Medullary cell sizes (µm)	57–81(–111) by 101–133(–154)	150–170(–190) by 304–330(–400)	Thick-walled; 62–66(–74) by 79–106 (–116)	100–120(–125)	50–65(–86)	261–329(–398)	103–120(–135)
Remarks	Outer medullary cells pigmented		All medullary cells pigmented	*[1]		Most cortical cells dome-shaped	*[2]

*[1] Presence of a distinct subcortex formed by 1 cell layer of strongly compressed cells.

*[2] This species has pigmented outer medullary cells, the most spherical medullary cells among these species, and gland cells more common at the margins.

occasional clusters of small, cylindrical branched stipes arise, 0.4–0.7 cm in length. At first, branching dichotomous in one plane, with conspicuous bifurcation of blades, except at damaged portions where new axes may form, always from margin. New branches and blades resulting from regrowth of damaged thallus with constricted, almost cylindrical bases. If this pattern repeated, segments of broken blades becoming connected by narrow, basal constrictions. Cortex composed of (1–)2 cell layers of mostly isodiametric cells, sometimes anticlinally elongated, and subcortex 1 cell layer thick, of strongly anticlinally compressed cells filled with floridean starch. Outer cortical cells 3.75–7.5 (mean = 5.8) µm by 6.25–11.8 (mean = 8.6) µm. No hair cells observed. Sharp transition between medulla and cortex. Medulla composed of 4(–5) cell layers of isodiametric cells closer to transition margin, and rounded to slightly compressed cells in middle portion of thallus; cells 154.7–184.6 (mean = 169.6) µm by 100–124.75 (mean = 120) µm.

Reproductive structures not found in epitype and other specimens from Louisiana.

Distribution: Gulf of Mexico: Louisiana. Caribbean Sea: Martinique.

Habitat: Subtidal, dredged from 75 m depths.

Specimens Studied: Holotype and epitype (US Alg. Coll.-204336). Epiparatypes: *NW Gulf of Mexico:* offshore Louisiana, dredged from R/V *Pelican* station 4.2 [27°58.090' N; 92°35.860' W], May 25, 2000, leg. S. Fredericq, LAF-5-25-00-4-2-1; and R/V *Pelican* station 3.2, June 30, 2001, leg. S. Fredericq, LAF-6-30-01-3-2-16 and LAF-6-30-01-3-2-8.

Remarks. Two morphologically similar deepwater specimens of *G. mammillaris* (Fig. 6B–C) and *G. occidentalis* (Fig. 11A) were recently collected from offshore Louisiana. The two were genetically different from each other and from any other flat *Gracilaria* species included in this study. The sequenced specimen of *G. mammillaris,* though genetically distinct, also displays some morphological similarities in habit with some atypical nonreproductive specimens of *G. hayi* sp. nov., *G. galetensis* sp. nov., and *G. oliveirarum* sp. nov.

Much confusion surrounds the taxonomic status of the poorly defined *G. mammillaris.* The original description of *Rhodymenia mammilaris* (Montagne 1842) is short, and the holotype (Fig. 6A) from Martinique is small and fragmentary, making the delineation of this species obscure and ambiguous. Dawson (1941) considered the taxon to be "Species inquirendae." Limited information about vegetative, reproductive, and anatomical features of the type specimen and confusion about the species limits of morphological variation have resulted in huge variation reported for compressed to flattened species of *Gracilaria* in the tropical western Atlantic. Almost any somewhat similar specimen with thin, strap-shaped, dichotomously branched thalli with obtuse or rounded terminal portions has been referred to this species name (e.g., Taylor 1960; Joly 1965;Schnetter and Schnetter 1967; Rodriguez de Rios 1972; Schneider 1975; Schneider and Searles 1991; Littler and Littler 2000). The taxonomic confusion surrounding *G. mammillaris* has resulted in misidentifica-

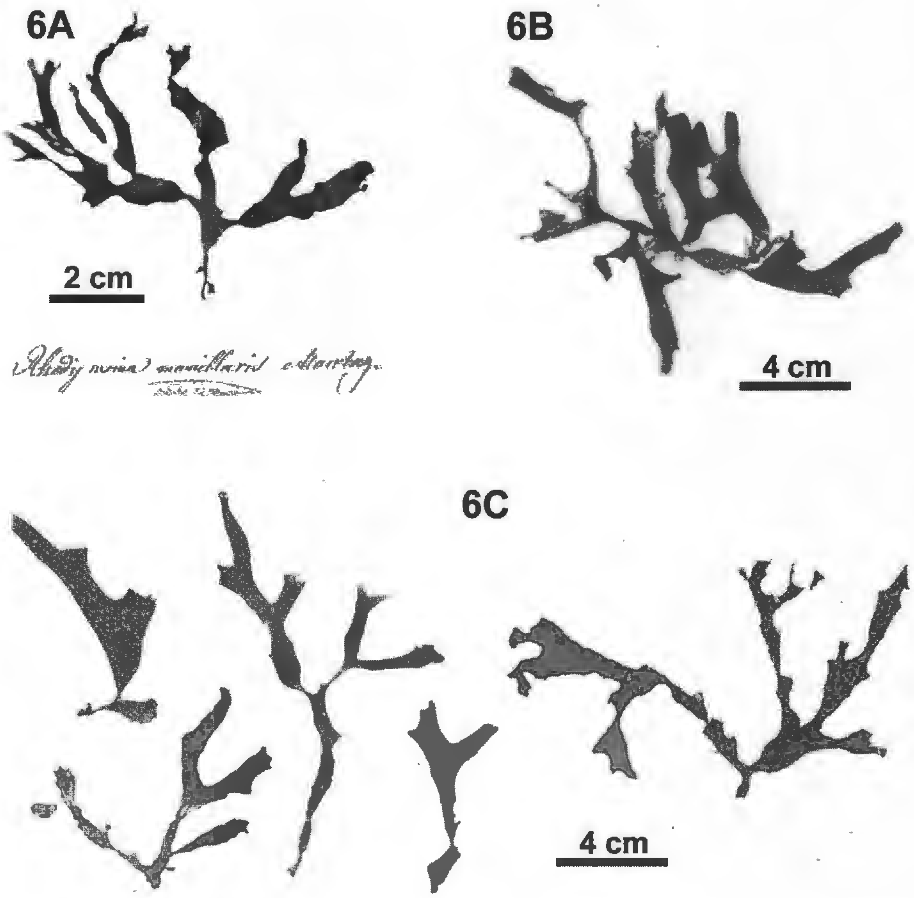

Fig. 6. ***Gracilaria mammillaris*** **(Montagne) Howe. 6A, Holotype of** ***Rhodymenia mammillaris*** **Montagne (PC). 6B, Epitype (US Alg. Coll.-204336), dredged from deep water offshore Louisiana, Gulf of Mexico. 6C, Para-epitypes showing habit variation (US Alg. Coll.-204374; LAF).**

tions and has led many phycologists to report different male reproductive features for algae collected in different geographic areas (Bird and McLachlan 1984). In some instances, the reported features under certain environmental conditions all overlap (see e.g., Taylor's 1960 descriptions of *G. cuneata, G. mammillaris,* and *G. ornata*) and sometimes can be found in what we now recognize to be distinct species. Currently in the literature *G. mammillaris* is considered to have wide distribution in the western Atlantic, ranging from North Carolina (Schneider 1975) to Brazil (Oliveira Filho 1977). However, many of the species previously included in the *G. mammillaris* assemblage are now recognized to be genetically distinct species. Thus the distribution range of actual *G. mammillaris* remains unclear, and the literature reports for this species should be considered with skepticism.

The diagnosis of *Rhodymenia mammillaris* (Montagne 1842) is of a membranous alga, of fleshy and cartilaginous texture, with linear branches with obtuse apices that are irregularly dichotomous branched, above a narrow base. These vegetative features are in agreement with *G. mammillaris* and several other species found within the *G. mammilaris* lineage. Among the most important observations of Montagne was that the gonimoblasts of *R. mammillaris* are composed of "thick filaments" *(inter filamenta crassa).* Montagne's type specimen was probably a drift specimen. In this study, morphologically studied and genetically confirmed specimens of *G. mammillaris,* including the epitype, were restricted to deepwater (~75 m depth) sites in the northwest Gulf of Mexico. It is most likely that *G. mammillaris* is a subtidal or deeper-water species, and records of this alga from the intertidal should be critically reexamined.

Gracilaria hayi Gurgel, Fredericq et J. Norris, sp. nov. (Fig. 7A–F, Tab. 2)

Type Locality: Caribbean Panama: on coral rubble, sand plain off Galeta Reef platform (fronting STRI Galeta Marine Lab., Smithsonian Tropical Research Institute), 13 m depth, Galeta Point [9°24'18" N, 79°51'48.5" W], Republic of Panama.

Holotype: US Alg. Coll.-29046 (Fig. 7A; specimen no. 5 of 22 of Hay and Norris 1984), leg. M. E. Hay, MEH-1023, Sept. 8, 1979.

Isotypes: US Alg. Coll.-29097 (Fig. 7B; specimen no. 20♂ of 22); LAF; UC.

Misapplied Names: *Gracilaria cuneata* sensu Taylor, Mar. algae eastern... Americas, p. 448, 1960 (in part); Hay and Norris, Hydrobiologia 116/117, fig. 4b, 1984 [non *Gracilaria cuneata* Areschoug, Nova Acta Uspal., ser. 3, p. 351, 1854; Ganesan, Carib. J. Sci. 30, pp 124–129, figs. 1–11, 1994]. *Gracilaria mammillaris* sensu Schneider, Taxon 24, p. 643, 1975; Hanisak and Blair, Hel. Meeres. 42, tabs. 1, 3, 5, 1988; Schneider and Searles, Seaweeds... Southeastern U.S., p. 323, figs. 374–376, 1991; Littler and Littler, Carib. reef plants, p. 116, 2000 [non *G. mammillaris* (Montagne) Howe, Flora Bermuda, p. 515, 1918].

Thalli 5–10(–15) cm alti complanati, stipite cylindrico, laminis ramosis dichotome usque ad subdichotome (5–)14–16(–25) mm latis marginibus laevibus, tenibus usque ad 100 µm crassis; cortex, 1–2 stratus cellularum transversaliter compressarum, (6–)8–10 µm x (2.5–)5.0–7.5 µm; cellilae pilis a nobis non visa; transitio inter corticem medullamque acuta; medulla 3–5 strata magnarum cellularum. Tetrasporangia dispersa super laminam. Spermatangia dispersa, valdosi textorii-typi. Cystocarpis 1000–2000 µm diametero; leviter constricta ostiolo centrali; cellulae tubulosae nutriciae prominentes pericarpio supero.

Thalli of variable size, 5–10(–15) cm tall; with roundish holdfast below cylindrical stipe, 1–2 cm long, bearing flat, basally cuneate blades, (5–)14–16(–25) mm wide, mostly dichotomously to subdichotomously branched and terminating with broad, lobed, bifurcated round to obtuse apices. Strap-shaped to broad axes and branches, sometimes with small, lateral proliferations or bladelets. Undamaged apices, regenerating tips, and new mature branches typically with bifurcated, "heart-shaped" apices. Blades thin, up to 100 µm thick in transverse sections. Cortex composed of (1–)2 cell layers of periclinally compressed cells; outer cortical cells (6.25–)8–10 µm by (2.5–)5.0–6.5 µm. Occasional with small gland cells. Hair cells not observed. Sharp transition between medulla and cortex. Medulla composed of 3–4(–5) cell layers of large, rounded to oval cells, 50–65(–86) µm.

Tetrasporangia scattered over blades. Cystocarps hemispherical, wide-based, scattered on upper surfaces of main axes, 1000–2000 µm in diameter, and slightly constricted at base where protruding from thallus; with a centrally located ostiole. Gonimoblasts at maturity nearly completely filling cystocarp cavity and composed of regular thin-walled cells. Transition zone at base of cystocarp composed of rounded cells; tubular nutritive cells prominent in upper part of carposorophyte. Carposporangia organized in tightly packed files. Pericarp composed of 12–14 cells layers, 180–200 µm thick; lower pericarp cells isodiametric, squarish in middle, and anticlinally elongate at margin of pericarp. Spermatangia scattered on blade surfaces, shallow textorii-type.

Etymology: This species is named for our colleague and collector of this alga, Dr. Mark E. Hay (Teasley Professor of Environmental Biology, Georgia Institute of Technology, Atlanta, Georgia). In residence at STRI's Galeta Marine Lab., Mark made extensive collections of marine algae (US Alg. Coll.) and contributed several important phycological and ecological studies from this unique region.

Distribution: Western Atlantic: Florida, Panama.

Habitat: On coral rubble or rocks; subtidal reefs and sand plains, 5–15(–26) m depths.

Specimens Studied: Holotype (US Alg. Coll.-29046) and isotypes. Paratypes: *Caribbean Panama:* (fronting STRI Galeta Marine Lab.), Galeta Point, Galeta Reef slope, on coral, 6–8.5 m, leg. M. E. Hay, MEH-113, May 18, 1978 (US Alg. Coll.-29041); sand plain off Galeta Reef platform, on coral rubble, 9–13 m depths, leg. M. E. Hay, MEH-383 (Fig. 7C: specimen no. 11), Nov. 3, 1978 (US Alg. Coll.-29046), MEH-697, April 23, 1979 (US Alg. Coll.-29062), MEH-734, May 13, 1979 (US Alg. Coll.-29065), MEH-908, June 8, 1979 (US Alg. Coll.-29090); Galeta sand plain,12–15 m depth, leg. B. Wysor and W. Kooistra, BW-737 (Fig. 7D: topotype sequenced voucher), BW-01010, Sept. 21, 1999 (both LAF). *Atlantic Florida:* South Hutchinson I. (ocean side), Fort Pierce, drift (Fig. 7E: cystocarpic; sequenced voucher), leg. C. F. D. Gurgel s.n., April 1998 (LAF); north jetty of Ft. Pierce Inlet, on rocks, leg. N. J. Eiseman and M. C. Benz, s.n. (Fig. 7F), April 4, 1977 (HBOI-1480); off St. Lucie Inlet, 25 m depth, leg. T. Askew and R. Avent, s.n., July 24, 1975 (HBOI-548).

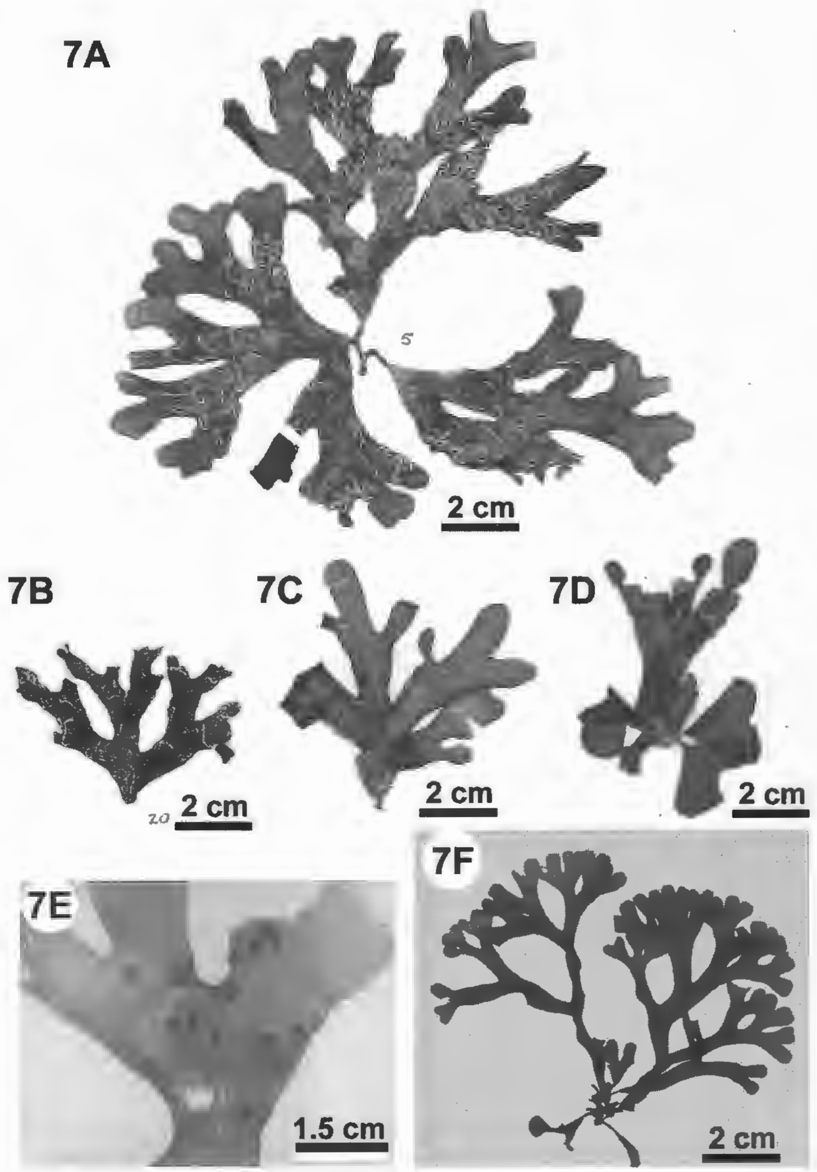

Fig. 7. *Gracilaria hayi* Gurgel, Fredericq et J. Norris, sp. nov. 7A–E: Range of variation in shape of habit and degree of branching. 7A–D: Specimens from sand plain off the Galeta Reef platform, Galeta Point, Caribbean Panama. 7A, Holotype (US Alg. Coll.-29046). 7B, Isotype (US Alg. Coll.-29097, no. 20♂). 7C, Paratype (US Alg. Coll.-29046, M.E. Hay-383, no. 11). 7D, Sequence voucher from the type locality (LAF; B. Wysor-737). 7E–F: Specimens from vicinity of Fort Pierce, east coast of Florida. 7E, Cystocarpic sequence voucher, South Hutchinson I. (LAF). 7F, North jetty of Fort Pierce Inlet (HBOI-1480).

Remarks: Sequenced isolates were from topotype specimens of *G. hayi* collected on the subtidal sand plain off Galeta Reef, Caribbean Panama (Figs. 1, 7D). Specimens of *G. hayi* from the east coast of Florida (drift material from Fort Pierce) were also sequenced (Figs. 1, 7E). These Florida specimens (e.g., Fig. 7E–F) exhibited a habit of specimens previously reported for the southeastern United States but misidentified as *G. mammillaris* (Hanisak and Blair 1988; Schneider 1975; Schneider and Searles 1991).

One of the thinnest flat species of *Gracilaria* in the western Atlantic (only up to 100 µm thick), *G. hayi* is apparently a common but highly variable species. Specimens of *G. hayi* from Galeta Point, Caribbean Panama, typically exhibit a cuneate base (see Fig. 7A–D; also Hay and Norris 1984, fig.4B). The cuneate nature of the blades can also sometimes be seen in other genetically distinct western Atlantic species of *Gracilaria,* such as some specimens of *G. cuneata, G. curtissiae, G. galetensis,* and *G. mammillaris.* The biotic or physical environment can also alter the characteristic branching pattern and shape of the cuneate blades. Herbivory, thallus damage or breakage, and thallus regrowth can result in atypical phenotypes with a high degree of convergence to some other species. Thus taxonomic identification of individual atypical specimens can often be difficult, especially if they are fragmentary, dwarfed, or otherwise modified. The morphology of its undamaged branches and apices and its thin anatomy are the most promising characters to distinguish *G. hayi* from other flattened Caribbean species.

Gracilaria galetensis Gurgel, Fredericq et J. Norris, sp. nov.
(Fig. 8A–F, Tab. 2)

Type Locality: Caribbean Panama: attached to coral, 3.3–10.5 m depths, on Galeta Reef slope (fronting STRI Galeta Marine Lab., Smithsonian Tropical Research Institute) [9°24'18" N, 79°51'48.5" W], Galeta Point, Republic of Panama.

Holotype: US Alg. Coll.-029115 (Fig. 8A, upper left), leg. J. A. Kilar, JAK-1758, May 28, 1979.

Misapplied Names: *Gracilaria* “sp. 1” of Hay and Norris, Hydrobiologia 116/117, figs. 3a, 5–6, 1984. *Rhodymenia divaricata* sensu Schneider and Searles, Phycologia 15, p. 58, 1976; Blair and Hall, Northeast Gulf Sci. 4, p. 128, 1981; Schneider and Searles, Seaweeds...Southeastern U.S., p. 347, fig. 410, 1991 [non *Rhodymenia divaricata* Dawson, Allan Hancock Pac. Exp. 3, p. 141, pl. 23, fig. 31, 1941].

Thalli erecti, solitarii, delicati, carnosi, 8–16(–20) cm alt., 5–8 mm lat. in mediparte laminae, affixi per substratum haptero parvo rotundo. Thallus complanatus omnino, praeter stipem basalem parvum cylindricalem versus leviter compressum. Stipes coriaceus, 0.8–1.0 cm long., 1.0–1.5 mm lat. saepe dichotomi-subdichotomi. Ordines ramificationis magis 4–5 interdum trichotomi. Laminae lineares marginibus irregularibus laevibus, 1.1–1.8 cm lat. ad ramificationes. Apices rotundi, oblongi, simplices. Rami lineares ad basem numero variabili constrictionum palmatascentes. Cortex 1–2(–3) stromaticus. Medulla 4–5-stromatica transitione gradatim versus corticem.

Algae erect, solitary, delicate, fleshy, dark rose red, 8–16(–20) cm tall, (5–)6–8 mm wide in middle part of blade, 254–275 µm thick, attached to substratum by small round holdfast. Thallus flattened throughout with except for small cylindrical to slightly compressed, coriaceous basal stipe, 0.8–1.0 cm long by 1.0–1.5 mm in diameter, often 1–2(–3) times dichotomously to subdichotomously branched. Higher branching, 4th–5th orders, sometimes trichotomous. Blades straplike with smooth irregular margins, 1.1–1.8 cm wide at branches; apices rounded, oblong, simple. Branches linear, with variable degree of constriction at base, sometimes numerous, giving a palmate aspect to blade. Branches commonly may develop from broken apices as a result of regeneration of damaged tips. Cortex composed of 1–2(–3) rows of pigmented cells of variable size and shape but mostly anticlinally elongated, 3.75–10.0 (mean = 5.3) µm by 5.0–12.5 (mean = 8.5) µm, with gradual transition toward medulla. Hair cells common but inconspicuous, 11.25–13.75 (mean = 12.81) µm by 7.5–11.25 (mean = 9.4) µm. Medulla composed of 4–5 rows of round to isodiametric cells, most slightly compressed, 101.27–153.14 (mean = 133.2) µm by 56.81–111.15 (mean = 81.51) µm. Outermost medullary cells strongly compressed, sometimes pigmented.

Tetrasporangia cruciate, scattered on mid to upper thallus. Cystocarps hemispherical, urceolate, scattered on upper surface of main axes, 300–800 µm tall by up to 1000 µm in diameter, slightly constricted at base. Pericarp composed of 12–14 cell layers, 180–200 µm thick; pericarp cells outwardly rounded to isodiametric, inwardly periclinally compressed just above carposporangial mass. Cystocarp with wide-based gonimoblasts at maturity nearly filling cystocarp cavity, and composed of large, thick-walled cells. Carposporangia organized in tightly packed branched files. Spermatangia scattered on thallus, shallow textorii-type.

Etymology: The species epithet *galetensis* is named for the pristine coral reef and mangrove swamps of Isla Galeta. These unique and beautiful habitats, near the northeast entrance to the Panama Canal, are part of the natural and historical heritage of Isla Margarita, Caribbean Panama (Batista de Vega 2001). Twelve of the more than 60 red algal species recorded for Galeta are sympatric species of *Gracilaria,* and this high diversity in such a small area can be considered the largest number of sympatric species of a single red algal genus in the world (Hay 1981; Hay and Norris 1984).

Distribution: Western Atlantic: North Carolina, South Carolina, Florida, Panama.

Habitat: Attached to coral rubble and rocks; subtidal, 4–13 m depths.

Specimens Studied: Holotype (US Alg. Coll.-029115). Paratypes: *Caribbean Panama:* on coral rubble, 8–13 m depths, subtidal sand plain off Galeta Reef platform (fronting STRI Galeta Marine Lab.), Galeta Point, Republic of Panama, leg. M. E. Hay, MEH-499, March 10, 1979 (US Alg. Coll.-

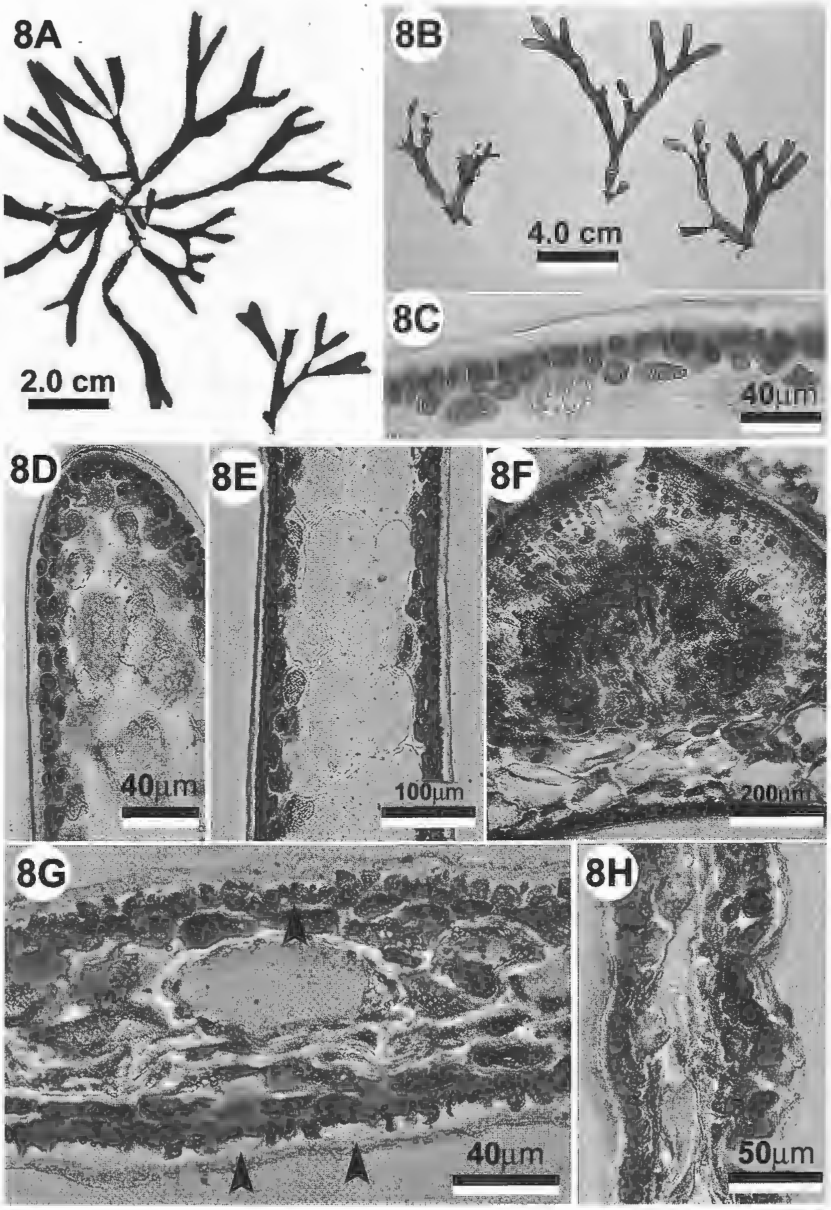

Fig. 8. *Gracilaria galetensis* Gurgel, Fredericq et J. Norris, sp. nov., from the subtidal sand plain off Galeta Reef, Caribbean Panama. 8A, Holotype, cystocarpic specimen at left (US Alg. Coll.-029115). 8B, Sequenced voucher specimens, showing habit variation. 8C, Detail of cortex. 8D–E, Detail of cortex–medulla transition. 8F, Transection of cystocarp. 8G, Transection of spermatangial thallus, showing shallow textorii-type spermatangial pits (arrowheads). 8H, Transection showing tetrasporangial initials.

029059), MEH-690, April 18, 1979 (US Alg. Coll.-029424), MEH-1024, Sept. 8, 1979 (US Alg. Coll.-029471); leg. B. Wysor, BW-715, June 20, 1999, BW-946, (Aug. 30, 1999), BW-1293, Oct. 19, 1999 (all LAF).

Remarks: Specimens of *G. galetensis* sequenced in this study were relatively common on the subtidal sand plains of Galeta Reef (Hay and Norris 1984, as *G.* sp. 1). Despite their distinct genetic differences (Fig. 1, Tab. 2), *G. galetensis* is very similar to *G. occidentalis* (Figs. 11A, 12A–D) and the type specimen (Fig. 11B). These taxa have smooth, elongated linear, straplike blades of variable width with rounded, obtuse or sometimes bifurcated apices. The lanceolate apices seen in undamaged phenotypes of *G. galetensis* and not observed in *G. occidentalis* help separate them.

Though some *Gracilaria* species resemble some species of *Rhodymenia* Greville (Rhodymeniaceae, Rhodymeniales), the sexual reproductive features readily separate the two genera. Western Atlantic species of *Rhodymenia* usually have a larger number of rounded medullary cells and lack cortical gland cells, useful features for distinguishing them from similar-looking species of *Gracilaria.*

Gracilaria oliveirarum Gurgel, Frederciq et J. Norris, sp. nov.
(Fig. 9A–D, Tab. 2)

Type Locality: Venezuela: on rocks and coral rubble, shallow subtidal, La Vela de Coro, Estado Falcon.

Holotype: US Alg. Coll.-204328 (Fig. 9B), July 12, 1999, leg. C. F. D. Gurgel, J. E. Conde, and C. Carmona (FG-12).

Isotype: LAF (Fig. 9A).

Misapplied Name: *Gracilaria textorii* sensu Rodriguez de Rios, Ernstia 38, p. 2, figs. 1–14, 1986 [non *Gracilaria textorii* (Suringar) DeToni, Syll. algarum...3, p. 27, 1895].

Thalli 1-pauci fasciculis, complanati, normaliter ligulatioides, plerumque 10–14 cm alt., 0.6–1.2 cm lat., exorientes haptero parvo discoideo, 2–4 mm diam. Ramificatio axium principalium dichotoma aut subdichotoma uniplanata, trichotoma-polychotoma interdum. Cortex 1–2-stromaticus, medulla 4–5-stromatica transitione abrupto versus corticem. Medulla cellularum magnarum ovoidearum centro 304–400 µm x 150–190 µm.

Algae one to few in clusters, flattened, usually straplike, mostly 10–14 cm tall, 0.5–1.2 cm wide (sometimes up to 2.0 cm broad at branch dichotomy), 500(–750) µm thick, branching common and irregularly along margins or at apices; arising from small discoid holdfast, 2–4 mm in diameter. Main axes dichotomous to subdichotomous branched in one plane; sometimes trichotomous to polychotomous branched as a result of development of branch initials at broken or grazed tips. Cortex of 1(–2) cells of variable size and shape, 3–5(–9) µm in diameter; subcortex inconspicuous, 1 cell layer of small vari-

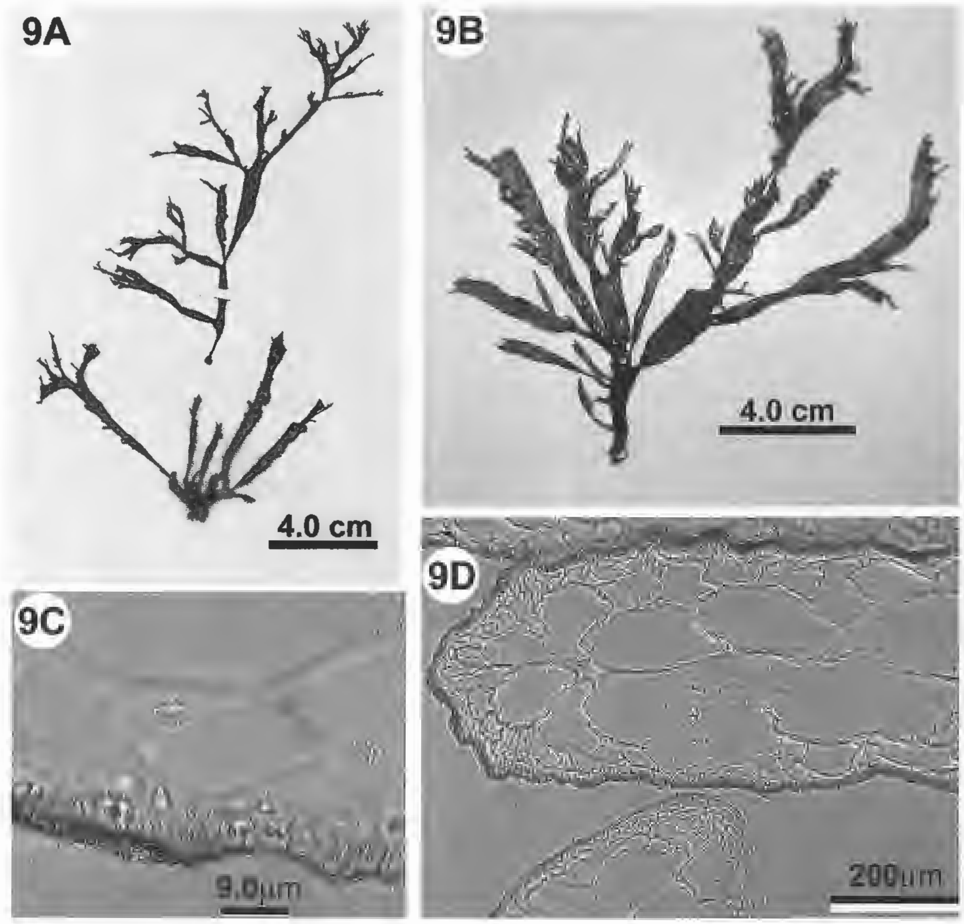

Fig. 9. *Gracilaria oliveirarum* Gurgel, Fredericq et J. Norris, sp. nov., from La Vela de Coro, Estado Falcon, Venezuela. 9A, Isotypes (LAF). 9B, Holotype (US Alg. Coll.-204328). 9C, Transection showing marked transition of cortex–medulla. 9D, Transection showing inner medullary cells.

able shaped cells, mostly radially elongated. Transition between cortex and medulla abrupt. Medulla of 4–5 cell layers, inner medulla usually of 2 large compressed ovoid cells in center, 304–400 (mean = 329) µm by 150–190 (mean = 170) µm. Reproductive structures not seen.

Etymology: In recognition of their contributions to our knowledge of Brazilian marine algae and the systematics of *Gracilaria,* we name this species *oliveirarum* ("of the Oliveiras") for Dr. Eurico Cabral Oliveira Filho and his daughter Dra. Mariana C. Oliveira (Professors, Universidad do São Paulo, São Paulo, Brazil).

Distribution: Western Atlantic: Venezuela.

Habitat: Growing on small rocks and coral rubble spread over sand bottoms in protected, shallow subtidal environments.

Specimens Studied: Holotype (US Alg. Coll.-204328) and isotype. Paratypes: *Venezuela:* La Vela de Coro, Playa Barranquila, Estado Falcon, July 14, 1999, leg. C. F. D. Gurgel, J. E. Conde, and C. Carmona, s.n.

Remarks: Some specimens of *G. oliveirarum* can be similar in habit to small specimens of *G. curtissiae,* making the distinction between these somewhat similar morphs difficult, especially when dealing with small immature specimens. When fully grown, however, the two can be easily distinguished (Tab. 2), with *G. oliveirarum* usually having thinner 500(–750) µm and narrower (0.5–1.0 cm), often irregularly branched blades, with most branches turned toward the apices, whereas *G. curtissiae* usually has thicker (500–1000 µm) and broader (1.0–3.5 cm) lanceolate blades with distinct bi- to tripartite (palmate) branchlets along the margins (Fig. 13A–B). There are also differences, seen in transverse sections, in their anatomy. The medulla of *G. oliveirarum* is usually 4–5 cell layers with the 2 conspicuously compressed central medullary cells, and cortical cells of variable shape (mostly elongated) and size (Fig. 9C–D). In contrast, *G. curtissiae* has a 3–4-celled medulla composed of larger, less compressed central cells, and a cortex of isodiametric cells with conspicuous cortical hairs and gland cells (Fig. 13C–D).

The reported *G. textorii* from the Caribbean (Rodriguez de Rios 1986) is incorrect, and these specimens are now recognized to be *G. oliveirarum.* Though the literature suggests that the Pacific and Atlantic Oceans share several species of Gracilariaceae, critical studies of reputed shared taxa such as *G. verrucosa* (Hudson) Papenfuss or *G. bursa-pastoris* have indicated that this is not the case. A phylogeny based on *rbc*L (Fig. 1) places *G. textorii* from Japan far from any flattened species of *Gracilaria* from the Caribbean. Although juvenile specimens of *G. curtissiae* and *G. occidentalis* are somewhat close to *G. textorii,* none of the other foliose species sequenced in this study is genetically similar enough to *G. textorii* to be even placed in the same intrageneric *Gracilaria* subgroup. Even among the most derived clades within *Gracilaria* that are characterized by flattened species with textorii-type spermatangia (Yamamoto 1978), there is one clade composed of Caribbean species *(G. occidentalis, G. flabelliforme, G. ornata, G. curtissiae,* and *G. apiculata)* and another composed of South African and Asian species *(G. beckeri, G. capensis, G. vieillardii, G. spinulosa,* and *G. textorii)* (Gurgel and Fredericq 2003). The latter clade, indicating a phylogenetic affinity among Japanese, Taiwanese, and east South African biogeographic regions, supports an existing ancient dispersal hypothesis that some *Gracilaria* taxa reached the Atlantic from its center of dispersal in the southeastern Asia region through a southern route (Hommersand 1990).

Gracilaria smithsoniensis Gurgel, Fredericq et J. Norris, sp. nov. (Fig. 10A–D, Tab. 2)

Type Locality: Caribbean Panama: attached to coral rubble, 8–13 m depths, subtidal sand plain off Galeta Reef platform (fronting STRI Galeta Marine Lab., Smithsonian Tropical Research Institute), Galeta Point [9°24'18" N, 79°51'48.5" W],Republic of Panama.

Holotype: US Alg. Coll.-29464 (Fig. 10A; specimen no. 36♂ on herbarium sheet of Hay and Norris 1984), leg. M. E. Hay, MEH-991, July 11, 1979.

Isotypes: US Alg. Coll.-204330 (specimen nos. 24, 26, 29, and 32 shown in Fig. 10B); US Alg. Coll.-204331 (specimen no. 17 shown in Fig. 10B); US Alg. Coll.-204333 (specimen nos. 27–28 shown in Fig. 10B).

Misapplied Name: *Gracilaria* "sp. 2" of Hay and Norris, Hydrobiologia 116/117, figs. 2b, 5–6, 1984.

Thalli parvi, 3–5.5 cm. alt., angusti, 2–2.5 mm lat., tenues, affixi per substratum haptero parvo rotundo, compressi omnino, regulariter dichotomi ramosi angula lata uniplanata; habitus variabilis, stipe cylindrico ad leviter compressum in specimina robusta. Apices lati, rotundi, simplices. Ramuli raro. Cortex 1–2-stromaticus, medulla 5–6-stromatica transitione abrupto versus corticem. Cellulae medullosae parvae, isodiametrae.

Algae compressed throughout, 3.0–5.5 cm tall, with narrow 2.0–2.5 mm wide, and thin (up to 300 µm), regularly dichotomously branched axes, frequently branching in one plane at wide angles; presence of basal stipe, cylindrical to slightly compressed and 1.0–3.5 cm long in more robust specimens, attached by small round holdfast. Habit variable, ranging from thalli with narrow axes and coarse, wiry texture to more delicate thalli with wider axes. Branches mostly from main axes, with simple broad, rounded apices; branchlets rarely present. Cortex of 1–2 rows of variable shaped cells, with sharp transition between cortex and medulla; hair cells absent. In transverse section, at middle portion of blade, cortical cells mostly periclinally elongated, 3.75–6.25 (mean = 5.62) µm by 5.0–7.5 (mean = 6.5) µm, becoming anticlinally elongated at margin. Medulla of 5–6 layers of small, isodiametric, pigmented cells with relatively thick cell walls, 79–116 (mean = 110) µm by 61.75–74.10 (mean = 65.7) µm.

Tetrasporangia cruciately divided, scattered over blade surfaces. Cystocarps hemispherical, scattered and protruding on thallus surface, 1–2 mm in diameter and slightly constricted at base. Pericarp, composed of 12–14 cell layers, 170–200 µm thick; pericarp cells isodiametric, not tightly packed, becoming anticlinally elongate at outer margin. Cystocarp wide-based; gonimoblasts at maturity completely filling cavity and composed of large, elongate thick-walled inner gonimoblast cells; tubular nutritive cells extending deep into margins of lower pericarp region. Transition zone at base of cystocarp composed of 3–4 layers of small cells. Carposporangia organized in tightly packed files. Spermatangia of the shallow textorii-type, scattered over mid to upper blade surface.

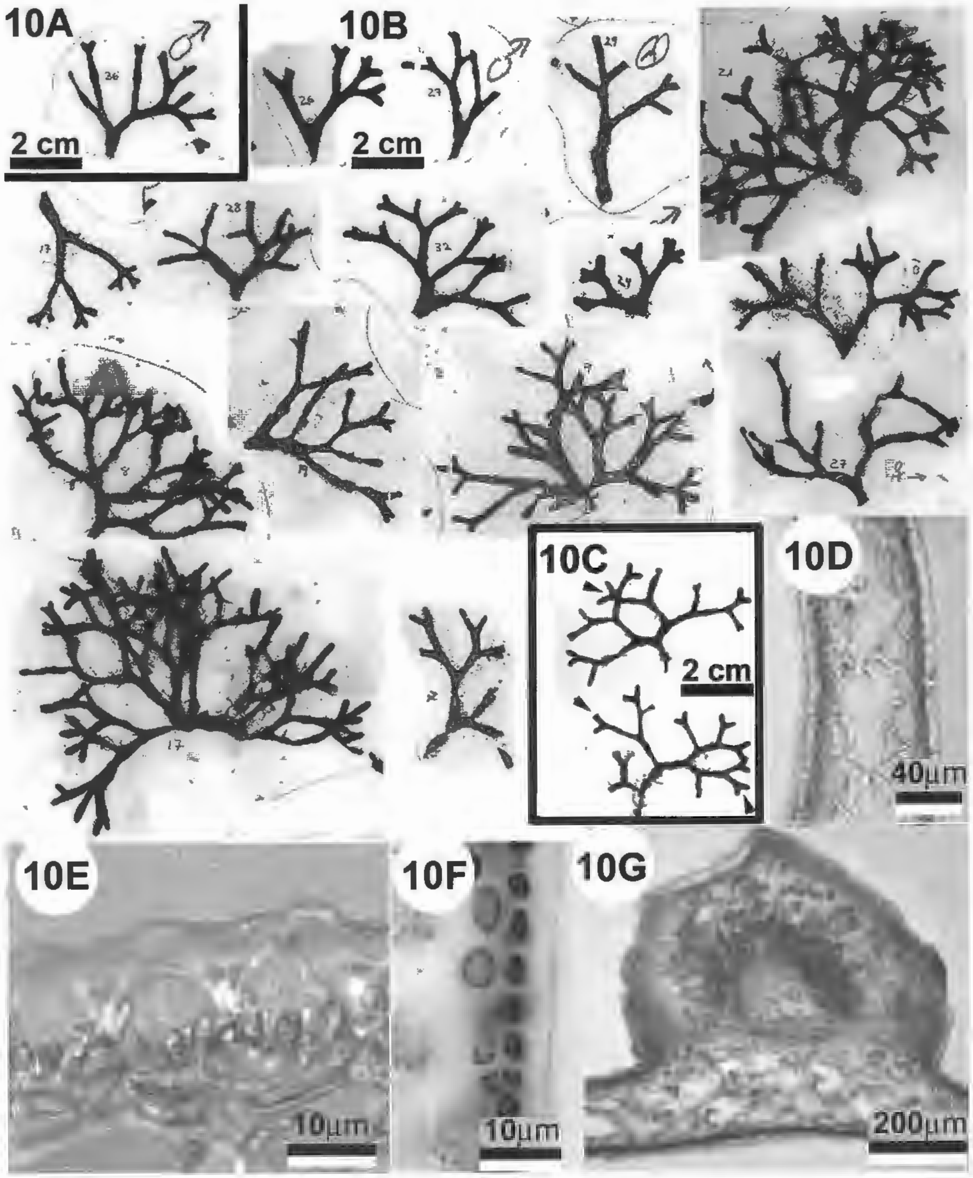

Fig 10. *Gracilaria smithsoniensis* Gurgel, Fredericq et J. Norris, sp. nov., from subtidal sand plain off Galeta Reef, Caribbean Panama. 10A, Holotype (US Alg. Coll-029464, no. 36 spermatangial thallus). 10B, Specimens from study of Hay and Norris (1984) showing phenotypic variation in isotypes (US Alg. Coll.-204330, nos. 24, 26, 29, and 32; US Alg. Coll.-204331, no. 17; and US Alg. Coll.-204333, nos. 27♂, 28), and paratypes (US Alg. Coll-29465 (nos. 9, 19, 21, and 27♀

(cont. right)

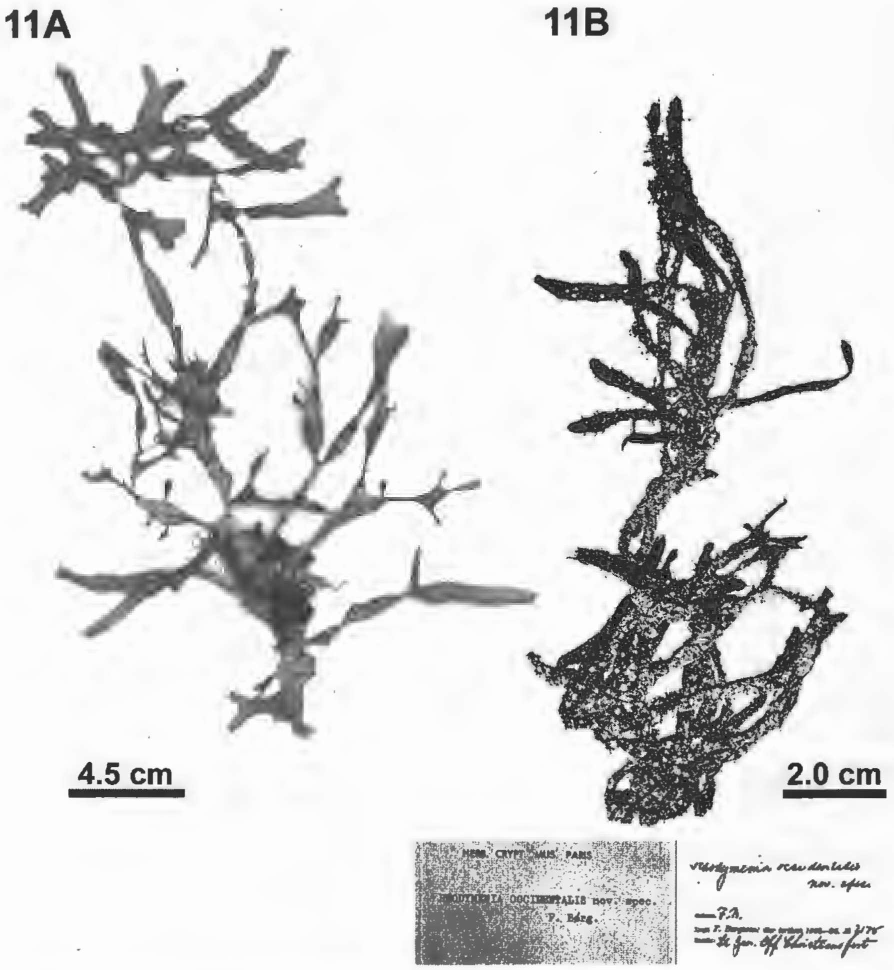

Fig. 11. *Gracilaria occidentalis* (Børgesen) Bodard. 11A, Habit of dredged specimens from offshore Louisiana, Gulf of Mexico. 11B, Type specimen of *Rhodymenia occidentalis* Børgesen [=*G. occidentalis*] (C 2178).

and (US Alg. Coll.-29474; nos. 7, 8, 10 and 17). 10C, Sequenced vouchers (BW-737; LAF). 10D, Transverse section through thallus, showing abrupt cortex–medulla transition. 10E, Transection through spermatangial thallus, showing shallow, textorii-type spermatangial conceptacles. 10F, Detail showing cortical cells in nonfertile thallus. 10G, Transection of mature cystocarp.

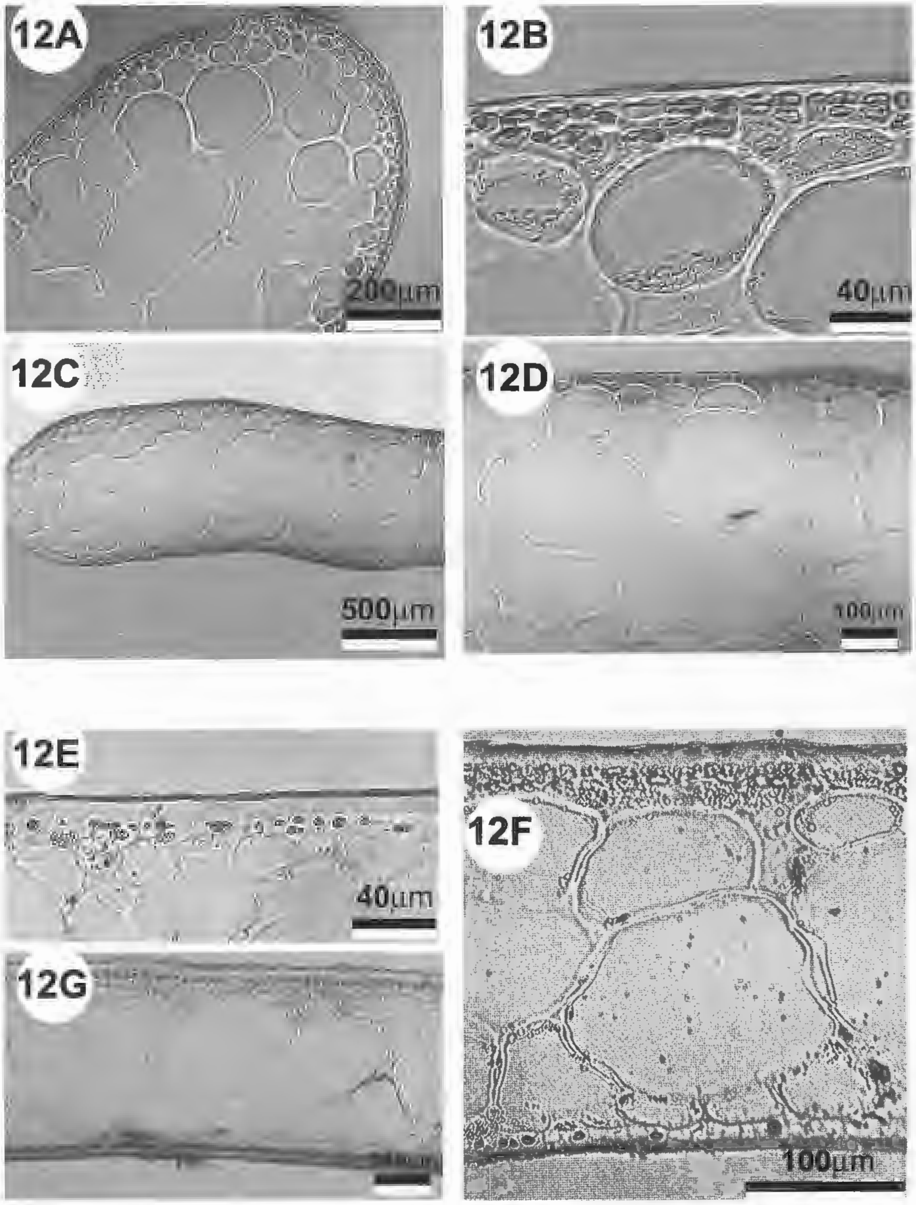

Fig. 12. ***Gracilaria occidentalis*** **(Børgesen) Bodard and** ***G. mammillaris*** **(Montagne) Howe, transverse sections through middle portions of thalli showing details of cortex, cortex–medulla transition, shape of medullary cells, and thallus thickness. 12A–D,** ***G. occidentalis.*** **12E–G,** ***G. mammillaris.***

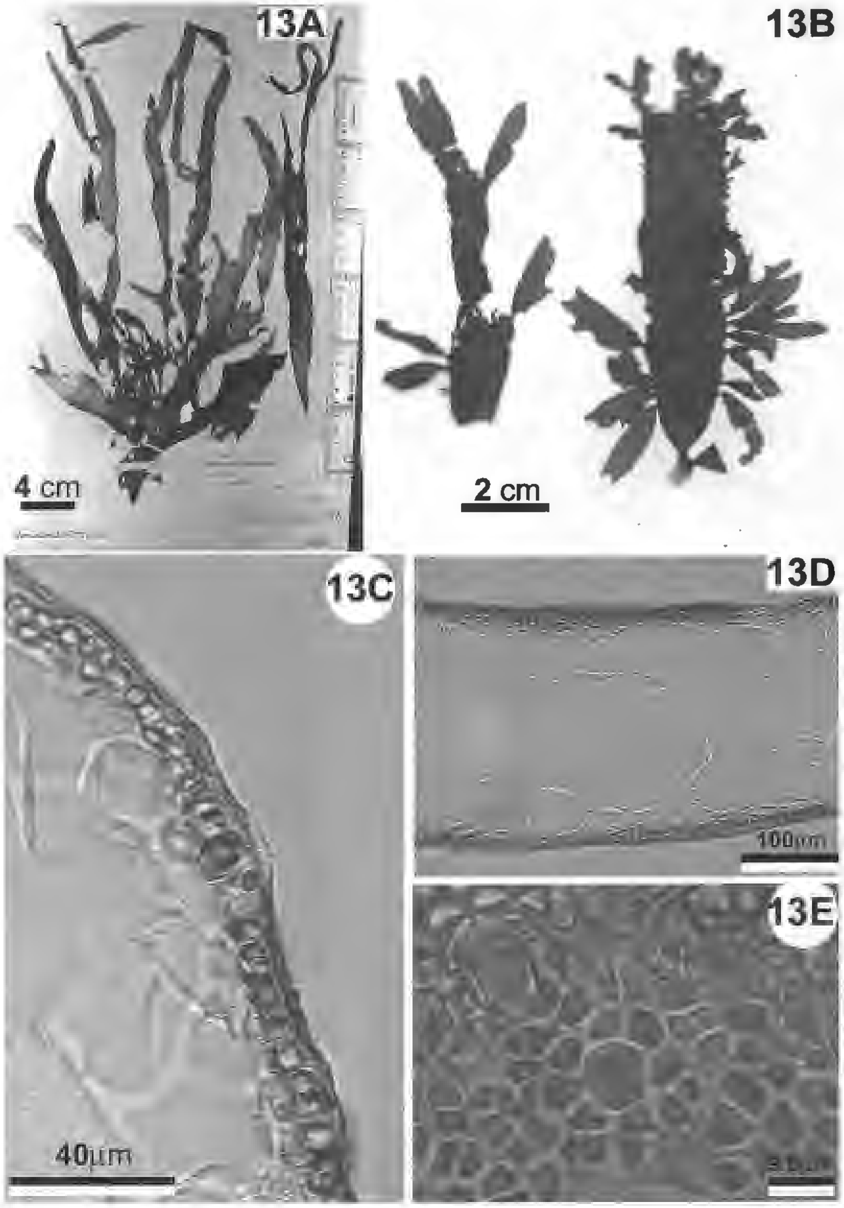

Fig. 13. ***Gracilaria curtissiae*** **J. Agardh. 13A, Lectotype specimen (Agardh Herbaium, LD-2953). 13B, Habit of specimens from La Vela de Coro, Estado Falcon, Venezuela. 13C, Detail of cortex; note the single gland cell in thin cortex, marked cortex–medulla transition. 13D, Transverse section through thallus. 13E, Surface view showing two circular, refringent gland cells.**

Etymology: This species epithet *smithsoniensis* is named after the Smithsonian Tropical Research Institute, with particular reference to the STRI Galeta Marine Laboratory located on the Galeta Reef platform, from which researchers have contributed to our knowledge of the marine and terrestrial biology and geology of Caribbean Panama.

Distribution: Western Atlantic: Panama.

Habitat: Attached to coral rubble and rocks, on subtidal sand plain; 8–14 m depths.

Specimens Studied: Holotype (US Alg. Coll.-29464) and isotypes. Paratypes. *Caribbean Panama:* on coral rubble, 8–13 m depths, subtidal sand plain off Galeta Reef platform (fronting STRI Galeta Marine Lab.), Galeta Point, Republic of Panama, leg. M. E. Hay, MEH-377, Nov. 3, 1978 (US Alg. Coll.-29388), MEH-437, Dec. 8, 1978 (US Alg. Coll.-29396), MEH-453, Jan. 9, 1979 (US Alg. Coll.-29400), MEH-965A, May 17, 1979 (US Alg. Coll.-29151), MEH-1010, Aug. 22, 1979 (US Alg. Coll.-29465; Fig. 10B), MEH-1028, Sept. 8, 1979 (US Alg. Coll. 29474-29476; Fig. 10B); leg. B. Wysor, BW-737 (sequence voucher; Fig. 10C), BW-738, both June 20, 1999, BW-862, July 24, 1999.

Remarks: Of the flattened, western Atlantic species of *Gracilaria, G. smithsoniensis* is one of the easiest to recognize due to its small delicate habit and narrow axes with regular dichotomous branching. The specimen of *G. smithsoniensis* (Fig. 10C) sequenced in this study was identical to *Gracilaria* "sp. 2" of Hay and Norris (1984) and was collected from the same locale, the subtidal sand plain, off the Galeta reef.

Gracilaria smithsoniensis, *G. hayi,* and *G. galetensis,* together with *G. domingensis* Sonder ex Kützing, *G. blodgettii* Harvey (=*G. cylindrica* Børgesen, see Fredericq and Norris 1992), and another unidentified species (Hay and Norris 1984, as "*G.* sp. 3"), are the most abundant species of algae on the sand plains off Galeta Reef, Panama. The percentage in reproductive thalli of these species typically increases in August to late November, just after the onset of the dry seasons (Hay and Norris 1984).

Conclusion

Among all major internal clades in the overall phylogeny of the genus *Gracilaria* sensu lato (including *Hydropuntia*), there currently are only three lineages that do not contain flattened species, the "*Gracilaria chilensis* lineage," the "*G. cornea* lineage," and the "*G. pacifica* lineage"; all remaining clades have species with at least one flat or strongly compressed thallus (Gurgel and Fredericq 2003).

Of the two *Gracilaria* lineages focused on in this study (Fig. 1), the "*G. venezuelensis* lineage" is the least morphologically variable, and its 3 species and 1 subspecies can easily be distinguished from one another based on overall habit morphology. In contrast, the "*G. mammillaris* clade" is composed of species whose morphological variations occasionally overlap, sometimes making their taxonomic identification by morphological comparisons alone difficult, especially when only small, fragmentary, and sterile specimens are available. The molecular analysis of flat species of *Gracilaria* in this study revealed that species with similar habit are in fact distinct genetic entities, which helps explain the taxonomic confusion in the literature. Despite the molecular differences discovered, the morphological delineation of genetically distinct but vegetatively similar taxa remains a difficult task.

This study provides evidence that the total number of distinct *Gracilaria* species in the western Atlantic is much larger than previously recognized (e.g., Taylor 1960; Schneider and Searles 1991; Wynne 1998). Further, we have found more distinct phenotypes of *Gracilaria* species in the tropical western Atlantic with dissimilar genetic signatures (DNA sequences). These genetically distinct species either do not fit any known species, available description, or type material or agree morphologically with more than one (albeit often vague or incomplete) diagnoses. The taxonomic resolution of poorly known species, especially those with overlapping morphologies, will be resolved only after molecular DNA sequence analysis and critical comparative morphological studies, particularly of the ontogeny of reproductive structures, are completed. Abundant collections from throughout the geographic as well as habitat ranges are important for the complete assessment of the full range of morphological variation for many species.

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Literature Cited

Abbott, I. A. 1985. New species of *Gracilaria* Grev. (Gracilariaceae, Rhodophyta) from California and Hawaii. In: Tax. Econ. Seaweeds 1, pp. 115–121.

Abbott, I. A. 1995. A decade of species of *Gracilaria* (sensu lato). In: Tax. Econ. Seaweeds 5, pp. 185–194.

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu. xv + 477 pp.

Abbott, I. A., et al. 1985. The red alga *Gracilaria* Greville (Gracilariaceae, Gigartinales): Introduction. In: Tax. Econ. Seaweeds 1, pp. 67–68.

Abbott, I. A., Zhang Junfu, and Xia Bangmei. 1991. *Gracilaria mixta*, sp. nov. and other western Pacific species of the genus (Rhodophyta: Gracilariaceae). Pacific Sci. 45(1):12–27.

Agardh, J. G. 1901. Species genera et ordines algarum, seu descriptiones succinctae specierum, generum et ordinum, quibus algarum regnum constituitur. Vol. 3, Pt. 4. Supplementa ulteriora et indices sistens. Malmström, Lund. [vi]+149 pp.

Batista de Vega, G. 2001. Defending Isla Margarita: A natural and historic heritage of Colon, Panama. Nemesix, Colon, Republic of Panama.Nemesix. 48 pp.

Bellorin, A. M., Oliveira, M. C., and Oliveira, E. C. 2002. Phylogeny and systematics of the marine algal family Gracilariaceae (Gracilariales, Rhodophyta) based on small subunit rDNA and ITS sequences of Atlantic and Pacific species. J. Phycol. 38:551–563.

Bhattacharya, D., Elwood, H. J., Goff, L. J., and Sogin, M. L. 1990. Phylogeny of *Gracilaria lemaneiformis* (Rhodophyta) based on sequence analysis of its small subunit ribosomal RNA coding region. J. Phycol. 26:181–186.

Bird, C. J. 1995. A review of recent taxonomic concepts and developments in the Gracilariaceae (Rhodophyta). J. Appl. Phycol. 7:255–267.

Bird, C. J., and. McLachlan, J. 1982. Some underutilized taxonomic criteria in *Gracilaria* (Rhodophyta, Gigartinales). Bot. Mar. 25:557–562.

Bird, C. J., and McLachlan, J. 1984. Taxonomy of *Gracilaria*: Evaluation of some aspects of reproductive structure. Hydrobiologia 116/117:41–46.

Bird, C. J., McLachlan, J., and Oliveira, E. C. 1986a. *Gracilaria chilensis* sp. nov. (Rhodophyta, Gigartinales) from Pacific South America. Can. J. Bot. 64:2928–2934.

Bird, C. J., Nelson, W. A., Rice, E. L., Ryan, K. G., and Villemur, R. 1990. A critical comparison of *Gracilaria chilensis* and *G. sordida* (Rhodophyta, Gracilariales). J. Appl. Phycol. 2:375–382.

Bird, C. J., and Oliveira, E. C. de 1986. *Gracilaria tenuifrons* sp. nov. (Gigartinales, Rhodophyta), a species from the tropical western Atlantic with superficial spermatangia. Phycologia 25:313–320.

Bird, C. J., Oliveira, E. C. de, and McLachlan, J. 1986b. *Gracilaria cornea,* the correct name for the western Atlantic alga hitherto known as *G. debilis* (Rhodophyta, Gigartinales). Can. J. Bot. 64:2045–2051.

Bird, C. J., Ragan, M. A., Crichley, A. T., Rice, E. L., and Gutell, R. R. 1994. Molecular relationships among Gracilariaceae (Rhodophyta): Further observations on some undetermined species. European J. Phycol. 29:195–202.

Bird, C. J., Rice, E. L., Murphy, C. A., and Ragan, M. A. 1992. Phylogenetic relationships in the Gracilariales (Rhodophyta) as determined by 18S rDNA sequences. Phycologia 31:510–522.

Bodard, M. 1967 [1966]. Les *Gracilaria* et Gracilariopsis au Sénégal. Ann. Fac. Sci., Dakar 19:27–55.

Børgesen, F. 1932. A revision of Forsskål's algae mentioned in Flora Aegyptico-arabica and found in his herbarium in the Botanical Museum of the University of Copenhagen. Dansk Bot. Ark. 8(2):1–15, 1 pl.

Candia, A., González, M. A., Montoya, R.,Gómez, P., and Nelson, W. 1999. Comparison of ITS RFLP patterns of *Gracilaria* (Rhodophyceae, Gracilariales) populations from Chile and New Zealand and an examination of interfertility of Chilean morphotypes. J. Appl. Phycol. 11:185–193.

Chang, C. F. and Xia Bang Mei. 1976. Studies on Chinese species of *Gracilaria*. Stud. Mar. Sinica 11:91–163, pls. 1–2. [in Chinese with English abstract]

Dawson, E. Y. 1941. A review of the genus *Rhodymenia* with descriptions of new species. Allan Hancock Pac. Exped. 3(8):123–181.

Dawson, E. Y. 1949. Studies on northeast Pacific Gracilariaceae. Allan Hancock Found. Publ., Occas. Pap. 7:1–105.

Dawson, E. Y. 1961. Marine red algae of Pacific Mexico, Pt. 4: Gigartinales. Pacific Naturalist 2(5):191–343.

Dreckmann, K. M. 2002. El género *Gracilaria* (Gracilariaceae, Rhodophyta) en el Pacífico centro-sur mexicano. In: Sentíes, G. A., and Dreckmann, K. M. (eds.), Monografías ficológicas, pp. 77–118. Universidad Autónoma Metropolitana–Iztapalapa, México D.F.

Dreckmann, K. M., and Pérez-Herández, M. A. 1994. Macroalgas bentónicas de la laguna de Tampamachoco, Veracruz. México. Rev. Biol. Tropica 42:715–717.

Edwards, P. 1970. Illustrated guide to the seaweeds and sea grasses in the vicinity of Port Aransas, Texas. Contrib. Mar. Sci. 15 (Supplement):1–27.

Felsenstein, J. 1985. Phylogenies from gene frequencies, a statistical problem. Syst. Zool. 34(3): 300–311.

Fredericq, S., and Hommersand. M. H. 1989a. Proposal of the Gracilariales, ord. nov. (Rhodophyta) based on an analysis of the reproductive development of *Gracilaria verrucosa*. J. Phycol. 25:213–227.

Fredericq, S., and Hommersand. M. H. 1989b. Comparative morphology and taxonomic status of *Gracilariopsis* (Gracilariales, Rhodophyta). J. Phycol. 25:228–243.

Fredericq, S., and Hommersand. M. H. 1990. Diagnoses and key to the genera of the Gracilariaceae (Gracilariales, Rhodophyta). Hydrobiologia 204/205:173–178.

Fredericq, S., and Norris, J. N. 1985. Morphological studies on some tropical species of *Gracilaria* Grev. (Gracilariaceae, Rhodophyta): Taxonomic concepts based on reproductive morphology. In: Tax. Econ. Seaweeds 1, pp. 137–155.

Fredericq, S., and Norris, J. N. 1992. Studies on cylindrical species of western Atlantic *Gracilaria* (Gracilariales, Rhodophyta): *G. cylindrica* Børgesen and *G. blodgettii* Harvey. In: Tax. Econ. Seaweeds 3, pp. 211–231.

Freshwater, D. W., and Rueness, J. 1994. Phylogenetic relationship of some European *Gelidium* (Gelidiales, Rhodophyta) species, based on *rbc*L nucleotide sequence analysis. Phycologia 33:187–194.

Ganesan, E. K. 1989. Taxonomy of the economically important seaweeds of Venezuela, 1. *Gracilaria*: *G. lacinulata* (Vahl) Howe Prox. Bol. Instit. Oceanogr. Venezuela, Univ. Oriente, Cumaná 28(1–2):85–97.

Ganesan, E. K. 1994. Morphology and taxonomy of the little-known species *Gracilaria cuneata* J. E. Areschoug (Gracilariales: Rhodophyta) from Venezuela. Carib. J. Sci. 30(1–2):124–129.

Gargiulo, G. M., De Masi, F., and Tripodi, G. 1992. Morphology, reproduction and taxonomy of the Mediterranean species of *Gracilaria* (Gracilariales, Rhodophyta). Phycologia 31:53–80.

Garth, J. S. 1945. Geographical account and station records of *Verlero* III in Atlantic waters. Allan Hancock Atlantic Exped., Report No. 1: [ii] + 1–106.

Gavio, B., and Fredericq, S. 2002. *Grateloupia turuturu* (Halymeniacae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. European J. Phycol. 37:349–359.

Goff, L. J., and Coleman, A. W. 1988. The use of plastid DNA restriction endonuclease patterns in delineating red algal species and populations. J. Phycol. 24:357–368.

Goff, L. J., Moon, D. A., and Coleman, A. W. 1994. Molecular delineation of species and species relationships in the red algal agarophytes *Gracilariopsis* and *Gracilaria* (Gracilariales). J. Phycol. 30:521–537.

Greuter, W., et al. 2000. International code of botanical nomenclature. Koeltz Scientific Books, Kőnigstein. xviii + 474 pp. [Regnum Vegetabile vol. 138.]

Guiry, M. D., and Freamhainn, M. T. 1986. Biosystematics of *Gracilaria foliifera* (Gigartinales, Rhodophyta). Nordic J. Bot. 5(6):629–636.

Gurgel, C. F. D. 2001. Phylogeny, taxonomy and biogeography of the Gracilariaceae (Gracilariales, Rhodophyta) with emphasis on taxa from the western Atlantic. Ph. D. dissertation. University of Louisiana at Lafayette. [Univ. Michigan Press, Ann Arbor; Proquest/Bell and Howell Infor. and Learning Co., Microfilm UMI33029835] [xi] +273 pp.

Gurgel, C. F. D., and Fredericq, S. 2003. Systematics of the Gracilariaceae (Gracilariales, Rhodophyta): A critical assessment based on *rbc*L sequence analysis. J. Phycol. 39, in press.

Gurgel, C. F. D., Fredericq, S., and Norris, J. N. 2003a. *Gracilariopsis silvana* sp. nov., *G. hommersandii* sp. nov., and *G. cata-luziana* sp. nov., three new species of Gracilariaceae (Gracilariales, Rhodophyta) from the western Atlantic. Hidrobiologica 13(1):53–64. [also e-published: 2003. Constancea 83 (P.C. Silva Festschrift):electronic version]

Gurgel, C. F. D., Liao, L., Fredericq, S., and Hommersand, M. H. 2003b. Systematics of *Gracilariopsis* Dawson (Gracilariales, Rhodophyta) based on *rbc*L sequence analysis and morphological evidence. J. Phycol. 39:154–171.

Hanisak, M. D., and Blair, S. M. 1988. The deep-water macroalgal community of the east Florida continental shelf. Helogoländer Meeresuntersuchungen 42:133–163.

Hay, M. E. 1981. Herbivory, algal distribution, and the maintenance of between-habitat diversity on a tropical fringing reef. Amer. Nat. 118:520–540.

Hay, M. E., and Norris, J. N. 1984. Seasonal reproduction and abundance of six sympatric species of *Gracilaria* Grev. (Gracilariaceae; Rhodophyta) on a Caribbean subtidal sand plain. Hydrobiologia 116/117:63–72.

Hillis, D. M., and Huelsenbeck, J. P. 1992. Signal, noise, and reliability in molecular phylogenetic analyses. J. Heredity 83:189–195.

Hillis, D. M., Allard, M. W., and Miyamoto, M. N. 1993. Analyses of DNA sequence data: Phylogenetic inference. Methodol. Enzymol. 224:456–487.

Holmgren, P. K., Holmgren, N. H, and Barnett, L. 1990. Index herbariorum. Part 1: The herbaria of the world. 8th ed. International Association of Plant Taxonomy, New York Botanical Garden, Bronx, NY. x + 693 pp. [Regnum Veg. vol. 120]

Hommersand, M. H. 1990. Biogeography of the marine red algae of the North Atlantic Ocean. In: Garbary, D. J., and South, G. R.(eds.), Marine algae of the North Atlantic, pp. 349–410. NATO ASI Series, Vol. 22. Springer-Verlag, Berlin and Heidelberg.

Hommersand, M. H., Fredericq, S., and Freshwater, D. W. 1994. Phylogenetic systematics and biogeography of Gigartinaceae (Gigartinales, Rhodophyta) based on sequence analysis of *rbc*L. Bot. Mar. 37: 193–203.

Intasuwan, S., Gordon, M. E., Daugherty, C. H., and Lindsay, G. C. 1993. Assessment of allozyme variation among New Zealand populations of *Gracilaria chilensis* (Gracilariales, Rhodophyta) using starch-gel electrophoresis. Hydrobiologia 260/261:159–165.

Joly, A. B. 1965. Flora marinha do litoral norte do Estado de São Paulo e regiões circunvizinhas. Bol. Fac. Filosfia, Ciênc. Letr. Univ. São Paulo 294 (Ser. Botânica 21):1–393, pls. 1–59.

Kapraun, D. F. 1993. Karyology and cytometric estimation of nuclear DNA content variation in *Gracilaria, Gracilariopsis* and *Hydropuntia* (Gracilariales, Rhodophyta). European J. Phycol. 28:253–260.

Kapraun, D. F., Dutcher, J. A., and Freshwater, D. W. 1993. Quantification and characterization of nuclear genomes in commercial red seaweeds: Gracilariales and Gelidiales. Hydrobiologia 260/261:679–688.

Kapraun, D. F., Lopez-Bautista, J. M., Trono, G., and Bird, K. T. 1996. Quantification and characterization of nuclear genomes in commercial red seaweeds (Gracilariales) from the Philippines. J. Appl. Phycol. 8:125–130.

Kylin, H. 1930. Über die Entwicklungsgeschichte der Florideen. Lunds Universitets Årsskrift, ny foeljd, Avd. 2, 26(6):1–104, pls. 1–28.

Kylin, H. 1932. Die Florideenordnung Gigartinales. Lunds Univ. Årsskr., ny foeljd, Avd. 2, 28(2):1–88, pls. 1–28.

Kylin, H. 1956. Die Gattungen der Rhodophyceen. C.W.K. Gleerups, Lund. xv + 673 pp.

Lin, S. M., Fredericq, S., and Hommersand, M. H. 2001. Systematics of the Delesseriaceae (Ceramiales, Rhodophyta) based on LSU rDNA and *rbc*L sequences, including the Phycodroideae, subfam. nov. J. Phycol. 37:881–899.

Littler, D. S., and Littler, M. M. 2000. Caribbean reef plants. OffShore Graphics, Washington D.C. 542 pp.

McLachlan, J. 1979. *Gracilaria tikvahiae* sp. nov. (Rhodophyta, Gigartinales, Gracilariaceae), from the northwestern Atlantic. Phycologia 18(1):19–23.

Meneses, I., and Abbott, I. A. 1987. *Gracilaria* and *Polycavernosa* from Micronesia. Micronesica 21:187–200.

Millar, A. J. K. 1997a. Studies on terete species of Australian *Gracilaria*. In: Tax. Econ. Seaweeds 6, pp. 103–109.

Millar, A. J. K. 1997b. Some flattened species of *Gracilaria* from Australia. In: Tax. Econ. Seaweeds 6, pp. 111–123.

Montagne, C. 1842. Botanique. Plantes cellulaires. In: Ramon de la Sagra, Historie physique, politique et naturelle de l'île de Cuba. Arthus Bertrand, Paris. [v] + x + 549 pp.

Norris, J. N. 1985. Studies on *Gracilaria* Grev. (Gracilariaceae, Rhodophyta) from the Gulf of California, Mexico. In: Tax. Econ. Seaweeds 1, pp. 123–135.

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

Oliveira Filho, E. C. de. 1977. Algas marinhas bentonicas do Brasil. Thesis, Univ. Sao Paulo, Inst. Biociencias, Sao Paulo, Brazil. 407 pp.

Oliveira Filho, E. C. de. 1984. Taxonomic criteria in the genus *Gracilaria* Grev. (Rhodophyta). Hydrobiologia 116/117:55–58.

Oliveira, E. C. de, Bird, C. J., and McLachlan, J. 1983. The genus *Gracilaria* (Rhodophyta, Gigartinales) in western Atlantic: *Gracilaria domingensis, G. cervicornia* and *G. ferox*. Can. J. Bot. 61:2999–3008.

Rice, E. L., and Bird, C. J. 1990. Relationships among geographically distant populations of *Gracilaria verrucosa* (Gracilariales, Rhodophyta) and related species. Phycologia 29(4):501–510.

Rodriguez de Rios, N. 1972. Contribution al estudio sistematico de las algas macroscopicas de las costas de Venezuela. Acta Bot. Venez. 7:219–324, map, pls. [1]–[40].

Rodriguez de Ríos, N. 1986. *Gracilaria textorii* (Suringar) De Toni, una nueva addicion a la flora de algas marinas de Venezuela (Rhodophyta, Gracilariaceae). Ernstia 38:1–11.

Schneider, C. W. 1975. Taxonomic notes on *Gracilaria mammillaris* (Mont.) Howe and *Gracilaria veleroae* Dawson (Rhodophyta, Gigartinales). Taxon 24:643–646.

Schneider, C. W., and Searles, R. B. 1976. North Carolina marine algae, VII: New species of *Hypnea* and *Petroglossum* (Rhodophyta, Gigartinales) and additional records of other Rhodophyta. Phycologia 15(1):51–60.

Schneider, C. W., and Searles, R. B. 1991. Seaweeds of the Southeastern United States: Cape Hatteras to Cape Canaveral. Duke Univ. Press, Durham, NC. xiv + 553 pp.

Schnetter, R., and Schnetter, M. 1967. Notas sobre unas especies del orden Gigartinales (Rhodophyceae) en la costa Atlántica de Colombia. Mitt. Inst. Colombo-Aleman Invest. Cien. 1:45–52.

Scholfield, C. I., Gacesa, P., Price, J. H., Russell, S. J., and Bhoday, R. 1991. Restriction fragment length polymorphism of enzymically-amplified small-subunit rRNA-coding regions from *Gracilaria* and *Gracilariopsis* (Rhodophyta): A rapid method for assessing 'species' limits. J. Appl. Phycol. 3:329–334.

Silva, P. C. 1952. A review of nomenclatural conservation in the algae from the point of view of the type method. Univ. Calif. Publ. Bot. 25:241–324.

Silva, P. C. 1994. Report to the Committee for Algae: 2. Taxon 43:257–264.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. Univ. Calif. Publ. Bot. 79:1–1259.

Sjöstedt, L. G. 1926. Floridean Studies. Lunds Univ. Årsskr., ny foeljd, Avd. 2, 22(4):1–95.

Steentoft, M., Irvine, L. M., and Bird, C. J. 1991. Proposal (1015) to conserve the type of *Gracilaria*, nom. cons., as *G. compressa* and its lectotypification (Rhodophyta: Gracilariaceae). In: Nicolson, D. H. (ed.), Proposals to conserve or reject. Taxon 40:663–666.

Swofford, D. L. 2002. PAUP*: Phylogenetic analysis using parsimony (and other methods). Version 4.0, beta release version 10. Sinauer, Sunderland, MA.

Taylor, W. R. 1928. The marine algae of Florida, with special reference to the Dry Tortugas. Papers from the Dry Tortugas, 25. Carnegie Inst. Wash. Publ. 379:1–219, pls. 1–37.

Taylor, W. R. 1942. Caribbean marine algae of the Allan Hancock Expedition, 1939. Allan Hancock Atlantic Exped., Report No. 2: 1–193.

Taylor, W. R. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. University of Michigan Press, Ann Arbor. ix + 870 pp.

Tsuda, R. T., and Abbott, I. A. 1985. Collecting, handling, preservation, and logistics. In: Littler, M. M., and Littler, D. S. (eds.), Handbook of phycological methods, Vol. 4. Ecological field methods: Macroalgae, pp. 67–86. Cambridge University Press, Cambridge and New York.

Westernhagen, H. 1974. Food preferences in cultured rabbitfishes (Siganidae). Aquaculture 3:109–117.

Withell, A. F., Millar, A. J. K., and Kraft, G. T. 1994. Taxonomic studies of the genus *Gracilaria* (Gracilariales, Rhodophyta) from Australia. Austral. Syst. Bot. 7:281–352.

Womersley, H. B. S. 1996. The marine benthic flora of Southern Australia, Part IIIB: Gracilariales, Rhodymeniales, Corallinales and Bonnemaisoniales. Australian Biological Resources Study, Canberra. 392 pp. [Flora of Australia Suppl. Ser., no. 5]

Wynne, M. J. 1998. A checklist of benthic marine algae of the tropical and subtropical western Atlantic: First revision. Beih. Nova Hedwigia 116. J. Cramer, Berlin and Stuttgart. iii + 155 pp.

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

Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25(2):97–152, pls. 1–49.

ADDITIONAL RECORDS OF *GRACILARIA* FROM THAILAND

Khanjanapaj Lewmanomont and Anong Chirapart

Abstract

Three species of *Gracilaria—G. longirostris, G. multifurcata,* and *G. rhodymenioides*—are reported from Thailand. All of them are new records for the country, adding to the 15 species previously reported.

Introduction

Previous studies of the genus *Gracilaria* from Thailand identified 15 species (Abbott 1988; Lewmanomont 1994, 1995; Chirapart and Ruangchauy 1999). Of these, 11 species were from the Gulf of Thailand and only 7 from the Andaman Sea. Many specimens are still unidentified due to lack of fertile plants, especially cystocarpic and spermatangial plants, which are important for species determination. Collection of specimens has been done continuously, adding more species to previous records.

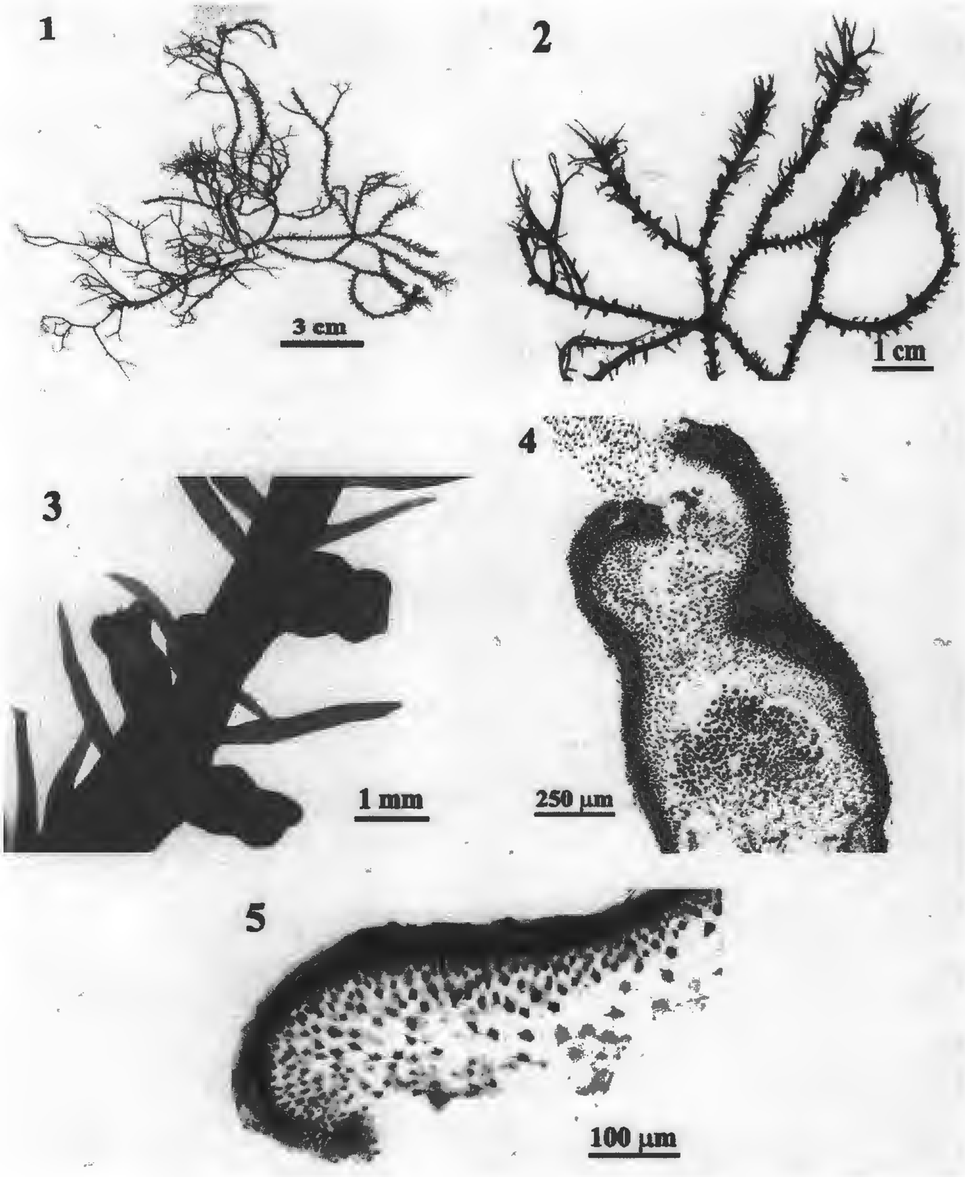
Materials and Methods

Specimens were collected from southern peninsular Thailand, along the west coast of the Gulf of Thailand and the Andaman Sea. Some were preserved in a 4% solution of formaldehyde in seawater, and some were made into herbarium specimens. Microscopic observations were made from sections cut with razor blades under a stereomicroscope and stained with 1% aniline blue, fixed with 1% hydrochloric acid and mounted in 25% Karo syrup. All specimens are kept at the Faculty of Fisheries, Kasetsart University, Bangkok.

Description of Species

Gracilaria longirostris Zhang et Wang, Tax. Econ. Seaweeds 5, pp. 197–205, figs. 1–19, 1995. (Figs. 1–5)

Plant dark brown, erect to decumbent, to 13 cm high, arising from a small discoid holdfast, with percurrent axis and 2–3 orders of branching (Fig. 1). Main axis cylindrical throughout, about 1.5 mm in diameter, becoming narrower in higher-order branches. Percurrent axes covered with numerous small branchlets radially attached in all directions (Fig. 2). Specimens adhering imperfectly to paper on drying.



Figs. 1–5. ***Gracilaria longirostris.*** **Fig. 1, Habit of cystocarpic plant. Fig. 2, Branches with many small branchlets and cystocarps. Fig. 3, Enlarged portion showing pomegranate-like cystocarps. Fig. 4, Longitudinal section through 2-chambered cystocarp. Fig. 5, Section of pericarp, showing the arrangement of cells.**

In transverse section, thallus consisting of a cortex of 2–3 layers of small, oblong to ovoid cells 3–8 µm by 2.8–5.0 µm, outermost layers of cells pigmented; medulla of large parenchymatous cells 100–160 µm by 150–220 µm, with walls 5–8 µm thick; transition of cells from medulla to cortex abrupt.

Cystocarps numerous on main axis and first order of branches, prominently protruding, globose to double-chambered (Figs. 3, 4), 1–2 mm high and 1.0–1.3 mm wide, slightly constricted at base; rostrum short to very elongated, apex often lobed. Pericarp thin, 100–160 µm, consisting of 7–10 layers of cells (Fig. 5), inner layers with stellate plastids and obscure cell walls. Gonimoblast consisting of small star-shaped cells with obscure cell walls connected by elongated arms. Traversing filaments lateral, rare.

Type Locality: Guangdong Province, China.

Collection Site: Bang Gra Noi, Phetchaburi Province, on the west coast of the Gulf of Thailand about 200 km from Bangkok.

Remarks: The specimens are similar to *Gracilaria longirostris* described by Zhang et al. (1995) in having large, prominently protruding cystocarps, some with the distinctive pomegranate-like shape. The specimens from Thailand do not show the elongated, simple to branched beaks of those from China. The morphological features of fronds and cystocarps are, however, similar. The Thai plants were growing on shoreline sandbags at the mouth of a small canal connected to the sea, a habitat similar to that of the holotype specimens from China, which were collected from shallow intertidal shells or gravel in a small canal with some fresh water flowing into it (Zhang et al. 1995).

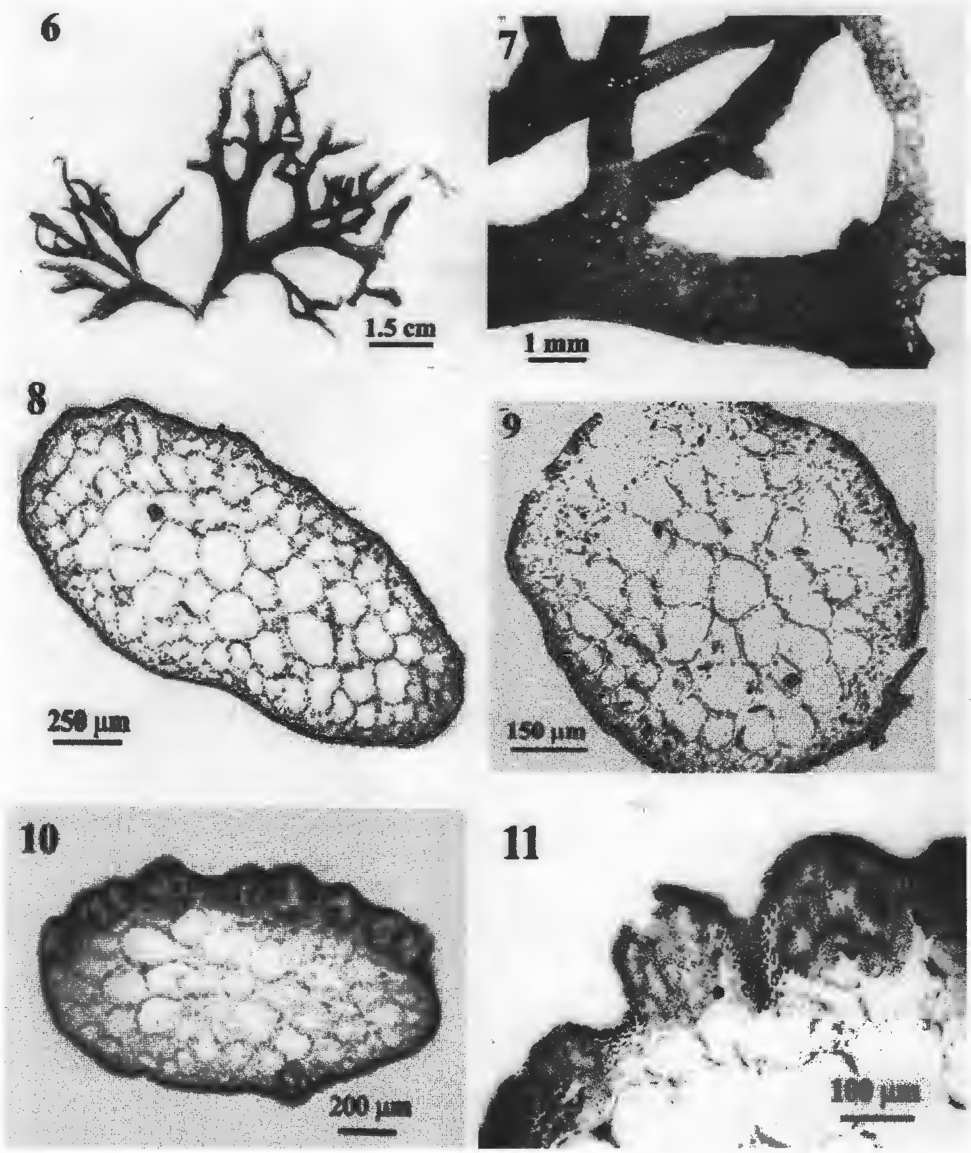
Gracilaria multifurcata Børgesen, Kongel. Danske Vidensk. Selsk. Biol. Meddel 21(9), pp. 42–44, figs. 15–16, 1953. (Figs. 6–16)

Synonyms: *Polycavernosa multifurcata* (Børgesen) Chang et Xia, Stud. Mar. Sinica 3, p. 123, 1963; *Hydropuntia multifurcata* (Børgesen) Wynne, Taxon 38, pp. 477, 1989.

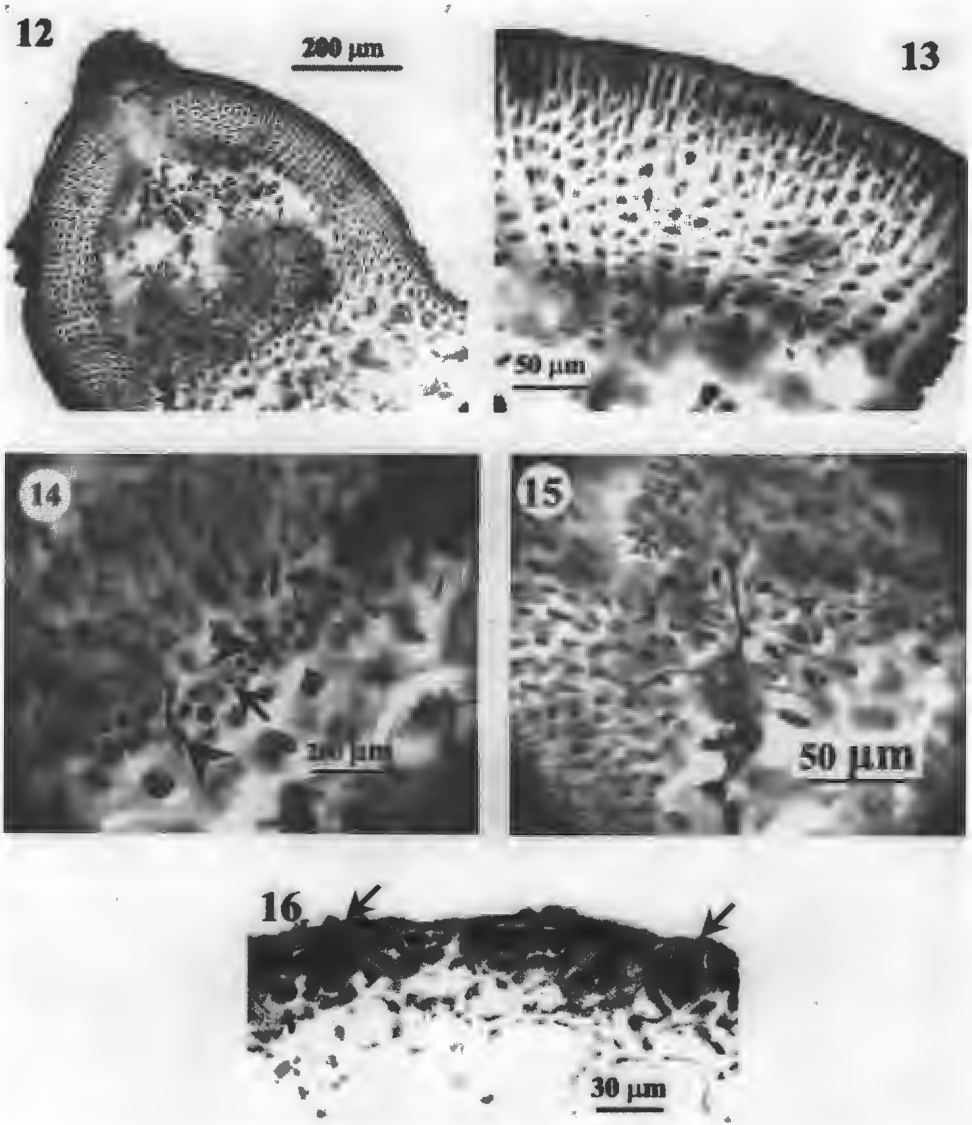
Plant erect, growing from a small discoid holdfast, 2.0–3.5 cm high; di- to trichotomously branched up to 6 orders (Fig. 6). Lower segments compressed 1–2 mm wide, 600 µm thick (Fig. 8), becoming narrower and thicker in higher-order branches, upper-order branches subterete to terete, 1 mm or less in diameter (Fig. 9), apices acute. Plants not adhering well to paper upon drying.

In transverse section, cortex consisting of 1–2 layers of pigmented cells, cells in outermost layer spherical to oval, 4–6 µm tall and 3–4 µm in diameter; medulla 7–8 layers of cells across, transition of cells from medulla to cortex gradual. In compressed portions of thallus, medullary cells oval, innermost medullary cells 150 µm by 220 µm, cell walls thin, 2–4 µm thick.

Cystocarps globose, up to 1 mm in diameter, slightly constricted at base and slightly rostrate (Fig. 12). Pericarp 150–200 µm thick, fastigiate arrangement, up to 15 layers of cells with obscure cell walls (Fig. 13). Gonimoblasts of large cells with obscure cell walls, basal part forming a sill of 2 layers of



Figs. 6–11. *Gracilaria multifurcata.* Fig. 6, Habit of male plant. Fig. 7, Surface view of male conceptacles. Fig. 8, Transverse section of lower part of thallus, showing compressed form. Fig. 9, Transverse section of upper part of thallus, showing terete form. Fig. 10, Transverse section of male plant, showing multi-cavitied conceptacles. Fig. 11, Section of male plant, showing protruding male conceptacles.



Figs. 12–16. *Gracilaria multifurcata.* Fig. 12, Longitudinal section of cystocarp. Fig. 13, Section of pericarp, showing arrangement of cells. Fig. 14, Longitudinal section of cystocarp, showing thin sill (arrow) and absorbing filament (arrow head). Fig. 15, Thick and branched basal absorbing filament. Fig. 16, Transverse section of tetrasporic plant, showing tetrasporangia (arrows).

small cells (Fig. 14). Basal traversing filaments many, thick and branched (Fig. 15), some lateral.

Spermatangial conceptacles multicavitied, width and depth almost the same, 150–220 µm, numerous on one surface and few on the other (Fig. 10). Mature conceptacles protruding from surface, wartlike structures, to 300 µm in diameter (Figs.7, 11).

Tetrasporangial conceptacles with unmodified cortical layer; tetrasporangia cruciately divided, up to 18 µm tall and 10 µm in diameter (Fig. 16).

Type Locality: Pointe aux Sables, Mauritius, South Africa.

Collection Site: Ao Khao Kwai, Ranong Province, Andaman Sea, forming cushions on rope at intertidal level.

Distribution: Indian Ocean (Silva et al. 1996), southwestern Pacific Ocean (Millar 1997), and Malaysia (Terada et al. 2000).

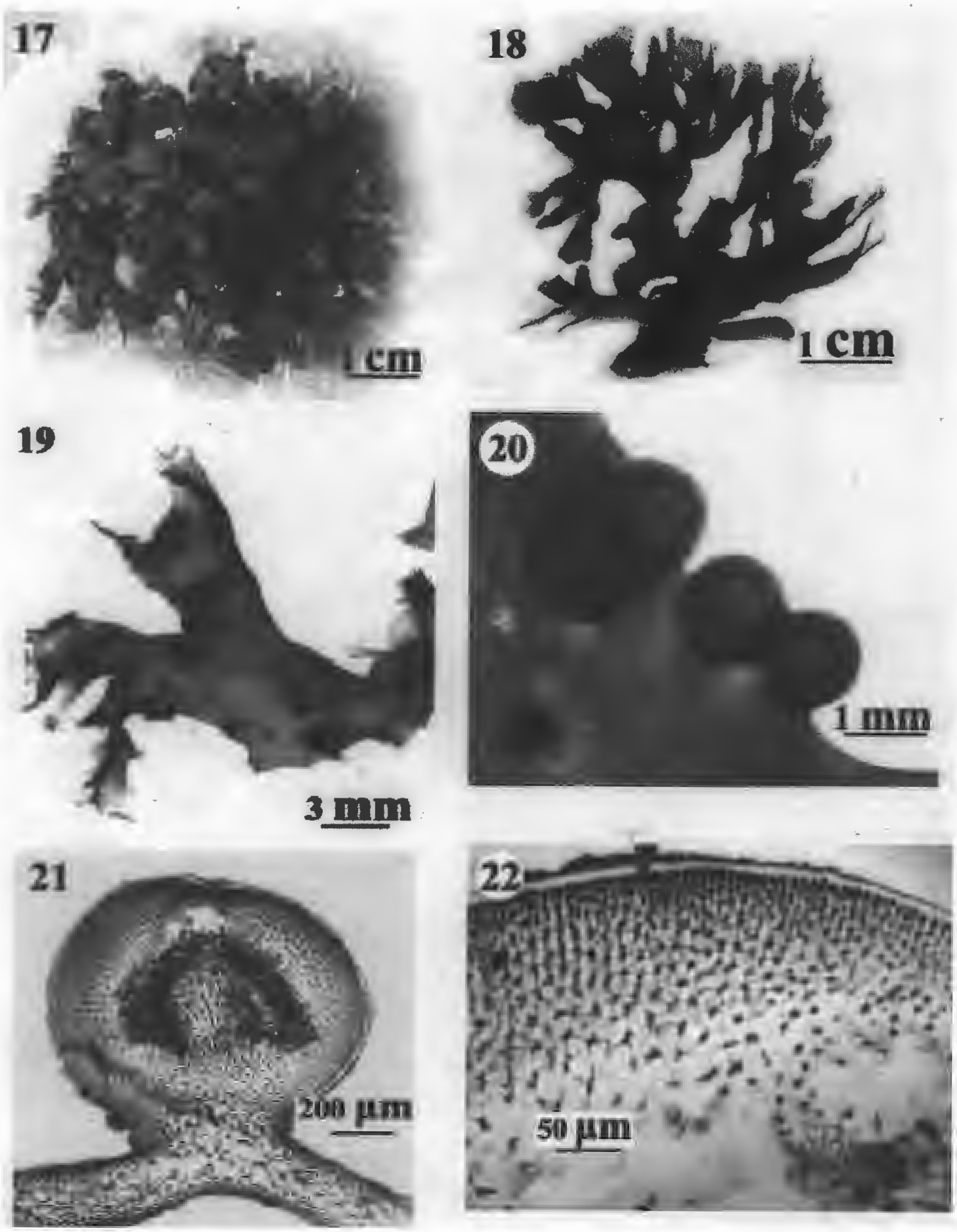
Remarks: The Thai plants are similar to the Australian plants reported by Millar (1997) but much smaller. The Australian plants are up to 22 cm high, up to 22 mm wide at the dichotomies, and 1.2 mm thick, whereas the Thai plants reach only 3.5 cm high, 1–3 mm wide, and 600 µm thick. The Thai plants are, however, similar in size to the Mauritius plants described by Børgesen (1953) as forming extensive cushions about 4 cm high, 1–2 mm broad, and 500 µm thick. The Malaysian plants described by Terada et al. (2000) are 4–16 cm long, up to 2 mm wide, arising from a small discoid holdfast with prostrate rhizome, forming an entangled mass. In external appearance and size, the Thai plants also resemble *G. abbottiana* described by Hoyle (1978) from the Hawaiian Islands. These two are different in compressed portions of thalli: the Thai plant is compressed below, becoming subterete to terete above, whereas *G. abbottiana* is terete below, becoming elliptical to compressed above. In addition, the male conceptacle of the Thai plant is of the multicavitied polycavernosa-type, unlike the verrucosa-type of *G. abbottiana*.

Gracilaria rhodymenioides Millar, Tax. Econ. Seaweeds 6, pp. 114–118, figs. 5–12, 1997. (Figs. 17–28)

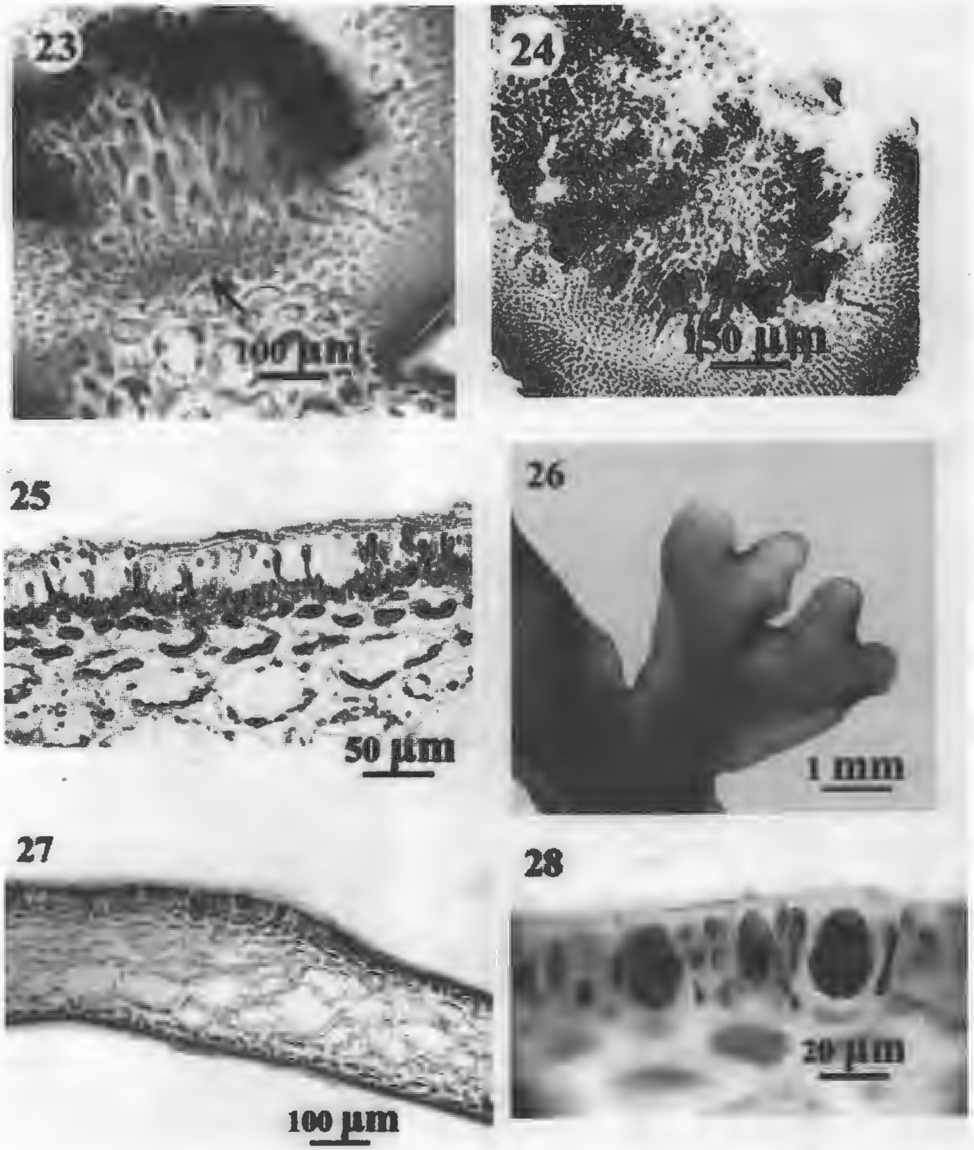
Plant cartilaginous, erect to horizontally spreading, growing in loose to dense tuft (Figs. 17, 18), 2–5 cm high. Prominent stipe, 3–7 mm long and 2–4 mm diameter. Blades flattened, spreading widely from stipe into an erect plant or decumbent and parallel to substratum, with di- or trichotomously to irregularly divided fronds, 2–7 mm wide, up to 1.5 cm at the point of branching, 200–250 µm thick, with entire margins and obtuse apices. Blades of fertile plants sometimes incurved.

In transverse section, plant consisting of a cortex of 1–2 layers of pigmented oval cells, 5–8 µm tall and 3–5 µm in diameter; medulla of large parenchymatous cells, 40–120 µm by 40–80 µm, with walls 4–6 µm thick; transition of cells from medulla to cortex abrupt.

Cystocarps large, present on both surfaces, mainly on underside (Fig. 19) and at blade margin (Fig. 20), globose, constricted at base, non-rostrate (Fig.



Figs. 17–22. *Gracilaria rhodymenioides.* Fig. 17, Habit of plants growing in tuft. Fig. 18, Habit of plant with thick stipe. Fig. 19, Female plant with cystocarps on lower surface. Fig. 20, Enlarged cystocarps on lower surface and at margin. Fig. 21, Longitudinal section of cystocarp. Fig. 22, Section of pericarp, showing arrangement of cells.



Figs. 23–28. *Gracilaria rhodymenioides*. Fig. 23, Longitudinal section of cystocarp, showing large gonimoblasts and thick sill (arrow). Fig. 24, Basal and lateral absorbing filaments. Fig. 25, Transverse section of male plant, showing textorii-type spermatangia with modified elongated cortical cells. Fig. 26, Part of tetrasporic plant with thick uplifting patches. Fig. 27, Transverse section of tetrasporic plant, showing tetrasporangia on surface. Fig. 28, Tetrasprangia with modified elongated cortical cells.

21), up to 2.2 mm in diameter. Pericarp thick, 200–280 µm, up to 18 layers of cells with obscure cell walls (Fig. 22); cells of outer layers ovoid to oblong, middle layers with stellate plastids connected by elongated arms, innermost layers small and compressed. Gonimoblast consisting of moderate to large cells with obscure cell walls; basal part of gonimoblast forming thick sill of 4–5 layers of small cells (Fig. 23). Traversing filaments many basal, few lateral (Fig. 24) and occasionally at upper portion.

Spermatangial conceptacles of deep textorii-type, confluent, present on one side of blade, elevating from surface to form a thick patch to 50 µm thick with modified, elongated cortical cells (Fig. 25). Spermatangial plants pale in color.

Tetrasporangial conceptacles with modified cortical layer in thick nemathecial patches (Fig. 26), present only on one side of blade (Fig. 27), pinkish in color. Mature tetrasporangia cruciately divided (Fig. 28), 20–35 µm tall and 14–20 µm in diameter.

Type Locality: Coffs Harbour, New South Wales, Australia.

Collection Site: Ta Mong Lai, Prachuap Khiri Khan Province, on the west coast of the Gulf of Thailand.

Remarks: The Thai plants are quite similar in external appearance and anatomical features to *G. rhodymenioides* from Australia described by Millar (1997) and Millar and Xia (1999), except that the Thai plants seem to be smaller, only up to 4 cm high, whereas the Australian plants reach 11 cm high. In addition, no male plants bearing spermatangia have been discovered in the Australian plants, whereas the Thai specimens show the deep textorii-type in the male plants.

The specimens from Thailand also resemble *G. vieillardii* from Australia (monoecious specimen MELU 24327) (Withell et al. 1994) in the horizontally spreading blades and the presence of tetrasporangia on one side of the blade only. The Thai plants appear to differ from *G. vieillardii* in having entire margins, whereas the latter species shows many spines on the blade margins.

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Literature Cited

Abbott, I. A. 1988. Some species of *Gracilaria* and *Polycavernosa* from Thailand. In: Tax. Econ. Seaweeds 2, pp. 137–150.

Børgesen, F. 1953. Some marine algae from Mauritius: Additions to the parts previously published. Kongel. Danske Vidensk. Selsk. Biol. Meddel. 21(9):1–62, 2 plates.

Chirapart, A., and Ruangchauy, R. 1999. A new record of *Gracilaria, G. rubra* C. F. Chang et B. M. Xia from Thailand. In: Tax. Econ. Seaweeds 7, pp. 137–143.

Hoyle, M. D. 1978. *Gracilaria abbottiana* sp. nov. (Rhodophyta, Gigartinales): A second intertidal species of *Gracilaria* from the island of Oahu, Hawaii. Phycologia 17(3):299–303.

Lewmanomont, K. 1994. The species of *Gracilaria* from Thailand. In: Tax. Econ. Seaweeds 4, pp. 135–148.

Lewmanomont, K. 1995. *Gracilaria urvillei* (Montagne) Abbott: A new record for Thailand. In: Tax. Econ. Seaweeds 5, pp. 223–226.

Millar, A. J. K. 1997. Some flattened species of *Gracilaria* from Australia. Tax. Econ. Seaweeds 6, pp. 111–123.

Millar, A. J. K., and Xia Bangmei. 1999. The genus *Gracilaria* and *Gracilariopsis* from Norfolk Island, Southwestern Pacific. In: Tax. Econ. Seaweeds 7, pp. 113–119.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. University of California Press, Berkeley. 1259 pp.

Terada, R., Kawaguchi, S., Masuda, M., and Phang, S. M.. 2000. Taxonomic notes on marine algae from Malaysia: III. Seven species of Rhodophyceae. Bot. Mar. 43:347–357.

Withell, A. F., Millar, A. J. K., and Kraft, G. T. 1994. Taxonomic studies of the genus *Gracilaria* (Gracilariales, Rhodophyta) from Australia. Austral. Syst. Bot. 7:281–352.

Zhang, Junfu, Xia Bangmei, Wang Yongchuan, and Pan Guoying. 1995. Additions to the species of *Gracilaria* from China. In: Tax. Econ. Seaweeds 5, pp. 197–205.

A COMPARISON OF THE NUTRITIONAL CONTENT OF HAWAIIAN *GRACILARIA* SPECIES

Karla J. McDermid and Brooke Stuercke

Abstract

Four species of *Gracilaria* commonly eaten in Hawaii, *G. coronopifolia* J. Agardh, *G. parvispora* Abbott, *G. salicornia* (C. Agardh) Dawson, and *G. tikvahiae* McLachlan, from five locations, including wild, pond-raised, and tank-cultured populations, were analyzed for ash, protein, carbohydrate, lipid, caloric, vitamin, and mineral content. Tank-cultured *G. coronopifolia* and *G. salicornia* showed protein values above 10% of dry weight. Soluble carbohydrate content ranged from 14.3 to 24.6% of dry weight. All samples contained less than 4.5% crude lipid. The highest energy value was measured in *G. tikvahiae* (1856.8 cal/g). A number of *Gracilaria* samples contained measurable quantities of beta carotene, niacin, and several minerals. Inter- and intraspecific variation in nutritional composition may be due to environmental as well as genetic factors.

Introduction

Species of *Gracilaria* are well known as sources of commercial agar (Lewis et al. 1988; Armisen 1995) and are often the subject of studies on taxonomy (Abbott 1985; Bird 1995; Terada and Yamamoto 2000), agar quality (Santos and Doty 1983; Guerin and Bird 1987; Hurtado-Ponce and Umezaki 1988; Oyieke 1994; Murano 1995; Freile Pelegrin et al. 2002), cultivation (Santelices et al. 1984; Smith et al. 1984; Edding et al. 1987; Santelices and Doty 1989; Dawes 1995; Friedlander and Levy 1995; Buschmann et al. 2001), molecular biology (Goff et al. 1994; Lim et al. 2001; Bellorin et al. 2002), and ecology (Hoyle 1978; Gao et al. 1993; Sfriso et al. 1994; Kain and Destombe 1995; Molloy and Bolton 1995; Glenn et al. 1999). *Gracilaria* species are also consumed as "sea vegetables" for the "whole-piece" food market (Fortner 1978; Abbott 1988). In Hawaii, *Gracilaria* species known as *limu manauea* and *limu ogo* are usually eaten fresh with raw fish in Hawaiian *poke* dishes, but they are also sold pickled, salted, prepared as Japanese-style *namasu* or Korean *kim chee,* and even dried in packages of "instant *poke*" (Abbott 1978, 1988, 1996). The State of Hawaii reported the harvest and sales of 4,240 pounds of wild *Gracilaria* in 2001 with a value of US$10,785 (DNLR 2002), which would account for an estimated 5% of the total quantity of cultured species.

Nine species of *Gracilaria* are present in the Hawaiian Islands (Abbott 1999). *Gracilaria abbottiana* Hoyle, *G. coronopifolia* J. Agardh, *G. dawsonii* Hoyle, *G. dotyi* Hoyle, *G. epihippisora* Hoyle, and *G. parvispora* Abbott are endemic species; *G. lemaneiformis* (Bory) Greville is indigenous. *Gracilaria salicornia* (C. Agardh) Dawson, an species introduced to the Hawaiian Islands, is also widely distributed in the Indian and warm Pacific Oceans (Silva et al. 1996). In 1987, *G. tikvahiae* McLachlan was brought to the Hawaiian Islands from Florida for use in commercial mariculture, in order to offset the low market supplies of *G. parvispora* (Abbott 1999). Although the nutritional composition has been analyzed for some *Gracilaria* species from the Caribbean (Burkholder et al. 1971), China (Fan et al. 1993), India (Marolia et al. 1982), Japan (Arasaki and Arasaki 1983; Ito and Hori 1989), Malaysia (Norziah and Ching 2000), Mexico (Robledo and Freile Pelegrin 1997), Pakistan (Qasim 1986), and the Philippines (Portugal et al. 1983), published information on Hawaiian *Gracilaria* nutritional value is limited (Reed 1907; Harry 1934). A recent study of the proximate, vitamin, and mineral composition of 22 species of edible Hawaiian seaweeds included data on 3 *Gracilaria* species (McDermid and Stuercke, in press). This workshop paper examines not only interspecific differences in ash, protein, carbohydrate, lipid, caloric, vitamin, and mineral content of Hawaiian *Gracilaria* but also intraspecific variation among wild and cultivated populations from different islands.

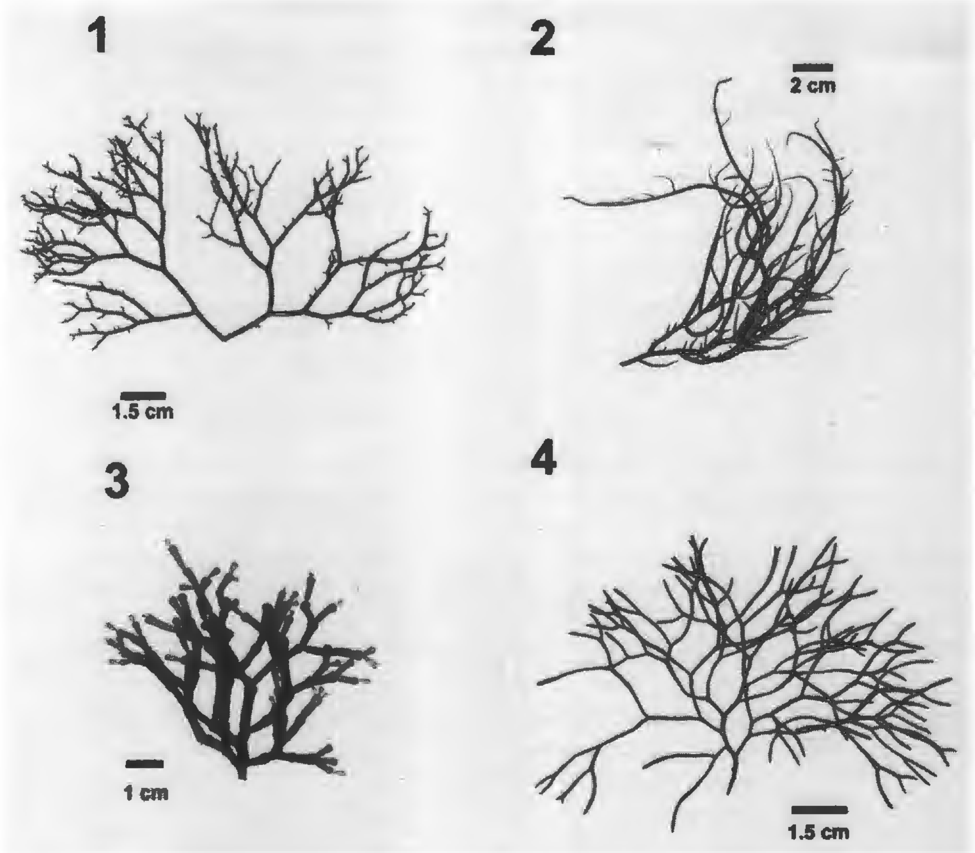
Materials and Methods

Collection. Samples of *G. coronopifolia, G. parvispora, G. salicornia,* and *G. tikvahiae* (Table 1 and Figs. 1–4) were collected in food-grade plastic bags (approximately 1 kg fresh weight consisting of at least 20 different thalli from each population) and transported to the laboratory in insulated containers. Samples were identified to genus and species on the basis of morphological and anatomical characteristics per Abbott (1999). Voucher specimens were selected, photographed, and prepared as dried herbarium specimens deposited in the Bishop Museum herbarium in Honolulu (BISH).

Sample Preparation. Within 6 hours of collection, fresh plants were thoroughly washed three times in filtered seawater. Any epiphytic algae, invertebrates, sand, or debris were removed. Samples were divided into portions (50–200 g each), spun in a salad spinner for 30 s to remove excess water, and then weighed (wet weight). All portions were placed on aluminum foil trays and dried to a constant weight at 60°C in an air oven. The key part of this procedure was to dry the sample to a constant weight before bacterial decay could begin, and at a temperature that caused the least modification of chemical composition. The dried samples were then ground into a fine powder (to pass through a 1 mm sieve) in a coffee grinder or analytical mill (IKA A11) and then stored in air-tight, labeled glass jars in a refrigerator at 4°C. All chemical analyses were conducted in triplicate on dried ground material, except in ash determination, for which 5 replicates were used. All values were reported relative to the dry weight of the seaweed. Mean values and standard error (*SE* = standard deviation/square root of the sample size) were calculated.

Table 1. Hawaiian *Gracilaria* Species Collected and Analyzed

Species	Coll. #	Location, Island	Date coll.
G. coronopifolia	NC012	Royal Hawaiian Sea Farms, Hawaii	11/20/01
G. parvispora	NC003	Royal Hawaiian Sea Farms, Hawaii	10/23/01
G. parvispora	NC031	Ke Kuaaina Hanauna Hou, Molokai	03/12/02
G. salicornia	NC006	Onekahakaha Beach Park, Hawaii	10/24/01
G. salicornia	NC007	Royal Hawaiian Sea Farms, Hawaii	10/30/01
G. salicornia	NC010	Heeia Fish Ponds, Oahu	11/07/01
G. salicornia	NC025	Kaneohe Bay, Oahu	02/13/02
G. salicornia	NC032	Ke Kuaaina Hanauna Hou, Molokai	03/12/02
G. tikvahiae	NC009	Royal Hawaiian Sea Farms, Hawaii	11/06/01
G. tikvahiae	NC011	Royal Hawaiian Sea Farms, Hawaii	11/13/01
G. tikvahiae	NC013	Royal Hawaiian Sea Farms, Hawaii	11/27/01



Figs. 1–4. Fig. 1, Tank-cultured *Gracilaria coronopifolia* (NC012), Hawaii. Fig. 2, Pond-grown *G. parvispora* (NC031), Molokai. Fig. 3, Wild *G. salicornia* (NC025), Oahu. Fig. 4, Tank-cultured *G. tikvahiae* (NC009), Hawaii.

Water Content of Fresh Plants. The water content of the fresh material was calculated as the difference between the dried sample weight and the spun wet weight for each of the portions of the total sample.

Ash Determination. Ash content was determined by heating the samples for 4 h at 500°C following the Association of Official Analytical Chemists (1995) methods as modified by Robledo and Friele Pelegrin (1997).

Total Protein Analysis. The Lowry method was used for protein determination (Lowry et al. 1951; Harrison and Thomas 1988). The samples were digested in 1 N NaOH, then allowed to react with an alkaline copper citrate solution and Folin-Ciocalteau phenol reagent to measure protein concentration colorimetrically based on absorptions at 660 nm in a Beckman Coulter DU 640 spectrophotometer and compared to a bovine serum albumin standard.

Soluble Carbohydrate Content. Soluble carbohydrates were extracted from samples in 5% trichloroacetic acid, and concentrations were determined by the phenolic sulfuric acid colorimetric method outlined in Dubois et al. (1956) and used on Mexican seaweeds by Robledo and Friele Pelegrin (1997). Percent soluble carbohydrate was calculated based on absorptions at 490 nm in a Beckman Coulter DU 640 spectrophotometer and compared to a glycogen standard.

Crude Lipid Analysis. A gravimetric method was used similar to that of Chan et al. (1997) in which crude lipid was extracted in a chloroform/methanol (2:1, v/v) mixture, then purified according to Folch et al. (1957) and evaporated to dryness under a stream of filtered nitrogen gas and weighed.

Caloric Value. Pressed pellets of 0.1–0.2 g of dried powder were combusted in a Parr 1425 Semimicro Calorimeter standardized with benzoic acid. Total calories were calculated on an ash-free basis (Carefoot 1985).

Vitamin A, B complex, and C Analyses. Samples were sent to an independent chemical analysis laboratory (Industrial Labs in Denver, Colorado, USA). This lab uses methodologies as specified by the Association of Official Analytical Chemists, the Institute for Nutraceutical Advancement, the Food and Drug Administration, and the American Association of Cereal Chemists. Vitamin B complex and vitamin C content of the seaweed samples was determined using HPLC, and beta carotene content was measured spectrophotometrically.

Mineral Analyses. Samples of dried ground material were sent to an independent laboratory for analysis (Waters Agricultural Laboratories, Georgia, USA). This lab uses official methods of analysis of the Association of Official Analytical Chemists and the Association of Florida Phosphate Chemists.

Statistical Analysis. Data for total protein, soluble carbohydrate, crude lipid, and caloric content were analyzed statistically. First, each data set was checked for equal variance by using Bartlett's and Levene's tests. One-way analysis of variance (ANOVA) was carried out for each nutritional component. Tukey's pairwise comparison test was employed to differentiate where the differences existed between groups.

Results

This study completed the nutritional analysis of 4 species of *Gracilaria*, including 2 native and 2 introduced species, from five different locations in the Hawaiian Islands, including wild, pond-grown, and tank-cultured populations (Table 2). Water content of fresh plants was consistently high, ranging from 89.3 to 92.9%. Ash content ranged from 44.3 to 61.7% of dry weight (Fig. 5). Tank-cultured *G. salicornia* (NC007) and *G. coronopifolia* (NC012) both showed protein values above 10% of dry weight (Fig. 6). Soluble carbohydrate values ranged from 14.3 to 24.6% of dry weight (Fig. 7). All samples contained less than 3% crude lipids (Fig. 8), except *G. salicornia* from Molokai ponds (NC032) and *G. salicornia* from tanks on the island of Hawaii (NC007), 4.4% of dry weight and 3.4% of dry weight, respectively. The highest energy value was measured in *G. tikvahiae* (1856.8 cal/g), and the lowest was found in *G. salicornia* (702.2 cal/g) (Fig. 9).

The 11 sample variances were found to be homogeneous. ANOVA indicated that there was a significant difference among the *Gracilaria* samples for total protein ($P < 0.001$), soluble carbohydrate ($P < 0.001$), crude lipid ($P = 0.048$), and calories ($P < 0.001$). Where two samples were significantly different from each other ($P < 0.001$) for a nutritional characteristic, that component (protein, carbohydrate, lipid, and calories) is listed in the appropriate box in Table 3. *Gracilaria salicornia* (NC025) from Kaneohe Bay showed the greatest number of statistically significant pairwise differences (21 out of a possible 40). Protein content was the significantly different component in 28 of the 55 possible paired comparisons. In terms of lipids, however, no pair of samples met the criteria for Tukey's pairwise comparison.

A number of samples showed high amounts of beta carotene (vitamin A) (Table 4). For instance, the beta carotene concentration in wild *G. salicornia* from Kaneohe Bay, Oahu, was 230 IU/gram dry weight. Niacin (vitamin B_3) was present in measurable quantities in *G. coronopifolia, G. salicornia,* and *G. tikvahiae*. Only *G. parvispora* exhibited detectable levels of riboflavin (vitamin B_2), and vitamin C could be quantified only in *G. tikvahiae*. Several minerals were abundant in the *Gracilaria* samples, notably potassium (K), boron (B), zinc (Zn), manganese (Mn), and iron (Fe) (Table 5). Iron values ranged from 79 to 356 ppm based on dry weight. Calcium (Ca) content was low, ranging from 0.18% in *G. coronopifolia* to 0.96% in *G. salicornia.*

Gracilaria salicornia samples were collected from three of the eight main Hawaiian islands from wild, pond-raised, and tank-cultured populations. A comparison of proximate constituents among *G. salicornia* samples showed no consistent patterns (Fig. 10). Pond-grown *G. salicornia* (NC032 and NC010) showed the highest amounts of ash: 61.7% of dry weight. Tank-cultured *G. salicornia* (NC007) was significantly higher in protein than the wild and pond-grown samples. Overall, wild *G. salicornia* (NC025 and NC006) contained the highest amount of carbohydrates and the lowest quantity of lipids.

Table 2. Proximate Compostition and Caloric Content of Hawaiian *Gracilaria* Species

Species (Coll. #)	Water (%)	Ash (%)	Total Protein (%)	Soluble Carbs (%)	Crude Lipid (%)	Calories (cal/g)
G. coronopifolia (NC012)	89.4 ± 0.1	53.4 ± 0.1	10.5 ± 1.3	15.2 ± 0.3	2.1 ± 0.1	1266.6 ± 90.2
G. parvispora (NC003)	91.5*	49.7 ± 0.5	8.3 ± 0.2	17.5 ± 1.5	2.7 ± 0.2	1345.6 ± 28.0
G. parvispora (NC031)	90.4 ± 0.1	48.1 ± 0.4	7.6 ± 0.4	22.9 ± 0.9	2.8 ± 0.3	1358.5 ± 66.4
G. salicornia (NC006)	90.4*	52.9 ± 1.1	5.6 ± 0.4	20.0 ± 0.7	2.4 ± 0.4	1012.7 ± 12.9
G. salicornia (NC007)	92.2*	57.3 ± 0.6	11.4 ± 0.1	14.3 ± 1.2	3.4 ± 0.7	928.0 ± 9.0
G. salicornia (NC010)	92.9 ± 0.4	61.7 ± 0.8	4.3 ± 0.5	18.5 ± 1.5	2.8 ± 0.4	799.5 ± 29.0
G. salicornia (NC025)	90.1 ± 0.2	49.5 ± 1.4	3.9 ± 0.4	24.6 ± 0.6	1.5 ± 0.1	1445.9 ± 52.5
G. salicornia (NC032)	92.2 ± 0.1	61.7 ± 0.4	4.6 ± 0.6	17.2 ± 0.27	4.4 ± 0.1	702.2 ± 29.7
G. tikvahiae (NC009)	90.5 ± 0.1	50.3 ± 0.3	8.3 ± 0.5	17.1 ± 0.2	1.6 ± 0.1	1171.1 ± 21.6
G. tikvahiae (NC011)	90.7 ± 0.1	48.8 ± 0.2	9.3 ± 0.5	14.9 ± 0.5	1.9 ± 0.2	1228.4 ± 27.8
G. tikvahiae (NC013)	89.3 ± 0.2	44.3 ± 0.1	9.5 ± 0.3	18.6 ± 0.4	2.1 ± 0.2	1856.8 ± 221.3

Values are mean ± standard error.
Water content is relative to total fresh weight. Ash, protein, carbohydrate, lipid, and energy values are relative to total dry weight.
*Standard error not calculated for this analysis.

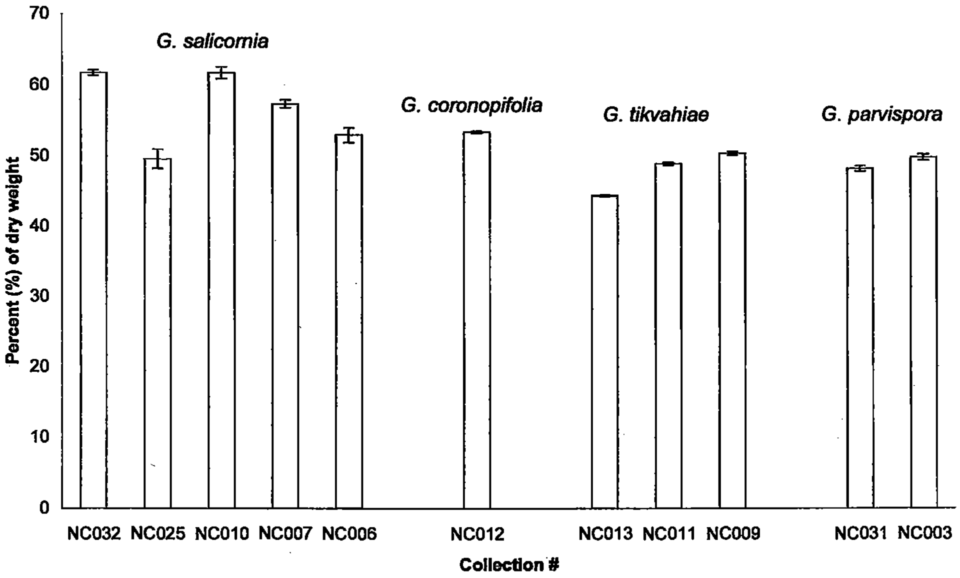


Fig. 5. Mean ash content (% of dry weight) of Hawaiian *Gracilaria* grouped by species. Bars indicate the standard error (SE) of the mean.

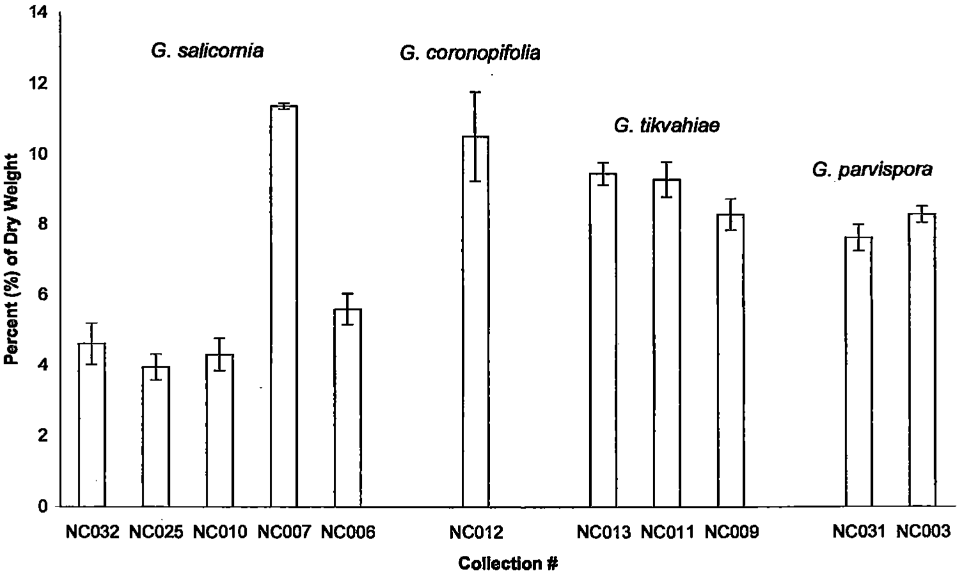


Fig. 6. Mean total protein content (% of dry weight) of Hawaiian *Gracilaria* grouped by species. Bars indicate the standard error (SE) of the mean.

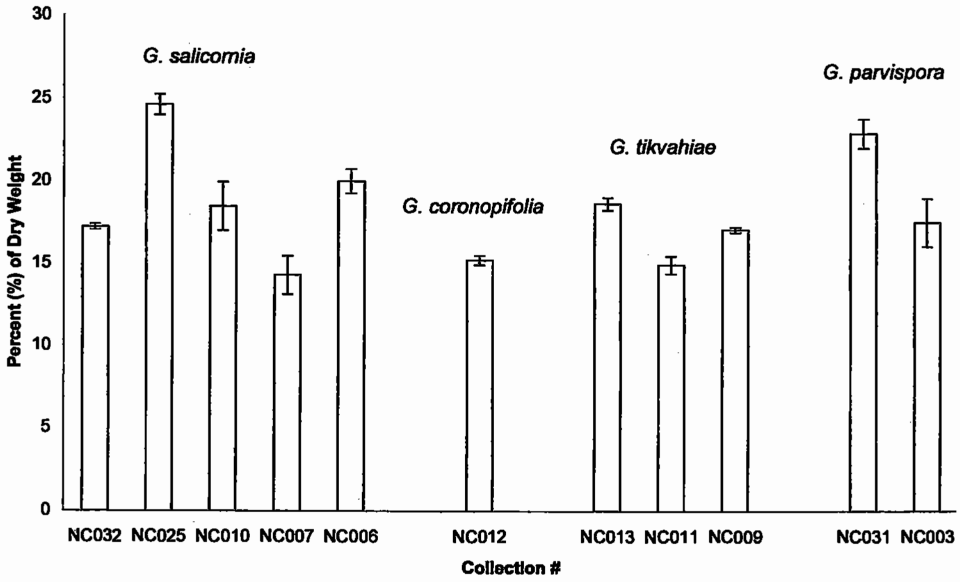


Fig. 7. Mean soluble carbohydrate content (% of dry weight) of Hawaiian *Gracilaria* grouped by species. Bars indicate the standard error (SE) of the mean.

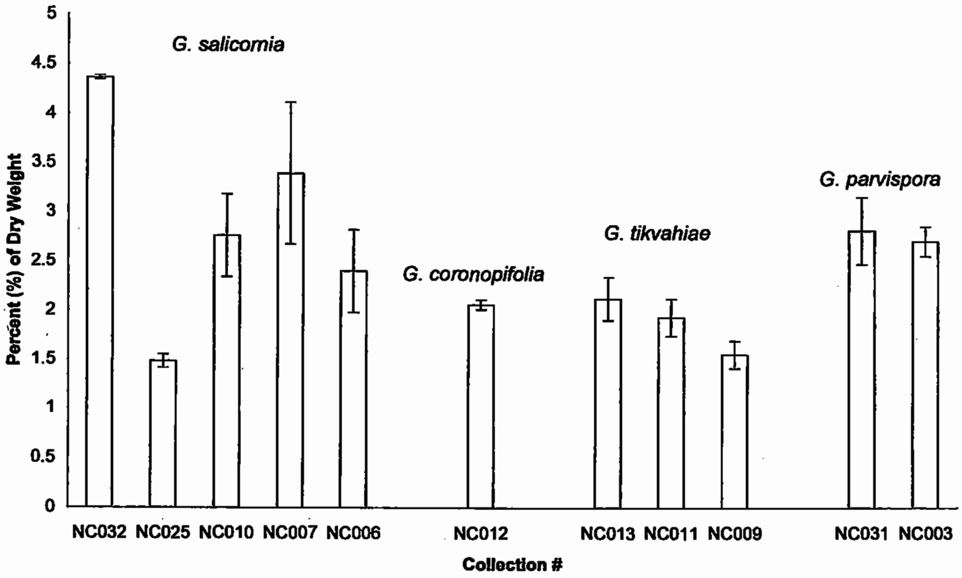


Fig. 8. Mean crude lipid content (% of dry weight) of Hawaiian *Gracilaria* grouped by species. Bars indicate the standard error (SE) of the mean.

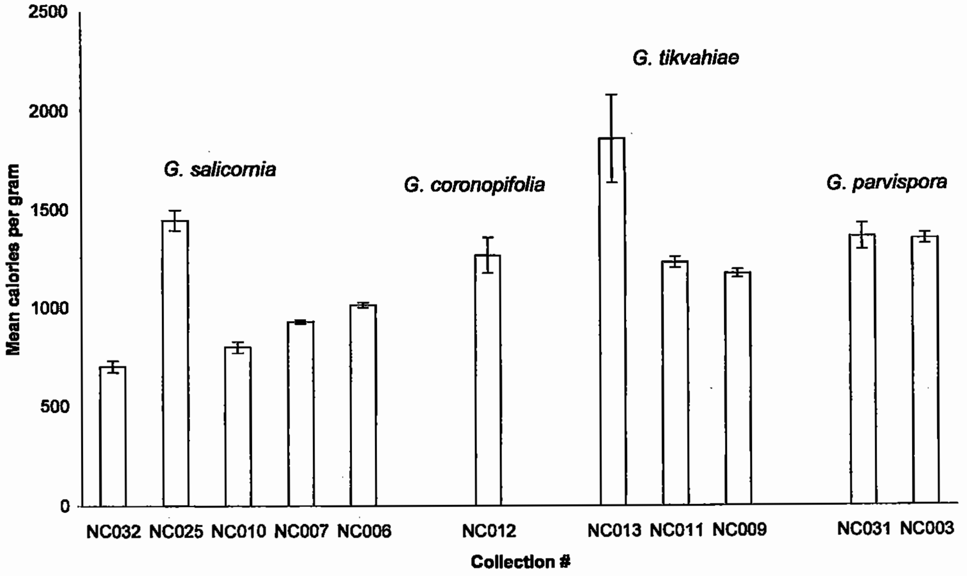


Fig. 9 Mean ash-free caloric content (calories/g of dry weight) of Hawaiian *Gracilaria* grouped by species. Bars indicate the standard error (SE) of the mean.

Discussion

The nutritional values reported in this paper for Hawaiian *Gracilaria* species are comparable to previous reports on *Gracilaria* species from around the world in Table 6. The ash content of Hawaiian *Gracilaria* species in the current study is higher than in previous studies. *Gracilaria coronopifolia* in this study contained 53.4% ash, which is considerably higher than ash values reported for the same species by other researchers: 17.8% (Reed 1907) and 20.9% (Portugal et al. 1983). Protein levels measured in the current study are within the range of those in most other studies. *Gracilaria salicornia* from China contained 11.34% protein (Fan et al. 1993), similar to tank-cultured *G. salicornia* in the present study. Hawaiian *Gracilaria* species showed a narrower range of carbohydrate values (14.3–24.6% of dry weight) compared to other *Gracilaria* species, whose carbohydrate values ranged from 25.8 to 68.1% of dry weight. Lipid values in this study show higher levels for *G. salicornia* (1.5–4.4% of dry weight) and *G. coronopifolia* (2.1% of dry weight) than in other studies on *G. salicornia* (0.4% of dry weight; Fan et al. 1993) and *G. coronopifolia* (0.1–0.8% of dry weight; Reed 1907; Portugal et al. 1983). Some of the variation in results among studies may be due to differences in methods; some authors, for example, determined protein content by

Table 3. Results of Tukey's Pairwise Comparison of *Gracilaria* Samples for Significant Difference in Proximate Composition and Calories

Collection #	NC003	NC006	NC007	NC009	NC010	NC011	NC012	NC013	NC025	NC031	NC032
NC003		•	•	•	•	•	•	•	•	•	•
NC006	Calories		•	•	•	•	•	•	•	•	•
NC007	Protein	Carbos Protein		•	•	•	•	•	•	•	•
NC009	n.s.	n.s.	Protein		•	•	•	•	•	•	•
NC010	Calories Protein	n.s.	Protein	Protein		•	•	•	•	•	•
NC011	n.s.	Carbos Protein	n.s.	n.s.	Protein		•	•	•	•	•
NC012	n.s.	Carbos Protein	n.s.	n.s.	Protein	n.s.		•	•	•	•
NC013	Calories	Calories Protein	Calories Carbos	Calories	Calories Protein	Calories	Calories		•	•	•
NC025	Carbos Protein	Calories Carbos	Calories Carbos Protein	Carbos Protein	Calories Carbos	Carbos Protein	Carbos Protein	Calories Carbos Protein		•	•
NC031	Carbos	n.s.	Calories Carbos Protein	Carbos	Calories Carbos Protein	Carbos	Carbos Protein	Calories	Protein		•
NC032	Calories Protein	n.s.	Protein	Calories Protein	n.s.	Calories Protein	Calories Protein	Calories Protein	Calories Carbos	Calories Carbos Protein	

Nutritional component listed if $P< 0.001$.
n.s. = no significant difference.

Table 4. Vitamins A, B_2, B_3, and C Content of Hawaiian *Gracilaria* samples

Species (Coll. #)	A IU/g	B_3 mg/g	B_2 mg/g	C mg/g
G. coronopifolia (NC012)	15	0.70	–	–
G. parvispora (NC003)	–	–	–	–
G. parvispora (NC031)	–	–	0.006	–
G. salicornia (NC006)	60	–	–	–
G. salicornia (NC007)	26	–	–	–
G. salicornia (NC010)	8	–	–	–
G. salicornia (NC025)	230	0.08	–	–
G. salicornia (NC032)	55	0.10	–	–
G. tikvahiae (NC009)	–	0.20	–	–
G. tikvahiae (NC011)	–	0.30	–	0.3
G. tikvahiae (NC013)	41	0.22	–	–

All values based on dry weight.
Blank values indicate that vitamin content not detected at method detection limit.

measuring nitrogen (N) and then multiplying the value by 6.25, while others used the Lowry method, which is specific for protein.

In this study on Hawaiian *Gracilaria*, interspecific differences in ash, protein, carbohydrate, lipid, caloric, vitamin, and mineral content as well as intraspecific variation among wild and cultivated populations from different islands were found. For instance, tank-cultured *G. coronopifolia, G. parvispora,* and *G. tikvahiae* contained the highest amounts of nitrogen and phosphorus. Wild *G. salicornia* exceeded all other *Gracilaria* samples in terms of beta carotene concentration. In contrast, *G. parvispora* samples from two different islands—Molokai and Hawaii—displayed similar values for all constituents. Variation among samples may be due to different environmental conditions, especially nutrient content of ambient seawater; however, temperature, light, and water motion may also affect the proximate, mineral, and vitamin composition of seaweeds. In addition, age, health, and reproductive state can influence allocation of resources within plants and may account for variation in nutritional composition of seaweeds. Genetic differences among species and among populations may control biochemical composition. Further studies are needed to assess the interaction of these factors. Controlled laboratory or aquaculture farm experiments would be valuable to determine the relationships among genetic strains, nutrient levels in seawater, and nutritional composition of seaweeds.

Table 5. Comparison of Selected Minerals in Hawaiian *Gracilaria* Based on Dry Weight

Species	Coll. #	N %	P %	K %	Mg %	Ca %	S %	B ppm	Zn ppm	Mn ppm	Fe ppm	Cu ppm
G. coronopifolia	NC012	3.04	0.38	22.16	0.34	0.18	5.25	244.47	42.12	57.11	135.98	1.90
G. parvispora	NC003	2.78	0.26	18.12	0.40	0.20	4.14	224.40	12.98	20.98	120.09	1.56
G. parvispora	NC031	1.48	0.15	16.00	0.49	0.38	3.99	242.00	8.00	48.00	198.00	3.00
G. salicornia	NC006	1.12	0.17	17.97	0.51	0.73	3.95	404.24	16.39	10.27	355.89	5.13
G. salicornia	NC007	0.71	0.27	23.11	0.44	0.34	2.77	336.28	8.72	12.45	107.80	2.30
G. salicornia	NC010	1.12	0.13	22.24	0.41	0.28	3.45	412.56	12.57	303.87	356.79	4.81
G. salicornia	NC025	0.70	0.16	18.30	0.47	0.96	5.35	442.00	6.00	3.00	79.00	2.00
G. salicornia	NC032	0.90	0.16	25.70	0.37	0.28	3.51	386.00	14.00	18.00	99.00	5.00
G. tikvahiae	NC009	2.52	0.38	22.05	0.32	0.22	3.64	227.29	10.49	28.25	238.97	2.13
G. tikvahiae	NC011	2.75	0.39	19.27	0.42	0.22	3.15	258.26	13.51	67.19	299.28	3.44
G. tikvahiae	NC013	2.77	0.31	17.41	0.44	0.22	4.25	250.59	16.72	21.51	162.55	2.67

Table 6. Nutritional Composition of *Gracilaria* Species in Previous Studies

Species	Ash (%)	Protein (%)	Carbs (%)	Lipid (%)	Source
G. arcuata Zanardini	26.4	9.9	55.1	1.3	Portugal et al. 1983
G. changii (B. Xia et Abbott) Abbott, Zhang, et Xia	22.7	6.9	–	3.3	Norziah and Ching 2000
G. chorda Holm	36.0	19.4	35.2	0.3	Fan et al. 1993
G. cornea [=*Hydropuntia correa* (J. Agardh) Wynne]	29.1	5.5	–	–	Robledo and Freile Pelegrin 1997
G. coronipifolia J. Agardh	20.9	9.8	41.8	0.8	Portugal et al. 1983
G. coronopifolia	17.8	7.9	61.4	0.1	Reed 1907
G. corticata (J. Agardh) J. Agardh	–	–	–	1.1	Marolia et al. 1982
G. corticata	–	–	–	2.9	Qasim 1986
G. domingensis (Kützing) Sonder ex Dickie	40.3	8.2	47.2	0.2	Burkholder et al. 1971
G. eucheumatoides Harv.	17.9	5.3	61.1	2.7	Portugal et al. 1983
G. heterocladia Zhang et Xia	46.0	8.8	36.7	0.2	Fan et al. 1993
G. salicornia (C. Agardh) Dawson	47.5	11.4	25.8	0.4	Fan et al. 1993
G. sjoestedtii Kylin	21.0	30.0	42.6	0.7	Fan et al. 1993
G. sp.	17.8	7.9	–	0.1	Arasaki and Arasaki 1983
G. verrucosa (Hudson) Papenfuss	2.5	2.3	–	0.2	Arasaki and Arasaki 1983
G. verrucosa	11.0	9.6	68.1	1.0	Portugal et al. 1983

Blank values indicate that the nutritional component was not tested.

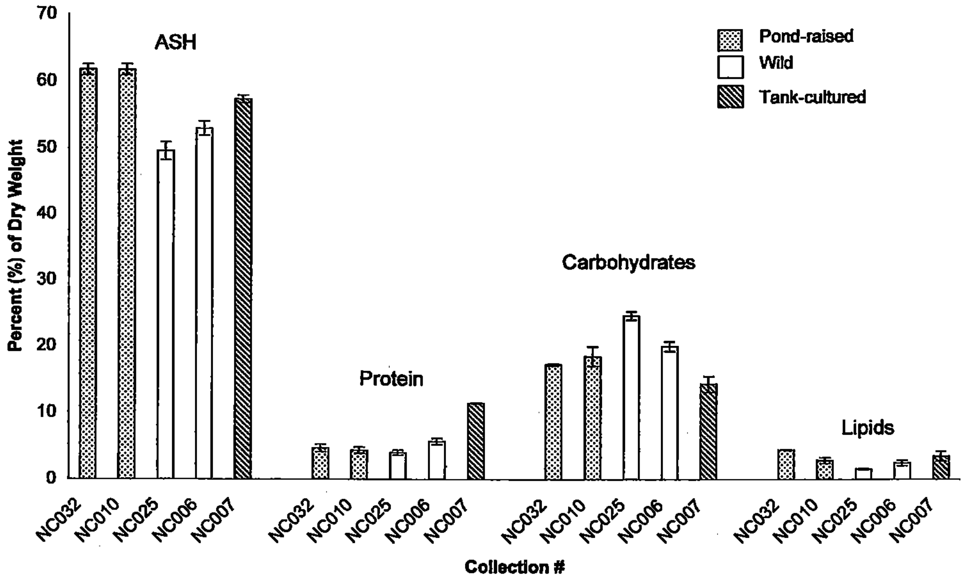


Fig. 10. Comparison of proximate constituents (% of dry weight) in wild, pond-raised, and tank-cultured *G. salicornia*. Bars indicate the standard error (SE) of the mean.

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Literature Cited

Abbott, I. A. 1978. The uses of seaweed as food in Hawaii. Econ. Bot. 32:409–412.

Abbott, I. A. 1985. *Gracilaria* from Hawaii: Key, list, and distribution of the species. In: Tax. Econ. Seaweeds 1, pp. 85–87.

Abbott, I. A. 1988. Food and food products from seaweeds. In: Lembi, C. A., and Waaland, J. R. (eds.), Algae and human affairs, pp. 135–147. Cambridge University Press, Cambridge.

Abbott, I. A. 1996. Limu: An ethnobotanical study of some Hawaiian seaweeds. National Tropical Botanical Garden, Lawai, Kauai. 39 pp.

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu. 477 pp.

Arasaki, S., and Arasaki, T. 1983. Vegetables from the sea. Japan Publishing, Tokyo. 196 pp.

Armisen, R. 1995. World-wide use and importance of *Gracilaria*. J. Appl. Phycol. 7:231–243.

Association of Official Analytical Chemists. 1995. Official methods for analysis. 16th ed. AOAC, Washington, D.C.

Bellorin, A. M., Oliveira, M. C., and Oliveira, E. C. 2002. Phylogeny and systematics of the marine algal family Gracilariaceae (Gracilariales, Rhodophyta) based on small subunit rDNA and ITS sequences of Atlantic and Pacific species. J. Phycol. 38:551–563.

Bird, C. J. 1995. A review of recent taxonomic concepts and developments in the Gracilariaceae (Rhodophyta). J. Appl. Phycol. 7:255:267.

Burkholder, P. R., Burkholder, L. M., and Almodovar, L. R. 1971. Nutritive constituents of some Caribbean marine algae. Bot. Mar. 14:132–135.

Buschmann, A. H., Correa, J. A., Westermeier, R., Hernandez-Gonzalez, M. D. C., and Norambuena, R. 2001. Red algal farming in Chile: A review. Aquaculture 194:203–220.

Carefoot, T. H. 1985. Calorimetry. In: Littler, M. M., and Littler, D. S. (eds.), Handbook of phycological methods: Ecological field methods: Macroalgae, pp. 479–491. Cambridge University Press, New York.

Chan, J. C. C., Cheung, P. C., and Ang Jr., P. O. 1997. Comparative studies on the effect of three drying methods on the nutritional composition of seaweed *Sargassum hemiphyllum* (Turn.) C. Ag. J. Agric. Food Chem. 45:3056–3059.

Dawes, C. P. 1995. Suspended cultivation of *Gracilaria* in the sea. J. Appl. Phycol. 7:303–313.

Department of Land and Natural Resources. 2002. Report to the governor, FYS 1999, 2000, 2001. State of Hawaii, Honolulu. 178 pp.

Dubois M., Gilles, F. A., Hamilton, J. K., Rebers, P. A., and Smith, F. 1956. Colorimetric method for the determination of sugars and related substances. Analyt. Chem. 28:350–356.

Edding, M., Macchiavello, J., and Black, H. 1987. Culture of *Gracilaria* sp. in outdoor tanks: Productivity. Hydrobiologia 151/152:369–374.

Fan X., Han L., and Zheng N. 1993. The analysis of nutrient components in some Chinese edible seaweeds. Chinese J. Mar. Drugs 12(4):32–38.

Folch, J., Lees, M., and Sloan-Stanley, G. H. 1957. A simple method for the isolation and purification of total lipids from animal tissues. J. Biol. Chem. 226:497–507.

Fortner, H. J. 1978. The limu eater, a cookbook of Hawaiian seaweed. Sea Grant Miscellaneous Report UNIHI-SEAGRANT-MR-79-01, UH Sea Grant College Program, Honolulu. 102 pp.

Freile Pelegrin, Y., Robledo, D., Pedersen, M., Bruno, E., and Ronnquist, J. 2002. Effects of dark and salinity treatment in the yield and quality of agar from *Gracilaria cornea* (Rhodophyceae). Cienc. Mar. 28:289–296.

Friedlander, M., and Levy, I. 1995. Cultivation of *Gracilaria* in outdoor tanks and ponds. J. Appl. Phycol. 7:315–324.

Gao, K., Aruga, Y., Asada, K., and Kiyohara, M. 1993. Influence of enhanced CO2 on growth and photosynthesis of the red algae *Gracilaria* sp. and *G. chilensis*. J. Appl. Phycol. 5:563–571.

Glenn, E. P., Moore, D., Akutagawa, M., Himler, A., Walsh, T., and Nelson, S. G. 1999. Correlation between *Gracilaria parvispora* (Rhodophyta) biomass production and water quality factors on a tropical reef in Hawaii. Aquaculture 178:323–331.

Goff, L. J., Moon, D. A., and Coleman, A. W. 1994. Molecular delineation of species and species relationships in the red algal agarophytes *Gracilariopsis* and *Gracilaria* (Gracilariales). J. Phycol. 30:521–537.

Guerin, J. M., and Bird, K. T. 1987. Effects of aeration period on the productivity and agar quality of *Gracilaria* sp. Aquaculture 64(2):105–110.

Harrison, P. J., and Thomas, T. E. 1988. Biomass measurements: Protein determination. In: Lobban, C. S., Chapman, D. J., and Kremer, B. P. (eds.), Experimental phycology: A laboratory manual, pp. 27–34. Cambridge Scientific Press, New York.

Harry, J. V. 1934. An investigation of the iodine content of Hawaiian marine foods. M.S. thesis, Chemistry, no. 44, University of Hawaii, Honolulu. 40 pp.

Hoyle, M. D. 1978. Reproductive phenology and growth rates in two species of *Gracilaria* from Hawaii. J. Exp. Mar. Biol. Ecol. 35:273–283.

Hurtado-Ponce, A. Q., and Umezaki, I. 1988. Physical properties of agar gel from *Gracilaria* (Rhodophyta) of the Phillipines. Bot Mar. 31(2):171–174.

Ito, K., and Hori, K. 1989. Seaweed: Chemical composition and potential food uses. Food Rev. Int. 5:101–144.

Kain, J. M., and Destombe, C. 1995. A review of the life history, reproduction and phenology of *Gracilaria*. J. Appl. Phycol. 7:269–281.

Lewis, J. G., Stanley, N. F., and Guist, G. C. 1988. Commercial production and applications of algal hydrocolloids. In: Lembi, C. A., and Waaland, J. R. (eds.), Algae and human affairs, pp. 205–236. Cambridge University Press, Cambridge.

Lim, P., Thong, K., and Phang, S. 2001. Molecular differentiation of two morphological variants of *Gracilaria salicornia*. J. Appl. Phycol. 13:335–345.

Lowry, O. H., Rosebrough, N. J., Farr, A. L., and Randall, R. J. 1951. Protein measurement with the Folin phenol reagent. J. Biol. Chem. 193:265–275.

Marolia, V.J., Joshi, S., and Mathur, H. H. 1982. Fatty acid composition of neutral lipids from some red algae. Indian J. Mar. Sci. 11:102–103.

McDermid, K. J., and Stuercke, B. In press. Nutritional composition of edible Hawaiian seaweeds. J. Appl. Phycol.

Molloy, F. J., and Bolton, J. J. 1995. Distribution, biomass and production of *Gracilaria* in Lüderitz Bay, Namibia. J. Appl. Phycol. 7:381–392.

Murano, E. 1995. Chemical structure and quality of agars from *Gracilaria*. J. Appl. Phycol. 7:245–254.

Norziah, M. H., and Ching, C. Y. 2000. Nutritional composition of edible seaweed *Gracilaria changgi*. Food Chem. 68:69–76.

Oyieke, H. A. 1994. The effect of phenotypic plasticity on agar from *Gracilaria salicornia* (J. AG) Dawson (Gracilariales, Rhodophyta) in Kenya. Bioresource Technology 49(3):267.

Portugal, T. R., Ladines, E. O., Ardena, S. S., Resurreccion, L., Medina, C. R., and Matibag, P. M. 1983. Nutritive value of some Philippine seaweeds, II. Proximate, amino acid and vitamin composition. Philipp. J. Nutr. (Oct.–Dec.): 166–172.

Qasim, R. 1986. Studies on fatty acid composition of eighteen species of seaweeds from the Karachi coast. J. Chem. Soc. Pak. 8:223–230.

Reed, M. 1907. The economic seaweeds of Hawaii and their food value. Annual report of the Hawaii agricultural experimental station 1906, pp. 61–88.

Robledo, D., and Freile Pelegrin, Y. 1997. Chemical and mineral composition of six potentially edible seaweed species of Yucatan. Bot. Mar. 40:301–306.

Santelices, B. J., and Doty, M. S. 1989. A review of *Gracilaria* farming. Aquaculture 78(2):95–133.

Santelices, B. J. Ohme, U., and Fonck, E. 1984. Managing wo;d crops of *Gracilaria* in central Chile. Hydrobiologia 116/117:77–89.
Santos, G. A., and Doty, M. S. 1983. Agar from some Hawaiian red algae. Aquat. Bot. 16(4):385–389.
Sfriso, A., Marcomini, A., and Pavoni, B. 1994. *Gracilaria* distribution, production and composition in the lagoon of Venice. Bioresource Tech. 50:165–173.
Silva, P. C., Basson, P. W., and Moe R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. University of California Press, Berkeley. 1259 pp.
Smith A., Nichols, H. K., and McLachlan, J. 1984. Cultivation of seamoss (*Gracilaria*) in St. Lucia, West Indies. Proc. Int. Seaweed Symp. 11:249–251.
Terada, R., and Yamamoto, H. 2000. A taxonomic study on two Japanese species of *Gracilaria*: *Gracilaria shimodensis* sp. nov. and *Gracilaria blodgetti* (Gracilariales, Rhodophyta). Phycol. Res. 48:189–198.

GRACILARIA HERMONII sp. nov. (GRACILARIACEAE, RHODOPHYTA), A COMPRESSED SPECIES FROM THE EAST COAST OF AUSTRALIA

Alan J. K. Millar

Abstract

Gracilaria hermonii sp. nov. is described from subtidal habitats on the eastern seaboard of Australia. Plants consist of erect, compressed to flattened branches that grow to heights of 22 cm, are 1.2 mm thick, and are up to 22 mm wide at dichotomies. Plants are regularly dichotomously, divaricately to alternately branched, often with small lateral branchlets (proliferations) bordering main axes. Apices are acute, tapered, and never rounded. Spermatangial conceptacles are of the poly-cavernosa-type. Traversing cells issue from base and lower sides of the gonimoblasts. Previously recorded from New South Wales as misidentifications of either *G. textorii* or more recently *G. multifurcata,* this eastern Australian taxon has been shown on closer inspection and comparisons with more specimens to be representative of an undescribed species.

Introduction

Australia is host to some 30 species of the commercially valuable red algal genus *Gracilaria* (Withell et al. 1994), of which 9 are distinctive by their compressed to flattened thallus branches (Withell et al. 1994; Millar 1997). Two species in particular—*G. textorii* (Suringar) De Toni and *G. multifurcata* Børgesen—have been confused with each other over the past decades, and it is only now that we are slowly getting a much clearer picture of the diagnostic features of each. Millar (1997) discussed the confusion, at least with eastern Australian populations, between *G. textorii* and *G. multifurcata* and made some progress in sorting out the charateristic features that allow their identification in the field.

Closer scrutiny of the Pacific Australian populations identified as *G. multifurcata* has shown that they cannot be allied to that species as it occurs at its type locality in Mauritius in the Indian Ocean. They do not, in fact, perfectly align with any existing species of *Gracilaria* and are therefore described herein as representing a new species. Millar (1997) has already provided a detailed description as well as illustrations of this species. The following, however, satisfies the ICBN regarding the necessary requirements for valid publication.

Description of Species

Gracilaria hermonii Millar sp. nov. (Figs. 1–4)

Misapplied Names: *Gracilaria multifurcata,* sensu Millar, Tax. Econ. Seaweeds 6, p. 111, figs. 13–19, 1997 [non *G. multifurcata* Børgesen, Kongel. Danske Vidensk. Selsk. Biol. Meddel. 21, pp. 42–44, figs. 15–16, 1953]. *Gracilaria textorii,* sensu May, CSIR Bull. 235, p. 43, pl. 8, fig. 2, pl. 9, fig. 1, 1948 (as f. *textorii*); sensu Millar and Kraft, Aust. Syst. Bot. 6, p. 28, 1993 [non *G. textorii* (Suringar) De Toni, Syll. algarum...3, p. 27, 1985].

Thallus coriaceus, erectus usque ad 22 cm altus; rami complanati usque ad 1.2 mm crassi et 22 mm lati ad furcas, ramificationibus regulariter dichotomis divaricatis vel alternis, axibus principalibus saepe ramulis parvis lateralibus (proliferationibus) marginatis; apices acuti angustati haud rotundati; cellulae medullosae usque ad 760 µm diametro, abrupte contractae versus cellulas corticales ad 10 µm diametro. Tetrasporangia cruciata obovata, 40 x 28 µm, per corticem ubique dispersa. Conceptacula spermatangialia illis polycavernosae similia. Cystocarpia papillata vel hemisphaerica , usque ad 1.3 mm diametro; pericarpium 12–15-stromaticum cellulis in seriebus anticlinalibus; cellulae peragrationes numerosae, e basi atque partibus infernis gonimoblasti orientes.

Thallus coriaceous, erect to 22 cm high; branches flattened to 1.2 mm thick and 22 mm wide at dichotomies, regularly dichotomously, divaricately to alternately branched, often with small lateral branchlets (proliferations) bordering main axes; apices acute, tapered, never rounded; medullary cells to 760 µm in diameter tapering abruptly to cortical cells to 10 µm in diameter. Cruciately divided tetrasporangia scattered thoughout cortex, obovate, 40 µm by 28 µm. Spermatangial conceptacles of the polycavernosa-type, shallow to deeply imbedded. Cystocarps papillate to hemispherical, to 1.3 mm in diameter; pericarp consisting of 12–15 layers of cells in anticlinal rows; traversing cells numerous, issuing from base and lower sides of gonimoblast.

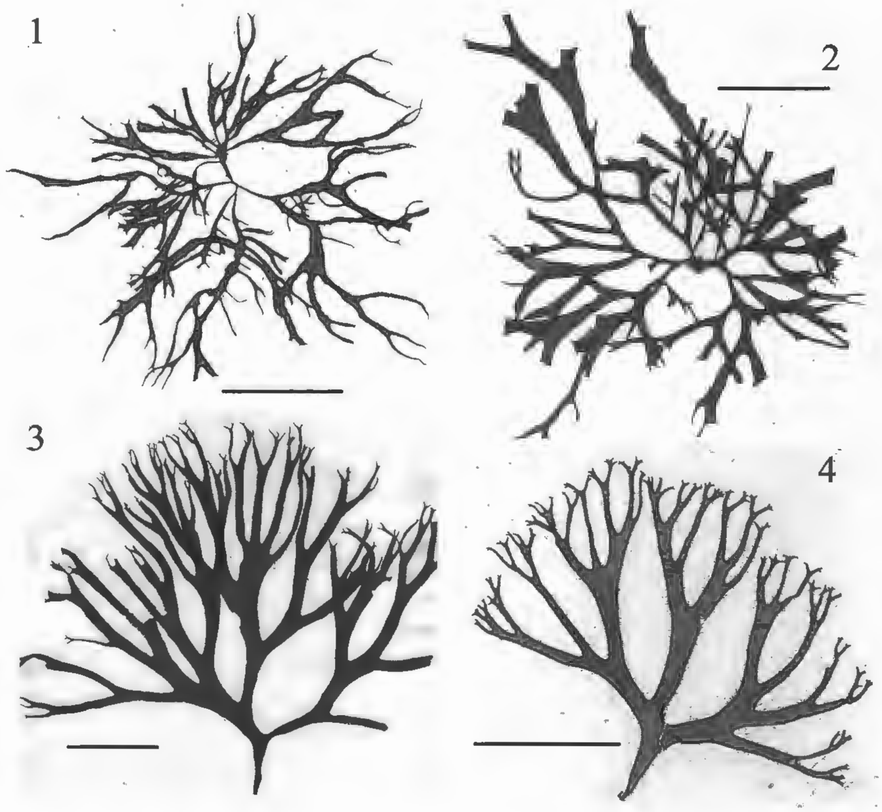
Holotype: NSW 292774, leg. A. J. K. Millar and P. G. Richards, May 19, 1993 (Fig. 1).

Type Locality: West side of Cabbage Tree Island, northeast of Port Stephens entrance, New South Wales, Australia.

Distribution: Southwestern Pacific Ocean from northern Queensland south to Botany Bay, New South Wales.

Etymology: Named in recognition of the late Hermon Slade, whose lasting legacy in the form of the Hermon Slade Foundation has funded much of the research that led to the discovery that this species was undescribed.

Specimens Examined: Queensland, Great Barrier Reef, Ribbon Reef 4, 32 m deep, A. Siotas, November 21, 1985, MELU A041735–41737; Moreton Bay, Fishermans Island, drift, V. May 795, December 24, 1943, NSW 391386;



Figs. 1–4. *Gracilaria hermonii* Millar sp. nov. Fig. 1, Cystocarpic holotype, NSW 292774. Fig. 2, Tetrasporic isotype, NSW 292775. Fig. 3, Paratype from Botany Bay displaying di- to tetrachotomies, NSW 391387. Fig. 4, Paratype from Botany Bay displaying trichotomies, NSW 429375. All scales = 50 mm.

V. May 792, April 1943, NSW 391385. New South Wales, Port Stephens, west side of Cabbage Tree Island, 11 m deep, A. Millar and P. Richards, May 19, 1993, NSW 289173, 292774–76, 4293–91 (all isotypes). Woy Woy, Hawkesbury River, trawled, V. May 791, February 9, 1943, NSW 391384. Botany Bay, A. Lucas, January 1912, NSW 391387; February 1905, NSW 391388; Sandringham, Sans Souci, A. Lucas, January 1904, NSW 391389; Weeny Bay, drift, V. May 887, February 20, 1945, NSW 391381, 391382; Quibray Bay, drift, A. Millar, April 6, 1989, NSW 289173–75.

Discussion

Millar (1997) suggested that the New South Wales populations, initially identified as *G. textorii* and later as *G. multifurcata,* represent a new species. Many more specimens of the Australian taxon have since been collected, and it is now clear that this species is a strictly subtidal, deepwater (11–35 m) taxon. It is now hard to imagine Børgesen's Mauritius entity (Børgesen 1953), which grows only intertidally on exposed rocks forming extensive cushions in the Indian Ocean, to be the same species as the purely erect, solitary and freestanding, strictly subtidal species from the eastern Pacific. Millar (1997) equated the Australian plants with *G. multifurcata* mostly because of their shared characters of deeply immersed, polycavernous spermatangial conceptacles, flattened branches with acute branch apices, and cartilaginous texture. Although these characters are indeed useful at the specific level in the genus *Gracilaria,* other features should be taken into consideration. The branches of *G. multifurcata* are much narrower (1–2 mm), thinner (500 µm), and shorter (4–5 cm) than those of *G. hermonii,* which are up to 22 mm wide, 1.2–2 mm thick, and grow to heights of 22 cm. Medullary cell sizes are also at odds between the two species (150 µm in diameter in *G. multifurcata* vs. 760 µm in *G. coriacea*). Adding to this their grossly different habits (forming cushions vs. free and erect), habitats (intertidal vs. deep subtidal), and branching patterns (irregular vs. regularly dichotomous), there seems little doubt as to their respective identities.

Acknowledgments

Sincere thanks to Dr. Isabella Abbott and Dr. Karla McDermid for the invitation to participate in the Ninth Workshop and to the California Sea Grant Program for financial aid. The Hermon Slade Foundation funded much of the fieldwork associated with this discovery. Drs. Ryuta Terada, Bangmei Xia, Khan Lewmanomont, and Anong Chirapart offered like-minded discussions on *Gracilaria* species. Thanks also to Dr. Peter Wilson for translating the Latin description.

Literature Cited

Børgesen, F. 1953. Some marine algae from Mauritius. Additions to the parts previously published. Kongel. Danske Vidensk. Selsk. Biol. Meddel. 21(9):1–62.
Millar, A. J. K. 1997. On some flattened species of *Gracilaria* from Australia. In: Tax. Econ. Seaweeds 6, pp. 111–123.
Withell, A. F., Millar, A. J. K., and Kraft, G. T. 1994. Taxonomic studies of the genus *Gracilaria* (Gracilariales, Rhodophyta) from Australia. Austral. Syst. Bot. 7:281–352.

GRACILARIA EPHEMERA sp. nov. (GRACILARIALES, RHODOPHYCEAE), A FLATTENED SPECIES FROM SAMOA, SOUTH PACIFIC

Posa A. Skelton, G. Robin South, and Alan J. K. Millar

Abstract

Gracilaria ephemera sp. nov. is a flattened, ephemeral species discovered in a subtidal, man-made pond in Samoa, South Pacific. A suite of vegetative and reproductive characters distinguishes *G. ephemera* from about 40 known flattened *Gracilaria* species. Its relatively small size (10 cm tall and frond widths to 5 mm) separates it from at least 17 flattened taxa. The lack of proliferations or dentations distinguishes it from another 9 species, and its cartilaginous texture and branching arrangement is unlike remaining flattened *Gracilaria* species. Cystocarpic plants show traversing filaments in all but the basal portions of the gonimoblast. Tetrasporangia are scattered throughout the blade and are embedded in the cortex without any modification to the cortical cell rows. The lack of spermatangial plants hinders a conclusive placement of *G. ephemera* at the subgeneric level. The population, which was abundant in 2000 and 2001, disappeared in October 2002 and has not been found since at any other site in Samoa.

Introduction

Gracilaria species are economically important algae that are harvested for agar (Tseng and Xia 1999). The cosmopolitan genus contains over 150 species (Tseng and Xia 1999; Abbott 1999), of which most have terete to subterete thalli. About 40 flattened or compressed species of *Gracilaria* are known (Hoyle 1994; Millar 1997), of which 14 are reported from the Indo-Pacific region (Nelson 1987; Silva et al. 1987, 1996; Millar 1997; Tseng and Xia 1999).

Only 2 species of *Gracilaria* have been recorded from the Samoa Islands (13–15°S, 168–173°W), both by Grunow (1874): *G. lichenoides* Linnaeus [=*G. edulis* (Gmelin) Silva] and *G. confervoides* (Linnaeus) Greville [=*G. verrucosa* (Hudson) Papenfuss]. As is now well documented, records of the European *G. verrucosa* (Hudson) Papenfuss from Japan, China, Thailand, Philippines, California, Micronesia, and Taiwan have been shown to represent distinct and separate taxa (Abbott et al. 1985; Abbott 1988; Yamamoto and Trono 1994; Zhang and Xia 1988; Yamamoto and Yamaguchi 1997). It is thus likely that the record of *G. verrucosa* from Samoa is also erroneous.

Interestingly, all attempts to survey the Samoa Islands until now have failed to find any *Gracilaria* species, including those recorded by Grunow more than 100 years ago. It was therefore surprising when a chance visit to a man-made pond (110 m by 50 m) in the capital Apia in 2000 revealed a population of a markedly flattened species. The depth of the pond is 2.5 m at high tide, and the substratum is of fine muddy sand overlying rubble and rocks. The pond was artificially created on the foreshore of a reclaimed area near Apia Harbor and was used as an entertainment site during the 7th South Pacific Festival of the Arts held in 1996. A narrow opening exists between the pond and the sea, allowing sea water exchange. It is in the middle part of the pond and adjacent to the pilings that supported the stage that the bed of *Gracilaria* was found. Subsequently, further anthropogenic, physical alterations have been carried out at the site, including restriction of the water flow. In July 2002, the population of the flattened *Gracilaria* was reduced significantly and by October 2002 no more specimens were found. Surveys of neighboring sites have failed to produce any other populations.

Comparison of the Samoan *Gracilaria* species with other flattened species led us to believe that it represents a new species, which we herein describe as *Gracilaria ephemera* sp. nov.

Materials and Methods

Specimens were collected from the pond (13°48'88"S, 171°46'85"W) at approximately 1 m depth and preserved in a 5% formalin/seawater solution. Hand sections were made with single-edged razor blades and stained in an aniline blue solution made according to the methods of Millar (1990) before mounting them in a 30% Karo solution (corn syrup in distilled water and thymol crystals). Permanent slides were made using a stronger (60–80%) Karo solution and sealed with a clear nail varnish.

Digital images were taken using Nikon Coolpix 990/995 digital cameras and were enhanced and arranged using the Adobe Photoshop ver. 6.

Voucher specimens are deposited at the South Pacific Regional Herbarium (SUVA-A), Royal Botanic Gardens, Sydney (NSW), and Hokkaido University (SAP).

Results

Gracilaria ephemera sp. nov. Skelton, South and Millar (Figs. 1–7)

Holotype: Matagialalua Pond, Apia, leg. P. A. Skelton and G. R. South, Aug. 20, 2000 (SUVA-A 7042♀); Isotypes in Royal Botanic Gardens, Sydney (NSW 458043, 458044, 497528, 497532).

Paratypes: Matagialalua Pond, Apia, leg. G. R. South and R. V. Tuivaiti, March 25, 2001 (SUVA-A 6950-51).

Thallus ad 10 cm altus (altitudine), atropurpureus, cartilagineus, erectus, haptero discoideo usque ad aliquot frondes exoriens; axes ubique compressi, 400–625 m crassi (crassitie), vel teretes non nisi aliquot mm basim, ad 5 mm lati (latitudine) parte latissima sub divisionibus dichotomis (infra divisiones dichotomas); rami dichotomi regulatim ad 6 ordines, spatio 8–15 mm inter ramos; apices obtusi vel parum attenuati; medulla ex cellulis magnis subsphaericis incoloratis 120–200 µm x 75–120 µm constans, magnitudo cellularum extrorsus decrescens ad 2–3 strata cellularum pigmentosum corticalium; cellulae interiores cortiales periclinaliter compressae, subsphaericae vel elongate 10–17.5 µm x 5–7.5 µm; cellulae exteriores corticales plus minusve anticlinaliter elongatae, cubiformes vel subsphaericae, 5–7.5 µm x 5 µm.

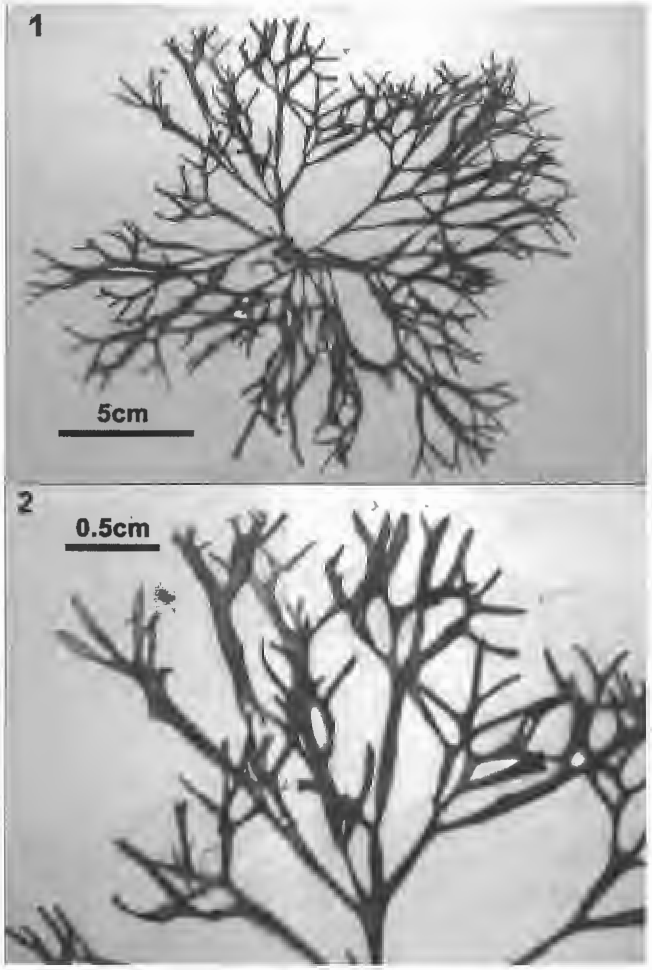
Cystocarpia hemisphaerica leniter basi constrictaque, 875–1125 µm diametro, ubique in superficiebus ambabus laminae dispersa sed in apicibus et partibus basalibus rariora; ostiolum rostratum; pericarpium zonatum, ex 21–23 stratis cellularum constans; ca 6 strata interiora ex cellulis cytoplasmatibus stellaribus leniter pigmentosis constantia; pars exterior ex 15–18 stratis cellularum anticlinaliter compressarum valde pigmentosarumque constans; filamenta peregrantia numerosa, ad 30 µm diametro et 200 m longa (longitudine), cellulas gonimoblasti pericarpiique ubique in cystocarpio praeter partem basalem concatenantia; gonimoblastus ex cellulis magnis angularibus pseudoparenchymatis constans, sine cellula coalescenti; carposporangia terminalis in seriebus linearibus, sphaerica aut ovoidea, 15–30 µm diametro.

Tetrasporangia dispersa, ovata, ad 19.5 µm diametro, a cellulis corticalibus non mutatis circumcincta.

Plantae masculae non observatae.

Plants to 10 cm tall, dark purple, cartilaginous, erect, up to several fronds arising from discoid holdfast (Fig. 1); axes flattened throughout, 400–625 µm thick, or terete only for few millimeters from base, to 5 mm broad with broadest section below dichotomous divisions (Figs. 1, 2); branches regularly dichotomous, to 6 orders; distance between branches 8–15 mm; apices obtuse to slightly tapered (Fig. 2); medulla of large subspherical, non-pigmented cells, 120–200 µm by 75–120 µm, size decreasing gradually outwardly to 2–3 layers of pigmented cortical cells (Figs. 5, 6); inner cortical cells periclinally compressed, subspherical to elongated 10–17.5 µm by 5–7.5 µm; outer cortical cells more or less anticlinally elongated, cuboidal to subspherical, 5 µm by 5–7.5 µm.

Cystocarps hemispherical and weakly constricted at base, 875–1125 µm in diameter, scattered throughout and on both sides of blade, but scarcer in apices and basal parts; ostiole rostrate; pericarp zonate, composed of 21–23 cell rows; ca 6 inner rows with stellate cytoplasm, weakly pigmented (Fig. 3); outer part of 15–18 layers of anticlinally compressed, strongly pigmented cells; traversing filaments numerous (Figs. 3, 4), to 30 µm in diameter, 200 µm long, joining gonimoblast and pericarp cells in all but basal section of cystocarp; gonimoblast consisting of large, angular, pseudoparenchymatous cells, lacking fusion cell; carposporangia terminal, in linear series, rounded or ovoid, 15–30 µm in diameter.

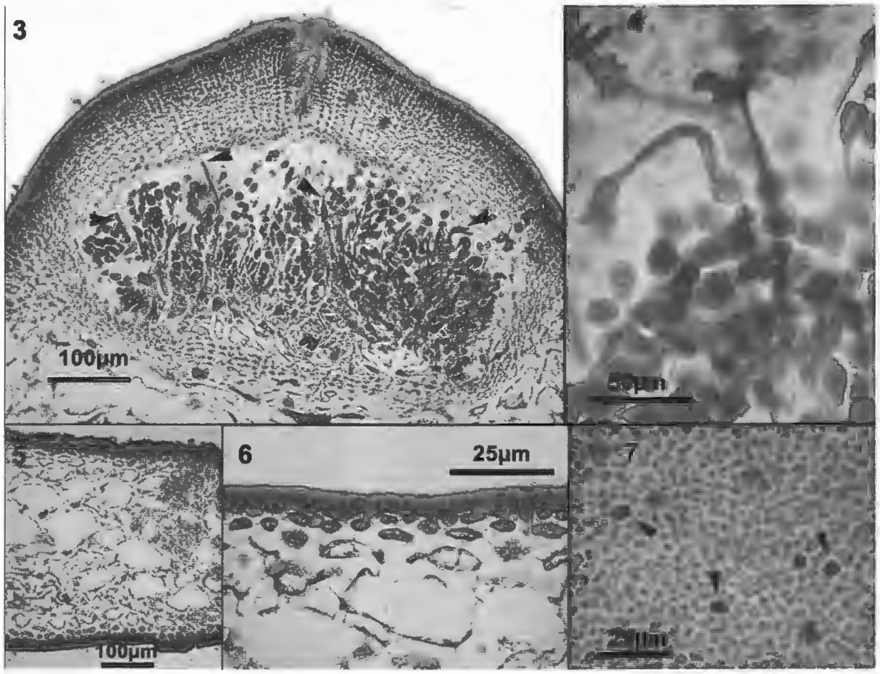


Figs. 1–2. *Gracilaria ephemera* sp. nov. Fig. 1, Habit showing several erect fronds arising from the holdfast. Fig. 2, One of the erect fronds showing obtuse to slightly tapering apices.

Tetrasporangia scattered, oval, to 19.5 µm in diameter, surrounded by unmodified cortical cells (Fig. 7).

Male plants not seen.

Etymology: The specific epithet refers to the plant's apparent ephemeral or short-lived presence in the type locality.



Figs. 3–7. *Gracilaria ephemera* sp. nov. Fig. 3, Vertical section of cystocarp showing traversing filaments confined to the mid to upper portion of the pericarp (arrows). Fig. 4, Detail of traversing filaments. Fig. 5, Transverse section showing larger medullary cells grading toward smaller cortical cells. Fig. 6, Detail of cortex, usually with 2–3 pigmented cell layers. Fig. 7, Surface view of tetrasporic material showing scattered tetrasporangia (arrows).

Discussion

Approximately 38 of all known *Gracilaria* species are flattened or compressed, and 15 of these are recorded from the tropical Indo-Pacific region. *Gracilaria ephemera* is distinguished from all flattened species by a suite of vegetative characters including plant size, smooth margins, and cartilaginous texture (Table 1). Of the 15 Indo-Pacific species, *G. ephemera* is distinguished from *G. foliifera* (Forsskål) Børgesen, *G. mannarensis* Umamaheswara Rao, *G. textorii* (Sur.) De Toni, *G. truncata* Kraft, and *G. vieillardii* Silva by its smaller size (10 cm tall by 5 mm wide versus >10 cm tall by >15 mm wide). The proliferations or dentations found in *G. denticulata* Schmitz ex Mazza, *G. eucheumatoides* Harvey, *G. millardetii* (Mont.) J. Agardh, *G. punctata* (Okamura) Yamada, *G. spinigera* Dawson, and *G. halogenea* Millar clearly separate them

Table 1. Comparison of *G. ephmera* to Other Flattened *Gracilaria* Species

Species	Distribution	Height (cm)	Width (mm)	Marginal Proliferation or Dentition	Stipe Terete/ Subterete
G. abbottiana Hoyle	Hawaii (endemic)	3	4	None	Yes
G. corallicola Zanardini	Mediterranean	6	10	NS	NS
G. crispata Setchell et Gardner	Northeast Pacific	7–8	10–50	Yes	NS
G. cuneata Areschoug	Caribbean	18	12	Yes	No
G. cuneifolia (Okamura) Lee et Kurogi	Northwest Pacific	20	50	Yes	No
G. cunninghamii Farlow in J. Agardh	Northeast Pacific	20	8	Yes	NS
G. curtissiae J. Ag.	Caribbean	40	35	NS	NS
G. dawsonii Hoyle	Hawaii (endemic)	7	6	None	Yes
G. denticulata Schmitz ex Mazza	Indian Ocean	7.5	1	Yes	No
G. ecuadoreanus (Taylor) Dawson	Galapagos	9	50	NS	NS
***G. ephemera* Skelton et al.**	**Samoa**	**10**	**5**	**Yes**	**No**
G. eucheumatoides Harvey	Northwest Pacific, Indo-Pacific	7	10	Yes	Yes
G. foliifera (Forsskål) Atlantic, Borgesen	Mediterranean, Caribbean, Indo-Pacific	30	15	Yes	Yes
G. glomerata Zhang et Xia	Northwest Pacific	4.5	2	None	Yes
G. halogenea Millar	Australia (eastern)	40	15–20	Yes	Yes
G. incurvata Okamura	Northwest Pacific, Southwest Pacific	20	150	Yes	No
G. mammillaris (Mont.) Howe	Atlantic, Northeast Pacific	14	7	None	Yes
G. mannarensis Umamaheswara Rao	Indian Ocean	12	60	NS	NS
G. mayae Millar	Australia	30	130	None	NK
G. millardetii (Mont.) J. Ag	Indian Ocean	6	3	Yes	NS
G. multifurcata Borgesen	Indian Ocean	16	2	None	Yes
G. multifurcata sensu Millar (1997)	Australia	22	22	Yes	NS
G. peruana Piccone et Grunow	Peru	20	10	NS	NS
G. punctata (Okamura) Yamada	Northwest Pacific, Southwest Pacific	5	15	Yes	Yes
G. rhodymenioides Millar	Australia, Norfolk Is.	11	15	None	Yes
G. rubrimembra Dawson	Northeast Pacific	12	25	Yes	Yes

(cont. pp. 237–239)

Table 1. ***(cont.)***

Species	Texture	Tetrasporangia cortex modified/ diameter µm	Traversing filaments	Reference
G. abbottiana	Coriaceous*	slightly modified; 19	Present	Hoyle 1978
G. corallicola	Coriaceous	NS	NA	Hoyle 1994
G. crispata	NS	slightly modified; 18–21(25–35)	Penetrate pericarp	Dawson 1949; Setchell & Gardner 1924
G. cuneata	Membranous	NS	NS	Taylor 1960
G. cuneifolia	Membranous	Modified; 17–23	Mainly upper textorii-type	Okamura 1933–1942; Lee & Kurogi 1977
G. cunninghamii	NS	Modified; size NS	Penetrate pericarp	Dawson 1949
G. curtissiae	Membranous	NS	NS	Taylor 1960
G. dawsonii	Coriaceous	some modification; 15–30	Numerous, penetrate pericarp	Hoyle 1994
G. denticulata	NS	11–20	Present but rare	Seagrief 1980; Withell et al. 1994
G. ecuadoreanus	NS	Unmodified; 15	Present but in small number	Dawson 1949
G. ephemera	**Cartilaginous**	**Unmodified; 19.5**	**Present** textorii-type	**this study**
G. eucheumatoides	Cartilaginous	15–20	NS	Yamamoto 1978
G. foliifera	NS	20–35	NS	Taylor 1960
G. glomerata	Cartilaginous	NK	NK	Zhang & Xia 1994
G. halogenea	Cartilaginous	Modified; 24	Sides and upper	Millar 1990
G. incurvata	Coriaceous	Texture NS; 25–38	Abundant penetrate pericarp	Okamura 1929–1932
G. mammillaris	Membranous	Slight modification; 25–35	Numerous textorii-type	Schneider 1975
G. mannarensis	Coriaceous	NS	NS	Hoyle 1994
G. mayae	NS	not NK	Numerous textorii-type	Millar 1997
G. millardetii	NS	NS	Numerous penetrate gonimoblast	Børgesen 1943
G. multifurcata	Cartilaginous	Unmodified cortex; 30	Confined to floor hydropuntia	Børgesen 1953; Terada et al 2000
G. multifurcata	Pliable leathery	Texture NS; 28	numerous	Millar 1997
G. peruana	Coriaceous	NS	NS	Hoyle 1994
G. punctata	Membranous	slightly modified; size NS	Present but few	Yamamoto 1978
G. rhodymenioides	Membranous	Unmodified cortex; size NS	Numerous textorii-type	Millar 1997
G. rubrimembra	Membranous	Modified cortex; 20–30	Numerous	Dawson 1949

*According to I. A. Abbott (pers. comm.), *G. abbottiana* is not coriaceous; NS = Not stated by the author; NK = Not yet known for the species.

Table 1. Comparison of *G. ephmera* to Other Flattened *Gracilaria* Species *(cont.)*

Species	Distribution	Height (cm)	Width (mm)	Marginal Proliferation or Dentition	Stipe Terete/ Subterete
G. skottsbergi Taylor	Galapagos	8	30		
G. spinigera Dawson	Northeast Pacific, Southwest Pacific	15	12	Yes	Yes
G. spinulosa (Okamura) Chang et Xia	Northwest Pacific	9	8	Yes	Yes
G. srilankia (Chang et Xia) Withell et al.	Northwest Pacific, Indo-Pacific	4	5	None	Yes
G. stipitata Withell et al.	Australia	8	9	Yes	Yes
G. sublittoralis Yamada et Segawa	Northwest Pacific	25	50	rarely proliferous	Yes
G. symmetrica Dawson	Northeast Pacific	18	4	None	Yes
G. tepocensis (Dawson) Dawson	Northeast Pacific	25.5	2–3(5.5)	None	Yes
G. textorii (Sur.) De Toni	Northeast Pacific, Northwest Pacific, Indo-Pacific	20	20	Yes	Yes
G. truncata Kraft	Indo-Pacific	32	15	Yes	Yes
G. vieillardii P. Silva	Northwest Pacific, Indo-Pacific	8.5	35	Yes	Yes
G. yamamotoi Zhang et Xia	Northwest Pacific	7	3	None	Yes

from *G. ephemera*. The coriaceous character of *G. corallicola* Zanardini as well as its distribution in the Adriatic Sea separates it from *G. multifurcata* Børgesen, *G. rhodymenioides* Millar, *G. srilankia* (Chang and Xia) Withell, Millar and Kraft, and our plant. *Gracilaria rhodymenioides* is distinguished from *G. ephemera* by its membranous texture and wider blades (to 15 mm). The smaller size of *G. srilankia* (3–4 cm tall) with a single, linear, and vertically aligned blade arising from an undivided stipe (Withell et al. 1994) distinguishes it from *G. ephemera.*

In regards to the reproductive structures, the subgeneric system of Yamamoto (1975, 1978) based on spermatangial conceptacles is useful in grouping flattened (as well as other) *Gracilaria* species. As is currently conceived, 4 subgenera are recognized on the basis of spermatangial conceptacles (Yamamoto 1975, 1978; Tseng and Xia 1999). Subgenus *Gracilariella,* or the chorda-type, is characterized by continuous superficial spermatangia, whereas subgenus *Textoriella,* or the textorii-type, is characterized by shallow cup-shaped conceptacles. Subgenus *Gracilaria,* the verrucosa-type, is characterized by deep pot-shaped conceptacles, and the polycavernosa-type is characterized by multiple cavities borne near the periphery of the thallus.

Table 1. *(cont.)*

Species	Texture	Tetrasporangia cortex modified/ diameter µm	Traversing filaments	Reference
G. skottsbergii	Firmly Fleshy	NS	Present	Dawson 1949
G. spinigera	NS	Modified cortex; 20–25	Present	Dawson 1949
G. spinulosa	Membranous	NS	Present at top only, textorii-type	Withell et al. 1994
G. srilankia	NS	NS	NS	Withell et al. 1994
G. stipitata	Tough to soft pliable	Modified cortex; 16–24	Mainly basal, rarely above	Withell et al. 1994
G. sublittoralis	Leathery	Modified cortex; 28–35(–53)	Abundant	Yamamoto 1978
G. symmetrica	Membranous	Unmodified cortex; 30	Abundant	Dawson 1949
G. tepocensis	Membranous	Modified cortex; 18–20	Abundant	Dawson 1961
G. textorii	Coriaceous or membranous	Modified cortex; 23–30	Abundant textorii-type	Yamomoto 1978
G. truncata	NS	Unmodified cortex; 30–40 x 20–30	Common in lower gonimoblast	Kraft 1977; Nelson 1987
G. viellardii	Pliable	Unmodified cortex; 6–12	Rare, basal only polycavernosa-type	Withell et al. 1994
G. yamamotoi	Coriaceous	NK	Absent	Zhang & Xia 1994

The majority of the flattened *Gracilaria* species fall into the textorii-type (e.g., *G. textorii*), the polycavernosa-type (e.g., *G. multifurcata*), or the verrucosa-type (e.g., *G. truncata, G. abbottiana,* and *G. sublittoralis*). Some species may exhibit both polycavernosa- and verrucosa-types (e.g., *G. multifurcata* sensu Millar 1997:119, figs. 16, 17). Because spermatangial plants have not yet been discovered for *G. ephemera,* its subgeneric placement is uncertain.

When *Gracilaria* species are distinguished, tetrasporangial characters are rarely considered, although the modification of the cortex, the scattered tetrasporangia versus those borne in nemathecia or sori, and tetrasporangial size have been used by Dawson (1949) to distinguish *G. veleroae* Dawson [=*G. mammillaris* (Mont.) Howe] and *G. symmetrica* Dawson from *G. crockeri* Dawson [=*G. tepocensis*], *G. rubrimembra* Dawson, *G. vivesii* Howe [=*G. textorii*], and *G. skottsbergii*. The tetrasporangia of *G. ephemera* are scattered throughout the blade and fall within a small group of flattened *Gracilaria* species that do not exhibit a modified cortex, such as *G. rhodymenioides, G. viellardii, G. ecuadoreanus* (Taylor) Dawson, and *G. multifurcata*. The tetrasporangial size of *G. ephemera* (to 19.5 µm in diameter) is within the size range of most flattened species, except *G. foliifera* (20–35 µm), *G. incurvata* Okamura and *G. mammillaris* (Mont.) Howe (both 25–35 µm), *G. multifurcata* (28–30 µm), *G. sublittoralis* Yamada and Segawa (28–35[–53] µm), *G. textorii* (23–30 µm), and *G. halogenea* (24–40 µm).

In the cystocarp, the position of traversing filaments may be useful in grouping some *Gracilaria* species, similar to the current subgeneric system based on spermatangial arrangements. Yamamoto (1978) attempted to establish the relationship between spermatangial patterns and the presence or absence of nutritive filaments (also called traversing filaments in this paper; see his fig. 29). He suggested that the chorda-type always lacks nutritive filaments, whereas nutritive filaments are found in the textorii-type. The verrucosa-type is similar in regard to the presence of nutritive filaments to the textorii-type, although some species within the former group may lack nutritive filaments altogether. Yamamoto acknowledged the use of nutritive filaments as an "unreasonable" taxonomic character, relegating it as a subsidiary element, whereas he retained the spermatangial patterns as a fundamental character.

The appearance and then sudden disappearance of *G. ephemera* are noteworthy, especially since both seem to have been the result of anthropogenic activities. The location of the pond associated with Apia Harbor makes *G. ephemera* a possible introduced species. From whence this new species came, though, is a mystery, and comparisons with described species have failed to find a match. The fact that the pond is well protected with a reduced number of grazers may have given the alga a better chance of survival once it was established than it would have had along the fringing reefs or the more exposed, shallow lagoons. The removal of the stage and the placement of a concrete block at the mouth of the narrow opening restricting water flow in early 2002 may have led to its disappearance. Surveys of the fringing and subtidal habitats adjacent to the pond have so far failed to find any *Gracilaria* plants.

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Literature Cited

Abbott, I. A. 1988. The red algal genera *Gracilaria* and *Polycavernosa*: Additional species from the western Pacific. In: Tax. Econ. Seaweeds 2, pp. 127–129.

Abbott, I. A. 1999. Section III. Gracilariales—Introduction. In: Tax. Econ. Seaweeds 7, p. 87.

Abbott, I. A., Chiang, Y. M., Fredericq, S., Norris, J. N., Tsuda, R. T., Xia Bangmei, and Yamamoto, H. 1985. The red alga *Gracilaria* Greville (Gracilariaceae, Gigartinales). In: Tax. Econ. Seaweeds 1, pp. 67–83.

Børgesen, F. 1943. Some marine algae from Mauritius: III. Rhodophyceae: Part 2. Gelidiales, Cryptonemiales, Gigartinales. Kongel. Danske Vidensk. Selsk. Biol. Meddel. 19: 1–85.

Børgesen, F. 1953. Some marine algae from Mauritius. Additions to the parts previously published. Kongel. Danske Vidensk. Selsk. Biol. Meddel. 21:1–62.

Dawson, E. Y. 1949. Studies of northeast Pacific Gracilariaceae. Allan Hancock Found. Publ. Occas. Pap. 7:1–105.

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

Grunow, A. 1874. Algen der Fidschi-, Tonga- und Samoa-Inseln, gesammelt von Dr. E. Graeffe. J. Museums Godeffroy [Hamburg] 3:23–50.

Hoyle, M. D. 1978. *Gracilaria abbottiana* sp. nov. (Rhodophyta, Gigartinales): A second intertidal species of *Gracilaria* from the island of Oahu, Hawaii. Phycologia 17(3):299–303.

Hoyle, M.D. 1994. *Gracilaria dawsonii* sp. nov. (Rhodophyta, Gigartinales): A second flattened species from the Hawaiian islands. In: Tax. Econ. Seaweeds 4, pp. 85–94.

Kraft, G. T. 1977. Transfer of the New Zealand red alga *Tylotus proliferus* (Gracilariaceae, Gigartinales) to the genus *Gracilaria.* New Zealand J. Bot. 15:495–502.

Lee, I. K., and Kurogi, M. 1977. On the taxonomic position of *Rhodymenia cuneifolia* Okamura (Rhodophyta). Bull. Jpn. Soc. Phycol. 25:113–118.

Millar, A. J. K. 1990. Marine red algae of the Coffs Harbour Region northern New South Wales. Austral. Syst. Bot. 3:293–593.

Millar, A. J. K. 1997. Some flattened species of *Gracilaria* from Australia. In: Tax. Econ. Seaweeds 6, pp. 111–123.

Nelson, W. A. 1987. The New Zealand species of *Gracilaria* Greville (Rhodophyta, Gigartinales). New Zealand J. Bot. 25:87–98.

Okamura, K. 1929–1932. Icones of Japanese algae, Vol. 6. Tokyo. 203 pp.

Okamura, K. 1933–1942. Icones of Japanese algae, Vol. 7. Tokyo. 116 +70 + 41 pp.

Schneider, C. W. 1975. Taxonomic notes on *Gracilaria mammillaris* (Mont.) Howe and *Gracilaria veleroae* Dawson (Rhodophyta, Gigartinales). Taxon 24 (5/6):643–646.

Seagrief, S. C. 1980. Seaweeds of Maputaland. In: Bruton, M. N., and Cooper, K. H., Studies on the ecology of Maputaland, pp. 18–41. Rhodes University, Grahamstown, and the Wildlife Society, Durban.

Setchell, W. A., and Gardner, N. L. 1924. Expedition of the California Academy of Sciencs to the Gulf of California in 1921. The marine algae. Proc. Calif. Acad. Sci., ser. 4, 12:695–949.

Silva, P. C., Basson, P. W., and Moe, R. L. 1996. Catalogue of the benthic marine algae of the Indian Ocean. Univ. Calif. Publ. Bot. 79:1–1259.

Silva, P. C., Meñez, E. G., and Moe, R. L. 1987. Catalog of the benthic marine algae of the Philippines. Smithsonian Contr. Mar. Sci. 27:1–179.

Taylor, W. R. 1960. Marine algae of the eastern tropical and subtropical coasts of the Americas. Ann Arbor: University of Michigan Press. ix + 870 pp.

Terada, R., Kawaguchi, S., Masuda, M., and Phang, S. M. 2000. Taxonomic notes on marine algae from Malaysia: III. Seven species of Rhodophyceae. Bot. Mar. 43:347–357.

Tseng, C. K., and Xia Bangmei. 1999. On the *Gracilaria* in the western Pacific and the southeastern Asia region. Bot. Mar. 42:209–217.

Withell, A. F., Millar, A. J. K., and Kraft, G. T. 1994. Taxonomic studies of the genus *Gracilaria* (Gracilariales, Rhodophyta) from Australia. Austral. Syst. Bot. 7:281–352.

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

Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Bull. Fac. Fish. Hokkaido Univ. 25:97–152.

Yamamoto, H., and Trono, G. C., Jr. 1994. Two new species of *Gracilaria* from the Philippines. In: Tax. Econ. Seaweeds 4, pp. 95–101.

Yamamoto, H., and Yamauchi, H. 1997. A bisporangial sporophyte in the life history of *Gracilaria chorda* var. *exilis* (Gracilariaceae). In: Tax. Econ. Seaweeds 6, pp. 97–102.

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

Zhang Junfu (Chang, C.F.) and Xia Bangmei. 1994. Three foliose species of *Gracilaria* from China. In: Tax. Econ. Seaweeds 4, pp. 103–110.

NEW RECORD OF *GRACILARIA YAMAMOTOI* ZHANG et XIA (RHODOPHYTA) FROM JAPAN

Ryuta Terada and Junya Ueno

Abstract

Gracilaria yamamotoi Chang et Xia is newly recorded for Japan, where it grows at Tanegashima Island, the northernmost island of the Ryukyu Archipelago, southern Japan. This species is characterized by slender foliose blades with a discoid basal disc (holdfast), a short subterete stipe, entire margins, a dark purplish red color, and scarce traversing filaments between the dense gonimoblast and the pericarp. The Japanese specimens agree well with the original description of *G. yamamotoi* from China.

Introduction

Gracilaria (Gracilariaceae, Rhodophyta) is well represented on the shores of Japan, with 21 species recognized for the region (Yoshida 1998; Terada and Yamamoto 2000; Terada et al. 2000). Some species present mainly in southeast China (*G. firma* and others) are also known from the Ryukyu Archipelago in Japan (Chang and Xia 1976; Yamamoto 1978; Terada et al. 2000), suggesting that the algal flora of this region is similar to that of southern China. *Gracilaria yamamotoi* Zhang et Xia was originally described in 1994, based on specimens from Hainan Province, China (Zhang and Xia 1994). We confirmed this species at Tanegashima Island, in the northernmost of the Ryukyu Archipelago, southern Japan. In this paper we give a detailed description of this species as a new record for Japan.

Materials and Methods

Specimens collected at Injo, Tanegashima Island, Kagoshima Prefecture, on April 15, 2002, were preserved in ca. 5% formalin/seawater and prepared for microscopic observations. Sections were made with a freezing microtome and stained with 1% cotton blue in 50% glycerol/seawater. Specimens examined were deposited in the Herbarium of the Faculty of Fisheries, Kagoshima University.

Gracilaria yamamotoi Zhang et Xia, Tax. Econ. Seaweeds 4, p. 106, figs. 4–21, 1994. (Figs. 1–6)

Distribution: China (Hainan Island, Zhang and Xia 1994) and Japan (Tanegashima Island, this study).

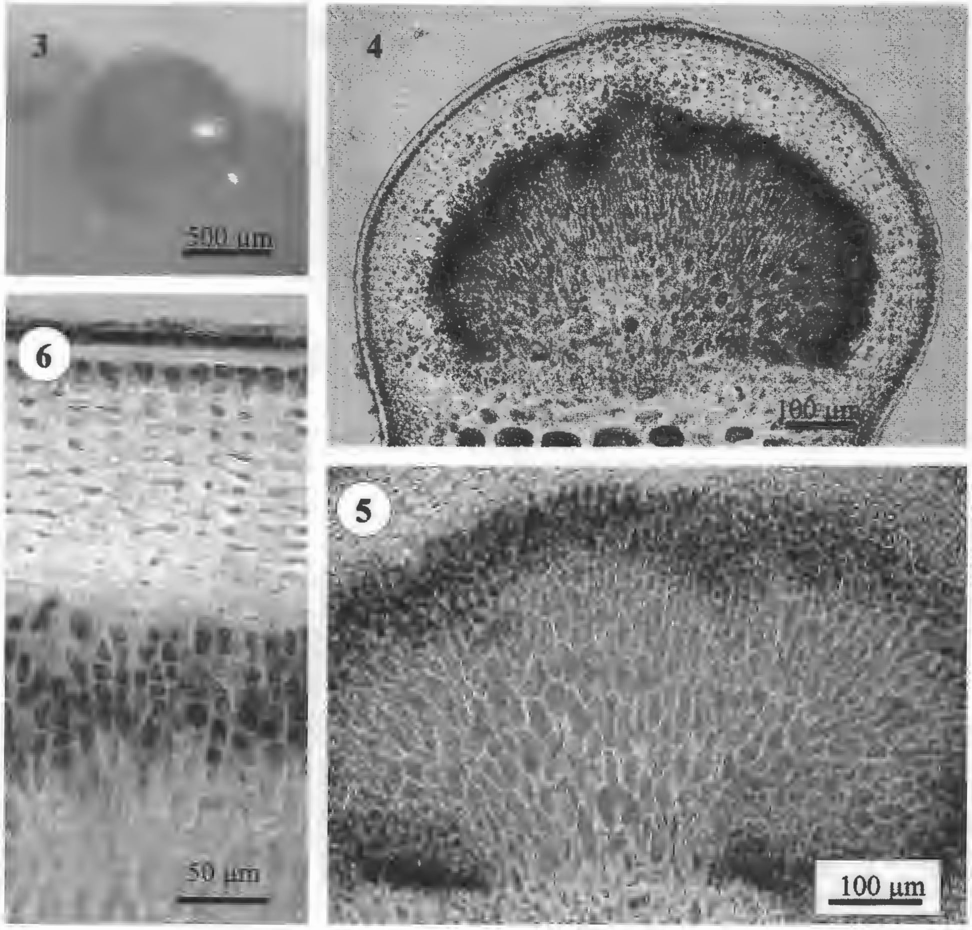
Figs. 1–2. *Gracilaria yamamotoi,* Tanegashima, Kagoshima Prefecture, Japan. Fig. 1, Herbarium specimen (cystocarpic, Terada 1444). Fig. 2, Detail of basal part, showing basal disc (holdfast) and stalk (liquid-preserved material).

Specimens Examined: Injo (Tanegashima Island, Kagoshima Prefecture), April 15, 2002, leg. R. Terada and J. Ueno (cystocarpic, Terada 1443–1444, Terada 1445a; tetrasporangial, Terada 1445b).

Plants grow on rocks in the lower intertidal zone. The thallus arises from a small discoid basal disc (holdfast) with a short subterete stipe and is up to 4 cm high (Figs. 1–2). It is foliose throughout, cartilaginous, dark purplish red in color, and does not adhere to herbarium paper when dried. Each blade is up to 12 mm long, 2 mm wide, and 350 µm thick and regularly or irregularly divides dichotomously or trichotomously 2–3 times in one plane. Margins are entirely smooth, and apices are slightly attenuated and rounded.

The thallus is multiaxial with a pseudoparenchymetous cortex and medulla. The medulla consists of 5 layers of cells 20–160 µm in diameter; the cortex consists of 2 layers of cells up to 8 µm long and 6 µm wide.

Cystocarps are formed on both surfaces of female gametophytes except for basal and apical parts. Mature cystocarps appear prominently on the bearing blades. They are globose, up to 1200 µm long by 1500 µm wide, with or without a slightly rostrate ostiole and a slightly constricted base (Figs. 3–4). Gonimoblasts consist of small cells up to 57 µm long and 25 µm wide (Fig. 5). Traversing filaments between the dense gonimoblast and the pericarp were



Figs. 3–6. ***Gracilaria yamamotoi,*** **female gametophytes, Tanegashima, Kagoshima Prefecture, Japan. Fig. 3, Cystocarp, showing globular shape. Fig. 4, Vertical section of cystocarp. Fig. 5, Vertical section of cystocarp, showing gonimoblast consisting of small cells. Fig. 6, Vertical section of the pericarp and terminal portion of carposporangia.**

not found in our specimens. The pericarp, up to 150 µm thick, consists of two kinds of tissue, the outer consisting of 2–4 layers of small and oblong cells, the inner one of 7–9 layers of horizontally long cells (Fig. 6). Tetrasporangia are scattered on the both surfaces of tetrasporophytes except for the basal and apical portions. Tetrasporangia, with cruciately arranged spores, are up to 40 µm long by 30 µm wide.

Spermatangia were not found in our specimens, but Zhang and Xia (1994) report that they are formed in shallow conceptacles up to 33 µm deep, on the entire surface of male gametophytes except for the apical and basal portions.

Japanese name: Hoso Kabanori (new name)

Discussion

Gracilaria yamamotoi was originally described by Zhang and Xia (1994) based on material from Hainan Province, China. It has been characterized by small gonimoblast cells, no traversing filaments in the cystocarp, and shallow textorii-type spermatangial conceptacles (Zhang and Xia 1994; Xia and Zhang 1999). The Japanese specimens reported here generally agree well with the original description morphologically and anatomically. However, the pericarp thickness of our materials, up to 150 µm, differs significantly from that reported in the type material (264–304 µm). We suggest that this difference is due to the ages of the cystocarps and their development.

Gracilaria yamamotoi closely resembles *G. textorii* (Suringar) Hariot in gross morphology, but the blades of the latter species are wider than those of our materials (Yamamoto 1978). Furthermore, the latter species has abundant traversing filaments in the cystocarp. Gross morphology of *G. yamamotoi* resembles that of *G. dawsonii* Hoyle (Hoyle 1994; Abbott 1999), but *G. dawsonii* also has abundant traversing filaments in the cystocarp.

Gracilaria yamamotoi also resembles *G. srilankia* (Chang et Xia) Withell, Millar et Kraft and *G. vieillardii* Silva because of its flattened blades. Our material clearly differs from the latter two species, which have of spines along the margins of the blades. Although *G. yamamotoi* has been reported only from southern China, we suggest that our records of its presence in Japanese waters extend the northernmost distribution of this species.

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Literature Cited

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu. 477 pp.

Chang, C., and Xia B. 1976. Studies on Chinese species of *Gracilaria*. Stud. Mar. Sin. 11:91–163, pls. 1–2.

Hoyle, M. D. 1994. *Gracilaria dawsonii* sp. nov. (Rhodophyta, Gigartinales): A second flattened species from the Hawaiian Islands. In: Tax. Econ. Seaweeds 4, pp. 85–94.

Terada, R., Baba, M., and Yamamoto, H. 2000. New record of *Gracilaria firma* Chang et Xia (Rhodophyta) from Okinawa, Japan. Phycol. Res. 48:291–294.

Terada, R., and Yamamoto, H. 2000. A taxonomic study on two Japanese species of *Gracilaria*: *Gracilaria shimodensis* sp. nov. and *Gracilaria blodgettii* (Gracilariales, Rhodophyta). Phycol. Res. 48:189–198.

Xia Bangmei and Zhang Junfu. 1999. Ahnfeltinales, Gigartinales, Rhodymeniales. In: Flora algarum marinarum sinicarum II, Rhodophyta, V. Science Press, Beijing. 201 pp.

Yamamoto, H. 1978. Systematic and anatomical study on the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, pls. 1–49.

Yoshida, T. 1998. Marine algae of Japan. Uchida Rhokakuho, Tokyo. 1222 pp.

Zhang Junfu and Xia Bangmei. 1994. Three foliose species of *Gracilaria* from China. In: Tax. Econ. Seaweeds 4, pp. 103–110.

PRESENCE OF A DIFFERENT *GRACILARIA* IN CHINA

Xia Bangmei and Wang Yongqiang

Abstract

A small species of *Gracilaria* that grows in the sublittoral (1–3 m) of lower salinity, at Qinglangang, Wenchang, Hainan Island, is similar to *G. lemaneiformis, G. bailinae,* and *G. chorda* in some morphological characters, especially the structure of the cystocarps; there are, however, differences among these taxa.

Description of Species

***Gracilaria* sp.** (Figs. 1–4)

Plants solitary, slender, and delicate, cylindrical throughout, 3–9 cm long from a discoid holdfast, without percurrent main axes, simple axes of 1–2 orders of dichotomous or alternate branches; branching flagelliform, up to 6–7 cm long; branches 0.5–1 mm in diameter; frond in transverse section consisting of medulla of large thin-walled cells, 216–349 µm by 149–198 µm in diameter, 2 layers of cells in cortex; transition from medulla to cortex abrupt.

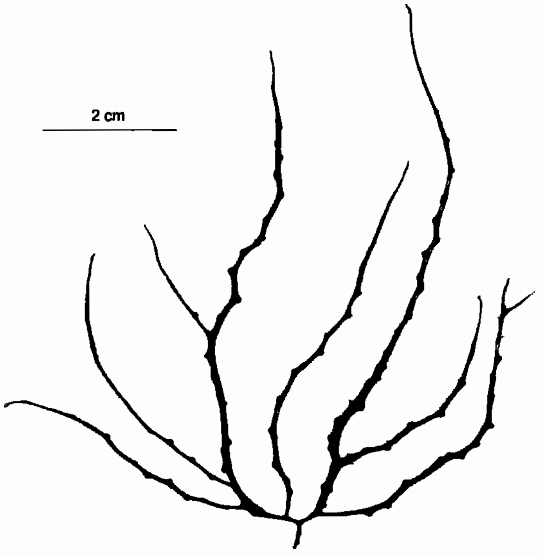

Fig. 1. Cystocarpic frond of *Gracilaria* sp. from Hainan Island.

Fig. 2. *Gracilaria* sp., transection of frond (dried material).

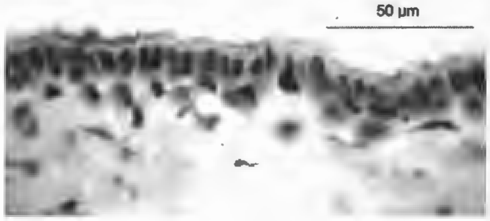

Fig. 3. *Gracilaria* sp., transection of part of frond, showing the cortex cells.

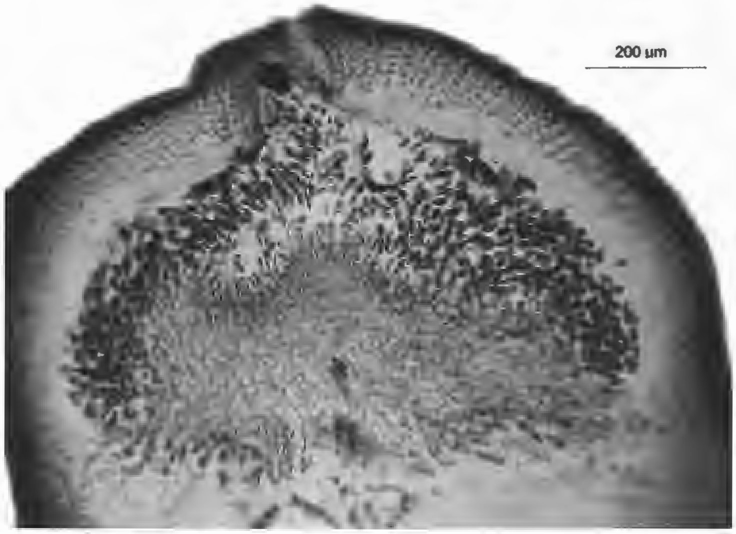

Fig. 4. *Gracilaria* sp., longitudinal section of cystocarp.

Table 1. Comparison of *Gracilaria* sp. with Its Three Closely Related Species

Characters	***G. lemaneiformis***	***G. bailinae***	***G. chorda***	***Gracilaria* sp. (AST 66–591)**
Mature frond	24–45(–200) cm long[a]	10–50(–70) cm long[d]	25–60 cm long[c] To 150(–200) cm long[e] To 60(–150) cm long[f]	6–9 cm long
Main axis percurrent	Frequently[a]	With or without[d]	Conspicuous[c] More or less traceable or distinctive[e]	Without
Branches	With or without more orders of branching, 0.5–3 mm diam.[a]	2–4 orders, 1–2(–3) mm diam.[d]	To 5 mm diam.[e] 2–3 mm diam., 1–2 orders[c]	0.5–1 mm diam, simple, 1–2 orders
Cystocarp	Globose, strongly basally constricted[a]	Subconical, unconstricted at bases[d]	Globose, slightly constricted at bases[f] Constricted at bases[e]	Subspherical, unconstricted at bases
Pericarp	10–14 layers[b] 116–182 µm thick, 10–14 layers[c]	76–100 µm thick, 7–8 layers[d]	To 120 µm thick, 8–10 layers[f]	53–66 µm thick, 5–7 layers

[a] Abbott 1999.
[b] Lewmanomont 1994.
[c] Chang and Xia 1976.
[d] Zhang and Xia 1988.
[e] Yamamoto 1978.
[f] Terada and Ohno 2000.

Cystocarps subspherical, 415–548 µm tall, 747–868 µm wide, nonrostrate and nonconstricted at bases, gonimoblasts consisting of many smaller cells; carpospores 16.5–23.1 µm by 9.9–11 µm in diameter; pericarp thin, consisting of 6–7 layers, 53–83 µm thick, without absorbing filaments.

Tetrasporangia (immature) ovoid. Spermatangia unknown.

Discussion

The *Gracilaria* sp. we describe here is morphologically somewhat like *G. lemaneiformis, G. bailinae,* and *G. chorda* in branching pattern, in the gonimoblast with many small cells, and in the pericarp, which lacks absorbing filaments. We also note differences in branching pattern, cystocarp features, and numbers of layers in the pericarp (Table 1). We are attempting to find more specimens in the field, especially alga with spermatangia, in order to finalize the taxonomic position. A name will be given after plants with male reproductive organs have been found.

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Literature Cited

Abbott, I. A. 1999. Marine red algae of the Hawaiian Islands. Bishop Museum Press, Honolulu.

Chang, C. F., and Xia B. M. 1976. Studies on Chinese species of *Gracilaria*. Stud. Mar. Sinica 11:91–163, pls. 1–2.

Lewmanomont, K. 1994. The species of *Gracilaria* from Thailand. In: Tax. Econ. Seaweeds 4, pp. 135–148, figs. 1–22.

Terada, R., and Ohno, M. 2000. Notes on *Gracilaria* from Tosa Bay and adjacent waters: I. *Gracilaria chorda*, *Garcilaria gigas* and *Gracilaria incurvata*. Rep. Bull. Mar. Sci. Fish. Kochi Univ. 20:81–88, figs. 1–19.

Yamamoto, H. 1978. Systematic and anatomical study of the genus *Gracilaria* in Japan. Mem. Fac. Fish. Hokkaido Univ. 25:97–152, pls. 1–49.

Zhang J. F. and Xia B. M. 1988. On two new *Gracilaria* from South China. In: Tax. Econ. Seaweeds 2, pp. 131–136, figs. 1–17.

Section VIII. *Laurencia* Species

INTRODUCTION

Isabella A. Abbott

The contribution by Ki Wan Nam of Korea on the *Laurencia* complex reinforces recent changes in the recognition of genera from *Laurencia* alone to *Chondrophycus* and *Osmundea.* It was previously easy to name a large number of specimens as *"Laurencia"* (for filing purposes), and to continue that when these changes involved taxa not recognized in Hawaii and much of the warm Pacific. Those days are over! Two of the rather common species in Hawaii, "old names" *L. undulata* and *L. cartilaginea,* are now in Chondrophycus. We have to look more carefully now to distinguish *Laurencia* from *Chondrophycus. Osmundea* is certain to show up in the central Pacific too. (It isn't only *Laurencia; Gigartina* has also undergone that kind of change, as will other genera. Did you see the paper that places all *Enteromorpha* species into *Ulva?*)

LAURENCIA COMPLEX: MORPHOLOGY OF *LAURENCIA PINNATA* (RHODOPHYTA), WITH A KEY TO KOREAN SPECIES

Ki Wan Nam

Abstract

The *Laurencia* Lamouroux (Rhodophyta) complex involves 3 similar genera, *Laurencia*, *Chondrophycus* (Tokida et Saito) Garbary et Harper, and *Osmundea* Stackhouse, whose generic delineations were recently newly defined based on some vegetative and reproductive structures. In this study, previously unknown developmental morphology of *L. pinnata* Yamada from Korea and Japan, which is superficially similar to other complanate species of the *Laurencia* complex, is studied in the context of the generic delineation. This species has a vegetative axial structure with a trichoblast and 4 pericentral cells, trichoblast-type spermatangial development, procarpic structure with 5 pericentral cells, and tetrasporangial production from pericentral cells. Among the pericentral cells in the vegetative axial segment, the first one is always produced below the basal cell of the trichoblast, then the second formed at some distance from the first, followed by the third and fourth in an alternating sequence. Spermatangial branches are produced from 1 of 2 laterals on the suprabasal cell of the trichoblast. Tetrasporangia are also abaxially produced from the existing third and fourth pericentral cells as in other *Laurencia* species. The fundamental vegetative and reproductive morphology confirms this species to be a member of *Laurencia* rather than of *Chondrophycus* or *Osmundea*.

Introduction

Recently, the *Laurencia* Lamouroux (1813) (Rhodophyta) complex, including more than 150 species with worldwide distribution, was separated into 3 genera—*Laurencia*, *Chondrophycus* (Tokida et Saito) Garbary et Harper, and *Osmundea* Stackhouse (1809), each of which was newly defined (Nam et al. 1994; Nam 1999; Garbary and Harper 1998). *Osmundea* is characterized by the combined features of the production of 2 pericentral cells in the vegetative axis, spermatangial development of the filament type, and tetrasporangial production from random cortical cells (Nam 1999). In contrast, *Laurencia* is circumscribed by the production of 4 pericentral cells rather than 2 in the vegetative axis, spermatangial development of the trichoblast type, and tetrasporangial production from particular pericentral cells (Nam 1999). *Chondrophycus* is delimited from *Laurencia* by the vegetative axis having 2 pericentral cells rather than 4. These 3 genera are, however, indistinguishable by external features. *Osmundea* is found on the Atlantic coast of Europe, around the Canary Islands, in the Mediterranean Sea, and along the Atlantic and Pacific coasts of North America (Dawson 1944; Dawson et al. 1960; Saito 1969, 1982; Furnari and Serio 1993a, b; Maggs and Hommersand 1993; Nam and Saito 1994; Nam et al. 1994; Cormaci et al. 1994). *Laurencia* and *Chondrophycus* are present throughout the Pacific Basin including Korea, Japan, China, the Philippines, Australia, and Hawaii (Kang 1966; Saito 1967; Saito and Womersley 1974; Cordero 1977; Zhang and Xia 1985; McDermid 1988a,b).

Laurencia pinnata Yamada was described from Enoshima, Japan (Yamada 1931). Since then, its presence has been reported mainly from the western Pacific (Yamada 1931; Kang 1966; Saito 1967; Saito and Womersley 1974; Cordero 1977; Zhang and Xia 1985). In those areas, this alga is a common species and is sometimes superficially confused with other complanate species of the *Laurencia* complex, such as *L. brongniartii* J. Agardh, *C. kangjaewonii* (Nam et Sohn) Garbary et Harper, and *O. pinnatifida* (Hudson) Lamouroux. In this paper, previously unknown vegetative and reproductive morphology of *L. pinnata* is studied in the context of the revised generic delimitation, and taxonomic features found in the species are compared with those of other Korean *Laurencia* and *Chondrophycus* species.

Materials and Methods

Data for this study were obtained from fresh, liquid-preserved, and herbarium specimens collected from Korea and Japan. Sectioning technique and methods for microscopic examination were the same as in Nam and Sohn (1994). Measurements are given as length by diameter. Voucher specimens have been deposited in the Herbarium of the Department of Marine Biology, Pukyong National University (formerly National Fisheries University of Busan), Korea.

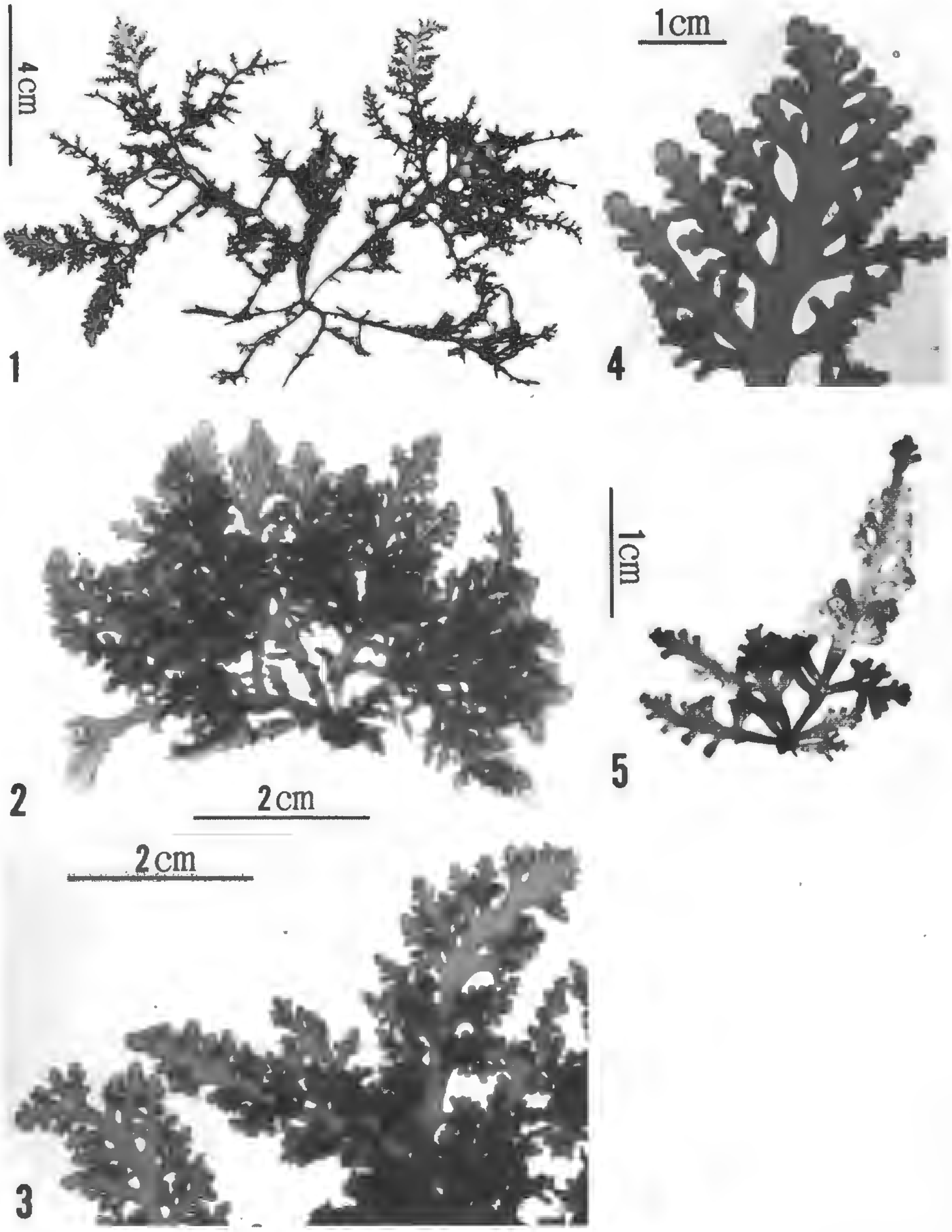
Results

Laurencia pinnata Yamada, Univ. Calif. Publ. Bot, p. 242, 1931. (Figs. 1–33)

Type locality: Enoshima, Sagami Province, Japan.

Distribution: Japan, Korea, China, Philippines (Yamada 1931; Kang 1966; Saito 1967; Cordero 1977; Zhang and Xia 1985).

Examined specimens: SAP 13872 (type). *Korea:* Tongbaeksum, Busan, leg. Nam, Aug. 10, 1983 (N831042–43⊕), June 6, 1986 (N860074⊕♀); Ilgwang, leg. Nam, Oct. 23. 1983 (N831041, 43⊕♂); Yangdong, leg. Nam, May 21, 1986 (N860075⊕). *Japan:* Shiragami, Hakodate, leg. Yamamoto, May 11, 1963 (S346, 48); Matsumae, Hakodate, leg. Yamamoto, April 7, 1962 (S347 sterile), April 23, 1963 (S349 sterile); Noro, June 25, 1977 (S860333–35⊕, S860336♂, S860337♀); Hakodate, leg. Suda, June 9, 1977 (S860338♂), leg. Yamamoto, June 15, 1978 (S860339–42⊕, 45–46⊕, 43♀, 47♀, 44♂, 48♂), June 22, 1978 (S860349♂, 51♀), June 6, 1978 (S860350⊕), July 7, 1978 (S860352⊕); Nagasaki, leg. Minamisato, April 1, 1986 (S860448); Boshu, leg. Sugiyama (Yendo 00370).



Figs. 1–5. ***Laurencia pinnata*** **Yamada. Fig. 1, Herbarium mounted tetrasporangial plant (N860074). Fig. 2, Female plant. Fig. 3, Details of tetrasporangial branches. Fig. 4, Details of female branches. Fig. 5, Male plant.**

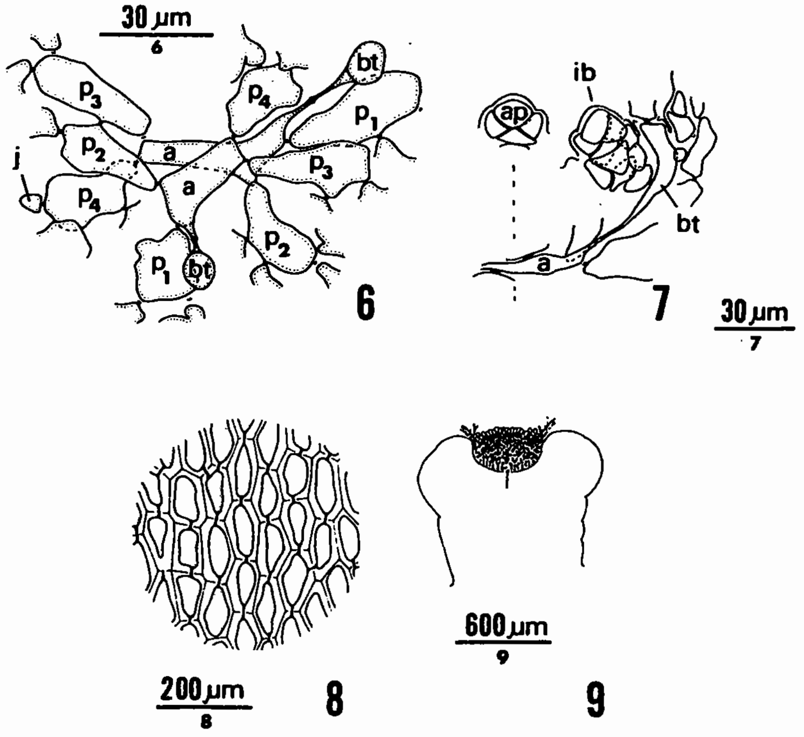
Habitat: On rock near lower tidal zone.

Habit: Thallus is 4–8 cm high (Fig. 1), forming loose clumps, occasionally epiphytic on other algae, distinctly compressed except near holdfast, brown or purplish brown, fleshy and soft in texture, adhering well to paper (Figs. 1–5). One or several erect axes arise from a discoid holdfast (Figs. 2, 5), at the broadest part 1.3–1.7 mm broad, usually without basal stoloniferous branches. Branching is somewhat patent, commonly distichous, repeatedly pinnate (Figs. 3, 4). Ultimate branchlets are slightly flattened, obtuse at the apices, 0.3–0.6 mm in diameter. In a collection from Busan, Korea, fertile plants of *L. pinnata* with small thallus size (ca 2 cm) were found; these seem to be an autumnal dwarf form of the species, mentioned by Kudou and Saito (1985).

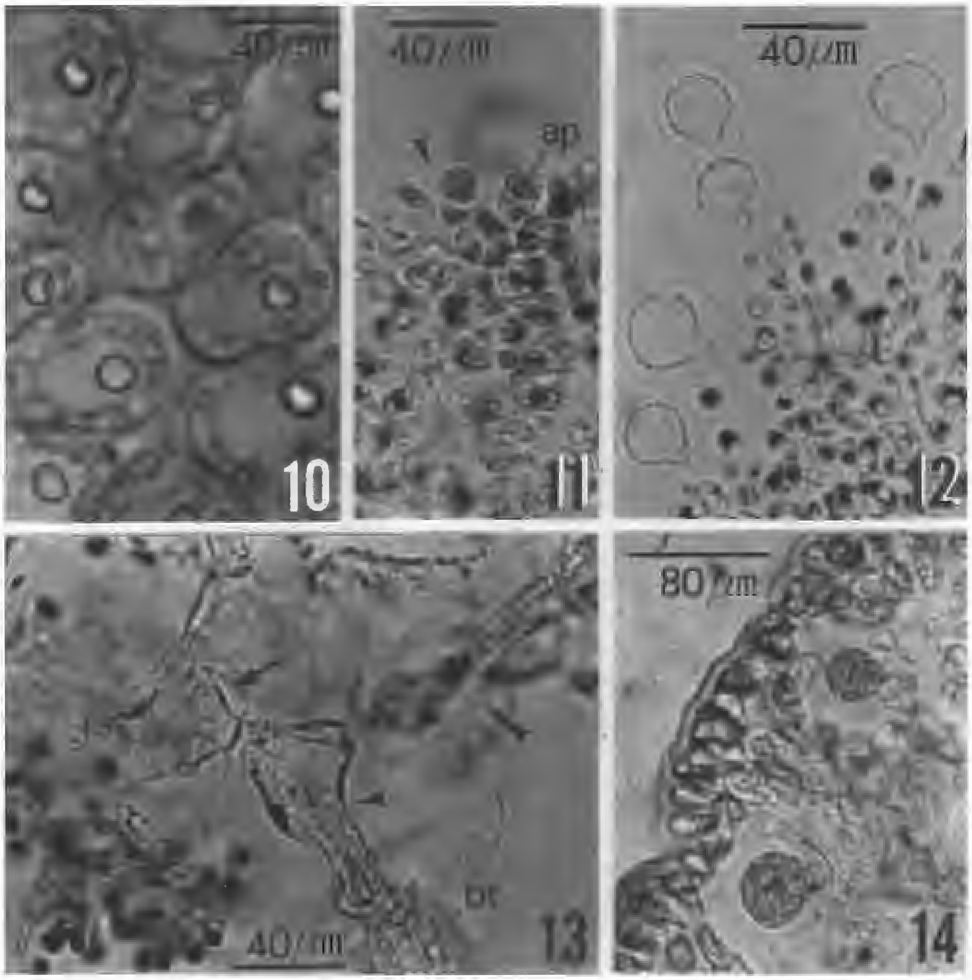
Vegetative morphology: Axial segments are obliquely cut off successively at 3 dividing faces from the apical cell, which is always sunk in the apical pit of branchlets. The resulting wedge-shaped axial segments are arranged in 3/8 spiral, clockwise or counterclockwise as seen from the apex (Figs. 6, 7). Each axial segment produces a trichoblast and 4 pericentral cells (Fig. 6). The first pericentral cell is always produced below the basal cell of the trichoblast, then the second at some distance from the first, followed by the third and fourth in an alternating sequence. Determinate filaments derived from the pericentral cells develop in one plane, giving rise to the strongly compressed thallus. Ordinary lateral branches are also successively produced from the axil of basal cells of trichoblasts (Fig. 7), which are arranged in one plane, with regular or irregular interval; this makes alternately, oppositely, or suboppositely distichous branching. Adventitious branchlets with subcortical origin on the major axis were not observed. Secondary cortication hardly occurs in branches except near the holdfast. Internal rhizoidal descending filaments are occasionally found between medullary cells at the base of thallus. Cortical cells project somewhat near the branchlet apex. In a transverse section of branchlets, cortical cells are neither elongated radially nor arranged like palisade cells. Secondary pit connections are present between cortical cells (Fig. 8). Medullary cells always lack lenticular thickenings in the walls. *Corps en cerise* are observed in both cortical and trichoblast cells in live material, 1 per cell, and measure 8–15 µm in diameter (Fig. 10).

Abbreviations for Figs. 6–33. a, axial cell; ap, apical cell; au, auxiliary cell; bs, basal sterile group; bsi, basal sterile group initial; bt, basal cell of trichoblast; c, central cell of procarp-bearing segment; cb, carpogonial branch; cg, carpogonium; fb, spermatangial branch; fp, fertile pericentral cell; fu, fusion cell; gi, gonimoblast initial; gl, gonimoblasts; ib, ordinary lateral branch initial; j, conjunctor cell; ls, lateral sterile group; lsi, lateral sterile group initial; p, pericentral cell; pc, primary cortical cells; po, postsporangial cover cell; pr, presporangial cover cell; rh, internal rhizoids; sb, sterile branch; sbc, suprabasal cell of trichoblast; sc, scar after shedding of trichoblast; sco, secondary cortex; sg, sterile cell group; smt, spermatangium; sr, secondary rhizoidal cortical cells; stk, stalk cell; su, supporting cell; t, tetrasporangium; tc, terminal sterile cell; ti, trichoblast initial; tr, trichogyne.

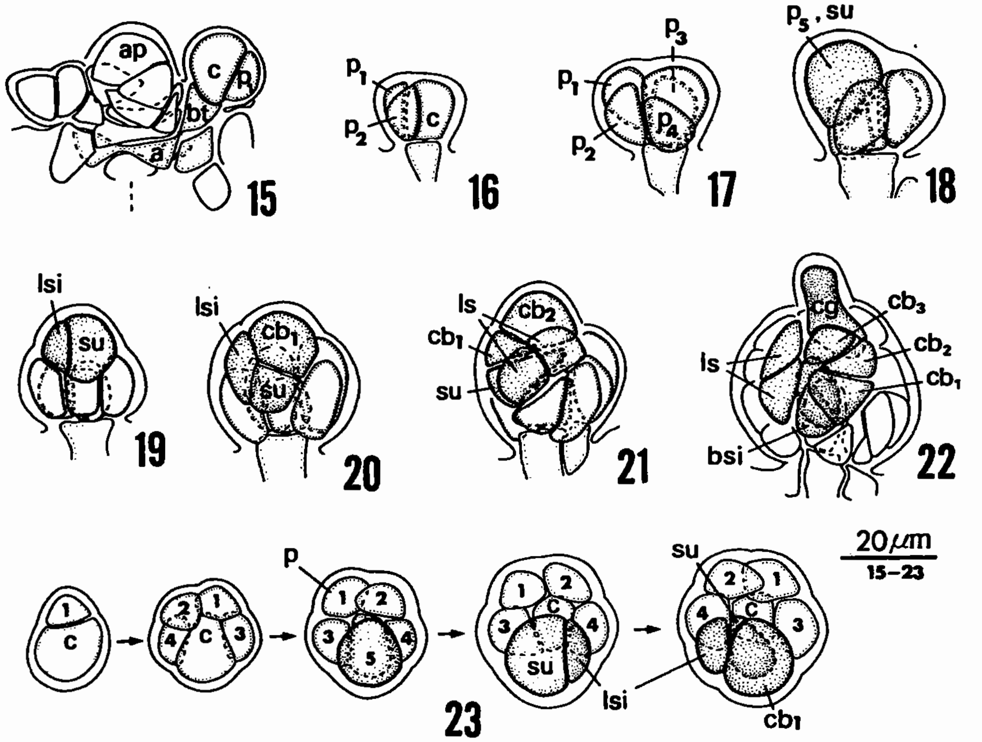
Reproductive morphology: Male branchlets are shortly turbinate, 1.0–1.2 mm in diameter. Male trichoblasts are produced in apical cup-shaped pits of the branchlets (Figs. 9, 11). Spermatangial branches are derived from 1 of 2 laterals on the suprabasal cell of the trichoblasts and terminate in 1 or occasionally in a row of 2 large sterile vesicular cells, 22–27 by 22–25 µm (Figs. 12, 13). It appears that production of pericentral cells in the axial segment of the spermatangial branches begins at the basal segment of the branches, then is extended upward to successive axial segments. Development of the pericentral cells seems to start in a very early stage, forming profuse branches composed of pericentral cell derivatives. Spermatangial mother cells are derived from these branches. Each spermatangial mother cell produces several ovoid spermatangia with an apical nucleus, 7–9 by 4–7 µm (Fig. 12). Mature spermatangial pits are 500–600 µm broad and up to 1.7–3.0 times as broad as deep.

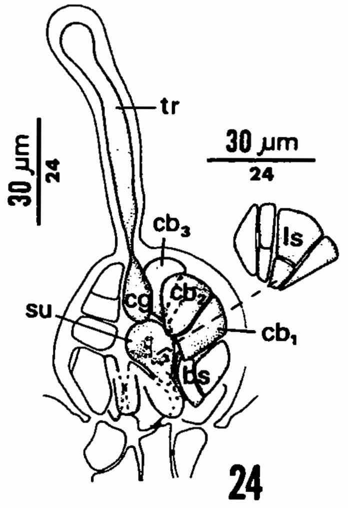


Figs. 6–9. ***Laurencia pinnata*** **Yamada. Fig. 6, Three superimposed vegetative axial segments. Fig. 7, Ordinary lateral branch initial on axil of basal cell of trichoblast. Fig. 8, Cortical cells with secondary pit connections in surface view of branches. Fig. 9, Male branchlet with cup-shaped spermatangial pit.**



Figs. 10–14. ***Laurencia pinnata*** **Yamada. Fig. 10, Cortical cells with *corps en cerise* in surface view. Fig. 11, Young male trichoblast (arrowhead) in median longitudinal section of branchlet. Fig. 12,. Spermatangial branches with terminal large vesicular sterile cells; note the cell terminating in a row of two. Fig. 13, Spermatangial (arrow) and sterile (double arrowhead) branches on suprabasal cell (arrowhead) of trichoblast. Fig. 14, Tetrasporangium produced abaxially from pericentral cell.**



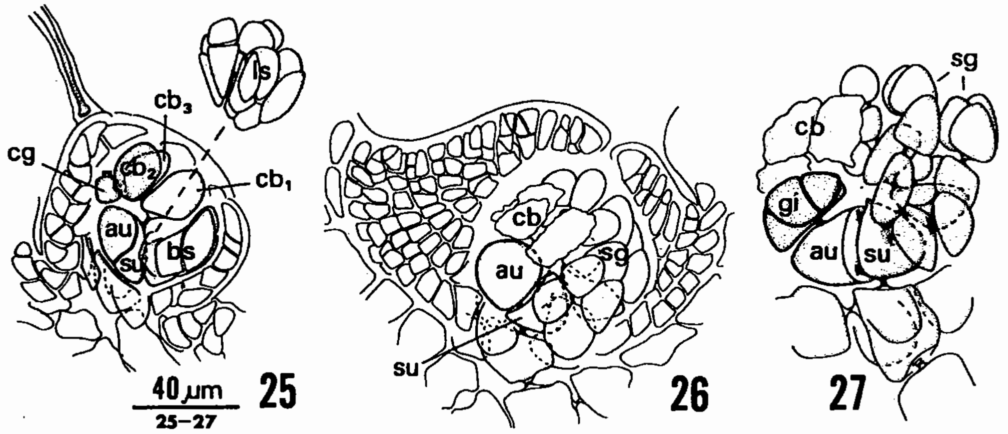


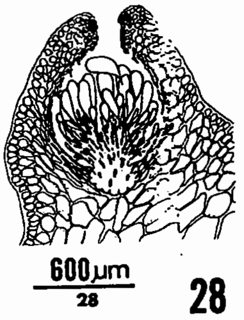
Figs. 15–24. ***Laurencia pinnata*** **Yamada.**
Figs. 15–22, Sequential developmental stages of procarp in longitudinal section of branchlets.
Fig. 23, Sequential developmental stages of procarp seen from branchlet apex.
Fig. 24, Mature procarp before fertilization.

Procarps are produced on the second segment (suprabasal cell) of the female trichoblasts in the apical pit of branchlets (Fig. 15). Five pericentral cells are cut off from the suprabasal cell (Figs. 15–18, 23). The first pericentral cell is abaxially formed by an oblique wall, then the second to the left or right of the first, followed by the third, fourth, and fifth cells in an alternating sequence. The fifth pericentral cell always acts as a supporting cell of a carpogonial branch (Fig. 18). The initial of the lateral sterile group is produced from the supporting cell (Fig. 19), followed by the carpogonial branch initial at a right angle to the lateral sterile group initial (Figs. 20, 21), and then the basal sterile group initial is formed underneath the carpogonial branch initial (Fig. 22). At the end of this stage, the carpogonial branch initial develops into a 4-celled branch, and the lateral sterile group initial divides into 2 or 3 cells (Fig. 22). The mature procarp has the supporting cell bearing the curved 4-celled carpogonial branch and 2 sterile groups, one lateral and one basal (Fig. 24). The first cell of the carpogonial branch is relatively large, and the second and third are wedge-shaped. The fourth cell (carpogonium) gives rise to a long trichogyne. The lateral and basal sterile group cells become densely cytoplasmic, composed of up to 6–8 cells and 3–4 cells, respectively, at the mature procarpic stage (Fig. 24).

After presumed fertilization, the trichogyne sheds from the terminal portion (Fig. 25). At the same time, the 4 cells of the carpogonial branch are fused with each other, although the fusion cell degenerates with development of gonimoblasts later (Figs. 26, 27). An auxiliary cell is also produced from the upper side of the supporting cell (Fig. 26). At this stage, cells of both sterile groups increase considerably in size and become more densely cytoplasmic. However, they also fuse with each other through enlargement of pit connections. In the young cystocarp, the space is almost filled with these sterile cell groups. The auxiliary cell cuts off a gonimoblast initial on its distal end, with its enlargement and gradual fusion to the supporting cell (Fig. 27). At the fully developed stage, both sterile cell groups consist of 25–35 cells or more. The gonimoblast initial is divided into a compact mass of gonimoblasts, then develops into numerous gonimoblast filaments by sympodial division. In this process, cells of sterile groups gradually disappear by absorption as nutrition. Thus, the gonimoblast filaments replace cystocarpic space occupied by sterile cell groups. The terminal cell of the gonimoblast filaments develops into a carposporangium (Fig. 28). Mature carposporangia are clavate, 300–400 by 70–100 μm. On the other hand, auxiliary and supporting cells are fused with neighboring cells, forming a large fusion cell at the base of the cystocarp (Fig. 28).

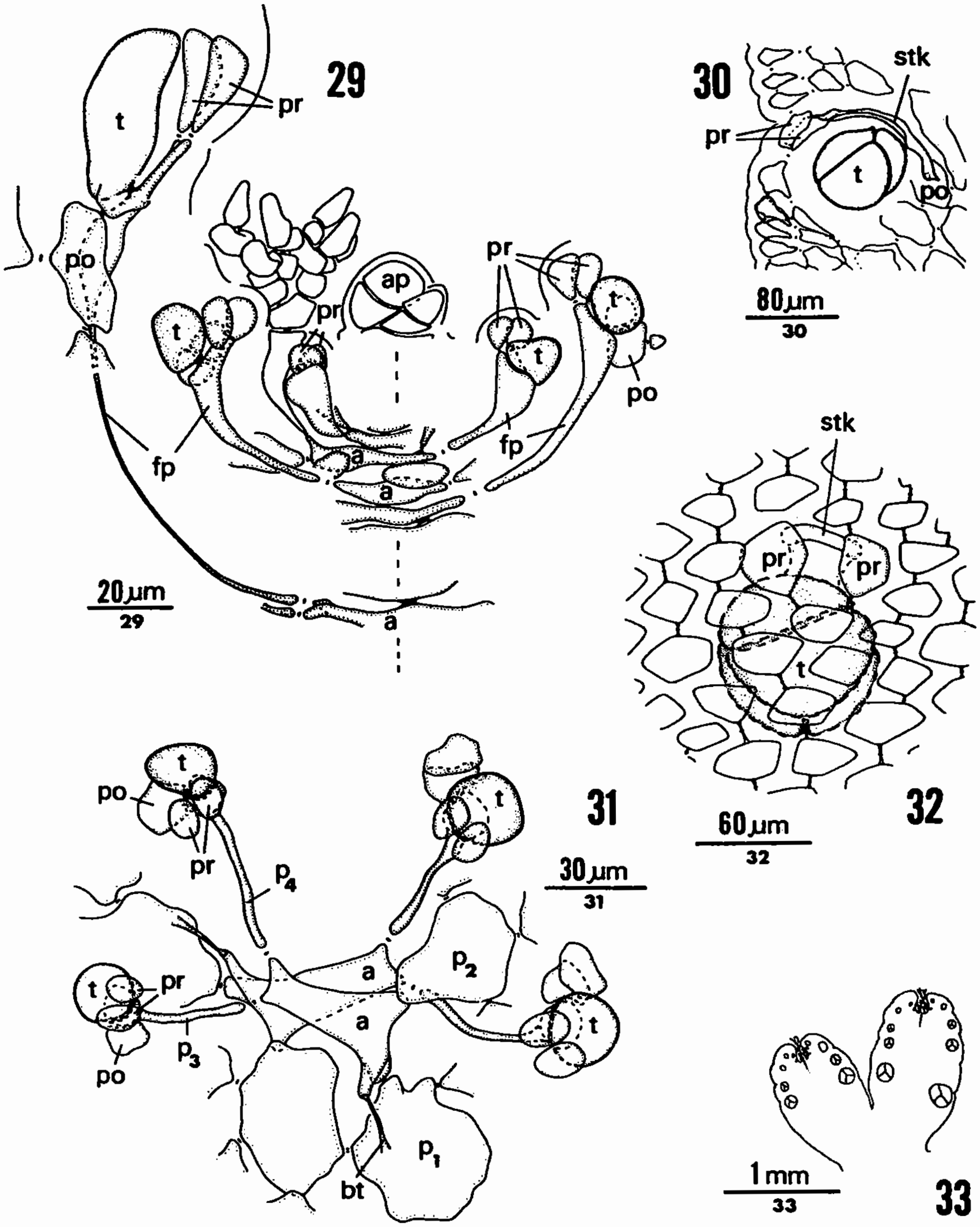
At the early young procarpic stage, pericarpic filaments are produced from 4 sterile pericentral cells in a procarp-bearing segment of trichoblast. These filaments continue to grow, forming a pseudoparenchymatous pericarp of 4–6 cell layers in the fully developed cystocarp. Mature cystocarps are ovoid with a non-protuberant ostiole, 1.1–1.2 by 1.0–1.2 mm (Fig. 28).





Figs. 25–28. *Laurencia pinnata* Yamada.
Figs 25–27, Procarpic development after presumed fertilization. Fig. 28, Mature cystocarp.

Tetrasporangial branchlets are somewhat cylindrical to clavate, 0.7–0.8 mm in diameter (Fig. 3). Tetrasporangia are abaxially produced from the existing third and fourth pericentral cells near the branchlet apex (Figs. 14, 29–31). Two pre- and one postsporangial cover cells are produced from the fertile pericentral cells before and after tetrasporangium production (Figs. 29, 31). The former cover cells remain undivided, forming a pair of large cells connected with adjacent cortical cells, whereas the latter cover cell develops into the corticating system around tetrasporangia (Figs. 29–30, 32). The 2 presporangial cover cells are arranged transversely to the stichidial axis in surface view (Fig. 32). Mature tetrasporangia divide tetrahedrally, measuring 160–200 µm in diameter (Figs. 30. 32). They show a parallel arrangement to the stichidial axis (Fig. 33).



Figs. 29–33. *Laurencia pinnata* Yamada. Figs. 29–30, Tetrasporangial development in median longitudinal section of stichidium. Fig. 31, Two superimposed tetrasporangial axial segments. Fig. 32, Tetrasporangium in surface view of stichidium. Fig. 33, Mature stichidia with parallel arrangement of tetrasporangia.

Discussion

As described above, *L. pinnata* shows a vegetative axis with 4 pericentral cells rather than 2, spermatangial structure of the trichoblast type rather than the filament type, and tetrasporangial production of pericentral cell origin rather than cortical cell origin. These features confirm that *L. pinnata* belongs to the genus *Laurencia*. As in other *Laurencia* species (see Nam 1999: Tab. 2), the first of 4 pericentral cells in a vegetative axial segment is produced underneath the basal cell of the trichoblast rather than at the side of the cell, then the second cell is produced some distance from the first, followed by the third and fourth in alternating sequence. As mentioned in previous works (Nam 1999; Nam and Choi 2000), this positional feature of the first pericentral cell in an axial segment, together with the vegetative axial structural type, seems also to be of phylogenetic significance in the *Laurencia* complex; in *Chondrophycus* (in species belonging to subgenera *Chondrophycus* Nam and *Kangjaewonia* Nam) and *Osmundea*, the first of 2 pericentral cells is formed at the side of a trichoblast basal cell (with the second formed at the other side of the cell). The number of pericentral cells in the procarp-bearing segment of female trichoblasts can be considered one of the significant taxonomic features in the *Laurencia* complex. A procarpic structure in *L. pinnata* was found to have 5 pericentral cells rather than 4 or 6 in the segment, as in many other species of *Laurencia* complex (Nam et al. 1994: Tab. 1). However, delayed formation of the auxiliary cell after presumed fertilization, which has been reported in some *Chondrophycus* species (Nam and Saito 1990k Nam and Sohn 1994k Nam 1999), was not observed in this species. It appears that delayed formation of the auxiliary cell is limited to some members of *Chondrophycus,* such as species belonging to subgenera *Chondrophycus* and *Kangjaewonia* (Nam and Sohn 1994; Nam 1999).

Laurencia pinnata plants are strongly compressed with bipinnate lateral branches with ultimate branchlets in opposite rows. Some *Laurencia* species, such as *L. elata* (C. Agardh) Harvey, *L. distichophylla* J. Agardh, and *L. brongniartii,* are similar to *L. pinnata* in having a compressed thallus with distichous branching. But these species differ in other features. *Laurencia elata* has a stoloniferous holdfast (but originally discoid), fastigiate branching, and abundant lenticular thickenings (Saito and Womersley 1974; Nam and Choi 2001), features not found in *L. pinnata*. *Laurencia distichophylla* differs from *L. pinnata* in having a clumped base (possibly stoloniferous) and occasionally lenticular thickenings (Saito and Womersley 1974). Among the species with a compressed thallus, *L. brongniartii* described from the West Indies is most similar to *L. pinnata* in habit, but these two species are readily distinguished by *corps en cerise* and the tetrasporangial arrangement with respect to the stichidial axis. The former species has 2–3 *corps en cerise* per cortical cell, and a tetrasporangial arrangement type intermediate between parallel and right-angle (Saito and Womersley 1974; Abe et al. 1998), whereas *L. pinnata*

Table 1. Comparison of Taxonomic Features Found in Korean Species of *Laurencia* and *Chondrophycus*

						Cortical cells		
Species	Thallus	Main leading branch	Pericentral cells in vegetative axis	Position of the first pericentral cell relative to trichoblast	Secondary pit connections	Arrangement	Projection	Corps en cerise/cell
L. obtusa	Terete	Present	4	Underneath	Present	NPD	Absent[†]	1
L. intricata	Terete	Absent	4	Underneath	Present	NPD	Absent[†]	(1)2–3(4)
L. nipponica	Terete	Present	4	Underneath	Present	NPD	Absent[†]	1
L. okamurae	Terete	Present	4	Underneath	Present	NPD	Absent[†]	1
L. venusta	Subterete or subcompressed	Not clear	4	Underneath	Present	NPD	Absent[†]	1
L. intercalaris	Terete	Present	4	Underneath	Present	NPD	Absent[†]	?
L. pinnata	Compressed	Not clear	4	Underneath	Present	NPD	Absent[†]	1
C. cartilaginea	Subcompressed or angular	Not clear	2	Side	Absent	NPD	Present	Absent
C. undulata	Compressed	Not clear	2	Side	Absent	NPD	Absent	Absent
C. kangjaewonii	Compressed	Not clear	2	Side	Absent	NPD	Absent	Absent
C. intermedia	Terete	Present	2	Underneath	Absent	PD	Absent	Absent
C. capituliformis	Terete	Present	2	Underneath	Absent	PD	Absent	Absent

NPD = non-palisade; PD = palisade; ? = unknown.

[†] Occasionally slightly projecting.

Table 1. *(cont.)*

Species	Spermatangial branches	Spermatangial nucleus	Pericentral cells in procarp-bearing segment	Auxiliary cell formtion	Arrangement of tetrasporangia	Tetrasporangial pericentral cells	Sterile pericentral cells in tetrasporangial axis	References
L. obtusa	SOL	Apical	5	N	Parallel	3rd, 4th	2	Nam (1990); Nam et al. (1994)
L. intricata	SOL	Apical	5	N	Parallel	3rd, 4th	2	Saito (1967); Nam (1990)
L. nipponica	SOL	Central	5	N	Parallel	3rd, 4th	2	Nam et al. (1991)
L. okamurae	SOL	Apical	5	N	Parallel	3rd, 4th	2	Saito (1967); Nam (1990)
L. venusta	SOL	Apical	5	N	Parallel	3rd, 4th	2	Nam et al. (2000)
L. intercalaris	Intercalary	Apical	?	?	?	?	?	Nam (1994)
L. pinnata	SOL	Apical	5	N	Parallel	3rd, 4th	2	This study
C. cartilaginea	STL	Apical	5	D	Right-angle	3rd*-5th*(6th*)	2	Nam & Saito (1990)
C. undulata	STL	Apical	5	D	Right-angle	3rd*-5th* (6th*)	2	Nam (1999)
C. kangjaewonii	STL	Apical	5	D	Parallel	3rd*-5th* (6th*)	2	Nam & Sohn (1994)
C. intermedia	SOL	Apical	4	N	Right-angle	2nd, 3rd*, 4th*, (5th*)	1	Nam & Saito (1995)
C. capituliformis	SOL	Apical	4	N	Right-angle	2nd, 3rd*	1	Nam & Saito (1995)

D = delayed formation of auxiliary cell after presumed fertilization; N = normal formation of auxiliary cell; SOL = with the development of spermatangial branches from one of the two laterals; STL = with development of spermatangial branches from two laterals on suprabasal cell of trichoblast, but one of the two remaining partly sterile; ? = unknown.

*Produced additionally.

has 1 *corps en cerise* per cell and a parallel arrangement of tetrasporangia. *Laurencia botryoides* (Turner) Gaillon, with a somewhat compressed thallus, is also readily distinguished from *L. pinnata* in having botryoidal branching and a right-angle arrangement of tetrasporangia (Saito and Womersley 1974; Nam 1990).

Osmundea pinnatifida, *Chondrophycus undulata* (Yamada) Gabary et Harper, and *C. kangjaewonii* also can be confused with *L. pinnata* (Okamura 1902; Yamada 1931; Kang 1966) because of superficial similarity among them. However, *O. pinnatifida* differs from *L. pinnata* in having 2 pericentral cells in the vegetative axial segment rather than 4, spermatangial development of the filament type rather than the trichoblast type, and tetrasporangial production from random cortical cells rather than from particular pericentral cells (Nam et al. 1994). *Chondrophycus undulata* and *C. kangjaewonii* are also readily distinguished from *L. pinnata* by the vegetative axial structure with 2 pericentral cells, absence of secondary pit connections between cortical cells, absence of *corps en cerise,* and tetrasporangial production from additional pericentral cells (Nam and Sohn 1994; Nam 1999). The features of spermatangial branches, tetrasporangial arrangement, and position of tetrasporangial pericentral cells are also important in distinguishing among those species (Table 1).

In Korea, 7 *Laurencia* and 5 *Chondrophycus* species are known (Table 1), but *Osmundea* is not found. *Laurencia pinnata* is distinct from these species in many vegetative and reproductive features: nature of the thallus (terete or compressed); presence or absence of a main leading branch; number of pericentral cells in the vegetative axis; position of the first pericentral cell relative to the trichoblast; presence or absence of secondary pit connections between cortical cells; presence or absence of a palisade-like arrangement and projection of cortical cells in ultimate branchlets; presence (and number of) or absence of *corps en cerise* in cortical cells; developmental aspects of spermatangial branches; position of spermatangial nucleus; number of pericentral cells in vegetative axial segments and the procarp-bearing segment of female trichoblasts; production position of tetrasporangia; and number of sterile pericentral cells in tetrasporangial axial segments.

Key to Korean Species of *Laurencia* and *Chondrophycus*

1\. Axial segment with 4 pericentral cells (*Laurencia*) 2
1\. Axial segment with 2 pericentral cells (*Chondrophycus*). 8
    2\. Fronds basically terete 3
    2\. Fronds basically compressed . . . .*L. pinnata*
3\. Cell wall thickenings always absent, thallus texture somewhat soft. 4
3\. Cell wall thickenings usually present or absent, thallus texture somewhat rigid 5

4. Cortical cells with 1 *corps en cerise*, thallus with main leading branch . . . . *L. obtusa*
4. Cortical cells with (1)2–3(4) *corps en cerise*, thallus without main leading branch . . . . *L. intricata*
5. Male trichoblast with intercalary spermatangia . . . . *L. intercalaris*
5. Male trichoblast without intercalary spermatangia 6
6. Spermatangium with central nucleus . . . . *L. nipponica*
6. Spermatangium with apical nucleus 7
7. Main leading branch not clear . . . . *L. venusta*
7. Main leading branch clear . . . . *L. okamurae*
8. Tetrasporangial axial segment with 2 sterile pericentral cells 9
8. Tetrasporangial axial segment with 1 sterile pericentral cells, cortical cells without secondary pit connections (subgen. *Palisada*) 11
9. With right-angle arrangement of tetrasporangia (subgen. *Chondrophycus*) 10
9. With parallel arrangement of tetrasporangia (subgen. *Kangjaewonia*) . . . . *C. kangjaewonii*
10. Cortical cells projecting near end of branchlets, cystocarps with protuberant ostioles . . . . *C. cartilaginea*
10. Cortical cells not projecting near end of branchlets, cystocarps without protuberant ostioles . . . . *C. undulata*
11. Cystocarps with protuberant ostioles . . . . *C. capituliformis*
11. Cystocarps without protuberant ostioles . . . . *C. intermedia*

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Literature Cited

Abe, T., Masuda, M., Kawaguchi, S., and Kamura, S. 1998. Taxonomic notes on *Laurencia brongniartii* (Rhodomelaceae, Rhodophyta). Phycol. Res. 46:231–237.

Cordero, P. A. 1977. Studies on Philippine marine red algae. Spec. Publ. Seto Mar. Biol. Lab. 4:1–258, 28 pls.

Cormaci, M., Furnari, G., and Serio, D. 1994. Two new species of *Laurencia* (Ceramiales, Rhodophyta) from the Mediterranean Sea: *Laurencia pelagiensis* sp. nov. and *Laurencia verlaquei* sp. nov. Jpn. J. Phycol. 42:365–375.

Dawson, E. Y. 1944. Some new Laurenciae from southern California. Madroño 7:233–240.

Dawson, E. Y., Neushul, M., and Wildman, R. D. 1960. New records of sublittoral marine plants from Pacific Baja California. Pacific Naturalist 1:3–30.

Furnari, G., and Serio, D. 1993a. The reproductive structure of the Mediterranean alga *Laurencia pelagosae* (Ceramiales, Rhodophyta). Eur. J. Phycol. 28:141–143.

Furnari, G., and Serio, D. 1993b. The distinction of *Laurencia truncata* (Ceramiales, Rhodophyta) in the Mediterranean Sea from *Laurencia pinnatifida*. Phycologia 32:367–372.

Garbary, D. J., and Harper, J. T. 1998. A phylogenetic analysis of the *Laurencia* complex (Rhodomelaceae) of the red algae. Cryptol. Algol. 19:185–200.

Kang, J. W. 1966. On the geographical distribution of marine algae in Korea. Bull. Pusan Fish. Coll. 7:1–125, 12 pls.

Kudou, K., and Saito, Y. 1985. Autumnal dwarf form of *Laurencia pinnata* Yamada. Jpn. J. Phycol. 33:77–78.

Lamouroux, J. V. 1813. Essai sur les genres de la famille des Thallasiophyte non articulées. Ann. du Mus. d'Hist. Nat. Paris 20:21–47, 115–139, 267–293, pls.5–13.

Maggs, C. A., and Hommersand, M.,H. 1993. Seaweeds of the British Isles, Vol. 1: Rhodophyta, Pt 3a. Ceramiales. Natural History Museum, London. 444 pp.

McDermid, K. J. 1988a. Section V. *Laurencia* (Rhodophyta, Rhodomelaceae) Introduction. In: Tax. Econ. Seaweeds 2, pp. 221–229.

McDermid, K. J. 1988b. *Laurencia* from the Hawaiian Islands: Key, annotated list, and distribution of the species. In: Tax. Econ. Seaweeds 2, pp. 231–247.

Nam, K. W. 1990. Morphotaxonomic studies of genus *Laurencia* (Rhodomelaceae, Rhodophyta). Ph. D Thesis, Hokkaido Univ., Japan. 492 pp., 49 pls.

Nam. K. W. 1994. Vegetative and male reproductive anatomy of *Laurencia intercalaris* sp. nov. (Rhodomealceae, Rhodophyta) in Korea. J. Plant Biol. 37:421–428.

Nam, K. W. 1999. Morphology of *Chondrophycus undulata* and *C. parvipapillata* and its implications for the taxonomy of the *Laurencia* (Ceramiales, Rhodophyta) complex. Eur. J. Phycol. 34:455–468.

Nam, K. W., and Choi, H. G. 2000. A detailed morphological study of the type species of *Osmundea* (Rhodomelaceae, Rhodophyta). Bot. Mar. 43:291–297.

Nam, K. W., and Choi, H. G. 2001. Morphology of *Laurencia clavata* and *L. elata* (Ceramiales, Rhodophyta) in relation to generic circumscription in the *Laurencia* complex. Eur. J. Phycol. 36:285–294.

Nam, K. W., Choi, H. G., Lee, S., Park, E. J., Kang, K. H., and Kim, Y. S. 2000. Vegetative and reproductive development of *Laurencia venusta* (Ceramiales, Rhodophyta). Cryptol. Algol. 21:97–110.

Nam, K. W., Maggs, C. A., and Garbary, D. J. 1994. Resurrection of the genus *Osmundea* with an emendation of the generic delineation of *Laurencia* (Ceramiales, Rhodophyta). Phycologia 33:384–395.

Nam, K. W., and Saito, Y. 1990. Morphology of *Laurencia cartilaginea* Yamada (Rhodomelaceae, Rhodophyta). Bull. Fac. Fish. Hokkaido Univ. 41:107–120.

Nam, K. W., and Saito, Y. 1994. A re-examination of *Laurencia hybrida* (Ceramiales, Rhodophyta) from the British Isles: Vegetative and reproductive morphology. Phycologia 33:34–41.

Nam, K. W., and Saito, Y. 1995. Vegetative and reproductive anatomy of some *Laurencia* (Ceramiales, Rhodophyta) species with a description *of L. maris-rubri* sp. nov. from the Red Sea. Phycologia 34:157–165.

Nam, K. W., Saito, Y., and Sohn. C. H. 1991. Vegetative structure and reproduction of *Laurencia nipponica* Yamada (Rhodomelaceae, Rhodophyta). Kor. J. Phycol. 6:1–12.

Nam, K. W., and Sohn, C.H. 1994. *Laurencia kangjaewonii* sp. nov. (Ceramiales, Rhodophyta) from Korea. Phycologia 33:397–403.

Okamura, K. 1902. Nippon soriu meii. 1st ed. Tokyo. 276 pp.

Saito, Y. 1967. Studies on Japanese species of *Laurencia,* with special reference to their comparative morphology. Mem. Fac. Fish. Hokkaido Univ. 15:1–81.
Saito, Y. 1969. On morphological distinctions of some species of Pacific North American *Laurencia.* Phycologia 8:85–90.
Saito, Y. 1982. Morphology and infrageneric position of three British species of *Laurencia* (Ceramiales, Rhodophyta). Phycologia 21:299–306.
Saito, Y., and Womersley, H. B. S. 1974. The Southern Australian species of *Laurencia* (Ceramiales: Rhodophyta). Austral. J. Bot. 22:815–874.
Stackhouse, J. 1809. Tentamen marino-cryptogamicum,... Mém. Soc. Imp. Nat. Moscou. 2:50–97.
Yamada, Y. 1931. Notes on *Laurencia,* with special reference to the Japanese species. Univ. Calif. Publ. Bot. 16:185–310.
Zhang J. and Xia B. 1985. Studies on the genus *Laurencia* of the Xisha Islands, Guangdong province, China. Stud. Mar. Sin. 24:51–67, pl. 1.

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