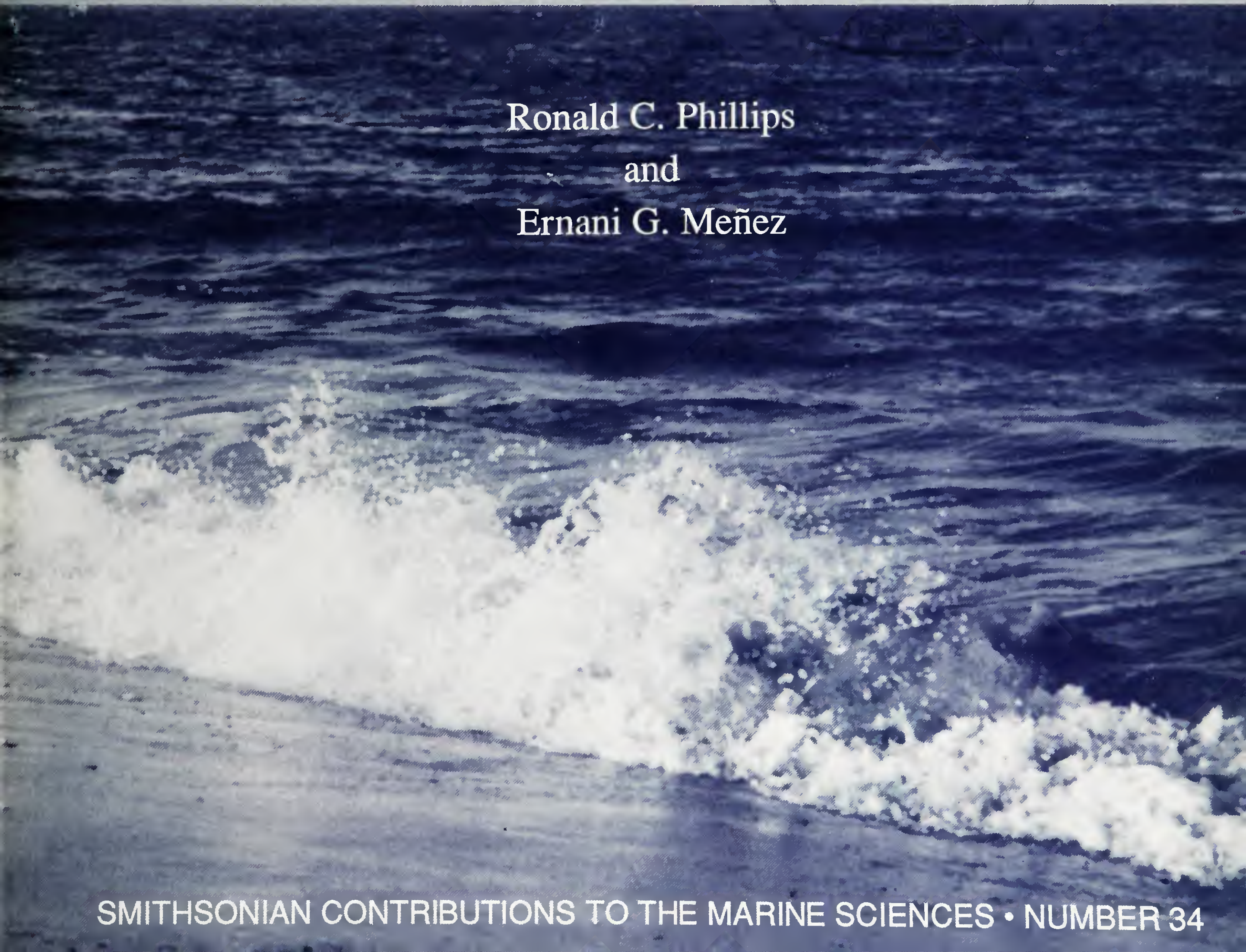
Seagrasses



Ronald C. Phillips
and
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SMITHSONIAN CONTRIBUTIONS TO THE MARINE SCIENCES • NUMBER 34

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SMITHSONIAN INSTITUTION PRESS
Washington, D.C.
1988

ABSTRACT

Phillips, Ronald C., and Ernani G. Meñez. Seagrasses. *Smithsonian Contributions to the Marine Sciences,* number 34, 104 pages, 4 tables, 57 figures, 39 maps, 1988.—This work presents general and current information on seagrass ecology, physiology, biology, distribution and evolution. Additionally, all known taxa of seagrasses are keyed to recognized species. Forty-eight species are described and illustrated, with accompanying maps to indicate their world distribution.

OFFICIAL PUBLICATION DATE is handstamped in a limited number of initial copies and is recorded in the Institution's annual report, *Smithsonian Year*. SERIES COVER DESIGN: Seascape along the Atlantic coast of eastern North America.

Library of Congress Cataloging in Publication Data
Phillips, Ronald C.
Seagrasses
(Smithsonian contributions to the marine sciences ; no. 34)
Bibliography p.
1. Seagrasses. 2. Helobiae. I. Meñez, Ernani G. II. Title. III. Series.
QK495.A14P47 1987 584'.742 87-23245

Contents

We dedicate this work to our colleague, Professor Hilconida P. Calumpong, Assistant Director,
Silliman University Marine Laboratory, Philippines, for her devotion and contributions
to the study of marine plants in the Philippines.

Seagrasses

Ronald C. Phillips and Ernani G. Meñez

Introduction

There are approximately 48 species of grass-like flowering plants found in the shallow-water coastal areas of the world between the Arctic and Antarctic Circles. These plants tend to develop extensive underwater meadows on muddy or sandy substrates, resembling fields of wheat. All seagrasses are monocots and are placed in one of two families, viz., Potamogetonaceae (9 genera, 34 species) and Hydrocharitaceae (3 genera, 14 species).

Seagrass meadows form extremely complex ecosystems that function through detritus-based food webs as well as herbivore webs. In the latter living seagrass plants as well as epiphytes on the plants are grazed. Seagrass meadows have recently been recognized as an important marine resource. The major functions of seagrasses were enumerated by Wood, Odum, and Zieman (1969): (1) the plants stabilize and hold bottom sediments even through the enormous stresses of hurricanes and temperate storms; (2) the leaves slow and retard water currents and waves, promoting sedimentation of particulate matter and inhibiting resuspension of organic and inorganic matter; (3) the meadow serves as a shelter and refuge for resident and transient adult and juvenile animals, many of which are of commercial and recreational importance; (4) the feeding pathways consist of both direct grazing on the leaves or epiphytes and detrital pathways; (5) the plants attain a high production and growth (leaves of some species can grow 5–10 mm per day); (6) the plants produce and trap detritus and secrete dissolved organic matter that tends to internalize nutrient cycles within the ecosystem.

The earliest work to be done on seagrass ecology was conducted by Danish investigators working on eelgrass (*Zostera marina* L.) from the Danish Biological Station in Copenhagen. The report by Petersen (1891), stating his belief that fish abundance in Denmark was due to eelgrass was the earliest report of its kind. Ostenfeld (1905, 1908) initiated extensive ecological studies on Danish eelgrass. Petersen and Boysen-Jensen (1911) assembled numerous data relating eelgrass growth, plankton density, and the quantity of deposited organic matter. Petersen (1913) listed Danish eelgrass standing stocks. Boysen-Jensen (1914) reported eelgrass production and its relation to the organic matter of the Danish sea bottom and made extensive chemical tests on eelgrass-based organic matter. Blegvad (1914, 1916) published two large papers on the food of invertebrates and fish in Danish marine waters. Petersen (1915, 1918) summarized the Danish work and assembled it into food chains and a quantitative food pyramid, all based on eelgrass. The overall concensus was that detritus formed from eelgrass in Danish waters formed the basis for the invertebrate animal communities that ultimately led to several species of food fish important to the Danish economy.

From 1929 to 1934, Setchell (1929, 1934, 1935) published studies on the phenology of eelgrass and the distribution of seagrasses.

From 1933 until approximately 1950 almost all seagrass research concerned the massive eelgrass epiphytotic (an epidemic disease in plants) that began on the Atlantic coast of North America in 1931 and was soon observed in Europe. By 1933 the so-called "wasting disease" had decimated 90% of all eelgrass in the North Atlantic (Tutin, 1942). Moffit and Cottam (1941) reported that along most areas of the Atlantic coast of the United States, 99% to 100% of standing stocks were destroyed in one year. A large amount of ecological work concerning the wasting disease was initiated in the eastern United States and in Europe, principally in England and France (Cottam, 1934; Dexter, 1944, 1950; Tutin, 1938).

In 1950 research began to veer away from the strictly applied bias of the 1930s and 1940s. Arasaki (1950a,b) published comprehensive studies on the ecology of eelgrass in Japan. In 1957, research on tropical seagrass species was initiated in Florida (USA). Phillips (1960) published a paper on the

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distribution and ecology of the Florida seagrasses. Following this paper, many investigators initiated intensive studies at several institutions on all components of the tropical seagrass ecosystems (Durako, Phillips, and Lewis, 1987).

In 1960, there were few published papers on seagrass ecology (Zieman, 1987). By 1978 a bibliography compiled by the Seagrass Ecosystem Study listed over 1,400 titles worldwide (Zieman, Bridges, and McRoy, 1978). By 1982 an analysis of South Florida seagrasses contained over 550 references (Zieman, 1982). From 1960 until 1970 seagrass work was largely descriptive and qualitative, with a movement toward quantitative studies. Conceptual models of the seagrass ecosystem were being developed by 1970. By 1980 increasingly robust models of the mechanisms by which the systems develop and maintain their productivity were proposed and used as guides for research.

In 1963, Phillips initiated comprehensive field studies, including transplantation, on eelgrass. In 1966, McRoy completed a voluminous study of eelgrass in Alaska. Den Hartog (1970) published a comprehensive monograph on seagrasses. In 1973, the National Science Foundation sponsored an international workshop that brought 38 scientists from 11 countries together in Leiden, The Netherlands, to determine what had been done on seagrasses and to formulate recommendations for future research. Since 1973, seagrass research has escalated in many parts of the world, particularly Japan, Australia, France, the Netherlands, India, Canada, Papua New Guinea, and the Philippines.

ACKNOWLEDGMENTS.—We wish to thank Dr. Joseph Zieman, University of Virginia, and Dr. Dieter Wasshausen, Smithsonian Institution, for their helpful criticism and advice. For the hospitality and support in expediting our seagrass project in the Philippines, we are indebted to Dr. Angel Alcala, Director, Silliman University Marine Laboratory and Hilconida Calumpong, University of California, Berkeley. Dr. Calvin McMillan, University of Texas, generously provided rarely collected female plants of *Halophila engelmannii*. Wordprocessing was done by Hilconida Calumpong, and Dr. Chris Meacham, also from the University of California, Berkeley, helped solved some computer incompatibility problems.

Ronald Phillips acknowledges the sabbatical leave grant and monies from the Institute for Research, Seattle Pacific University, which allowed him to complete his work. Ernani Meñez appreciates the travel and research support from the Smithsonian Institution Research Opportunities Fund.

The loan of herbarium material of seagrasses from the US National Herbarium, Smithsonian Institution, Washington, D.C., and the Rijksherbarium, Leiden, is gratefully acknowledged. This paper is based on research supported in part by the National Science Foundation, International Decade of Ocean Exploration, Living Resources Program under Grants OCE-24358 AOI, OCE76-84259, OCE77-25559, and OCE77-25559 AOI.

The Nature of the Species

Until recently seagrass taxonomists have not been confronted with any serious problems in defining species. There are 12 genera, each clearly delimited in morphology, and, for the most part, in function and environmental tolerances. There are relatively few (about 48) species distributed over the world. Except for *Zostera* (10 species), *Halophila* (11 species), and *Posidonia* (5 species), 9 genera have relatively few species.

In many areas and in many genera, it is difficult to find flowers of seagrasses. In some cases seagrasses do not produce any flowers or any appreciable abundance of flowers, e.g., *Halodule*, or the flowers are difficult to locate. In *Halodule* the flowers are produced under the sediment level and are only found in localized patches. In *Thalassia testudinum* the flowers may be hidden by the density of the vegetation. In many cases where collections have been made by visiting scientists in relatively inaccessible areas or in accessible areas but where no one is working on seagrasses, the collection time may occur during the non-reproductive season. Because of this, seagrass taxonomists have relied on morphological and anatomical criteria of seagrass vegetation in the description of new species.

Owing to the problems of growing seagrasses in culture under controlled conditions, little has been done until recently in the area of experimental taxonomy to define the range of physiological, morphological, and genetical variations in seagrass species. No one has yet attempted pollination experiments between species, but the work of McMillan on reproductive physiology (1976, 1982), McMillan and Phillips (1979a, 1981), and McMillan (1980) on isozymes, Zapata and McMillan (1979), and Phillips, McMillan, and Bridges (1981, 1983), Phillips, Grant and McRoy (1983), Jacobs (1982), and Orth and Moore (1983) have established that seagrass species are comprised of populations that are adapted to the selective influence of local habitat conditions over their distributional range. Some of these species and populations have broad tolerances and others have narrow tolerances to the environment. It is now known that plant morphology is influenced by the reaction of a population to its environment (Phillips and Lewis, 1983; McMillan, 1979; McMillan and Phillips, 1979a), and in certain cases can be highly plastic and variable. For example, *Zostera marina* appears to show such a plastic response. Depending on the degree of environmental stress that may be correlated with latitude, ocean, or stress correlated with a particular environmental factor at a particular site, leaf width may be quite variable. A variety of authors in the past have created either varieties or separate specific epithets for these adaptable, morphologically variable, species (*Zostera stenophylla* Rafinesque; *Z. angustifolia* (Hornemann) Reichenbach; *Z. serrulata* auctorum non Targioni-Tozz; *Z. oregana* S. Watson; *Z. pacifica* S. Watson; *Z. hornemanniana* Tutin; not to name the varieties). Setchell (1920, 1929) noted that leaves of *Z. marina* were narrower in the intertidal and in Alaska (Bering Sea) and along the entire Atlantic coast of

North America than leaves in the subtidal in those areas, and particularly in the subtidal from Alaska south of the Alaskan Peninsula to Baja California. Narrower leaves occur in winter than in summer. Ostenfeld (1908) recorded narrower subtidal leaves when the plants grew in sand than in mud. Setchell suggested that these narrower leaves were due to stress from greater annual or even tidal exposure or ranges of temperature. In the case of substrate differences, the stress could be a nutrient one. Field transplants across stress gradients have confirmed some of these observations. In certain cases populations show phenotypic plasticity and adapt readily to new sites with an accompanying increase or decrease in leaf width. In other cases populations show little change in leaf width and are said to be genotypically differentiated. It is thought that the latter populations are native to stressed locations.

Similarly, in the genus *Halodule,* there appears to be a certain amount of vegetative plasticity with respect to leaf morphology (width; tip: tricuspidate or bicuspidate). Plants in the field may demonstrate variability in these characters, depending on the tidal zone they are growing in, the age of the shoot, or of the leaf itself (Phillips, 1967). A recent extensive series of collections made throughout the tropical Atlantic indicated that leaf widths and tip forms were significantly different. Some populations produced wide leaves with tridentate tips (conforming to the description of *H. beaudettei*), while some were narrow with bicuspidate tips (like those of *H. wrightii;* Phillips, unpublished research). However, following a year in culture, the leaf tips proved to be highly modifiable with bicuspidate and tricuspidate tips on the same shoot. This variability appeared to correlate with the nutrient status of the environment (McMillan, 1983a). Plants with infrequently changed seawater displayed bicuspidate tips, while those growing in frequently changed seawater displayed tridentate leaf tips. All populations analyzed in the Atlantic had the same isozyme complement (McMillan, 1980).

The original collection of *H. wrightii* from Cuba (Type 3720) clearly contained two growth forms. One was very small (leaves <0.5 mm wide, only 1.0–1.5 cm long), while one was larger (leaves up to 1.0 mm wide; up to 4 cm long). Such growth forms occur commonly in the field, often side by side, but separated by tidal zone. The small one is located intertidally, while the larger one occurs from low tide into the subtidal. No comparative chromosomal studies have been made on these growth forms or on a systematic basis for the Atlantic populations of *Halodule.*

By themselves isozyme analyses and observations on leaf widths and leaf-tip form cannot "solve" the species problem in *Halodule.* Alternatively, studies done so far, including the culture studies performed, which demonstrate the plasticity of leaf-tip form, indicate that *Halodule* may consist of a restricted number of polymorphic species. This polymorphism can be observed as a variable morphology, but within one ocean system, isozymes do not differ. At this time, we cannot be more than tentative and conservative regarding the species question in *Halodule.*

Based on the work accomplished so far, we are limiting species in *Halodule* to three: *H. wrightii* for all populations in the Atlantic-East Pacific group; *H. uninervis* and *H. pinifolia* for populations in the Indo-West Pacific group. Extensive field collections from many populations, particularly in the tropical Atlantic area, are needed as well as intensive within-site collections, viz., intertidal and subtidal locations at individual sites. Morphological studies should be made, but studies are now required that will analyze chromosomal differences. Reciprocal transplants should be made across tidal zones and into other areas of differing environmental conditions to determine the full range of morphological and physiological tolerance characteristics inherent within a single population and other populations. Studies should be made on the relationship between nutrients and leaf morphology. These studies would elucidate morphological variability and expression of leaf width and tip form. When these studies are made, perhaps we could be more conclusive about "species status" in this seeming polymorphic genus.

Thus, we express caution in creating new seagrass species using just one technique alone. It appears that certain vegetative characters are modifiable by a variable environment. These characters should be tested before their use in taxonomy.

A variety of experimental and cytological methods is now available for use in seagrass taxonomy that were not available 10 years ago. Culture and chemical analytical methods are now available. The use of field experimental methods, such as transplanting, to determine the degree of adaptive tolerance and morphological variation in a population are available. More sophisticated microscopic methods, using the electron microscope, are also available. We strongly suggest that taxonomists use the available techniques before describing new species.

It is curious that two areas of the world have experienced radiative evolution within selected genera. In southern and western Australia, an area of minimal annual environmental change with extensive coastlines oriented along longitudinal axes, the genus *Posidonia* (5 species) and *Zostera* subgenus *Zosterella* (3 species) have produced many species. Of these 8 species, 7 are endemic to Australia. In Japan, there are 4 species in *Zostera* subgenus *Zostera,* three of which are endemic. These areas are worthy of intensive study.

Finally, it should be noted that relict populations occur in three areas of the world, viz., *Heterozostera* at one location in northern Chile; *Halodule* at Beaufort, North Carolina; and, *Cymodocea nodosa* in the Mediterranean. All these species denote highly tolerant, adaptable species, and all are pioneering or colonizing species in the ecological, successional sense. These areas of occurrence are also worthy of intensive study. It is possible that in these "relict areas," fossil evidence may be found of a much more luxuriant former flora or of a more extensive distribution of the species presently found in the area.

Thus, species concepts and techniques of species descriptions become directly related to the distributional studies and pattern interpretations of phytogeographers. Our treatment herein invokes a conservative approach to the species problem, and thus to phytogeographic interpretations.

Complementarity of Structure and Function

Requirements for Life in the Sea

According to Arber (1920) there are four properties that a marine vascular plant must possess for existence:

1. It must be adapted to life in a saline medium.
2. It must be able to grow when completely submerged.
3. It must have an anchoring system able to withstand wave action and tidal currents.
4. It must have the capacity for hydrophilous pollination.

Den Hartog (1970) added a fifth property: "Seagrasses must be able to compete successfully in the marine environment."

Seagrasses must be able to achieve vegetative and reproductive cycles in a saline medium while completely submerged. All species are securely anchored or are attached to the substratum. Seagrasses possess more or less strong rhizomes and show a tendency for gregarious growth. All seagrasses are well equipped for hydrophilous pollination.

Underwater pollination takes place in most genera. The filamentous shape of the pollen grains of all Potamogetonaceae facilitates their transport by water currents. *Halophila* and *Thalassia* have spherical pollen grains, but they also float as they are arranged in coherent, moniliform chains.

Occasionally, as the long filamentous pollen grains of *Phyllospadix* and *Zostera* are released into the water column, some are carried to the water surface by the motion of the water. Where the upper parts of the reproductive stalks reach the surface on an ebbing tide, surface pollination in these two genera is possible. Entirely submerged pollination is the usual condition for most *Zostera* and perhaps for *Phyllospadix.*

Enhalus acoroides is the only species that shows surface pollination. The pollen grains are large and globular. The flowers break off in the spathe and rise to the surface, where they have a short but independent existence. Pollination occurs on an ebbing or low tide when the long-coiled peduncles of the female flowers begin to uncoil, allowing the female flowers to reach the surface and trap the pollen masses. Thus, *Enhalus* appears to be the only seagrass with hydrophobous pollination.

Most seagrasses are dioecious and those that are monoecious show proterogyny (*Zostera, Heterozostera, Halophila decipiens*). Thus, cross-fertilization is the rule (den Hartog, 1970).

Depending on the species and whether they are temperate or tropical, seagrasses may be eurybiont or stenobiont for several environmental factors: temperature, salinity, depth, light, substrate, water motion. Eelgrass is probably the most eurybiont species with respect to most of these factors than any of the other species. Eelgrass is known to tolerate encasement in ice during the winter in Alaska (–6°C) and can endure brief substrate temperatures of 40.5°C. The most optimum stands of eelgrass occur in water temperatures varying from 10°–20°C. Eelgrass can grow in a range of salinity from freshwater (low tide opposite stream mouths) to 42‰ The best stands of eelgrass occur in a salinity range of 10–30‰. Eelgrass has been reported as growing over a depth range from 1.8 m above mean lower low water (MLLW) to –6.6 m deep Phillips, 1974b). Almost all seagrasses grow best on sandy-mud substrates. Individual species are found on sand (*Halodule* occasionally) or rock (*Phyllospadix, Amphibolis, Thalassodendron*). Most seagrasses occur in waters sheltered from wave action. Only *Phyllospadix* is limited to areas where there is considerable hydroturmoil. Most species grow best where tidal currents are moderate (up to 3.5 knots).

Only a few species grow below 20 m deep. Several species of *Halophila* occur to 40 m deep. *Posidonia oceanica* grows to 40 m deep in the Mediterranean. Except for pioneering species of *Halodule,* which are known to tolerate a wide range of salinity, temperature, and depth, most tropical species are relatively stenobiont. In the temperate zone where species usually do not compete with many, if any, other seagrass species, eurybiontism toward these environmental factors is observed.

Anatomical Features and Growth Patterns

Since the seagrasses are all aquatic plants, they achieve growth and complete vegetative and reproductive cycles while completely submerged and firmly anchored. Only a few adaptable species produce populations that endure alternating exposure to air and sometimes extremely dilute seawater at low tide. Fewer species yet are limited to intertidal life, e.g., *Zostera japonica,* which Harrison (1979) described as an opportunist with an ability to grow in the subtidal, and to "escape" direct competition with a taller, light-shading *Z. marina,* by enduring desiccation at low tide at a higher level on the beach.

Tomlinson (1974) stated that seagrasses persist by vegetative growth. Thus, in order to understand seagrass meadow persistence, recovery from stress and disturbance, rates of growth over the bottom, biomass, productivity, and other functional activities that seagrasses engage in, there is a need to understand the three major vegetative growth patterns of the seagrasses. All seagrasses demonstrate meristem dependence, i.e., the need for continually active shoot apical meristems to maintain populations. *Zostera* was thought to show a winter dormant condition, but is now known to remain active all winter along a broad latitudinal gradient in North America. Branching patterns among all species are of two types: (1) regenerative, which maintains the general form of the plant without leading to vegetative propagation (this pattern is the advanced one); (2) proliferative, which increases the number of indeterminate meristems and leads to vegetative propagation (this pattern is the more primitive one). A possible third pattern is shown in the genus *Syringodium* where all lateral meristems develop as short shoots, a type of proliferative branching, but where the proliferation is not ordered by the shoot itself, but by the perturbation of the environment. All three vegetative growth patterns are diagrammed in Figure 2.

The structural features of these hydrophytes have been found to relate directly to their function in the marine environment. All seagrasses possess a similar vegetative appearance, growth, and morphology (Tomlinson, 1974). Except for *Syringodium* (2 species), which has terete leaves, all species have flattened, blade-like leaves. Except for the genus *Halophila* (9 species), which has small ovate or ovate-linear leaves, all other species have small or very large linear, strap-like leaves. The second major morphological adaptation of seagrasses is an extensive rhizome-root system. Except for *Amphibolis* (2 species) and *Thalassodendron* (2 species) whose populations occur facultatively on coral or rock rubble, only *Phyllospadix* (5 species) occurs obligately on a rocky substrate. All other species are obligate on an unconsolidated substrate. This substrate is usually a mixture of mud and sand with a deep anoxic zone underlying an oxic surface layer only several millimeters thick (Fenchel and Riedl, 1970). Pioneering populations of *Zostera marina* may colonize on sand, while a colonizing species such as *Halodule wrightii,* a member of a multi-species system in the tropics, appears to require a coarse substrate with oxic conditions or is rooted at the surface in the oxic zone. All species of *Halophila* are rooted at the surface in the oxic zone. Ferguson, Thayer and Rice (1980) noted that flattened leaves and an extensive rhizome-root system are unique to submerged marine and estuarine plants and are adaptations to (1) life in flowing water; (2) restricted and differential penetration of light at different wavelengths in the water column; and (3) reduced rates of gas diffusion in the water relative to the air.

The following account of the structural features of the leaves and rhizomes/roots will be followed by an account of the functional features that result from and are complementary to the structural adaptations.

LEAVES.—Except for *Syringodium* whose leaves are terete, all genera have relatively thin, blade-like, and flattened leaves with a high surface-to-volume ratio. This provides an opportunity for maximal diffusion of gases and nutrients between the blades and water, a maximal photosynthetic surface, and a maximal exposure of the chloroplasts to incident radiation. In *Phyllospadix* the leaves may be oval in cross-section, owing to the abundance of sclerenchyma fibers. This does not interfere with photosynthesis as the chloroplasts in all species are densely packed in the epidermis. In *Thalassia testudinum* leaves are flat, but may swell up to 250% of their volume in the afternoon during the photosynthetic peak, thereby becoming oval. Some of the excess oxygen production escapes from the leaf margins and tips, while most cannot diffuse outward as fast as it is produced (Zieman, 1982). This oxygen accumulates in the leaf lacunae or is transported to the rhizome. The leaves lack stomata, but the cutin is thin, which allows gas and nutrient diffusion. The blades have a general absence of mechanical support, which gives them flexibility and pliability, allowing them to reflex in the water as the tide recedes. As the blades reflex, they exert a greater frictional drag on water currents, which (1) reduces current velocity, the diffusion barrier at the leaf surface (by creating localized turbulence), and sediment erosion within the meadow; and (2) increases organic-matter sedimentation and the refuge function of the meadow for animals. The leaves have large thin-walled aerenchyma that facilitate gas and solute diffusion within the leaf. Large areas of these cells adjoin on an extensive lacunal system, an open continuous system from the leaf tips through to the root tips. These lacunae give buoyancy to the leaves, allowing them to project erect in the water column, and comprise up to 70% of the total volume of a seagrass leaf. There are lateral plates and water-tight perforated diaphragms that interrupt the lacunae at intervals that protect the lacunae and the leaf from flooding if the leaf breaks or is chewed by herbivores (Zieman, 1982).

RHIZOMES/ROOTS.—The morphology of the rhizomes and roots complements that of their functions, viz., anchorage and absorption of nutrients. The rhizomes of most seagrasses have bundles of longitudinal sclerenchyma fibers in the inner and outer cortex that give a structural rigidity to the below-ground system. When growth is dense, the resulting rhizome mat can be very thick and tough. In addition, in the case of *Phyllospadix,* whose rhizomes often occur on the surface of rocks on wave-beaten coasts, there is a very thick hypodermis under the epidermis. The lacunae are extensive in the rhizomes and are continuous with those in the leaves. There is also in the roots a large air space to volume ratio. This appears to minimize the respiratory oxygen demand by the roots. It is known that the root respiratory oxygen comes from the leaves and that a gradient of oxygen exists from the leaf to the roots. Likewise, the major portion of the inorganic carbon used in photosynthesis comes from carbon monoxide in the roots, and a gradient exists from the roots to the leaves. This ability to transport oxygen from leaves to roots allows the roots to grow in an anoxic environment. It is now known that seagrass roots secrete oxygen into the sediment, creating an oxic microzone around the seagrass roots that allows the aerobic conversion of ammonium to nitrate and the uptake of metals and other minerals at the root surface (Iizumi, Hattori, and McRoy, 1980).

All seagrasses produce root hairs. The abundance of these hairs varies with the species. Eelgrass was found to produce an average surface area for root and root hairs of 48.2 and 138.9 mm^2/root, respectively, and an average 4,900 root hairs/root. In *Halodule wrightii* the average root and root hair surface areas were 34.8 and 19.2 mm ^{2}/root, respectively, and an average 8,500 root hairs/root (Smith, Hayasaka, and Thayer, 1979). It is felt that root hair development is genetically, not environmentally, controlled and that *Zostera* roots are much more efficient at nutrient uptake than those of *Halodule,* owing to a much greater root surface area. In the case of *Phyllospadix,* there are branched root hairs that obviously aid in increasing the surface area for anchoring the plant to the rock substrate without increasing the number of roots.

Seagrass plants exhibit dynamic interactions with the environment, which vary seasonally, with depth, with substrate texture and possibly with substrate nutrient levels. In the case of eelgrass, leaf to rhizome/root ratios vary along a sediment texture gradient where more roots are formed in mud than in sand. Winter ratios favor a dominance of roots, owing to a decline of the leaf biomass. Roots also appear to have greater biomass in the upper intertidal than in the lower intertidal.

Shoot density varies seasonally and with depth. Subtidal eelgrass may be 3–4 times more dense in summer than in winter. Many studies have documented the reduction in seagrass shoots with increasing depth. Backman and Barilotti (1976) placed canopies over eelgrass in shallow water, reducing downwelling and illuminance by 63%. Shoot density was decreased after only 18 days, and declined to 5% of the adjacent unshaded controls after 9 months.

Eelgrass leaf dimensions also vary seasonally and with depth. Not only are leaves narrower and shorter in winter at any one site, but they are narrower and shorter in the intertidal zone than in the subtidal zone. At the lowest edge of growth, however, the subtidal leaves are narrower and shorter than at the mid-depth of the subtidal growth. There are also less leaves on eelgrass shoots in winter than in summer (Phillips, 1972).

Eelgrass leaf dimensions in North America also vary along a latitudinal gradient. Leaves are narrower and shorter in the Gulf of California (Sea of Cortez), Mexico, in the Bering Sea, and along the entire Atlantic coast than those along the Pacific coast from Alaska to Baja California. It is thought that these smaller leaves reflect the stress of a much greater annual and diurnal range of water temperatures than is experienced by eelgrass in the Pacific Ocean.

PHYSIOLOGY

Submersion in a saline aqueous medium results in severe physiological and anatomical problems for plants rooted in the substrate. The anatomical problems are alleviated by the development of high surface-to-volume ratios of internal aerenchyma, lacunae, and of whole blades. The second problem, that of physiology, which affects nutrient acquisition and the adaptive tolerances of the whole plant to a variable environment, is another consideration.

Occasionally, two species such as eelgrass and *Z. japonica* may grow equally well in optimum light, but when the longer leaves of eelgrass overtop the smaller plants of *Z. japonica,* the latter may escape direct competition by growing at a higher tidal level (Harrison, 1982).

PRESSURE.—*Halodule uninervis* is known to undergo a severe decrease in net photosynthetic rate at an equivalent depth of 4 atm. This is due to a pressure squeeze on the leaf lacunae, restricting the amount of carbon monoxide the leaf can carry. Thus, the pressure squeeze on the lacunae results in a shallow depth of growth, even when saturation light intensities are sufficiently high to allow a much greater depth of growth (Beer and Waisel, 1982).

ADAPTIVE TOLERANCES.—A small amount of work has been done on variable temperature and salinity tolerances of seagrasses. In eelgrass, Biebl and McRoy (1971) documented an osmotic resistance to salinity changes from freshwater to 93^{0}/oo. At 124^{0}/oo leaves were killed. Positive net production and net photosynthetic rates were found from freshwater to 56^{0}/oo and were maximum at 31^{0}/oo. The net photosynthetic rate increased in an intertidal pool to 35°C, but only to 30°C in a subtidal population. *Thalassia testudinum* can tolerate water temperatures from 20°C to 36°C, but the maximum photosynthetic rate occurs from 28°C to 30°C. A combination of high temperature and low salinity can cause a great decline in *Thalassia* populations (Zieman, 1975). Photosynthetic rates decrease in both *Syringodium* and *Thalassia* with decreases in salinity below full-strength seawater. It is known that seagrasses have absolute tolerances to high salinity. *Halodule* can tolerate salinities up to 72^{0}/oo, *Thalassia* up to 60^{0}/oo, and *Syringodium* up to 40^{0}/oo (McMillan and Mosely, 1967).

Seagrasses produce local populations that show the selective influence of local habitat conditions (McMillan and Phillips, 1979a). A correlation of water temperatures and dates of flowering for populations of *Zostera* and *Thalassia* over broad geographic areas in North America showed that the date of visible flower expression is controlled by temperature progressions that follow winter minima. In both genera the data suggest genotypes at specific sites that respond to local temperature regimes. Even in vegetative plants, eelgrass from Alaska was found to be more heat resistant and cold tolerant than eelgrass further south. In tropical species populations of *Thalassia, Syringodium,* and *Halodule* from the northern Gulf of Mexico displayed a great tolerance to 2°C water, but those from the southern Gulf and tropical Caribbean were severely damaged at 2°C (McMillan, 1979). These differences were also reflected in differential flowering responses. *Thalassia* from the northern Gulf of Mexico was induced to flower at temperatures at or below 23°C, but those from the more tropical parts of the Caribbean flowered only at a slightly higher temperature, e.g., 24°C to 26°C (Phillips, McMillan, and Bridges, 1981).

Despite the amount of work done on floral initiation and expression as a response to critical water temperatures, we feel that much more critical study is needed to settle the question concerning the mechanism of seagrass flower production. In the case of eelgrass, the studies reported by Phillips, McMillan, and Bridges (1983) indicate that water temperature and not photoperiod is the critical factor. However, in no seagrass species has anyone related the age of a particular plant or meadow to flowering, the nutrient status of the substrate or the plants (viz., C:N ratio).

CARBON PROBLEMS.—Physiological problems in seagrasses arise from lowered gas concentrations and rates of diffusion several orders of magnitude lower than in air. There is an abundance of inorganic carbon in seawater in the carbonate buffer system. During active photosynthesis, however, the carbon in this buffer system is not available and much of the free carbon monoxide in the water is greatly reduced (Zieman and Wetzel, 1980; Zieman, 1982).

Seagrasses absorb inorganic carbon for use in photosynthesis as carbon monoxide or bicarbonate ion (HCO_3). The average pH of normal seawater is 7.8–8.2, a level at which free carbon monoxide is not abundant. During active photosynthesis, the pH may rise to 8.9 and even to 9.4 in tropical water. Above 8.9 there is no free carbon monoxide in the water, and the bicarbonate ion level is also greatly reduced. Thus, during active photosynthesis it would appear that the principal external source of inorganic carbon must come from the sediments. The difficulty of obtaining nutrients from the water is compounded by a quiescent water layer next to the seagrass leaf surface that results in a diffusion barrier up to 100 micromillimeters thick. This barrier may be interrupted by water turbulence and currents flowing past the leaf. A study done by Beer, Eshel, and Waisel (1977) indicated that the major source of carbon for photosynthesis for four species of seagrasses was the bicarbonate ion, which is much more abundant in the water at normal pH than free carbon monoxide. However, this study was performed using only leaf segments.

It is known that seagrasses demonstrate photorespiration, an enhanced respiration and carbon monoxide evolution in the light. While this may reduce photosynthetic efficiency, it does provide an internal source of carbon that may be used in photosynthesis. One study concluded that the carbon monoxide contribution from respiration, photorespiration, and the water columns was in excess of that needed for photosynthetic requirements for seagrasses.

Seagrasses can absorb carbon from the water by the leaves and from the sediments by the roots. Carbon transport through the plant can go both ways. In eelgrass up to 20% of the carbon removed from the water appears in the sediments, while up to 72% of that absorbed by the roots remains there; 25% is transported to the leaves and 3% is transferred to the epiphytes (Penhale and Thayer, 1980). In *Thalassia* only 1% of the carbon absorbed by the leaves is lost to the sediments.

Seagrasses are highly inefficient in using inorganic carbon. Only 5%–20% of that absorbed by the roots in eelgrass and *Thalassia* is fixed in photosynthesis, while in the pioneering species, *Halodule wrightii*, 89% of that absorbed is fixed. Some of the carbon lost from seagrasses is in the dissolved state (DOC). *Halodule* was found to lose only 2% of its fixed carbon, eelgrass loses an average 5%, while the rhizomes/roots on intact plants of *Thalassia* lose an average 8% (Wetzel and Penhale, 1979).

Seagrasses do not use carbon isotopes in the ratios found in nature. They differentiate in favor of the lighter and more mobile ^{12}C isotope (Zieman and Wetzel, 1980). Since species appear to accumulate relatively characteristic ratios of ^{13}C to ^{12}C, which are relatively preserved through the grazing and detritus food chains, C/C ratio signatures develop that can be used not only by physiologists, but also by persons studying trophic dynamics. Seagrass ratios are typical of C_4 plants, varying from −3 to −15 ppt. Two species of *Halophila* extend the range to −23 ppt. Typically, C_3 plants have a highly negative ratio of −24 to −36 ppt (poor in ^{13}C) (McMillan, Parker, and Fry, 1980).

NITROGEN.—Nitrogen has been identified as the nutrient most limiting to seagrass growth (McRoy and McMillan, 1977; Short, 1981). Most of the evidence for this comes from research on eelgrass. Nitrogen limitation is inconclusive for tropical species. This limitation exists during most of the growing season. There are three potential sources of nitrogen for seagrass growth: recycled nitrogen in the sediments, nitrogen in the water column, and nitrogen fixation. Living leaves contain a great quantity of nitrogen, but this becomes transported out of the leaf and reallocated as the leaf senesces. Thus, whole dead leaves are not responsible for much nitrogen cycling. While detritus is nitrogen poor, the particles become coated with a bacterial film that pumps a great deal of nitrogen and phosphorus into them. This nutrient-enriched detritus is carried to the sediments if the leaf baffle functions efficiently or may be flushed out of the system. In the sediments microbes and animals excrete ammonium that adds to the nitrogen pool. Dead seagrass rhizome/root material adds nitrates or nitrites to the sediments. It is known that the primary source of nitrogen for leaf production is recycled nitrogen from the sediments. Recently, it was found that oxygen transported from leaves to roots in eelgrass was excreted from the roots, creating an oxygenated microzone in the anoxic sediments. In this zone ammonium is oxidized to nitrite and nitrate for uptake by the roots.

There are highly significant correlations between the density of eelgrass vegetation, the organic matter in the sediment, fine sediments, and the total nitrogen pool. There is an increasing gradient in all four categories from unvegetated sediments to the edge of a meadow, to the mid-bed location. The nitrogen pool in the mid-bed is comprised of exchangeable ammonium, ammonium dissolved in the interstitial pores of the sediment, and total nitrogen. Very little nitrate is found in the sediments (Kenworthy, Zieman, and Thayer, 1982).

Nitrogen fixation by means of epiphytic blue-green algae is now known to occur in both the phyllosphere and in the rhizosphere of seagrasses (Patriquin and Knowles, 1972; McRoy and Goering, 1974; Capone, Penhale, Oremland, and Taylor, 1979; Zieman, 1982). Tropical species fix more nitrogen on the leaves than temperate species, but even in eelgrass this amount is probably important, owing to the great need for nitrogen. The phyllosphere nitrogen contributes primarily to the epiphytic community. Nitrogen fixed in the rhizosphere can supply 20%-50% of the nitrogen requirements of a seagrass meadow. Recently, endobacteria were found in the roots of eelgrass that were associated with nitrogen fixation.

PHOSPHORUS.—McRoy and Barsdate (1970) pioneered in the experimental study of nutrient uptake by determining that the eelgrass root system was the site of most of the phosphorus uptake by the plant. With the epiphytes removed, they determined that the plant was a phosphorus pump from the sediments to the water column. Phosphorus can enter the plant from the roots or the leaves, depending on which medium has the greatest concentration. In North Carolina, it was found that the phosphorus that enters the leaves remains in the leaves, but a small portion of that entering the root system is transported to the leaves and released to the epiphytes.

TRACE ELEMENTS.—Only a small amount of work has been done on uptake and cycling of microelements or trace elements. It is known that cadmium and manganese, particularly, remain complexed in the sediments under anoxic conditions. When the sediments are oxidized, the metals may become bioavailable. Eelgrass can absorb Cd and Mn through both the roots and the leaves, but the roots form a sink for cadmium. Old rhizomes and roots deposit their greater contents of Cd in the sediment sink, while Mn is more readily fixed by the leaves with little transport between the leaves and rhizomes/roots. A little Mn was found to enter the sediment sink.

Eelgrass in North Carolina absorbs a very high fraction of manganese, iron, copper and zinc contained in one year's accumulation of sediments (Wolfe, Thayer, and Adams, 1976). The animal component does not pick up much of the metals as it ingests detritus. The conclusions are (1) the eelgrass system can transport manganese and zinc out of the system via detrital flushing, but iron and copper tend to be conserved; (2) the largest metal fluxes are associated with *Zostera* production and sedimentation; and, (3) the flushing of detritus or fresh production is the single greatest export of metals from the eelgrass system. The eelgrass biomass is the largest reservoir of the four metals in the system. Various parts of the eelgrass plants and different beds in the North Carolina estuary differ significantly in the contents of these metals (Drifmeyer, Thayer, Cross, and Zieman, 1980). The live blades contain the most iron; and the attached dead leaves contain the most copper. It is interesting that iron, copper, and zinc increase in this sequence:

Live blades → Dead blades → Detritus

whereas manganese decreases.

Evolution and Geographic Distribution

EVOLUTION

In the Jurassic Period there was one continental land mass, Pangaea, and one giant warm sea, Panthalassia. A branch of Panthalassia, the Tethys Sea, intruded into Pangaea. Fossil evidence indicates that terrestrial angiosperms arose during the Jurassic (Raven and Axelrod, 1974; Stansfield, 1977), and became dominant in the Cretaceous. During the mid-Jurassic, Pangaea divided into two major land masses, a northern mass, Laurasia, which later became North America, Europe, and Asia, and a southern mass, Gondwana, which later became South America, Africa, Australia, India, and Antarctica (Figure 1).

Early in the Cretaceous an East Pacific Barrier (Ekman, 1934) formed that would have effectively prevented seagrass distribution. This barrier was a deep-sea formation, thousands of kilometers wide and without islands. Ekman (1934) noted that this barrier effectively separated the shelf fauna into West Pacific and Caribbean groups. During this time South America separated from Africa and slid westward. A little later Africa separated from Antarctica, and North America separated from Europe. During the Middle Eocene, South America finally separated from Australia, and at the end of the Late Eocene, India separated from Australia and migrated northward.

In the Miocene the Mediterranean was closed off from the Indian Ocean at the northern end of the Red Sea and the Persian Gulf, and the Panamanian Isthmus finally closed off the Atlantic Ocean from the Pacific Ocean. In the Miocene seas began to withdraw from the Near and Middle East, isolating the Mediterranean from the Indo-Pacific.

The earliest fossils related to seagrasses are dated from the Cretaceous. It is likely that a well-developed seagrass flora was present in this period, as well-developed fossils of at least two genera have been found, viz., *Archeozostera* (Zosterioideae) from Japan and *Thalassocharis* (Cymodoceoideae) from the Netherlands and Germany (cf., den Hartog, 1970, for an exhaustive review up to 1970).

At least three seagrass species occurred in the Basin of Paris during the Eocene: *Posidonia parisiensis* (Brongniart) Fritel, *Cymodocea serrulata* (R. Brown) Ascherson and Magnus, and *C. nodosa* (Ucria) Ascherson; both genera and the latter two species are still extant. *Cymodocea nodosa* has been found from the Pliocene and Quaternary in Emilia, Italy, while *C. serrulata* has been identified from the Miocene in Celebes, under the name *C. micheloti* Laurent and Laurent (Laurent and Laurent, 1926).

Several papers have been written on the development and distribution of seagrass floras at different geological periods, but these are only inferential, since they rely on the presence of foraminiferans presently associated with seagrasses (Brazier, 1975; Eva, 1980); from carbonate mud deposits similar to those presently associated with tropical seagrasses (Land, 1970; Petta and Gerhard, 1977; Bretsky, 1978); deposits of invertebrates, particularly mollusks, presently associated with seagrasses (Baluk and Radwanski, 1977; Hoffman, 1977); or even with deposits of sirenians that are known to be presently associated with tropical seagrasses (Domning, 1977, 1981). Based on these inferential data, the following historical account summarizes seagrass distribution as it is known.

Brazier (1975) stated that seagrass distributions fall into three associations:

1. *Zostera* association: *Heterozostera, Phyllospadix, Amphibolis, Posidonia.* These are predominantly temperate forms with bipolar distribution.
2. *Cymodocea* association: *Thalassodendron, Enhalus.* These are tropical genera that were and are absent from the Neotropics and tropical West Africa.
3. *Thalassia* association: *Halophila, Syringodium, Halodule.* These are also tropical seagrasses, but are absent from the Mediterranean.

Brazier (1975) reasoned that seagrasses encroached into the shallow subtidal waters of the warm Tethys Sea in the Late Cretaceous, indicating a modified Center of Origin Theory to account for seagrass evolution and distribution. McCoy and Heck (1976) noted that the fossil records show that corals, mangroves, and seagrasses were already intimately associated in the Cretaceous, indicating that these three groups co-occurred throughout the Tethyan and on through the Eocene-Miocene. They stated that seagrass distribution was worldwide in the Late Cretaceous before the breakup of Gondwana.

McCoy and Heck (1976) concluded that seagrass speciation was probably allopatric, occurring after the final separation of the continents, the Mediterranean from the Indian Ocean, and the Atlantic Ocean from the Pacific Ocean in the Miocene. However, the data indicate that the seagrass species from the four pantropical genera, which include the twin-species in the genera *Thalassia, Syringodium,* and *Halodule,* probably underwent sympatric speciation before these events, and probably as early as the Middle Cretaceous. Firstly, they could not have crossed the East Pacific Barrier that formed in the Cretaceous. No present-day seagrass has long-distance dispersal mechanisms. The three genera with buoyant fruits *(Posidonia, Enhalus,* and *Thalassodendron)* have restricted distribution (den Hartog, 1970). Secondly, it is almost certain that seagrasses would have migrated westward since the equatorial currents flowed westward. Thirdly, the presence of *Halodule wrightii* and *Halophila baillonis* along the Pacific coast of Central America shows relict populations cut off from the tropical Atlantic in the Miocene, with no tendency to spread westward. Fourthly, the three pairs of tropical twin-species show that they were formed before the Miocene when the Pacific Ocean was cut off from the Atlantic Ocean (den Hartog, 1970).

Not only do the data indicate that seagrasses migrated westward, but that the species formed a long time ago. *Halodule wrightii* and *Halophila baillonis* must have been in existence before the Miocene, as well as *H. decipiens,* which is pantropical. Fossil remains of *Cymodocea* from the European Eocene can be identified with still existing species. Therefore, the close resemblance that exists between the twin-species and also between many other seagrasses should be seen as a result of the very slow rate of evolutionary progress of the angiosperms in the relatively uniform marine environment (den

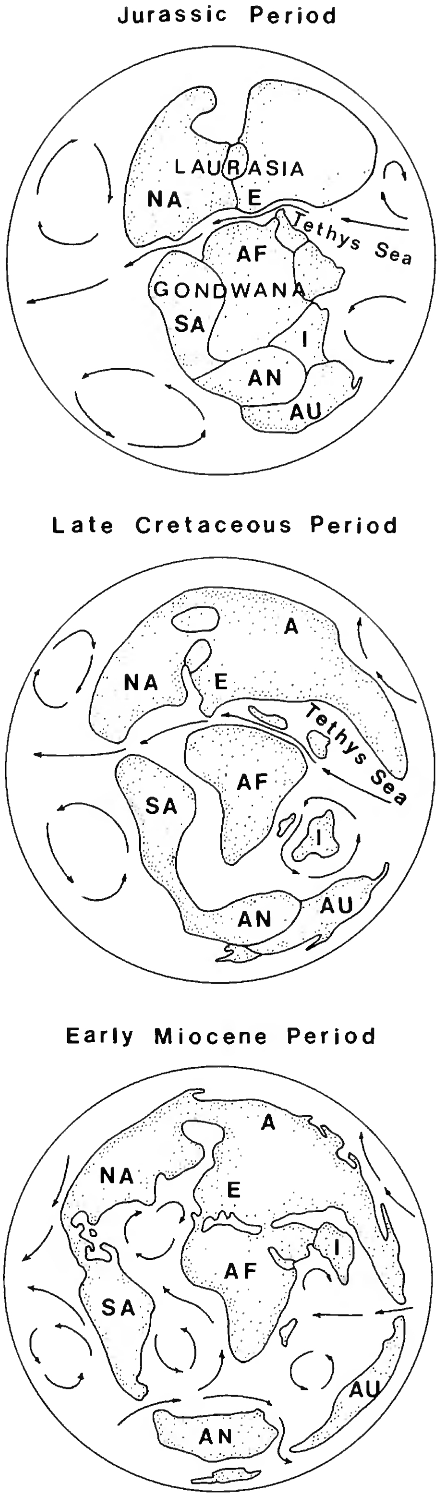


FIGURE 1.—Continental movements in the geological periods. NA = North America; A = Asia; E = Europe; SA = South America; AF = Africa; AN = Antarctica; I = India; AU = Australia. (Redrawn from Dott and Baten, 1981.)

Hartog, 1970). It is for this reason that the small population of *Heterozostera* in northern Chile (Phillips, Santelices, Bravo, and McRoy, 1983) is considered a relict one, a last remnant of a probable, much wider distribution on the Pacific coast of South America and left from a continuous area of distribution when Australia separated from South America about 50 million years B.C. in the Middle Miocene.

Lumbert, den Hartog, Phillips, and Dixon (1984) have recently shown a *Thalassodendron auricula-leporis* den Hartog, a *Cymodocea floridana* den Hartog, and a *Cymodocea* species, dating from the Eocene from Central Florida. All these forms belong to the *Cymodocea* association. This almost certainly demonstrates that seagrass distribution proceeded westward from the Tethys Sea at a relatively early date. It is not surprising that *Enhalus* has not been found among the fossils in the Caribbean. It is probably one of the last evolved genera and may never have reached the Caribbean (den Hartog, 1970). However, *Cymodocea* occurred during the Eocene in Europe and, at present, it occurs in subtropical seas. *Cymodocea serrulata, C. nodosa,* and *Posidonia parisiensis* occurred in the Basin of Paris during the Eocene (Fritel, 1910, 1914; Laurent and Laurent, 1926; Stockmans, 1932), and *Cymodocea-Posidonia* stands were widespread east of the Caribbean at least by Eocene times. *Thalassodendron* is also an old genus and has a present-day warm temperate species. The recent Indo-Pacific area of this genus shows a disrupted relict character. This genus must have had a much wider distribution in the past.

It is interesting that Eva (1980), also using foraminiferan data, suggested that a seagrass flora occurred in the Caribbean in Cretaceous times. He found a rich diversity of seagrass-adapted species in the Late Cretaceous deposits and concluded that their distribution in the Caribbean followed lines like that in the Tethyan region. Petta and Gerhard (1977) and Bretsky (1978) reported finds of carbonate muds in Colorado (USA) similar to those produced as carbonate flocks by *Thalassia* and its epiphytes today in the Caribbean (Phillips, 1960; Humm, 1964; Land, 1970; Patriquin, 1972).

No seagrass fossils have been recorded in the Paleocene, but Eva (1980) suggested their continued presence in the Caribbean.

In the Eocene there was a large expansion of seagrass growth (cf., *Cymodocea-Posidonia* growth in Europe and in the English Channel; seagrasses in the Caribbean). Brazier (1975) cited evidence that seagrasses presented a complete Tethyan distribution in the Early Eocene. Eva (1980) reported a great expansion of seagrass-related forams in the Caribbean in the Eocene (extending from Haiti to the Yucatan south to Panama). Dixon (1972), Randuzzo and Saroop (1976), and Lumbert, den Hartog, Phillips, and Dixon (1984) reported an abundant seagrass flora dating from the Eocene in central Florida. Lumbert, den Hartog, Phillips, and Dixon (1984) clarified the taxonomy of this flora. Brazier (1975) speculated that the *Cymodocea* association initiated its present-day distribution through the Mediterranean to the Indo-West Pacific in the Early Eocene and perhaps during the Paleocene.

Chesters, Gnauck, and Hughes (1967) recorded *Cymodocea* from the Oligocene on the Isle of Wight as well as in Florissant (Florida ?), USA.

Brazier (1975) suggested a pantropical expansion of the *Thalassia* association during the Early and Middle Miocene when temperatures were warmer. During this period the African continent moved northward. In Late Miocene waters cooled and the southern migration around Africa ceased. Baluk and Radwanski (1977) and Hoffman (1977) inferred an extensive tropical seagrass flora in Central Poland in the Middle Miocene, based on molluscan deposits. This developed, owing to a warm-water influx when the north end of the Persian Gulf was still open. This flora disappeared after the north end of the Persian Gulf was closed. Based on sirenian deposits, Domning (1977) theorized that a modest diversity of tropical seagrasses was present on the California coast in the Middle Miocene. When climates cooled in Late Miocene and into the Pliocene, the tropical seagrasses receded and *Zostera* subgenus *Zostera* and *Phyllospadix* colonized the area. This cooling trend restricted the northward movement of the stenothermal *Thalassia* association, but it probably left a relict population of the much more tolerant *Halodule* at Beaufort, North Carolina, when it receded.

GEOGRAPHIC DISTRIBUTION

Ascherson (1868), in his treatment of marine angiosperms, made a few remarks on disjunct distributions in some genera and compiled species lists in the various oceans. For the most part, the work was purely taxonomic. In 1871, Ascherson published the first paper on the geographical distribution of the seagrasses. This paper indicated the gaps in the knowledge and stimulated further collecting. He concluded that most of the species are confined to one of the temperate zones or to the tropical zone. Where they inhabit two zones, their occurrence in one is only marginal.

Nearly all seagrass species display continuous areas of distribution. In contrast, the distribution of genera show wide disjunctions. Further, there is an obvious agreement in the distribution of many species and genera. Ascherson (1871) noticed that closely related species (those that are very similar morphologically) generally occur separated from each other (e.g., *Cymodocea nodosa–C. rotundata*), while species that show more or less conspicuous differences often occur together (*C. rotundata–C. serrulata*). In that paper, Ascherson published the first seagrass distribution map.

Ostenfeld (1915) continued the study of the geographical distribution of seagrasses. By considering the systematic affinities and the distribution of land and sea in the past, Ostenfeld believed that a detailed study could possibly contribute to a better understanding of the evolution of seagrasses. In a detailed study of the phytogeographical aspect of the Mediterranean seagrass flora, Ostenfeld (1918) contributed to seagrass geography by compiling maps. Later, he published two sets of maps showing the distribution of all known species (Ostenfeld, 1927a,b).

Setchell (1920) approached the geographical distribution of seagrasses from an ecological point of view. He stressed in particular the influence of water temperature on the distributional pattern. In a later publication, Setchell (1929) applied his temperature interval scheme to the growth and development of *Zostera marina*. In 1935 Setchell prepared distribution maps of all species. Later contributions to the geography of seagrasses can be found in Moldenke (1940) and den Hartog (1964, 1967, 1970).

At present the geographic distribution of the seagrasses is well-known, although there are still several areas from which records are scarce. This is true in particular for South America. The entire Atlantic coast south of São Paulo, Brazil, is completely unknown for seagrasses, except for a leaf blade of an unknown zosteroid species recorded as washed ashore near Montevideo (Setchell, 1935). The beds of this species still have to be discovered, and additional material is necessary before this species can be described. Except for a small meadow of *Heterozostera tasmanica* in northern Chile (Phillips, Santelices, Bravo, and McRoy, 1983), there are no seagrasses known from the entire Pacific coast of South America, a distance of almost 9000 km. Setchell (1934) recorded only two species from South America: *Heterozostera tasmanica* (under the name *Zostera muelleri*) from Chile and *Halophila baillonis* from Pernambuco, Brazil. Den Hartog (1970) listed five seagrass species for the east coast of South America down to São Paulo, Brazil. None are known along the east coast south of São Paulo.

The African west coast needs exploration; only *Cymodocea nodosa* and *Halodule wrightii* have been reported. Nothing is known south of 10°N. Seagrasses are probably restricted to a few favorable places (Angola, Senegal, Mauritania).

There are many places from which information is meagre, or from which seagrasses are unknown. Among these under-collected areas are: Somalia, Mozambique, Southern Arabia, Iran, Pakistan, India, Burma, Borneo, Sumatra, Malacca, China, Korea, and the Russian areas along the Bering Sea. The Caribbean coast of South America is poorly known. The few records are from Venezuela and Colombia. The Caribbean and particularly the Pacific coasts of Mexico and Central America need more thorough investigation. The coasts of Mexico are almost unknown except for those of Baja California. The recent discovery of *Halodule wrightii* in the Gulf of California, Mexico, was the first report of *Halodule* on the Pacific coast of Mexico (McMillan and Phillips, 1979b), a location 3200 km northwest of the nearest reported population in Nicaragua, also on the Pacific coast.

Recently an extensive effort has been focused on the Philippine seagrass flora (Meñez and Calumpong, 1983, 1985; Meñez, Phillips, and Calumpong, 1983; Calumpong, Medalla, and Meñez, 1985). The work of this group and that of Tsuda from Guam cover a wide area of the Indo-Pacific.

Even in rather well-collected areas, there was a relatively recent discovery of *Zostera japonica* (under the name *Z. americana* den Hartog, 1970) in Washington State, USA. The species is now known to be distributed from Coos Bay in southern Oregon to southern British Columbia, Canada; Harrison and Bigley, 1982.

Phytogeographic patterns are apparent as a result of the interaction of populations of individual species with local environmental conditions. Individual species distributions extend to the limits of the adaptational tolerances of populations along gradients primarily of water temperature, but also of salinity, irradiance, suitable depth, substrate, and exposure. Thus, tropical and temperate conditions are based on the effects of ocean currents and local hydrological and atmospheric conditions. Species distribution is then the result of a dynamic interaction of these conditions with populational tolerances. A broader phytogeographic pattern is observed when groups of species show distributions that cluster or are generally similar.

Of 12 seagrass genera recognized at present, seven are characteristic for tropical seas (*Halodule, Cymodocea, Syringodium, Thalassodendron, Enhalus, Thalassia, Halophila*), while five are confined to temperate seas (*Zostera, Phyllospadix, Heterozostera, Posidonia, Amphibolis*). In this analysis we are adopting the ecological classification of tropical and temperate as defined by Setchell (1915, 1920): tropical and subtropical: mean water temperature for warmest month is 25°C and 20°C, respectively; warm temperate and cold temperate: 15°C and 10°C, respectively.

It is also true that these zones are not sharply divided as are the boundaries of the Tropics of Capricorn and Cancer on a map. Actual phytogeographic boundaries vary according to the steepness of the environmental factor gradient and the populational interaction with the gradient. Thus, several species that have their main distribution in the tropics or temperate zones have extended areas beyond these zones under the influence of north- or south-flowing warm- or cold-water currents, respectively, or other ecological factors.

One tropical species, *Halophila ovalis*, is rather eurythermic and extends southward to temperate South Africa and Tasmania, and as far north as the Suez Canal and Japan. There are at least two tropical genera that have produced species restricted to subtropical or even warm-temperate waters: *Cymodocea (C. nodosa, C. angustata,)* and *Thalassodendron (T. pachyrhizum)*. Alternatively, at least three species of the temperate genus *Zostera*, subgenus *Zosterella (Z. japonica, Z. capricorni, Z. capensis)*, extend into tropical waters.

The tropical seagrasses are not homogeneously distributed, but are concentrated in two large, but widely separated, areas. The Indo-West Pacific contains seven genera, of which two are confined to that area (*Thalassodendron* of the Potamogetonaceae; *Enhalus* of the Hydrocharitaceae). One genus is largely confined to the area (*Cymodocea* with one species, *C. nodosa*, in the Mediterranean and along the Atlantic coast of northwest Africa). The other four genera also occur in the tropical Atlantic Ocean, which includes the immediate Pacific coast of Central America (*Halodule* and *Syringodium* of the Potamogetonaceae; *Thalassia* and *Halophila* of the Hydrocharitaceae). The tropical Atlantic does not have one genus confined to it. The species, however, are different from those of the Indo-West Pacific, with the exception of one; *Halophila decipiens* is pantropical and locally extends beyond the tropics in the southern hemisphere, its southernmost locality being Sydney, Australia.

The tropical Atlantic area does have one endemic taxon on the supraspecific level, viz., *Halophila* section Americanae.

The seagrass flora in the southwest tropical Pacific, the Indo-Pacific region, presents a globally disjunct assemblage. Up to 11 seagrass species are found at any one location, and overall, about 32% of the total seagrass flora occurs in these Old World tropics. There are 15 strictly tropical species recorded from this region. Most species have a wide distribution covering almost the entire area, but there are five species with a more restricted distribution (*Halodule pinifolia, Halophila stipulacea, H. beccarii, H. spinulosa,* and *Thalassodendron ciliatum*).

There are at most only six seagrass species in four genera associated with the New World tropics in the tropical Atlantic Ocean and Pacific coast of Central America. The species of the tropical Atlantic-East Pacific group are less homogeneously distributed than those of the Indo-West Pacific group. The "center" of this group is the Caribbean, where three genera are represented by one species each and *Halophila* by four species. The other coastal areas have a much more impoverished flora, e.g., the west coast of Africa with one species (Feldmann, 1938), the east coast of Brazil with four species belonging to two genera, and the Pacific coast of Central America with two species (one each in *Halodule* and *Halophila*). The two species of the endemic *Halophila* section Americanae, inhabit different parts of the area. *Halophila engelmannii* is widely distributed along the northern coasts of the Gulf of Mexico, Cuba, and in the Bahama Islands, while *H. baillonis* has been found in the Lesser Antilles, the Pacific coast of Panama, and in Pernambuco, Brazil. *Thalassia testudinum* and *Syringodium filiforme* are strictly Caribbean.

Ostenfeld (1915) and Setchell (1935) theorized that the Caribbean seagrass flora and the Indo-Pacific one originated from a common ancestral flora that had a very wide distribution in tropical seas. When the upheaval of the Central American isthmus in the Miocene separated the Caribbean from the Indo-Pacific, these ancestral species diverged, resulting in the so-called twin species. These are pairs of species that show only slight morphological differences but have widely separated areas of distribution. It is almost certain that the species had differentiated before the Miocene, inasmuch as both *Halodule wrightii* and *Halophila baillonis* (of the endemic section Americanae) occur on both sides of the Panama Isthmus. *Halodule wrightii,* which is found throughout the tropical Atlantic, is reported (McMillan and Phillips, 1979b) in Pacific Mexico. The three pairs of twin species are:

Indo-West Pacific	Tropical Atlantic
Halodule uninervis	*Halodule wrightii*
Syringodium isoetifolium	*Syringodium filiforme*
Thalassia hemprichii	*Thalassia testudinum*

Finally, it is interesting that of the five genera that are more or less characteristic of the extra-tropical seas, there are two, *Zostera* and *Posidonia,* which have a bipolar distribution (den Hartog, 1970). This bipolarity can only be explained by an original area of distribution much larger than at present that encompassed both the temperate and tropical seas. In the course of time these genera must have been replaced in the tropics by more stenothermal species.

The disjunction in the distribution of *Posidonia* is the most striking. *Posidonia oceanica* is restricted to the Mediterranean. There are four species of *Posidonia* in western and southern Australia, which occur sympatrically with the three species of *Zostera* subgenus *Zosterella* in Australia. The fact that the differences between the Mediterranean and Australian species are rather profound indicates that the separation of the two groups took place at a relatively early time in the history of the seagrasses, presumably at least as early as the Late Eocene.

The disappearance of *Zostera* from tropical seas is not complete (den Hartog, 1970). Four of the eight species of the subgenus *Zosterella* still have populations in the tropics. It is readily apparent that the entire subgenus *Zosterella* is comprised of species with broad adaptive tolerances to temperature. The East Asian *Zostera japonica* has been found as far south as Vietnam; the East Atlantic *Z. noltii* has its southern border in Mauritania; the East Australian *Z. capricorni* was found as far north as the Torres Strait; while the East African *Z. capensis* is located largely within the tropics, even though its northernmost populations occur north of the equator.

The geographical distribution of *Z. noltii* is the most interesting, as it is the only species of the subgenus occurring beyond the Indo-Pacific area. It must have occurred in the Mediterranean before the closure of the Suez Isthmus in the Miocene. Moreover, it also occurs in the Caspian and Aral Seas, which today have no communication with the Mediterranean (cf., den Hartog, 1970).

The distribution of *Z. capricorni* also shows some interesting features: it occurs along the coasts of Queensland and New South Wales, is absent from Victoria and Tasmania, but has been found on the South Australian Kangaroo Island. The isolated occurrence on the latter island indicates that during the Oligocene and Miocene, when the Australian climate was much warmer, it must have had a continuous distribution in southeastern Australia. The species also occurs on North Island, New Zealand, and on Lord Howe Island. According to Knox (1963), New Zealand was an isolated land mass since the Upper Cretaceous. Without fossil evidence, it cannot be established whether its present distribution is the result of a later settlement after crossing the Tasman Sea under the influence of the West Wind Drift. Lord Howe Island could have served as a "stepping stone."

In the northern Pacific the genus *Zostera* underwent a further differentiation and evolved the subgenus *Zostera.* This subgenus is represented by several species in Japan in the northern Pacific, while only one of them, *Z. marina,* also occurs in the northern Atlantic. This species reached the Atlantic rather late. The isolated occurrence of the species in Hudson Bay is probably a relict one (Porsild, 1932). It is also noteworthy that it has been obtained from the Pleistocene of Montreal (Penhallow, 1900). The late appearance of *Z. marina* in the Atlantic is also supported by its absence from the Caspian Sea, which was connected temporarily with the Black Sea at the end of the Pleistocene. In the Black Sea the species is now common (den Hartog, 1970).

Two genera are restricted to the temperate zone of the southern hemisphere, viz., *Heterozostera* and *Amphibolis. Amphibolis,* which is restricted to the western and southern coasts of Australia, is the only completely extratropical genus of the subfamily Cymodoceoideae.

Vegetative and Reproductive Growth Patterns

The pattern of activity of the terminal meristem is the foundation for differences in vegetative growth patterns among seagrass species, their seasonalities, growth rates, biomass, and the rate of spread over the bottom by new rhizome and shoot production. In concert with physiological characteristics, this pattern of "meristem dependence" also determines whether a species will be a colonizing one or a climax one, inasmuch as it determines whether branching and new shoot production will be proliferative or merely regenerative (Tomlinson, 1974; Figure 2).

VEGETATIVE PATTERNS

All seagrasses tend to display a perennial habit. However, in at least two genera, *Halodule* and *Halophila,* populations can appear and disappear quickly. We cannot state categorically that all species and populations in these genera are perennial. It is surprising how few species have been analyzed as to their growth patterns: differences in tolerance to air exposure at low tide; seasonal differences in growth and abundance that relate to competition with other species; adjustments in growth needed for survival through inimical spatial positions or temporal periods. The work reviewed herein relates to eelgrass. Very little has been done on any other species.

Under most environmental conditions, eelgrass forms perennial stands. An increasing number of annual populations of eelgrass is being found on both coastlines of North America and in Europe. In the annual habit, the plants produce stalks with seeds, and the entire vegetative plant disappears at the end of the growing season. Seeds dropped in the sediment at the end of the growing season overwinter, germinate, and the population begins anew from seedlings during the following spring. Since annuality appears to be associated with locations of eelgrass in shallow water, in intertidal estuarine sites where the salinity becomes very dilute in winter, where air/water temperatures become very hot or cold, or where ice regularly scours intertidal plants away, there is a possibility that the annual habit is an environmentally induced one and not a fixed genetic pattern. Field- and laboratory-controlled experiments have rarely been made to determine this.

Keddy and Patriquin (1978) were the first to report annual eelgrass. They collected putative annual and perennial plants in Nova Scotia, Canada, and found that the seed crops of both types contained small percentages that became perennial and annual plants, respectively. Since the growth experiments were controlled, their results may indicate that the annual habit is a genetic one. In the Gulf of California (= Sea of Cortez) Mexico, all eelgrass, intertidal and subtidal, is annual. Summer water temperatures, up to 32°C, exceed the lethal limit for eelgrass. Since the plants produce seeds and release them from their attachment to the bottom before water temperatures reach the lethal point, eelgrass in the Gulf of California may also represent a true annual population. This response is thought to be an ultimate one (Phillips and Backman, 1983). However, in Izembek Lagoon, Alaska, intertidal eelgrass, which is annual, was transplanted to a subtidal location, where it adopted a perennial habit (Phillips and Lewis, 1983). This experiment clearly demonstrated a flexible, environmentally induced growth pattern.

For eelgrass on the Pacific coast of North America, there appears to be three vegetative growth patterns observed along latitudinal and local depth gradients:

1. Gulf of California, Mexico, where all eelgrass is annual. These populations appear to have a true annual habit.
2. Remainder of Pacific coast.
    a. Intertidal: predominantly perennial except where dilute salinities or very cold temperatures are encountered for extended periods. In such situations induced annuality may occur.
    b. Subtidal: perennial plants.

Thus, in North America, eelgrass is a phenoplastic halophyte with a conspicuous relationship between the degree of stress at both extremes of temperature and dilute salinity along latitudinal and depth gradients and the type of growth pattern observed. It appears that when the environmental stress approaches or exceeds the tolerances of the local vegetative population, that population is induced to flower and to produce seeds.

On the Pacific coast, *Zostera japonica,* which grows higher in the intertidal than eelgrass, is an opportunist, i.e., it can complete its life cycle in 6–7 months and overwinter as seed (Harrison, 1982). Along an r-K continuum, *Z. japonica* is an

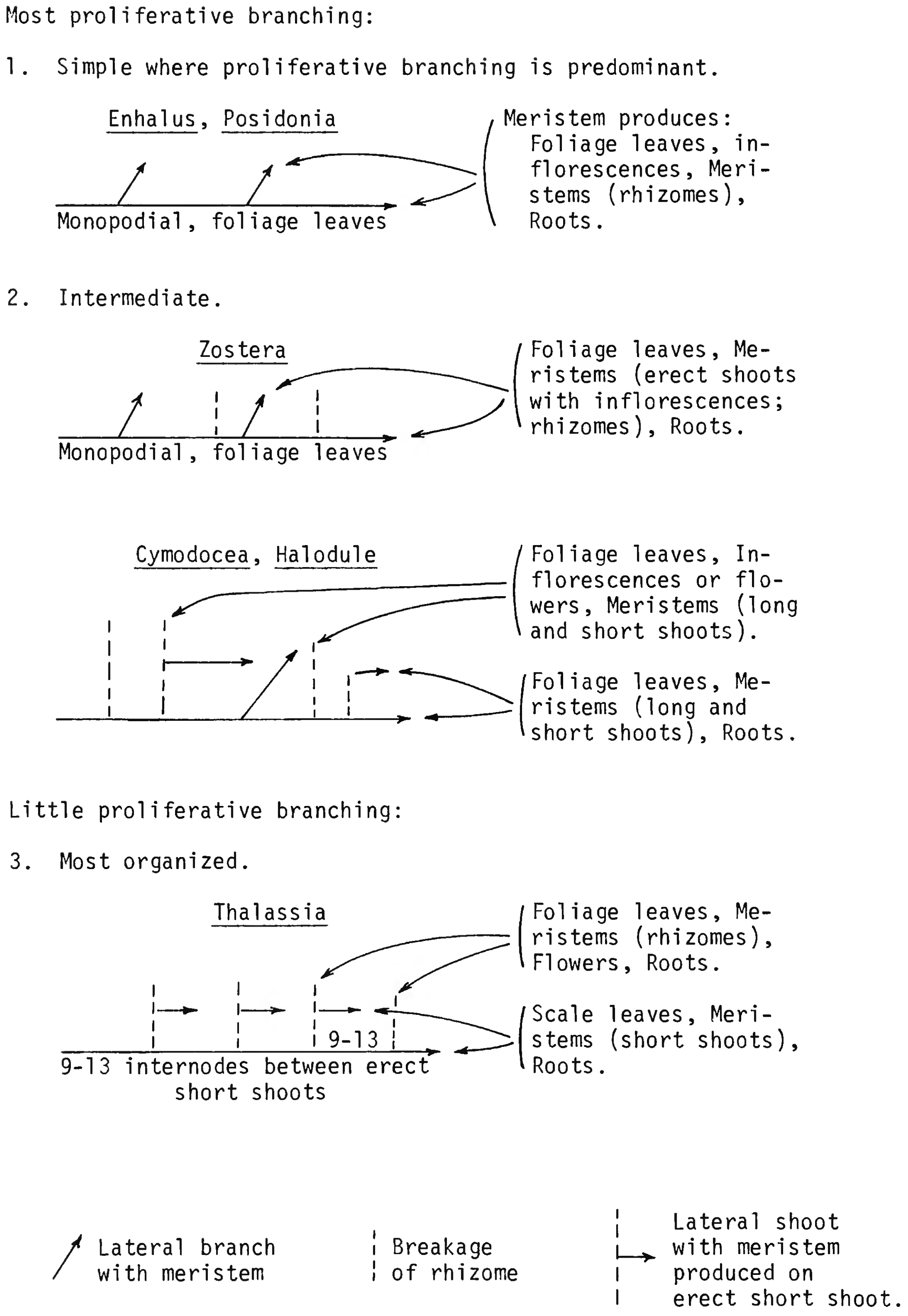


FIGURE 2.—Patterns of seagrass habit and proliferation (after Tomlinson, 1974).

r-strategist (Harrison, 1979). In southern Canada both species, however, show annual and perennial habits in the intertidal zone.

In Europe three vegetative patterns were reported for two *Zostera* species (Jacobs, 1982). *Zostera noltii:* (1) intertidal and subtidal populations overwinter by rhizomes and seeds. The seeds are of minor importance for propagation. This species is predominantly a perennial plant, but may display annuality if it encounters a less predictable environment in the upper intertidal zone. *Zostera marina:* (2) intertidal and brackish water populations are annual; (3) mid- and lower intertidal and subtidal populations are perennial.

These eelgrass patterns were applied to the classification of Grime (1979): (1) *Z. noltii*: stress-tolerant ruderal; (2) *Z. marina*: annual: competitive ruderal; perennial: competitor where ruderal is associated with low stress, high disturbance; stress tolerator is associated with high stress, low disturbance; competitor is associated with low stress, low disturbance. In the classification of Grime, stress is defined as those external constraints that limit the rate of dry matter production of a plant; disturbance is defined as those mechanisms that limit biomass by causing its partial or total destruction.

Recent studies have shown the ranges of adaptive tolerances and the intrapopulational genetic structure of seagrass species in a variety of habitats. This work concentrated on *Z. marina* and *Thalassia testudinum* and demonstrated traits in local populations that reflect the selective influence of water temperature and salinity (McMillan and Phillips, 1979a).

Field and experimental results have shown that seagrass populations may express phenotypic plasticity, genotypic differentiation, or both in their vegetative and reproductive growth relations to a given environment and site (Phillips and Lewis, 1983). Species may form genotypes that are selectively adapted to different habitats. Environmental factors that correlate with this genotypic selection are temperature, salinity, light, and combinations of temperature and light along a depth gradient.

Eelgrass from stressed environments appears to display genotypic differentiation, while that from less stressed environments shows more phenotypically plastic responses. The genotypically differentiated response correlates well with narrow tolerances to environmental factors. The phenotypically plastic response seems to enable broad tolerances to perturbations in the factors. One population in Izembek Lagoon, Alaska, demonstrated phenotypic plasticity when placed in an intertidal pool, but genotypic differentiation when placed in the intertidal zone, a location under high stress (Phillips and Lewis, 1983). The intertidal pool remains full of water at low tide and is much less stressed than is the intertidal zone.

The range of eelgrass extends latitudinally in the north temperate zone along gradients particularly of temperature and light. Along this gradient, it appears that in the center of the range and in local sites where conditions are least stressed, there is a higher incidence of phenotypic plasticity and greater adaptive tolerances to environmental conditions. At both ends of the distributional range, there is a relatively high incidence of genotypic differentiation with an accompanying restricted adaptive tolerance range to environmental conditions. Reciprocal transplants of eelgrass from Puget Sound, Washington, and Izembek Lagoon were made on two different occasions, using both intertidal and subtidal vegetative material. On both occasions Izembek Lagoon plants in Puget Sound died within six months, while the Puget Sound plants survived for a two-year monitoring period in Izembek Lagoon. It is possible that in the warmer waters of Puget Sound, the Alaskan eelgrass with narrower tolerances to temperature (genotypical response) displayed a reduced fitness. The plants from Puget Sound, which displayed a higher incidence of phenotypic plasticity, probably showed a wider range of tolerance to temperature and survived well in Alaska.

In the case of *Thalassia,* a tropical species, distribution is predominantly east to west with a less evident change in environmental conditions. There are locations in the northern Gulf of Mexico, where annual temperature extremes reflect continental-type climates (2°–30°C, annual range), but the populations are selectively adapted to these temperatures, and form genotypes that are different from those from the more homogeneous temperatures of the southern Gulf and Caribbean (McMillan, 1979). The field and experimental work done on *T. testudinum,* thus far, indicate that populations show rather narrow adaptive tolerances to light and temperature changes. *Thalassia* was transplanted across a depth gradient from 0.3 m to 8 m and 15 m locations in the Virgin Islands. In all cases, plants demonstrated genotypic differentiation (Phillips and Lewis, 1983). Extrapolating from experiments and observations conducted from all over the western tropical Atlantic Ocean, *Halodule,* on the other hand, appears to be a pioneering species with wide tolerances to a wide range of temperatures, salinities, depths, and substrates. Only in one case did *Halodule* exhibit a narrow response to environmental change. A small intertidal population with leaves (0.5–1.0 mm wide; 4–6 cm long) was transplanted into the same site at Craig Key in southern Florida. These plants expanded rapidly over the bottom and were healthy after two years (Lewis, Phillips, Adamek, and Cato, 1981).

It is concluded that in unispecific stands of the temperate eelgrass, both phenotypic plasticity and genotypic differentiation are found in the populations, occasionally in the same plant. The response pattern expressed is a function of the degree of environmental stress of the habitat in which the plants are growing. In the multi-specific tropical seagrass systems, it appears that *Thalassia* expressed only genotypic differentiation.

REPRODUCTIVE PATTERNS

FLOWER PRODUCTION.—In 1929 Setchell elaborated a system of 5°C temperature intervals to explain vegetative and reproductive patterns in eelgrass. These 5°C intervals, based on the mean maximum temperature for the warmest month, correlated with periods of vegetative development, flower production, anthesis, fruit development, and recrudescent rigor (decline of the vegetation when the temperatures became too high; Figure 3, after Setchell, 1929). All collections made for Setchell were taken in locations along the Atlantic coast of North America and one location in California. At these sites, the annual temperature ranges were either too great (Atlantic coast) or temperatures remained sufficiently high so that reproduction fit nicely into the 15°–20°C interval. However, in Puget Sound, Washington, new growth of vegetation and flowers appear in spring when water temperatures are still 7°C. Flowers are also produced in temperatures under 10°C in Nova Scotia, Canada. Recent research has substantiated the role of temperature proposed by Setchell, and also that seagrasses form populations that become adapted to local temperature regimes.

In the following treatment we will consider the frequency of flowering in eelgrass (the only species in which this aspect has been worked out), the phenological patterns of flowering in eelgrass and *Thalassia testudinum,* and the temperature regimes under which many seagrass species flower.

In North America there are two trends in the frequency of flowering of eelgrass. (1) In estuarine sites with large annual salinity fluctuations, the flowering response can be very high. This high percentage of flowering plants is usually limited to the intertidal zone, but it may also occur in the subtidal in estuaries with strong mixing characteristics. In Willapa Bay, Washington, the entire system is subjected to extremely dilute salinities during autumn (Nov–Dec) and again during spring (Mar–Apr). In some parts of the bay the flowering response is 100%. (2) In the subtidal along the Pacific coast there is a higher flowering percentage at the extremes of the range than in the center (Phillips, Grant, and McRoy, 1983).

Thus, the flowering response (% of shoots that are reproductive) reflects two types of spatial gradients, viz., broad latitudinal gradients where the greatest response occurs at both ends of the distribution (Table 1; Phillips, Grant, and McRoy, 1983), and a within-site gradient where the greatest response occurs in the intertidal and the least in the subtidal. These data suggest that: (1) higher temperatures provoke a greater flowering response; (2) fluctuating salinity regimes in the intertidal zone result in a greater flowering response; and (3) flowering appears as a response to stress that includes extremes of heat (Gulf of California, Mexico) or cold (Alaska), salinity, nutrients, or even the location of the plants within a particular meadow.

Recent studies on the phenology of *Zostera marina* and *Thalassia testudinum* confirm the conclusions of Setchell (1929) that seagrass floral expression and reproductive development are related to water temperatures. Flowering in these two taxa is related to increasing water temperatures that follow winter minima. Possibly, increased irradiance that may produce water earlier may explain earlier dates of flowering in populations at lower latitudes and in the intertidal zone at specific sites. Flowering times of eelgrass were compared on both coastlines in North America. It was found that populations on the Pacific coast always flower earlier at the same latitude than those in the Atlantic (Phillips, McMillan, and Bridges, 1983). At the same latitude, water temperatures on the Pacific coast are warmer at specific times than those on the Atlantic coast. This suggests that water temperature is the major influence in floral expression. In both *Zostera* and *Thalassia* there is evidence for variation and specialization of genotypes for flower development according to differing temperature regimes and habitats along their distributional ranges.

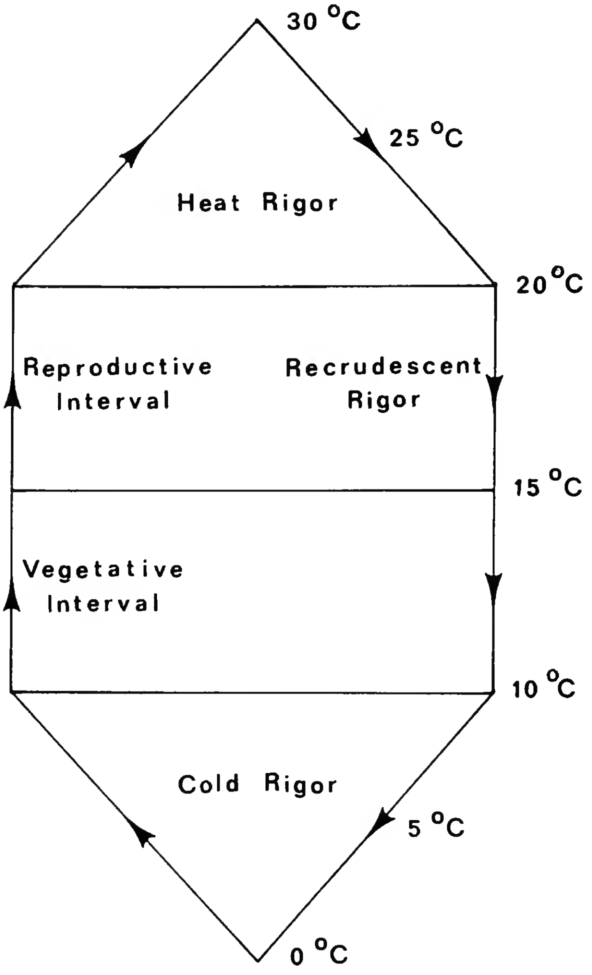


FIGURE 3.—Vegetative and reproductive patterns in eelgrass (Setchell, 1929).

SEED PRODUCTION.—Seed production and events related to this process, viz., flowering, seed release, dispersal, seed germination, and seedling growth, serve as a means of maintaining genetic diversity. In some places the dispersal of seeds to an unvegetated area may be the only significant

TABLE 1.—Flowering response of eelgrass in North America (Phillips, Grant, and McRoy, 1983).

Location	Tidal zone	Flowering response (% of all shoots)
Pacific coast		
Gulf of California, Mexico	Intertidal	100
	Subtidal	100
San Diego, California	Shallow subtidal	33
Oregon (40°N)	Upper intertidal	91
	Lower intertidal	33
	Subtidal	17
Washington (48°N)	Lower intertidal	100
Willapa Bay	Subtidal	100
Puget Sound	Intertidal	3–7
	Subtidal	4–11
Alaska		
South of the Alaska Peninsula (57°N)	Intertidal	4–10
	Subtidal	1–4
North of the Alaska Peninsula	Intertidal	36
	Intertidal Pool	8–13
Izembek Lagoon	Subtidal	13
Port Clarence, Norton Sound (northern extreme of eelgrass in Alaska)	Intertidal Lagoon	13–26
Atlantic Coast		
North Carolina (35°N)	Intertidal	10
	Subtidal	3
Rhode Island (41°N)	Intertidal	57
	Subtidal	8

mechanism for seagrass colonization.

There appear to be two basic spatial patterns evident in eelgrass seed production on the Pacific coast of North America (Table 2; Phillips, Grant, and McRoy, 1983). (1) There is a latitudinal correlation with seed production. Seed production is greatest at both extremes of the distributional range where the environmental extremes of temperature are greatest (Table 2). (2) There is a within-site correlation along a depth gradient in which seed production is greatest in the intertidal zone and is reduced in the subtidal zone. Seed production does not appear to be a function of any one variable, but genotypic responses selected for local habitat conditions have been suggested. It appears that seed production is related to the degree of environmental stress, i.e., extremes of temperature and/or salinity, irradiance, or desiccation.

SEED GERMINATION.—On the Pacific coast of North America, seed germination is indirectly correlated with latitude (Figure 4). In the Gulf of California, Mexico, seed germination is almost 100% in full-strength seawater. The percentage of seeds germinating demonstrates a declining gradient along an increasing latitudinal gradient in full-strength seawater (laboratory study; Table 3; Phillips, Grant, and McRoy, 1983). No correlation with latitude or germination percentage was observed using dilute seawater (10 $^{0}/_{00}$; Figure 4).

A series of studies reported the highest eelgrass seed germinations in dilute salinity (10 $^{0}/_{00}$). At 17 $^{0}/_{00}$ salinity seed germination was intermediate. Seed germination in the Gulf of California, Mexico, however, is directly correlated with water temperature (McMillan, 1983b).

Eelgrass seeds from the Atlantic coast of North America (Maine) and the Pacific coast (Puget Sound, Washington) were placed in screened boxes and anchored within seagrass beds in Puget Sound. After six months germination percentages of both were identical (~2%) and coincided with the laboratory results (0%–6.6%).

On the Atlantic coast of North America, eelgrass seed germination experiments were conducted in the field. There

TABLE 2.—Eelgrass seed numbers at sample locations along the Pacific Coast of North America.

Location	Tidal zone	Seed no.s/M^2
Gulf of California, Mexico		19,850
Puget Sound, Washington	Intertidal	2,059
	Subtidal	875–1,188
Alaska		
South of the Alaska Peninsula	Intertidal	(392)–6,861–7,140
	Subtidal	36,936
North of the Alaska Peninsula, Izembek Lagoon	Intertidal	8,112
	Intertidal pool	3,878–10,340
	Subtidal	1,469

TABLE 3.—Percent of eelgrass seed germination at various temperatures.

Location	Salinity (‰)	Percent at Temperature		
		5°	10°	15°
Gulf of California, Mexico	28	–	94	–
San Diego, California (33°N)	5	–	46	–
	10	–	30	–
	30	–	13.3	–
Puget Sound, Washington (48°N)	10	15–39.5	28.3–65.5	46–70
	17	–	13.1–26.6	–
	30	0.6–6	2–5	0.8–6
Maine (Atlantic Coast, 50°N)	5	–	68	–
	10	31	52	41
	30	–	10	5
Izembek Lagoon, Alaska (55°N)	28	–	0.9	–

was a strong positive correlation with water temperature (Orth and Moore, 1983). One study in the same area found a strong positive correlation with salinity (Lamounette, 1977).

Genotypic responses were suggested for eelgrass seed germination to account for local differences in timing of seed germination. We suggest that these genotypic responses relate to the specific factor that triggers seed germination at a particular site. From Baja California to Alaska on the Pacific coast, the annual range of temperature at any site does not exceed 8°C. In the Gulf of California (annual range is 13°–32°C), at all sites along the Atlantic coast of North America (annual range is 0°–27°C; up to 30°C in some places), and in the Bering Sea (annual range is –4°C to 20°C), the temperature range is extreme. Under these conditions water temperature and not dilute salinity may positively control seed germination in eelgrass.

Seed germination appears to occur throughout the year on both coastlines of North America, but there are seasonal peaks of germination when seedlings are found in large abundance. On the Pacific coast of North America, there is one peak during the year (April to July), while on the Atlantic coast there are two seasonal peaks (Orth and Moore, 1983). In the Chesapeake Bay one peak occurs in the late autumn-early winter, and a second peak in March (37% of all germinated seeds). Up to 66% of all germination occurs between December and March. Seeds on the Atlantic coast appear to be inhibited from germinating from June through August when water temperatures exceed 20°C. One peak occurs in spring before the water warms to 20°C, and the second peak in autumn after the water cools to 20°C. Seeds in the Gulf of California only experience one peak of germination, viz., late October or early November, after the water cools from the summer high of 32°C. The seeds are produced from March to May, but undergo an "induced" dormancy from June to November when water temperatures become elevated. This induced dormancy also occurs in seeds on the Atlantic coast.

It is doubtful that any seagrass seed has a true dormancy requirement. Germination experiments in the laboratory and field have shown that a small number of seeds of all species tested can germinate immediately upon formation. These experiments also show that a small number of seeds germinate throughout the year. Eelgrass seeds appear to maintain their viability for up to one year after their release. *Halodule* and *Syringodium* seed germination, on the other hand, was nearly continuous over three years (McMillan, 1983b). Some taxa may produce seeds with delayed development or with extended longevity, but these seeds do not seem to show a true dormancy.

The relative contribution of vegetative multiplication and sexual germination recruitment to maintain seagrass meadows and colonize new areas are becoming more clear. In seagrass meadows where stresses of environmental conditions (temperature, salinity, tidal ranges, currents) are not extreme, and where disturbance does not occur (wave action from storms; excessive herbivory or "blow-outs" as a result of digging activities of marine animals), the meadow is maintained by vegetative propagation of new shoots. Where stress is extreme and/or disturbances occur, seed germination and seedling recruitment are important. It is thought that colonization of the species in new areas occurs almost exclusively by seed deposition and seedling establishment. Seagrass seedling mortality is extremely high. In addition, most seagrass vegetation is buoyant and floats if it becomes detached. However, we have conducted experiments by merely placing detached eelgrass fragments (whole shoot with leaves and rhizomes/roots intact) on the substrate and covering the basal portion with sediment. These fragments established and quickly spread over the bottom. If detached fragments should lodge on suitable substrate long enough to take root, this could be an important mechanism for seagrass colonization in new areas. Vegetative fragments appear to be the principal means of dispersal in *Posidonia oceanica* along the French Mediterranean coast. Recently, detachable vegetative propagules (rhizome, roots, erect leafy stalks) were found on the terminal stems in *Heterozostera* and along the generative stalks of *Zostera mucronata* in Australia (Cambridge, Carstairs, and Kuo, 1983).

Den Hartog (1970) noted that of the genera with buoyant, floating fruits (*Posidonia, Thalassodendron, Enhalus, Thalassia*), all have a restricted distribution. However, seedling recruitment is needed for dispersal in local areas within the distribution.

In *Zostera* and *Syringodium* the entire generative stalk is released from the horizontal rhizome. This stalk with its remaining seed complement can float off, releasing seeds as they mature. Since stalks may float for an extended period (*Zostera* stalks floated in a tank for 2.5 months before decomposing and sinking), seeds may be carried great distances. Waterfowl that eat eelgrass seeds may help to

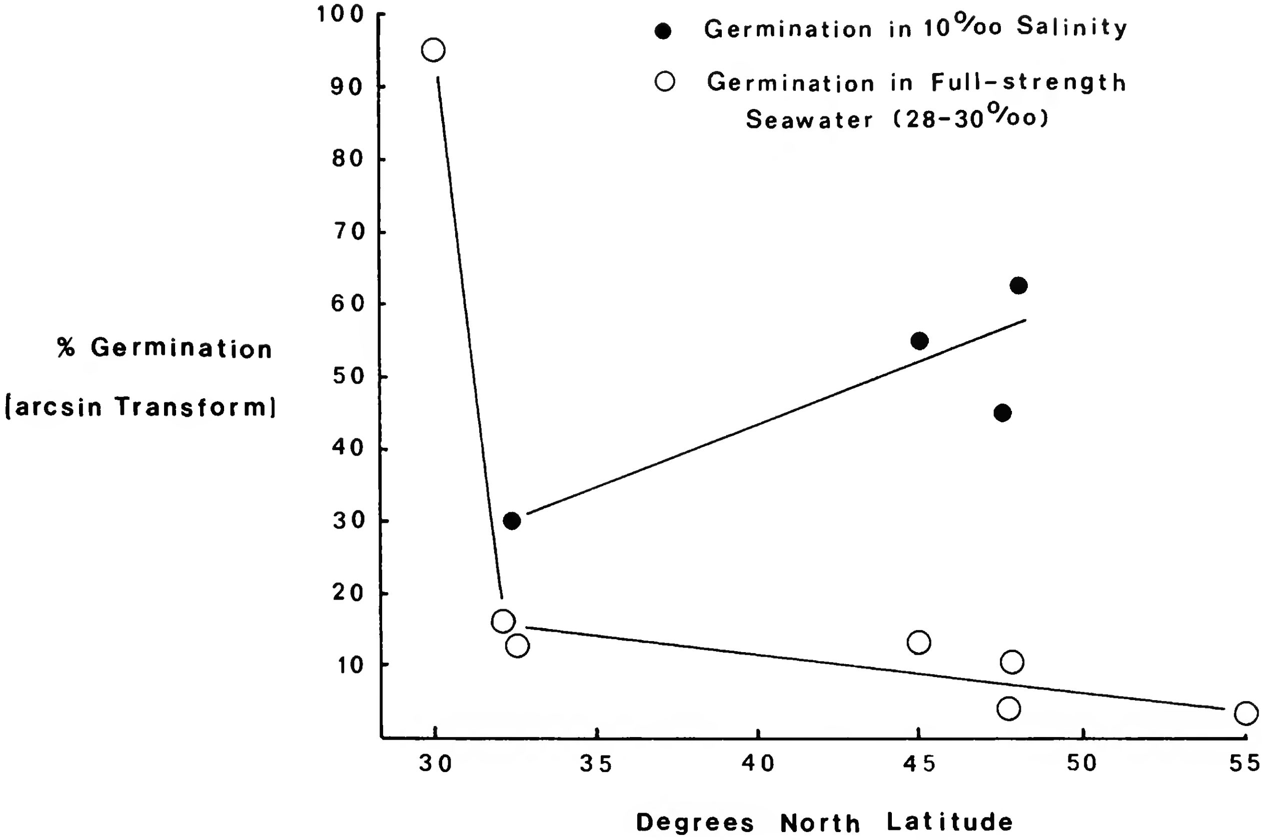


FIGURE 4.—Eelgrass seed germination experiments on the Pacific Coast of North America (from Phillips, Grant, and McRoy, 1983).

disseminate them. In Japan, eelgrass seeds were fed to ducks and recaptured after 24 hours following passage through the alimentary canals. Most seeds retained their ability to germinate. It is known that black brant geese may fly non-stop from Izembek Lagoon, Alaska, to their wintering grounds in Scammon's Lagoon, Baja California, Mexico, in 36 hours. Most birds stop at shorter distances along the Pacific coast.

Amphibolis fruits germinate on the female plant. The young seedlings break away from the plant when the leafy portion reaches 8 cm long, and may either sink immediately or float for great distances if caught in a current. When they sink, they settle "right-side up," owing to a ballasting of the base of the leafy stalk. In *Phyllospadix,* which grows on wave-beaten rocky shores, the fruit wall has two "hooked" arms that lodge around articulated coralline algae. New roots that emerge from the developing embryo have abundant sticky branched root hairs. It is unlikely that long-distance dispersal is effectively mediated by means of seeds in this genus unless a biological carrier intervenes (birds, fish). The flowering stalk, except in *P. torreyi,* is short and not released.

In *Halodule* and *Cymodocea* the one-seeded fruits are produced under the sediment surface. They apparently remain in the sediments until surface erosion occurs or until fish or skates disrupt the sediment. In this way they might roll along the sediment or be carried by a fish and deposited in another location. Species within both genera are colonizing species with very rapid growth. In *Halodule* flowers are patchy and of infrequent occurrence. In both genera maintenance of a meadow and geographic dispersal may be produced primarily by vegetative means.

The Seagrass Ecosystem

An ecosystem has been defined as a unit of biological organization comprised of a biotic and an abiotic component.

Up to 1973 most seagrass research was autecological or ecophysiological in approach. In 1973 the National Science Foundation sponsored an International Seagrass Workshop in Leiden, the Netherlands, attended by 38 scientists from 11 countries. This group assembled all known information on seagrasses, discovered what were the major gaps in our knowledge, and formulated recommendations as to future research. Among these recommendations was one to view the seagrass community as an ecosystem and that research on seagrasses be conducted from an ecosystem point of view.

CONCEPTUAL MODEL

The study of structural or functional components of a system alone is too static, since communities undergo change. The element of change is related neither to structure nor to function, as changes in structure inevitably cause changes in function. Therefore, dynamics of the community have to be regarded as a separate aspect in ecosystem research. In addition, the complex relations between the various components of an ecosystem have developed over extremely long periods and are the result of evolution, selection, and adaptational processes within each component. Consequently, each ecosystem has a firm root in the past, and the historical aspect cannot be omitted from ecosystem research (den Hartog, 1979).

Further, under more or less similar ecological circumstances rather similar communities are found. This may be ascribed to the complexity of relations between the various community components. By comparing a great number of similar communities, the overall traits and features can be developed into an idealized abstract model of the community, from which all local features are eliminated (den Hartog, 1979).

In designing a plan of study of a seagrass ecosystem, one might study each individual structural and functional component separately, and later assemble them into a holistic model. This approach is not adequate as the integration and biological regulation of the various structural elements are unaccounted for. One might organize the study around a theme, such as the succession of structural and process components. In this way not only do the individual components have to be studied and quantified, but the interrelationships of structural and process components must also be studied. In order to understand these connections, one must also study the historical aspect, viz., evolution, selection, and adaptational properties, through time. In such a study, there are predictive capabilities as well. Such a study would by definition remain integrated (Figure 5).

STRUCTURE

Several phytosociologists described the seagrass community as an extremely specialized one with a simple or poor degree of organization. At first glance the spatial structure of a seagrass community, characterized by one dominant species, appears simple, but an analysis of structural elements makes it clear that the spatial structure is rather complex.

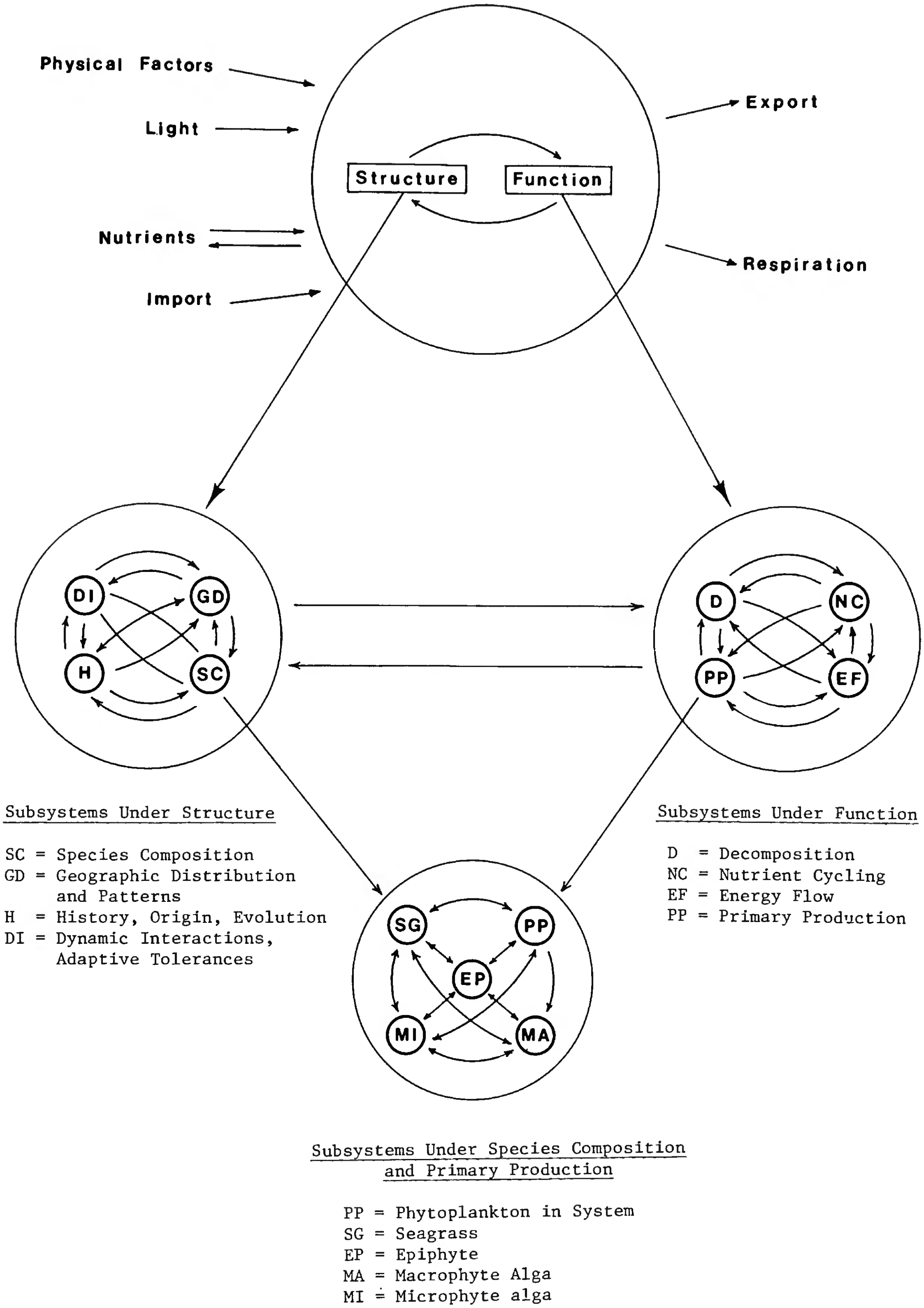
Inferences could have been made about this complexity a long time ago. From 1890 to 1918 Danish investigators compiled long lists of invertebrates and fish species associated with eelgrass meadows and their interactions with respect to trophic dynamics (Blegvad, 1914, 1916; Petersen, 1913, 1915). Work done at Woods Hole, Massachusetts, from 1911 to at least 1950, most of it related to the "wasting disease" problem, also resulted in long lists of algal epiphytes and invertebrates associated with eelgrass (Davis, 1913; Allee, 1923a,b). Much of this work from 1932 to 1950 described the consequences of the disappearance of eelgrass on the food animals in the eelgrass meadows of eastern North America.

Three-dimensional space created in the water column and substrate appears to be the most decisive factor for species diversity in the seagrass community. This has been shown for invertebrate and fish species, particularly (Coen, Heck, and Abele, 1981; Brown, 1982). The temporal pattern or periodicity (phenology) of seagrass systems depends mainly on climatic factors, such as temperature, precipitation, and wind strength. The annual cycle of the dominant seagrass species regulates to a high degree the floral and faunal composition of a number of subordinate structural elements, particularly the epiphytic algae and their grazers.

Structure consists of at least three major subcomponents that are interrelated: (1) floristic and faunistic composition; (2) arrangement of the organisms in space and time; and (3) interrelationships within the community and with the abiotic environment (cf., Table 4 for full listing). The spatial arrangement of seagrasses shows a number of characteristic patterns that can be divided into vertical, horizontal, and

TABLE 4.—Structural components of a seagrass ecosystem.

Component	Subcomponent
1. Species composition	
Flora	Seagrass plant Benthic algae (rhizophytic greens; microalgae in and on substrate; loose macroalgae) Epiphytic algae (on seagrass; on benthic algae) Endophytes (fungi, algae) Microbes
Fauna	Infauna Free-swimming (permanent; transient) Vertebrate grazers
Plankton	
Microbes	
2. Arrangement in space and time	Vertical and horizontal distribution Phenology Life history
3. Density in space and time	
4. Biomass in space and time	
5. Abiotic materials	Gases Nutrients Metals Physical factors Range of minimum to maximum gradient of change Quantity Distribution
6. Interrelationships between 1–5	



Subsystems Under Structure

SC = Species Composition
GD = Geographic Distribution and Patterns
H = History, Origin, Evolution
DI = Dynamic Interactions, Adaptive Tolerances

Subsystems Under Function

D = Decomposition
NC = Nutrient Cycling
EF = Energy Flow
PP = Primary Production

Subsystems Under Species Composition and Primary Production

PP = Phytoplankton in System
SG = Seagrass
EP = Epiphyte
MA = Macrophyte Alga
MI = Microphyte alga

FIGURE 5.—Conceptual model of a seagrass ecosystem.

three-dimensional. Vertical patterns are characterized by zonation and stratification. Horizontal patterns may be observed over geographic distances, or may be due to differences in bottom configuration or prevailing hydrodynamic conditions. The three-dimensional pattern is the way in which the species fill up the available space. This is probably the structural characteristic most decisive for the function of the community (den Hartog, 1979).

In many cases the most basic aspect of a study has not been approached, viz., the distribution, abundance, and phenological patterns of the seagrass itself, the framework of the system. It is becoming increasingly clear that trophic dynamics within a seagrass meadow may be more related to the food web concerned with grazing on the "brown felt" created by bacteria and epiphytes on the blades (Lewis and Hollingworth, 1982; Orth, Heck, and van Montfrans, 1984; Kitting, Fry, and Morgan, 1984), than on the more classical paradigm of the detritus-based webs. If this is substantiated, leaf longevity, number of leaf crops per year, and turnover rates of meadows will be extremely important aspects in defining seagrass ecosystem structure and function.

Numerous algal epiphytes are specific on seagrass blades (Harlin, 1980). These organisms on and associated with seagrass blades have life cycles and/or trophic relationships entrained to the longevity of individual leaves. Two excellent studies have demonstrated the importance of seagrass leaves in creating a substrate for extensive epiphyte communities and the interrelationship of these communities with epiphytic faunal communities (Nagle, 1968: eelgrass; Lewis and Hollingworth, 1982: *Thalassia testudinum*).

Not all seagrass communities contain all these structural elements. The pioneering communities are more simply structured than the climax communities. So far, no elaborate studies are available in which the framework consists of more than one species. It is not known whether the various coexisting seagrass species in a mixed community are sufficiently different in their anatomical and phytochemical properties to cause further differentiation in the form of development of species-specific epiphytic and epizoic associations (den Hartog, 1979).

FUNCTION

A study of the function or processes of a seagrass ecosysytem is an analysis of what the various components do. Basically, there are three major functional components: (1) the rate of energy flow through the system, including primary and secondary production and respiration; (2) the rate of material or nutrient cycling within the system, including decomposition; and (3) The degree of biological or ecological regulation in the ecosystem, including the regulation of organisms by the environment and vice versa. There is a need to study the contribution of each structural component to each of the three functional components. Several non-energetic properties, such as substrate accretion and stabilization, and the shelter and nursery functions, should be included.

RATE OF ENERGY FLOW

Primary production is the most essential function of the seagrass ecosystem. Production rates are remarkably high. However, there is a great need for investigators to standardize terms and methods used in deriving primary production. Often comparisons are made using data taken from standing crop methods (maximum minus minimum values), leaf marking methods, and ^{14}C uptake methods (Bittaker and Iverson, 1976). Often it is not clear if the underground biomass has been considered. As 50%–95% of the biomass of perennial species may be in the substrate, omission of the underground biomass may cause a considerable error.

There is also a need to analyze all compartments in primary production. Data on epiphyte, benthic macrophyte and microphyte algae, and phytoplankton are rare. The production of epiphytes can reach 50% of the seagrass production (Jones, 1968; Penhale, 1977; Borum and Wium-Andersen, 1980; Morgan and Kitting, 1984; Brouns and Heijs, 1986). Moreover, loose-lying algae between the seagrass plants may form a dense layer on the bottom of the seagrass beds, accounting for 10%–20% of the total above-ground biomass (Dawes, 1987). Considering the oxygen production, the photosynthetic activity of this algal mat is considerable. Data on the productivity of these algae are rare. Further, the productivity of phytoplankton above and between the seagrass must not be omitted. As an estimate, it is possible that the contribution of the seagrass component to the community productivity may be only 50% of the total in well-structured communities (den Hartog, 1979).

RATE OF NUTRIENT CYCLING

Many process-oriented investigators give much attention to turnover rate in seagrasses, the quotient between net primary production and average biomass. It is not necessary to link this parameter with primary production of the seagrass itself, as there is assimilation and dissimilation at all trophic levels within the system. Moreover, turnover rates of above-ground and below-ground parts may be different on the same seagrass plant (den Hartog, 1979). In order to give turnover values a more functional meaning, it is necessary to study decomposition processes in more detail.

Decomposition rates of the various plant and animal substances show great variation from almost no decomposition to instant decomposition. These rates determine whether nutrients will be returned quickly to the system or held in reserve. These rates could also influence the relative predominance of feeding types in a system (particulate feeders, grazers, etc.). If detritus is removed by suspension or deposit feeders, nutrient relationships in the sediment will be altered. On the other hand, if grazers are numerous, a significant amount of energy will be transported away from the system.

BIOLOGICAL REGULATION

Species composition affects biological regulation. Blue-green algae on or in the plant or substrate fix nitrogen for seagrass or epiphyte use. Owing to the high rate of use, nitrogen is considered a rate-limiting factor in the seagrass ecosystem. Seagrass density and biomass variations in space and time are reflections of the nitrogen pool (Short, 1981). These parameters in turn affect sediment accretion and stabilization, water clarity (which affects primary production), and further nutrient cycling. Features of the abiotic environment, viz., daily and annual ranges in temperature and salinity, wave activity, and tidal currents, regulate species composition and productivity values.

In a holistic sense, at least one major ecosystem property emerges when the system is intact, viz., the nursery function of a seagrass meadow. The vast interplay of structural and functional characteristics results in a dense, stable environment that forms refuge and shelter as well as food for a myriad of organisms. Some of these spend their lifetime in the meadow, while many spend only their juvenile life in it, or merely feed in it during a portion of a day, to pass on to an adjacent system to fulfill its life cycle.

DYNAMICS

Dynamics of a seagrass ecosystem refer to changes in the system in time. The main emphasis is on changes in the structure. However, changes in structure bring changes in function. The major process involved in ecosystem dynamics is succession, both structural and functional (process).

In structural succession, the seagrass system increases in differentiation, which is associated with changes in floristic and faunistic composition. These changes finally lead to a structure in which maximum diversity is coupled with the most efficient organization (den Hartog, 1979). It is also true that changes occur in system functions, viz., primary production and respiration increase as structure changes, more dissolved organic matter and detritus are formed, and biological regulation increases as more species are added and as the plants have a greater effect on modifying the physical environment in which they live.

Succession is a long-term process. Temporary disturbances due to weather or population explosions of grazers may cause quantitative and qualitative changes in the floristic and faunistic composition that may take more than a year to recover from. Succession may be obscured by long-term cyclic phenomena. There is a possible rhythm in the decline and increase of eelgrass vegetation in the North Atlantic, suggesting that the "wasting disease" of 1931–1933 was an extreme pulse in this rhythm (den Hartog, 1979).

RESEARCH PRIORITIES

There is a need to initiate long-term observations in selected areas relatively free of disturbance and human-related stress that will detect not only species changes in time, but also the limits of adaptability of individual flora and fauna. It must be pointed out that natural succession is a phenomenon that is almost impossible to study these days. The "steady state" was reached a long time ago in all marine waters. However, owing to increasing industralization, most coastal areas of the world are being subjected to impacts that lead to regression of the "climax" state of seagrass vegetation and secondary succession. These secondary successions are directed to a more or less rapid development of a new steady state.

There is a need to distinguish between what is a stress and a disturbance in seagrass systems. Further, the type and intensity of the stress as it affects the structure and function of the seagrass ecosystem should be studied. There is a need to determine the populational structure within a seagrass system, inasmuch as different populations may possess different adaptational tolerances to environmental pressures. Selective adaptational tolerances and populational survival could help explain the "steady state" or succession in the ecosystem. A knowledge of these aspects would allow a predictive capability that could aid in formulating policy aimed at conservation of the seagrass system.

In the marine environment three types of succession have been found in which seagrasses are involved (Figure 6; den Hartog, 1973). (1) The pioneering species is also the climax species (*Zostera*). (2) The seagrass is only a stage of succession toward a subtidal forest of Laminariales (Pacific coast of North America; *Phyllospadix torreyi* followed by *Macrocystis pyrifera* and *Eisenia arborea; Phyllospadix* persists in areas unsuitable for the kelps). (3) On solid substrates algal communities cause sanding-up and prepare a substrate suitable for seagrass colonization (*Thalassia testudinum* in the tropical Atlantic; *Posidonia oceanica* in the Mediterranean).

There is no indication that seagrass systems show a further succession, i.e., they are not a prelude to marsh or terrestrial systems.

The successional series described are derived from comparative field studies and deductions. There are few exact data available that have been followed over a period of years. We recommend that mapping of seagrass vegetation be done to record changes in an exact manner.

Conservation of Seagrass Ecosystems

IMPACTS

Following World War II, the need for housing, clothing, and food in many parts of the northern hemisphere, particularly in Europe and Japan, was very great. By necessity industrialization to satisfy these needs and to provide employment was

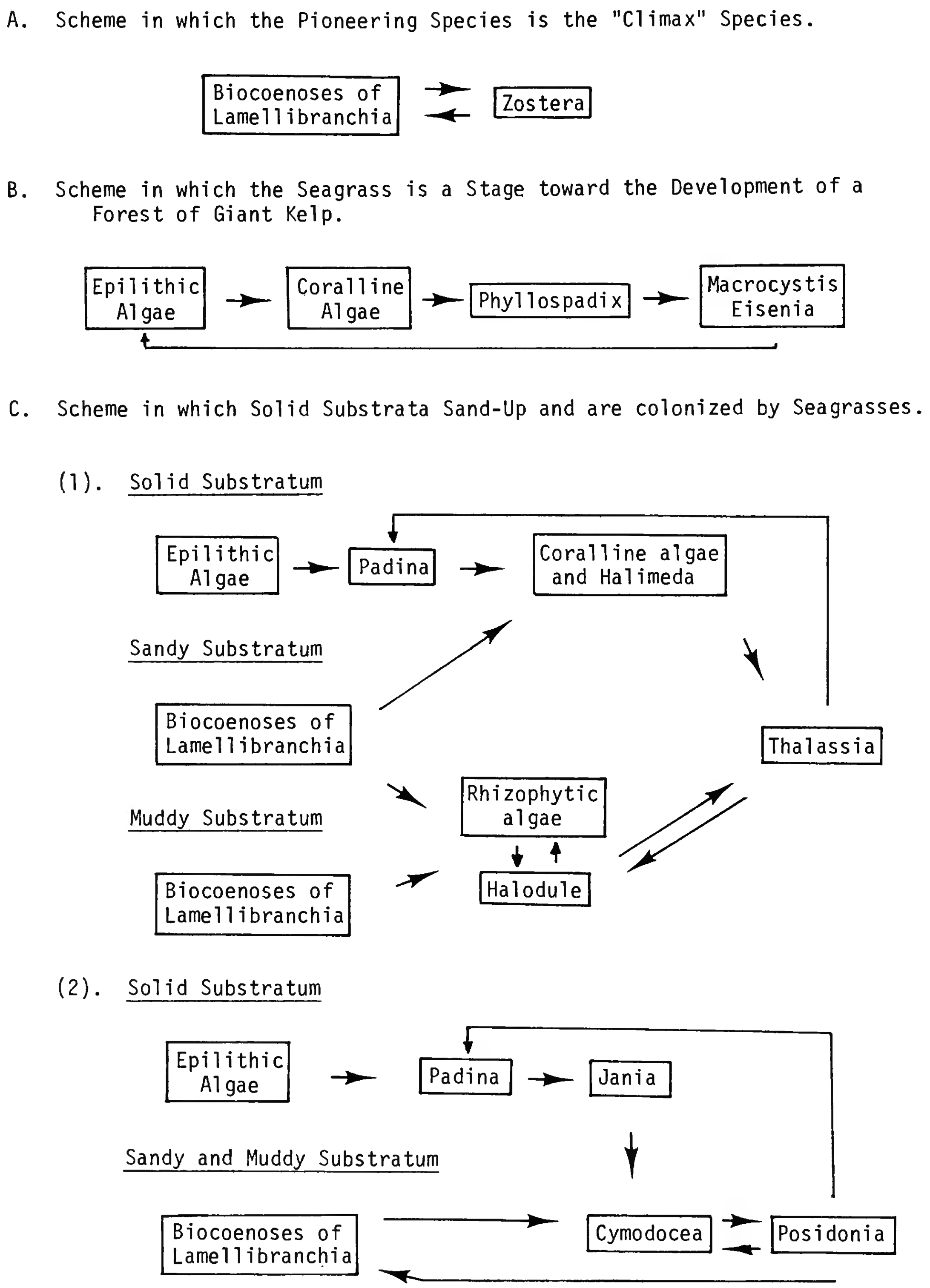


FIGURE 6.—Successional schemes in seagrass communities (after den Hartog, 1973).

rapid and intense. During the reconstruction period economic programs became international in scope with the development of international shipping and airline transportation systems. The economic boom that developed was accompanied by an escalation in the use of an abundant supply of cheap fossil fuels in every sphere of human activity. Forests were leveled for shelter, paper, and cardboard packing materials; land was cleared for agriculture and housing; size of cattle, sheep, and goat herds increased and all kinds of raw materials were acquired by the western nations to aid the reconstruction (Milne and Milne, 1951; Phillips, 1978; Thayer, Wolfe, and Williams, 1975).

Gradually, shallow coastal zones in the northern hemisphere received the impacts of these rapidly growing activities. As development and industrial activity intensified near the centers of population where the labor force was located, an increasing number of people moved from the farm to urban areas. Thus, demographic changes occurred that turned predominantly rural economies in the 1930s and 1940s to urban economies in the 1950s.

With fewer people left on the farms, farming became highly mechanized with the development and use of chemical fertilizers, pesticides and herbicides. Increasingly, people who had moved to the cities began to travel to resort locations along the coast for their holidays, then to buy second homes along the coast as their affluence grew. Finally, new cities developed and old ones enlarged along the coastal areas.

Human-related impacts on coastal areas in the United States were not readily observed until the mid-1950s. Extensive logging in the northeast and northwest USA occurred as early as 1900, allowing some silt to flow into estuaries, but there is no indication that this was a major problem to submerged aquatic vegetation. It was in the mid-1950s, following the sudden increase in the size of coastal cities and the development of hotels, motels (which accompanied the development of the motorway system during the administration of President Dwight D. Eisenhower), and holiday homes and resorts, that seagrass vegetation, as well as coral reef, marsh, and mangrove systems began to show signs of stress and decline.

Dredging in shallow bays in Florida, which contained vast, luxuriant, seagrass meadows, disrupted the ecology and resulted in erosion, siltation, and turbid water far removed from the construction activity (Taylor and Salomon, 1968; Phillips, 1974a). Maintenance dredging in shallow estuaries was required to allow increasing ship traffic to carry commercial products to ports in the coastal cities. With the population increase came the problem of where to dispose of the human and industrial waste. This sewage, if not directly toxic, has a fertilizer-effect on estuarine plant systems. Even if treated, it may stimulate phytoplankton growth and noxious benthic algae, leading to a decline in benthic vegetation.

In Long Island, New York, eelgrass was cleared from a large area as it was deemed a nuisance to swimmers at a newly-created beach (Burkholder and Doheny, 1968).

In the Pacific Northwest (Washington, Oregon, northern California), a drastic decline in the number of black brant geese, up to 90% to 99%, has been documented since 1981, owing to the disturbance and noise from an increasing use of boats near the large eelgrass meadows they require (Reiger, 1982).

In some areas, such as the Netherlands and the state of Florida, where field work began long ago, it has been possible to document the extent of loss of the seagrass resources. One study in Florida documented the loss of 80% of the seagrass stands in Tampa Bay alone from 1880–1980, owing to the decline in water quality (increasing turbidity, toxicity) coincident with the influx of people into the area (Lewis, Durako, Moffler, and Phillips, 1985). Studies done in some parts of Biscayne Bay near Miami documented the same trends (McNulty, 1970). Dredging and sewage disposal were the major factors causing seagrass declines in Christiansted Harbor, U.S. Virgin Islands, in the 1950s when the area developed into a major tourist resort (Dong, Rosenfeld, Redmann, Elliott, Balazy, Poole, Ronnholm, Kenisbery, Novak, Cunningham, and Karnow, 1972; Zieman, 1975). Even in Puget Sound, Washington, eelgrass stocks declined and are still declining near the City of Seattle, following large influxes of people in the early 1950s. In the Dutch Waddenzee profound changes in the abundance and location of eelgrass beds were recorded between 1869–1930, but these were regarded as normal long-term fluctuations with a dynamic equilibrium (Poldermann and den Hartog, 1975). In 1932, the "wasting disease" decimated the subtidal populations. After 1965, a general decline began of remaining stocks which is still in progress. While the exact cause is not determined, the decline appears to be related to the amount of increasing pollution (silt, toxic materials, viz., heavy metals, pesticides, PCB, detergents) carried by the river Rhine, which empties into the Waddenzee.

It is not realistic to believe that any seagrass system is without environmental impacts. Natural as well as human-related effects are observed. Natural impacts come from periodic and aperiodic disturbances from storms. Population explosions of sea urchins in the northeast Gulf of Mexico ravaged mixed beds of *Thalassia-Syringodium* over a length of 26 km and width of 5.9–9.2 km. The numbers of the urchin, *Lytechinus variegatus*, averaged 5.6/m^2, with as many as 63.6/m^2 at the leading edge. How the numbers became so high so quickly is not known (Camp, Cobb, and van Breedveld, 1973). Fish, rays, skates, and crabs disturb seagrass vegetation by resting on it, and/or foraging for food in it. Rays and crabs create holes in the meadow by digging. In the Chesapeake Bay, several hectares of eelgrass were removed by rays which scoured out the sediment to remove clams (Orth, 1975). Sirenians, such as the dugong, in the southwest Pacific graze extensively on seagrass. They use their snouts to shovel out strips of seagrasses, leaving open patches in the meadow (Domning, 1981; pers. obs., 1979). In Izembek Lagoon, Alaska, black brant geese consume 4% of the standing crop of eelgrass with no adverse impacts on the system. These birds crop only the leaves and thus leave the rhizome/root mat in the substrate (McRoy, 1966).

It is human activity, where impacts can be avoided or diminished, that constitutes the greatest concern for the health and survival of seagrass ecosystems. The list of human-related activities and impacts is very long. These include dredging projects for channel construction and maintenance and real estate development (Zieman, 1975, 1982). Other dredging-type impacts are caused by fishermen who drag nets and rakes to collect oysters, scallops, and clams (Thayer and Stuart, 1974). In several parts of the United States a hydraulic dredge was used to collect clams, a device that projects a stream of water onto the bottom, blasting trenches in the seagrass meadow up to 0.5 m deep and one meter wide (Godcharles, 1971). In Humboldt Bay, California, oyster dredging in eelgrass beds led to a 70% reduction in shoot density, as compared to a 33% reduction from other causes (siltation and turbid water from extensive upland logging, road building, and agricultural practices; Waddell, 1964). Boat propellers do much damage to seagrass meadows, especially in shallow tropical waters (Zieman, 1976). Dredging activities are extremely damaging to the seagrass ecosystem because they directly remove the plants and cause turbid water, as well as changing the redox potential of the sediments. This latter change may itself retard recovery by recolonizing propagules for extended periods. Heated water discharges from power generators have been released onto seagrass meadows. In Biscayne Bay, Florida, seagrasses died when the bay waters were heated to 5°C above ambient, while up to 60% of the growth died off at an elevation of 4°C above ambient (Roessler and Zieman, 1969). Such heated waters may disrupt the adaptive tolerances of species and also their reproductive cycles. The release of sewage and agri-chemicals by industries and farms fertilizes and blocks the functioning of the flora and fauna. A severe decline in eelgrass and other submerged aquatic vegetation has been documented in the Chesapeake Bay, coincident with the use of atrazine for upland maize cultivation (Correll and Wu, 1982). Flatfish in Elliott Bay, near Seattle, have liver tumors and are no longer fit for consumption, a fact directly attributable to the release of PCB from industry along the Duwamish River. These chemical additions may result in declining water clarity and plant density, biomass, and production. Even in remote areas oil drilling and increasing ship traffic related to oil brings the spectre of extensive negative impacts. In these cases seagrass ecosystems may be greatly affected and in no case may these systems be termed "natural" any longer.

RESEARCH PRIORITIES

It is now worthwhile to ask the question, "What is a natural unspoiled seagrass ecosystem?" If we can identify one, the next question will be, "By what criteria will we judge a meadow to be a natural, unspoiled meadow of seagrasses?" In order to properly assess environmental impact and consequences of proposed human activity in or adjacent to seagrass ecosysytems, it is imperative that there be systems available that can be observed and studied that are as free from human activity as possible. Only in this way will we obtain baseline data against which to measure adverse effects on a system.

An abundance of research in recent years has documented that seagrass ecosystems are complex structural and functional units. Component plant, animal, and microbial species are numerous, stratified, and possess diurnal and seasonal patterns of abundance and activity. Processes that result from these structural features are tightly coupled. Thus, it might be tempting to characterize a "natural" seagrass bed as one having the greatest abundance and diversity of species with the greatest rates of primary and secondary production. If it were possible to find even one unspoiled eelgrass or seagrass meadow, it might be possible to initiate such an analysis. However, it is well known that regional and local differences exist within each system, based on the adaptive tolerances of the seagrass species to the various environmental factors and even to fortuitous events. These plant differences result in differences in primary production, density, and biomass that relate to the refuge function of the system and how many and what types of animals occur in the system. Ideally, baseline studies should be made in "natural" regional and local seagrass meadows of each species. We suggest that criteria for the identification of "natural" meadows include: (1) maximum primary and secondary production for the area; (2) maximum diversity and abundance of plants and animals; (3) substrate consisting of a mixed mud and sand; (4) maximum seasonal density and biomass; (5) lack of introduced fertilizers, pesticides, herbicides, silt from upland development or sewage; (6) lack of mechanical disturbance from human activity (boat activity or dredging).

It is unfortunate that to find a natural or unspoiled seagrass ecosystem one must often travel great distances to coastal areas remote from human habitation and industrial activities. Only in these areas can anyone expect to find seagrass meadows without heated water discharges, sewage disposal, or some similar human-related influence. However, even in many of the third-world nations, much needed income is being derived from coastal timber removal, mining activities, and real estate development. Where remote unspoiled areas do exist, it may be possible to use research from the seagrass meadows found there as baseline data on the structure and function of a natural seagrass ecosystem. Areas with little human habitation still exist within the continental borders of the United States, but even along these coastlines, logging, roadbuilding, and agricultural activities have by now penetrated to the shore. It is only in extremely remote areas such as Izembek Lagoon, Alaska, in the northeast Gulf of Mexico, and along much of the southern and western coasts of Australia, where vast stretches of relatively undisturbed seagrass vegetation remain, that we have any chance of establishing research projects that will yield baseline data on a natural seagrass ecosystem.

Research projects are vitally needed in remote areas, even if they are expensive. The major problem is that it might be difficult to accept such data from remote areas if the application is needed hundred or thousands of kilometers away where the impacts are occurring. It is generally true that seagrass structural and functional characteristics are similar wherever they occur. However, the seagrasses themselves differ in adaptational tolerances and in growth patterns on an intrapopulational basis. Because of local microclimatic and even fortuitous reasons, species that may characterize a type of community might be lacking in specific local areas. Restricted regional studies on natural systems are vitally needed, as are studies on local systems even if they are impacted.

MANAGEMENT

We do not advocate the complete absence of human activity in or adjacent to seagrass meadows. However, the continued availability to humans of the biological resources of the seagrass ecosystem depends on either the maintenance of natural genetic and species diversity or a controlled reduction of this diversity, as in terrestrial agriculture. Since biological productivity is a function of the availability of nutrients, light, and temperature, the stability of natural systems is a function of the stability of these factors and the genetic and species diversity present. Human-induced impacts may lead to an increase in the short-term productivity, but they may also lead to an elimination of genotypes and species or to the spread of less desirable species.

We do advocate the identification and initiation of studies in representative natural seagrass beds in regional, local, and remote areas, so that we may know what constitutes harmful activity or even change in a seagrass ecosystem. Unless baseline data become available from natural, unspoiled systems, we will never have a measure of human activity in the ecosphere and will never attain wise management and stewardship of our natural resources.

ALIEN SPECIES

Indiscriminate human activity has allowed the introduction of alien or adventive seagrass species into other areas. *Zostera japonica* was undoubtedly introduced to the Pacific coast of North America, as was *Sargassum muticum,* when Japanese oysters were first brought to Willapa Bay, Washington, in 1925. This seagrass has now spread southward to Coos Bay, Oregon, and northward to southern British Columbia, Canada (Harrison and Bigley, 1982). Fortunately, it is not a noxious pest. Rather, it may be enhancing ecosystem and wildlife production. It does not compete with or exclude marsh or upland plant species and does not interfere with the much more desirable eelgrass. It grows mainly in the upper intertidal zone above eelgrass, and is a favorite food of black brant and other grazing waterfowl. *Halophila stipulacea,* a species of the Indo-Pacific, escaped into the Mediterranean with the opening of the Suez Canal in 1869 (Lipkin, 1972). A fragment was found at Rhodes in 1894. By 1923 the species was firmly established in many areas. It appears to be a euryhaline subtropical species, fragments of which were probably transported through the Canal on fishing nets that were then cleaned in harbors. *Halophila decipiens,* noted to be the only truly pantropical seagrass species, may owe its distributive abilities to ships, since it is unusually common around ports and harbors, often without companion species (den Hartog, 1970).

Division ANTHOPHYTA

Class MONOCOTYLEDONEAE

Order HELOBIAE

Key to the Genera of Seagrasses

1.	Leaves without a basal sheath	*Halophila*
	Leaves with a basal sheath	2
2.	Leaves bearing a ligule at junction of sheath and blade	3
	Leaves without a ligule	11
3.	Leaves with numerous tannin cells	4
	Leaves without tannin cells	9
4.	Leaves terete	*Syringodium*
	Leaves flat	5
5.	Leaf-bearing stem at each rhizome node	6
	Leaf-bearing stem not at each rhizome node	7

6. Leaf veins 3; roots unbranched . . . . ***Halodule***
   Leaf veins 7–17; roots branched . . . . ***Cymodocea***
7. Sheath persists as a bundle of fibers . . . . ***Posidonia***
   Sheath not persisting as bundle of fibers 8
8. Leaf blade margins spinulose; one unbranched or sparsely-branched erect stem on every fourth rhizome node . . . . ***Thalassodendron***
   Leaf blade margins entire; one profusely branched erect stem every 4–8 rhizome internodes . . . . ***Amphibolis***
9. Rhizomes congested with short compacted internodes (1–2 mm long) . . . . ***Phyllospadix***
   Rhizomes not congested, with longer internodes (more than 2 mm long) 10
10. Rhizome monopodial, herbaceous, with a short lateral shoot at each node . . . . ***Zostera***
    Rhizome sympodial, ligneous, with an erect unbranched, deciduous shoot at each node . . . . ***Heterozostera***
11. Sheath persisting as fibers; leaf blades 1.25–1.75 cm wide . . . . ***Enhalus***
    Sheath not persisting as fibers; leaf blades 0.5–1.0 cm wide . . . . . . ***Thalassia***

Family POTAMOGETONACEAE

Genus *Zostera*

Key to the Subgenera of *Zostera*

Leaf sheath closed and tubular, rupturing with age; reproductive shoot terminal; retinacula absent . . . . Subgenus ***Zostera***
Leaf sheath open with open margins overlapping; reproductive shoot lateral; retinacula always present . . . . Subgenus ***Zosterella***

Key to Species of *Zostera,* Subgenus *Zostera*

1. Rhizome suberect with extremely short internodes; leaf sheath persistent; leaf tip emarginate or notched . . . . ***Z. caespitosa***
   Rhizome creeping with elongate internodes; leaf sheath deciduous; leaf tip obtuse,mucronate 2
2. Seeds ridged . . . . ***Z. marina***
   Seeds smooth 3
3. Leaf tip obtuse to mucronate; reproductive shoot with fertile branches only at the base; seeds with anthocyanin spots . . . . ***Z. caulescens***
   Leaf tip truncate or emarginate; reproductive shoot without sterile branches; seeds without anthocyanin spots . . . . ***Z. asiatica***

Zostera asiatica Miki

FIGURE 7

CHARACTERISTICS.—Rhizome 5–6 mm wide with numerous roots and a leaf at each node. Internodes about 20 m long. Leaf sheath up to 25 cm long. Leaf blade up to 1.5 m long and 11–15 mm wide; veins 7–11; tip obtuse to truncate, often emarginate. Reproductive shoot up to 1.5 m long, sparsely branched, with several spathes. Spathal sheath 33–50 mm long and 4–5.5 mm wide. Spadix linear with 15–20 female and 15–20 male flowers. Fruit elongate–ellipsoid, 5–6.5 mm long; pericarp brown. Seed with yellowish brown testa, smooth.

NATURAL HISTORY.—Plants are confined to sheltered bays on sand in depths of 8–12 m.

DISTRIBUTION.—The species has been found in the Kuriles in the USSR and in two sites on Hokkaido in Japan (Map 1).

Zostera caespitosa Miki

FIGURE 8

CHARACTERISTICS.—Rhizome short with numerous roots and a leaf at each node. Internodes short, at most 5 mm long. Leaf sheath 5–15 cm long, persistent. Leaf blade up to 70 cm long and 3–6 mm wide; veins 5–7; tip obtuse, emarginate or centrally indented. Reproductive shoot 30–60 cm long, poorly branched with up to 10 spathes. Spathal sheath 35–60 mm long and 3–4 mm wide. Spadix linear with 10–12 female and 10–12 male flowers. Fruit ovoid, 3–3.5 mm long; pericarp brown.

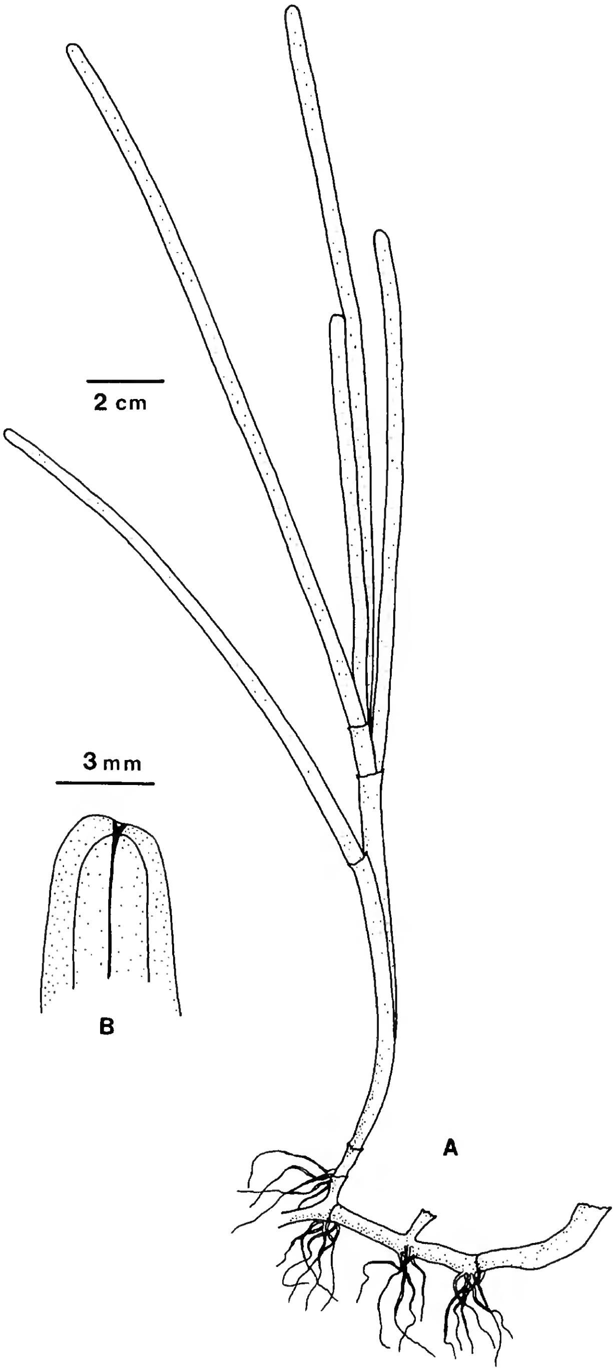


FIGURE 7.—*Zostera asiatica:* A, habit of plant; B, leaf tip.

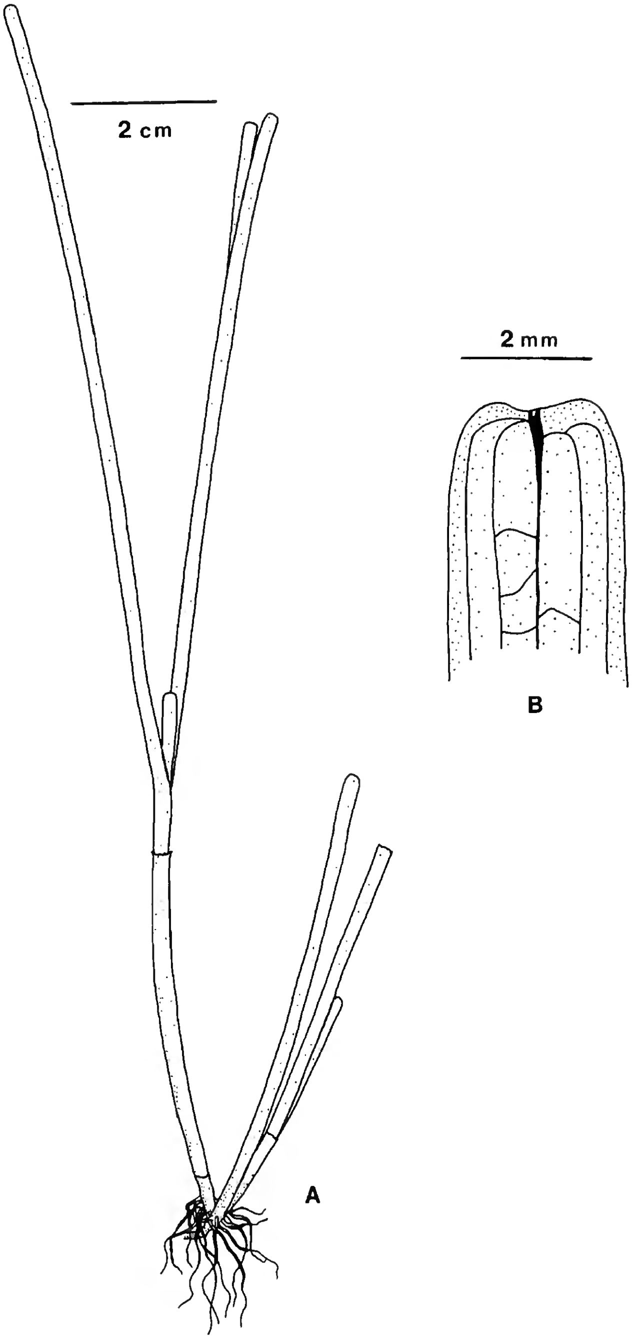


FIGURE 8.—*Zostera caespitosa:* A, habit of plant; B leaf tip.

Seed with brown testa, with 16–20 costae.

NATURAL HISTORY.—The species exists on sand in semi-exposed bays at 3–8 m depths. Plants flower in May.

DISTRIBUTION.—Reported only on the island of Honshu, Japan.

Zostera caulescens Miki

FIGURE 9

CHARACTERISTICS.—Rhizome 2–5 mm wide with numerous roots and a leaf at each node. Internodes 10–25 mm long. Leaf sheath up to 20 cm long, slightly wider than the blade. Leaf blade up to 60 cm long and 8 mm wide; veins 5–9; tip broadly obtuse. Reproductive shoot up to 1.5 m long, repeatedly branched with spathes only on the lower 2–3 branches. Spathal sheath 6.5–10 cm long and 2.5–5 mm wide. Spadix linear with about 20 female and 20 male flowers. Fruit elongate ellipsoid, 4 mm long; pericarp brown. Seed with light brown testa, almost smooth.

NATURAL HISTORY.—The species grows from 6–12 m deep in sheltered to semi-exposed bays on mud and sandy substrates. Flowering begins in April.

DISTRIBUTION.—Two locations in Korea (Kakijima near Mokpo; Ursan) and at one location in Japan (Horinouchi near Yokosuka on Honshu; Map 2).

Zostera marina Linnaeus

(Eelgrass)

FIGURE 10

CHARACTERISTICS.—Rhizome 2–5 mm wide with numerous roots and a leaf at each node. Internodes 10–35 mm long. Leaf sheath 5–20 cm long, wider than the blade. Leaf blade up to 2 m long and 1.5–12 mm wide; veins 5–11; tip obtuse, often slightly mucronate. Reproductive shoot up to 1.5 m long, repeatedly branched with numerous spathes. Spathal sheath 40–85 mm long and 2–4 mm wide. Spadix linear with up to 20 female and 20 male flowers. Fruit ellipsoid to ovoid, 2.5–4 mm long; pericarp brown. Seed with dark brown to straw-colored testa, with 16–25 distinct costae.

NATURAL HISTORY.—Eelgrass extends from the intertidal zone down into the subtidal, often in extensive meadows. It occurs in more or less sheltered areas on soft mud and on sand, but most often occurs on a mixed mud and sand substrate. It has also been found on gravel mixed with sand.

Depending on the area and the genotype, the salinity tolerance of the species is exceptional. It is a euryhaline species, occurring in the Baltic Sea in salinities as low as 6 ‰, but grows well in full-strength seawater. The depth of growth is influenced by water clarity, suspended matter in the water, the range and stage of the tide, wave action, the type of bottom, presence of storms, and the season of the year. In clear water it grows down to 30 m, but is limited to 1.2–2.0 m where the water is turbid. Eelgrass is most often found at a depth of 7–10 m deep where the water is clear.

Eelgrass is found where temperature declines well below the freezing point. Above 22°C the plants either produce flowers and seeds, becoming annual, or become moribund. According to Phillips, McMillan and Bridges (1983), flowering is a response to warming water temperatures which interact with local genotypes.

DISTRIBUTION.—Eelgrass is widely distributed in both the northern Pacific and Atlantic Oceans. It extends north of the Arctic Circle in northern Russia, presumably due to the warming influence of the Gulf Stream (Map 3).

Key to Species of *Zostera*, Subgenus *Zosterella**

1. Leaf tips tridentate . . . . *Z. mucronata*
   Leaf tips not tridentate 2
2. Seeds striate 3
   Seeds smooth 5
3. Leaf sheaths partially persistent as a scaly mass; testa with generally 16 longitudinal striae . . . . *Z. capricorni*
   Leaf sheaths not persistent; number of longitudinal striae more than 16 4
4. Leaf tips indented; retinacula obtuse; testa with generally 20 longitudinal striae . . . . *Z. muelleri*
   Leaf tips obtuse; becoming deeply indented with age; retinacula acute; testa with 24 longitudinal striae . . . . *Z. capensis*
5. Leaf tip indented when old; retinacula predominantly linear, acute . . . . *Z. noltii*
   Leaf tip predominantly obtuse, but may be indented with age; retinacula predominantly oblique, broadly triangular to elliptic, but may appear linear, predominantly obtuse . . . . *Z. japonica*

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* The use of characteristics, such as the shape of the leaf tip and the shape of the retinaculum, to separate species of *Zostera* should be discouraged. There is much variability observed from place to place, across tidal zones, and with age of the plant. Experimental techniques using controlled growth to define seagrass species should be discouraged. Additionally, *Z. novazelandica* has been deleted from the key. Following a study of vegetative plants of both *Z. novazelandica* and *Z. muelleri* (collected by RCP), we can observe no differences between these two species. Also, there are no differences detected between the descriptions of both species as given in den Hartog (1970).

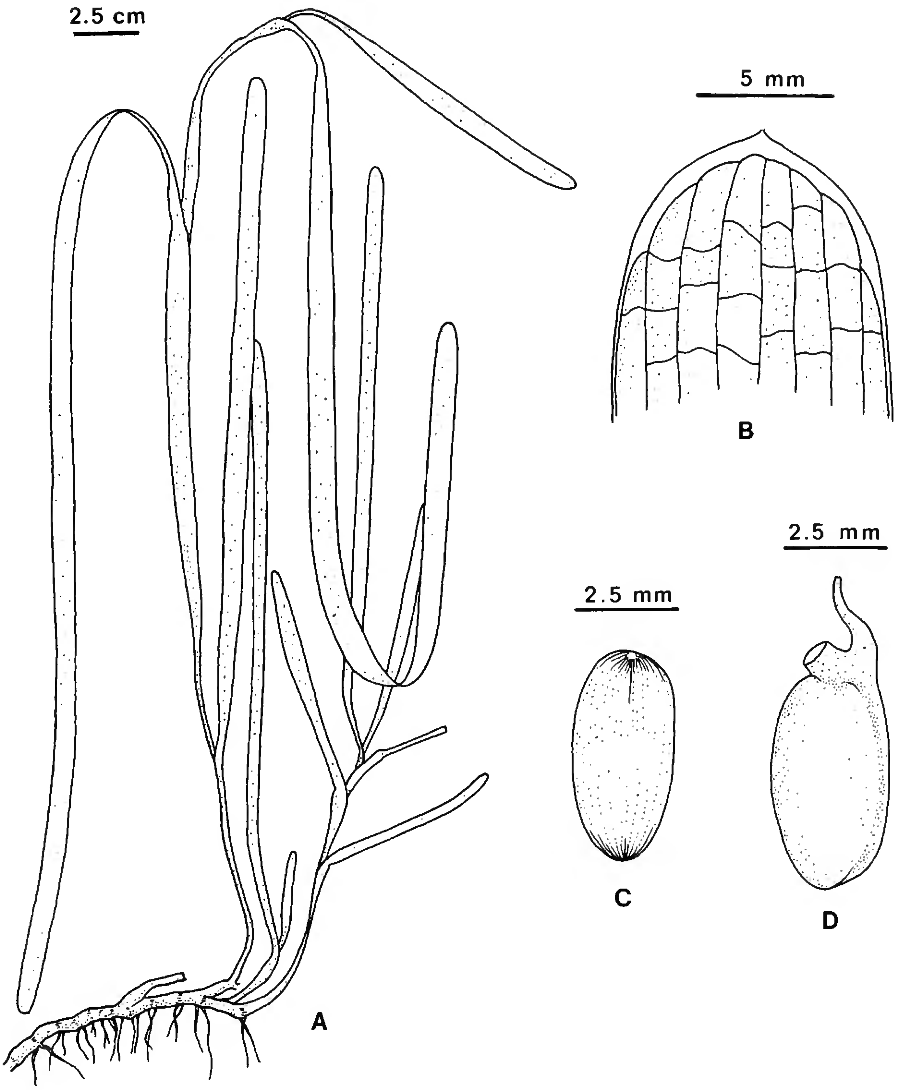

FIGURE 9.—*Zostera caulescens:* A, habit of plant; B, leaf tip; C, seed; D, fruit.

Zostera capensis Setchell

FIGURE 11

CHARACTERISTICS.—Rhizome 0.5–2 mm wide with 1–2 roots at each node. Internodes 3–35 mm long. Leaf sheath 1–5 cm long. Leaf blade 2–45 cm long and 0.5–2.5 mm wide; veins 3; tips obtuse, sometimes slightly emarginate, becoming deeply cleft with age. Reproductive shoot 0.5–10 cm long with 1–7 spathes. Spathal sheath 8–25 mm long and 1.5–2.5 mm wide. Spadix lanceolate with 3–5 female and 3–5 male flowers. Fruit ellipsoid, 2–2.5 mm long and 1 mm wide; pericarp dark brown. Seed with a reddish brown testa with 24 longitudinal striae.

NATURAL HISTORY.—The species occurs on intertidal flats and in lagoons. On intertidal flats the plants are small with leaves 20–30 cm long and with short reproductive shoots. Lagoonal plants are larger with leaves up to 115 cm long and have long reproductive stalks.

DISTRIBUTION.—Plants are found in South and East Africa from Kenya to Saldanha Bay on the Atlantic coast (Map 4).

Zostera capricorni Ascherson

FIGURE 12

CHARACTERISTICS.—Rhizome 0.75–2 mm wide, with 2 groups of roots at each node. Internodes 4–40 mm long. Leaf sheath 2–10 cm long. Leaf blade 7–50 cm long and 2–5 mm wide; veins 5; tip truncate, slightly denticulate. Reproductive shoot 1–30 cm long, with numerous spathes. Spathal sheath

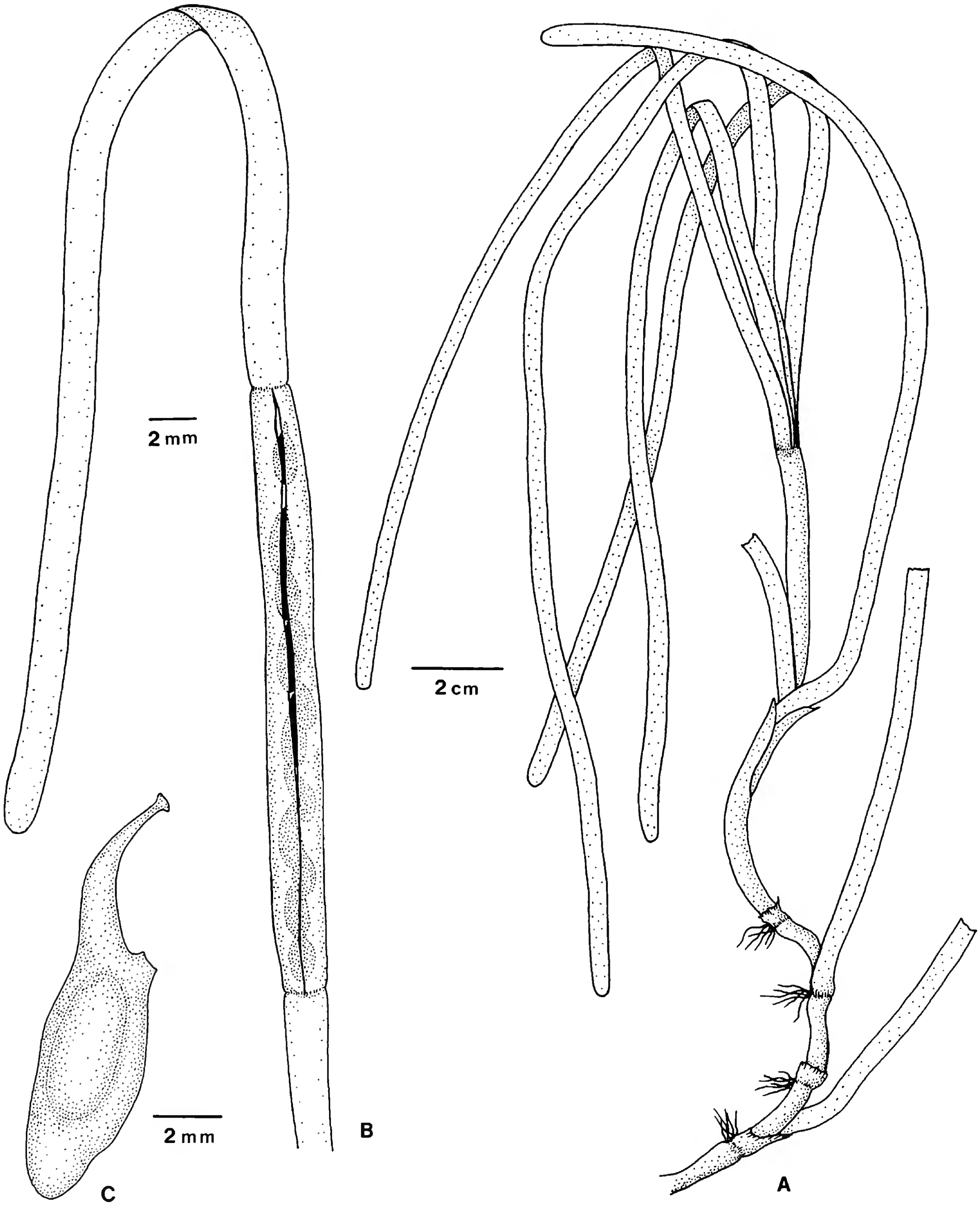

FIGURE 10.—*Zostera marina:* A, habit of plant; B, spadix; C, fruit.

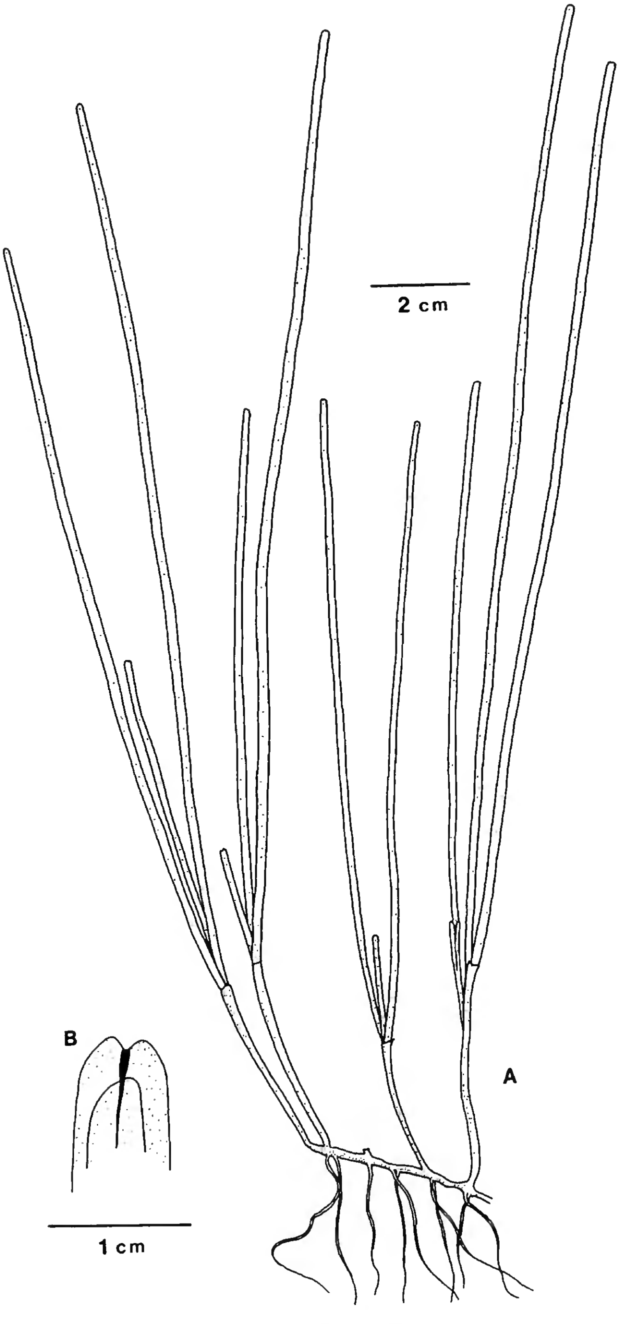

FIGURE 11.—*Zostera capensis:* A, habit of plant; B, leaf tip.

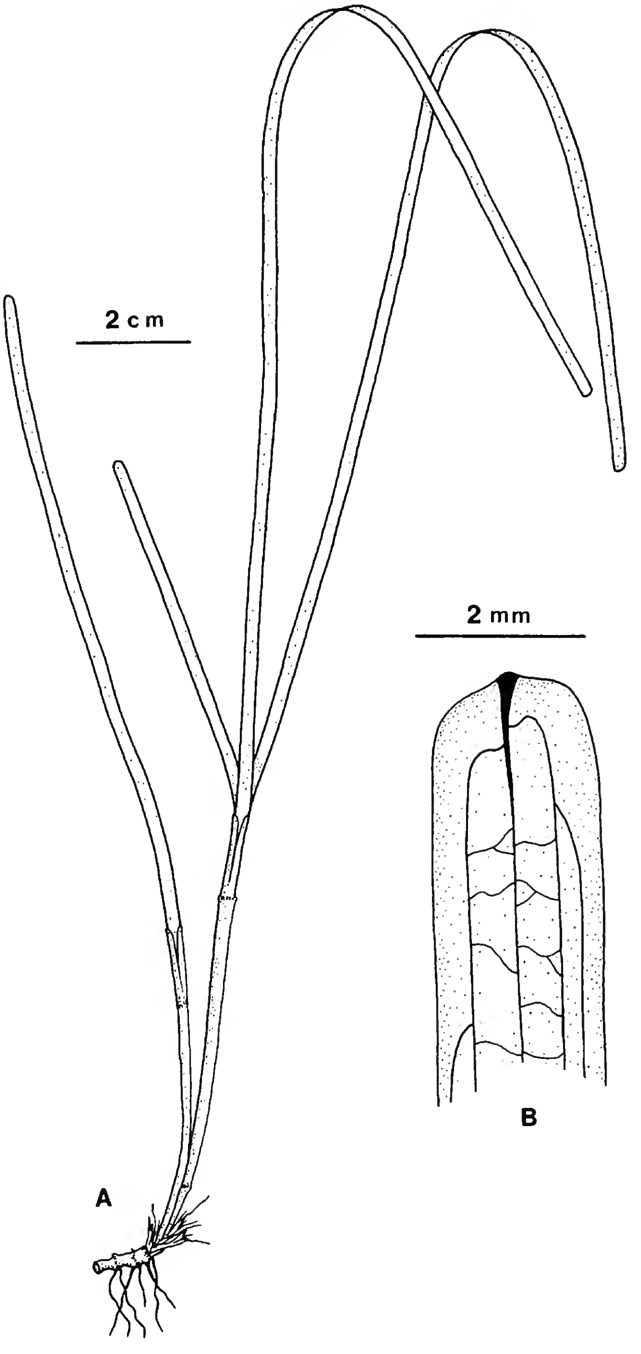

FIGURE 12.—*Zostera capricorni:* A, habit of plant; B, leaf tip.

14–26 mm long and 1.5–2 mm wide. Spadix linear to spathulate with 7–10 female and 7–10 male flowers. Fruit ellipsoid, 2 mm long and 1 mm wide; pericarp brown. Seed with a brown testa with generally 16 longitudinal striae.

NATURAL HISTORY.—The species is principally marine but may grow into brackish water in estuaries and lagoons. It may form extensive meadows down to 6 m deep. It is not common in the intertidal.

DISTRIBUTION.—Plants are found from New South Wales to Queensland in Australia. It has been reported from Thursday Island in the Torres Strait and on North Island, New Zealand. It was found on Kangaroo Island in South Australia (Map 5).

Zostera japonica Ascherson and Graebner

FIGURE 13

CHARACTERISTICS.—Rhizome 0.5–1.5 mm wide with 2 roots at each node. Internodes 3–32 mm long. Leaf sheath 1.25–6 cm long. Leaf blade 3–30 cm long and 0.75–1.5 mm wide; veins 3; tip obtuse, slightly emarginate in older leaves, often asymmetric. Reproductive shoot up to 2.5 cm long with 1–5 spathes in quiet water. Spathal sheath 10–17 mm long and 1.5–2 mm wide. Spadix lanceolate with 4–5 female and 4–5 male flowers. Fruit ellipsoid, 2 mm long; pericarp red-brown. Seed with a smooth brown testa.

NATURAL HISTORY.—The species is common on sheltered tidal flats, but also occurs in brackish coastal lagoons. On tidal flats leaves are short and narrow, while in lagoons leaves are long. In polluted estuaries the leaves are long and wide, and the plants remain vegetative.

DISTRIBUTION.—The species occurs from Sakhalin and Kamchatka to Vietnam (Map 6).

Zostera mucronata den Hartog

FIGURE 14

CHARACTERISTICS.—Rhizome 0.5–1.5 mm wide, with 2–3 roots at each node. Internodes 4–40 mm long. Leaf sheath 1.3–7.7 cm long. Leaf blade 2–22 cm long and 0.75–1.75 mm wide; veins 3; tip tridentate. Only vegetative plants have been found.

NATURAL HISTORY.—The species forms dense beds in the upper and mid-intertidal.

DISTRIBUTION.—Plants were found in St. Vincent Gulf and Spencer Gulf in South Australia, and in two locations in the southwestern part of Western Australia (Map 7).

Zostera muelleri Irmisch ex Ascherson

FIGURE 15

CHARACTERISTICS.—Rhizome 0.5–1.5 mm wide and with 2 roots at each node. Internodes 4–31 mm long. Leaf sheath 1.5–11 cm long. Leaf blade 5–30 cm long and 1–2 mm wide; veins 3; tip obtuse or truncate, more or less deeply notched. Reproductive shoot length variable, from 1 cm long in tidal habitats and up to 50 cm long in still water habitats; spathes 1–4 to several. Spathal sheath 16–55 mm long and 1.5–2.5 mm wide. Spadix linear-lanceolate with 4–12 female and 4–12 male flowers. Fruit ellipsoid, 2–3 mm long and 1–1.25 mm wide; pericarp brown. Seed with a testa with longitudinal striae.

NATURAL HISTORY.—The species is euryhaline, occurring on sheltered flats in marine waters, and penetrating into estuaries with brackish water.

DISTRIBUTION.—Plants occur in the southeast portion of South Australia throughout Victoria and on Tasmania (Map 8).

Zostera noltii Hornemann

FIGURE 16

CHARACTERISTICS.—Rhizome 0.5–2 mm wide with 1–4 roots at each node. Internodes 4–35 mm long. Leaf sheath 0.54 cm long. Leaf blade 6–22 cm long and 0.5–1.5 mm wide; veins 3; tip emarginate, often asymmetric, indented in older leaves. Reproductive shoot usually 10 cm long but varies from 2–25 cm; with 1–6 spathes. Spathal sheath 12–20 mm long and 1.3–2 mm wide. Spadix lanceolate with 4–5 female flowers and 4–5 male flowers. Fruit ellipsoid, 1.5–2 mm long; pericarp dark brown. Seed with smooth testa.

NATURAL HISTORY.—Intertidal flats; common from mean high water neap to mean low water neap. It is a euryhaline species. With decreasing salinity it grows deeper, and may become permanently submerged.

DISTRIBUTION.—The species occurs along the Atlantic coasts of Europe and around the British Isles, extending from southern Norway to Mauritania. It has also been found in the Mediterranean Sea, the Black Sea, and the Caspian and Aral seas (Map 9).

Genus *Phyllospadix*

Key to Species of *Phyllospadix*

1. Reproductive shoot branched with several spathes . . . . ***P. torreyi***
   Reproductive shoot with one spathe 2
2. Rhizome internodes with 6–10 roots . . . . ***P. scouleri***
   Rhizome internodes with 2 roots 3
3. Leaf tip truncate; retinacula obtuse, truncate, or retuse . . . . ***P. serrulatus***
   Leaf tip obtuse to slightly emarginate; retinacula acute 4
4. Rhizome internodes covered with reddish brown fibers . . . . ***P. iwatensis***
   Rhizome internodes covered with black fibers . . . . ***P. japonicus***

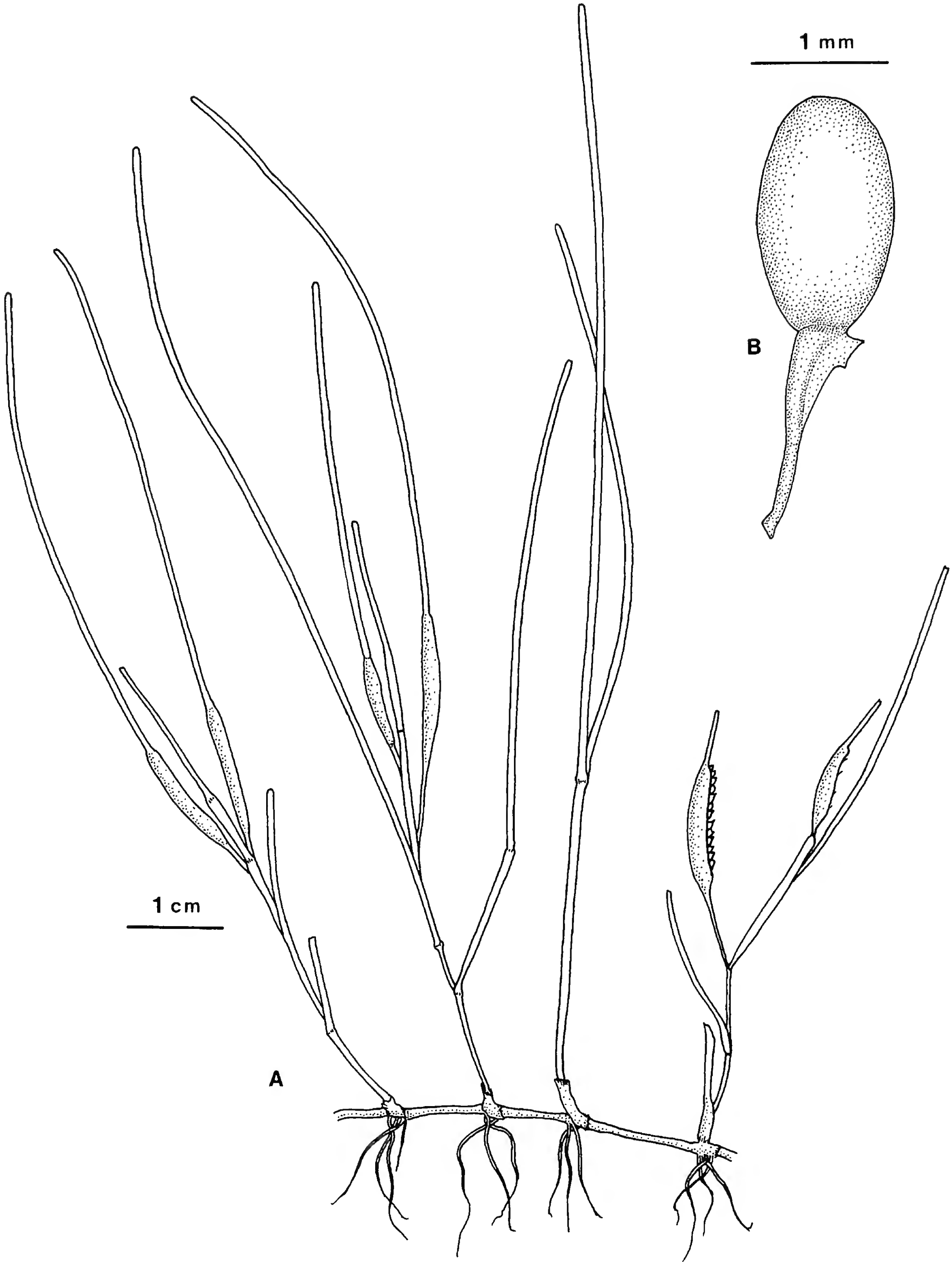

FIGURE 13.—*Zostera japonica:* A, habit of plant; B, fruit.

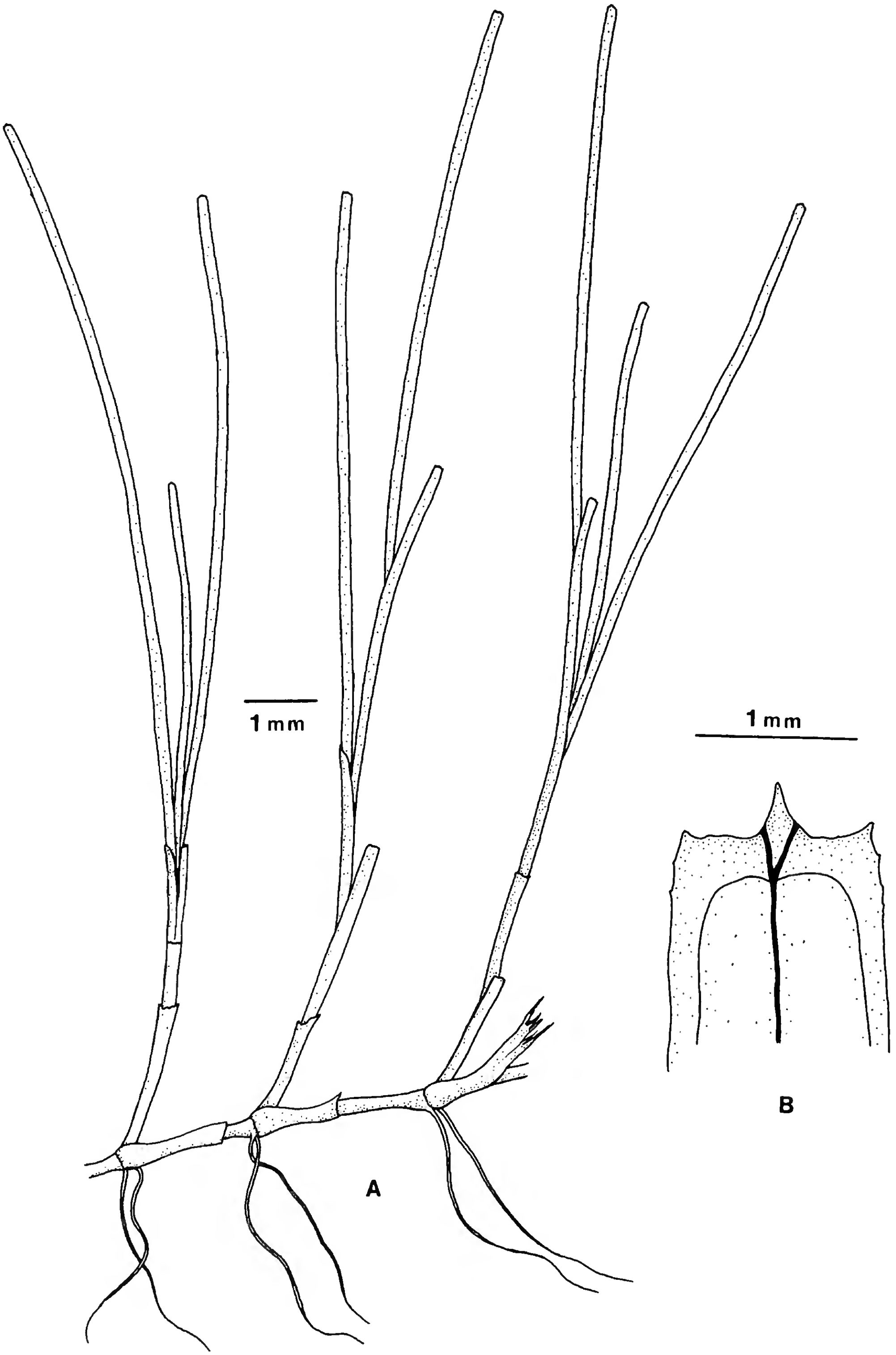

FIGURE 14.—*Zostera mucronata:* A, habit of plant; B, leaf tip.

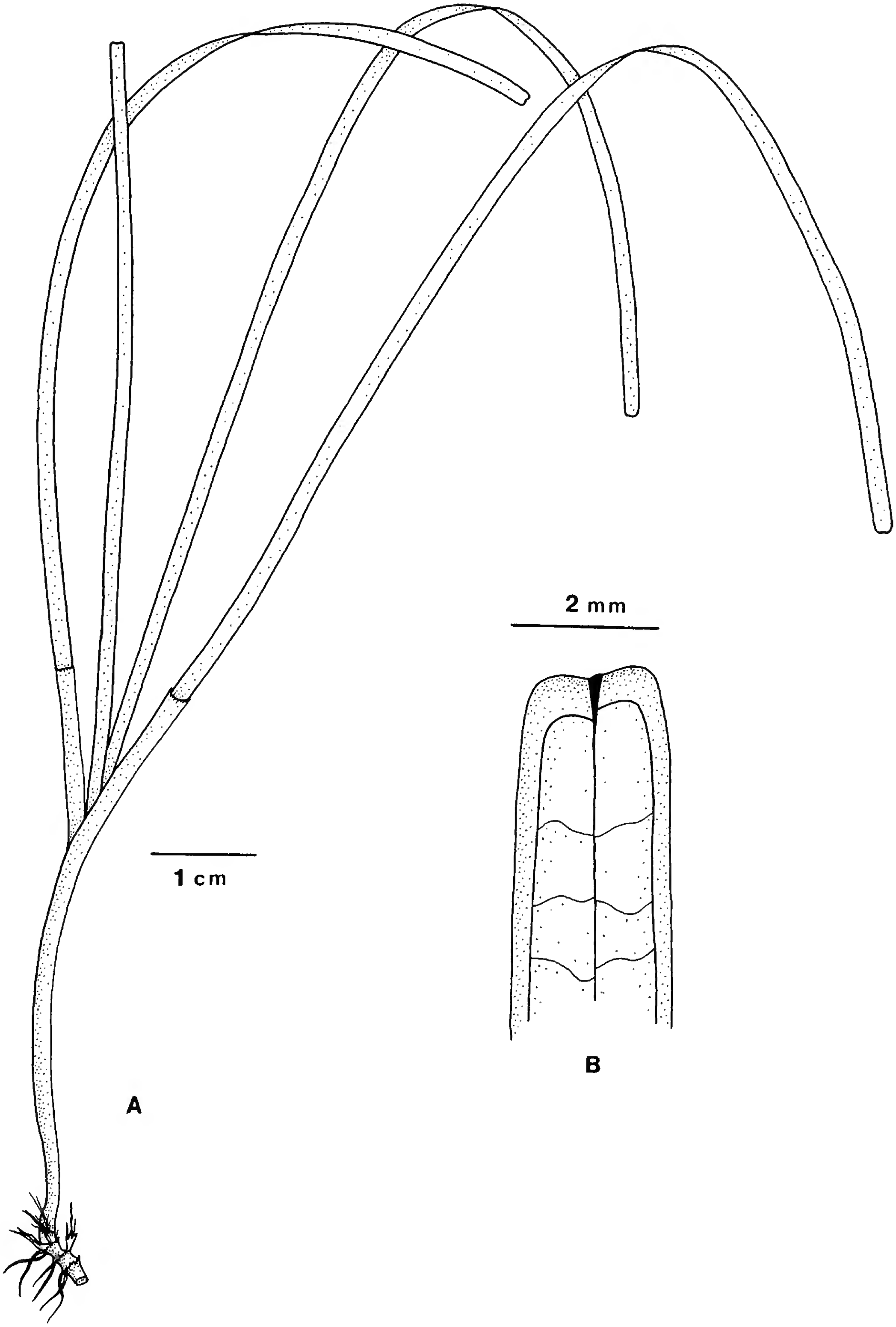

FIGURE 15.—*Zostera muelleri:* A, habit of plant; B, leaf tip.

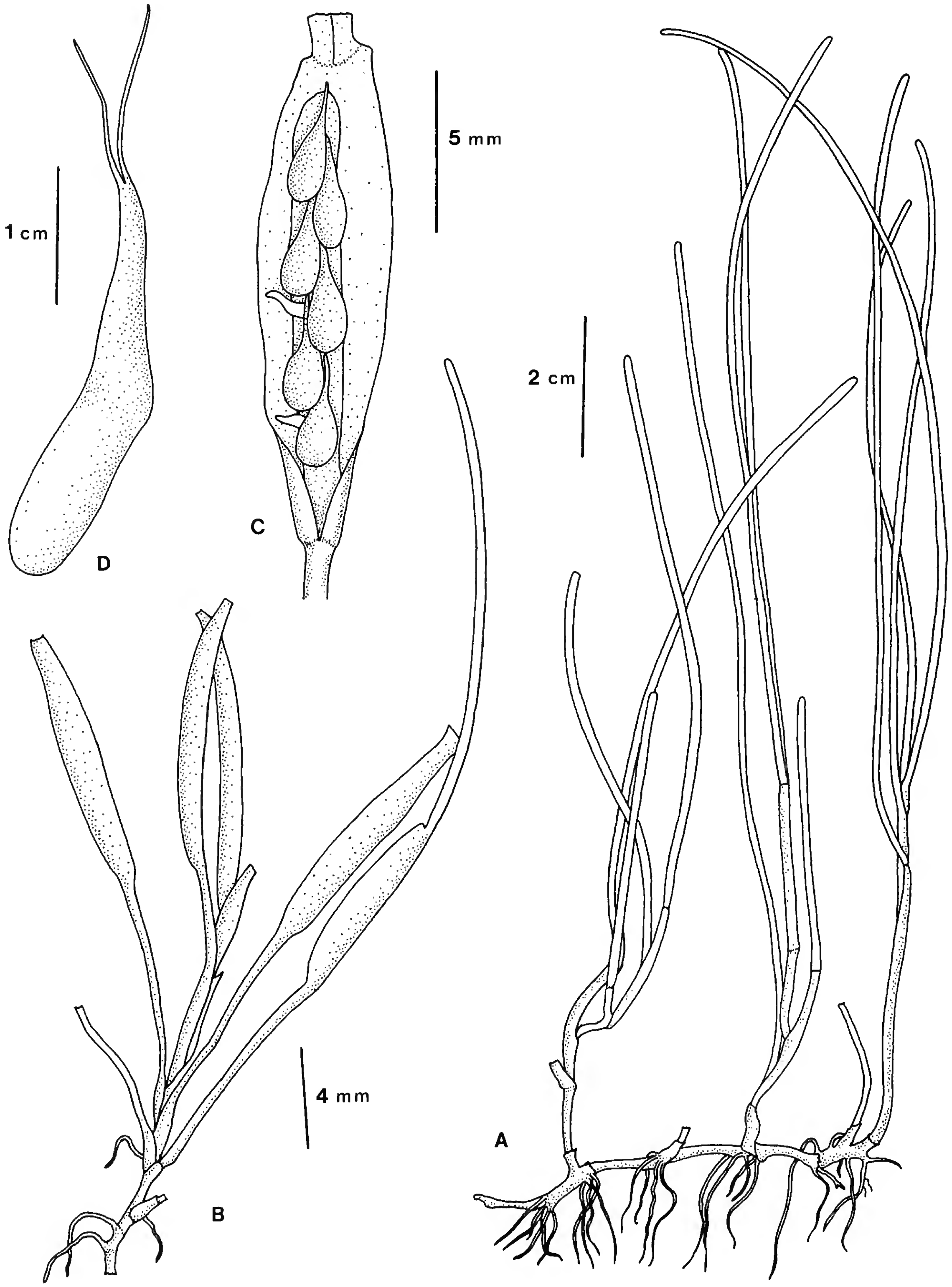

FIGURE 16.—*Zostera noltii:* A, habit of plant; B, fertile plant with spadices; C, spadix; D, female flower.

Phyllospadix iwatensis Makino

FIGURE 17

CHARACTERISTICS.—Rhizome internodes each with 2 roots; older part of rhizome covered with pale reddish brown fibers which may be 10 cm long; internodes 4–5 mm long. Leaf sheath up to 25 cm long. Leaf blade 1–1.5 m long and 1.15–4.5 mm wide; veins 5; tip obtuse, sometimes slightly emarginate. Reproductive shoot with one spathe. Spathal sheath 1.75–5.5 cm long and 6–8 mm wide. Spadix linear-lanceolate. Male spadix with 8–9 flowers; retinacula obliquely ovate to lanceolate, apex acute. Female spadix with 8–12 flowers; retinacula linear-lanceolate, apex acute. Fruit 2.25–3 mm long, 4–5 mm wide.

NATURAL HISTORY.—The species occurs on exposed coastlines but also in moderately sheltered locations. Plants may grow from low water to 8 m deep.

DISTRIBUTION.—Plants occur from northern Japan and from the Sakhalin and the Kuriles to the east and west coasts of Korea and on the Shantung coast of China. The northern limit of distribution coincides with the 0°C February isotherm, while the southern limit is the 11°C February isotherm (Map 10).

Phyllospadix japonicus Makino

FIGURE 18

CHARACTERISTICS.—Rhizome internodes each with 2 roots; older part of rhizome covered with black fibers which may be 4–5 cm long. Leaf sheath 4–20 cm long. Leaf blade 0.25–1 m long and 1–2.5 mm wide; veins 3; tip obtuse, slightly emarginate. Reproductive shoot with one spathe. Spathal sheath 3–4.5 cm long and 5–6 mm wide. Spadix linear-lanceolate. Retinacula on male spadix ovate-lanceolate, apex acute. Female spadix with 8–11 flowers; retinacula linear-lanceolate, apex acute. Fruit 2–2.5 mm long, 4–5 mm wide.

NATURAL HISTORY.—The species occurs on high energy coasts from low water to 10 m depth.

DISTRIBUTION.—Plants are found along southeast Honshu and from the west coast of Honshu from Sado Island southward. The northern limit of distribution coincides with the 10°C February isotherm (24°C August isotherm), while the southern limit is the 15°C February isotherm (27°C August isotherm).

Phyllospadix scouleri Hooker

FIGURE 19

CHARACTERISTICS.—Rhizome internodes each with 2 groups of 3–5 roots; older part of rhizome covered with pale yellow to grey fibers which may be 2–5 cm long; internodes predominantly 2–5 mm long and 6–7 mm wide. Leaf sheath 4–30 cm long. Leaf blade 0.5–2 m long and 1–4 mm wide; veins 3; tip obtuse, sometimes slightly truncate or centrally indented. Reproductive shoot predominantly 1–5 cm long with mostly one spathe. Spathal sheath 28–70 mm long and 2–6 mm wide. Spadix linear-lanceolate. Male spadix with generally 20 flowers; retinacula broadly ligulate, apex obtuse. Female spadix with 14–26 flowers; retinacula linear to ligulate, apex obtuse, less often acute or truncate. Fruit 4–5 mm long, 5 mm wide.

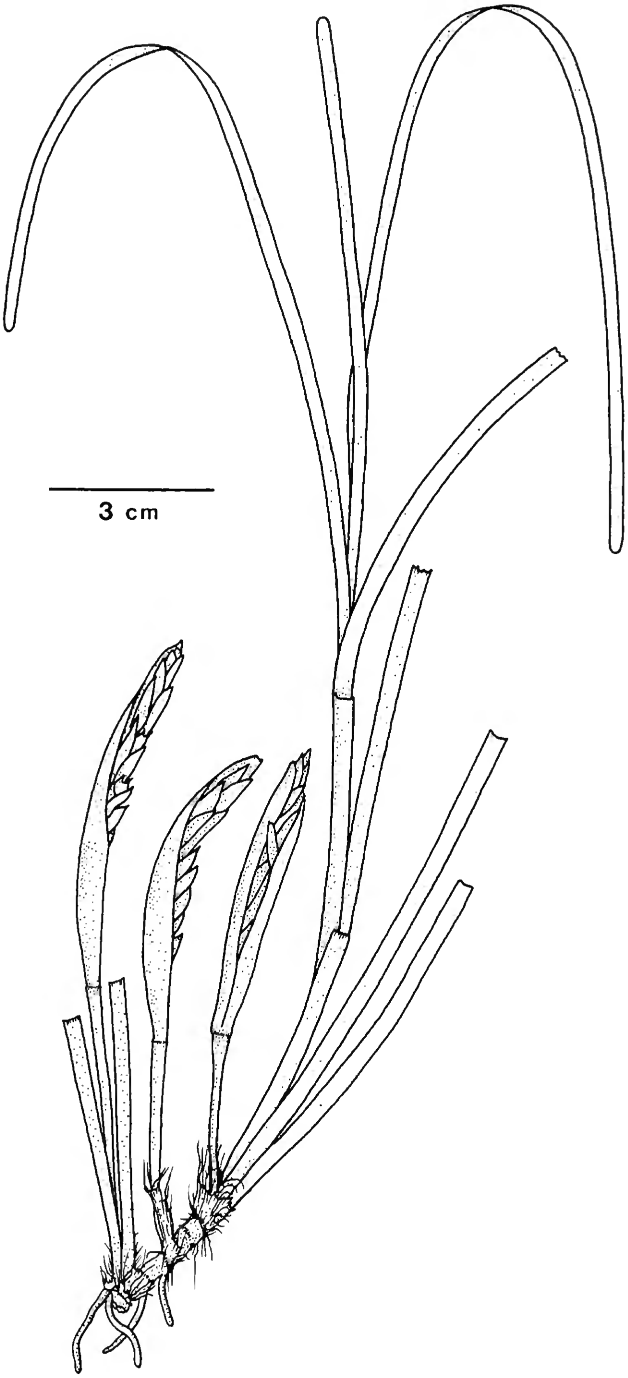

FIGURE 17.—*Phyllospadix iwatensis:* habit of plant.

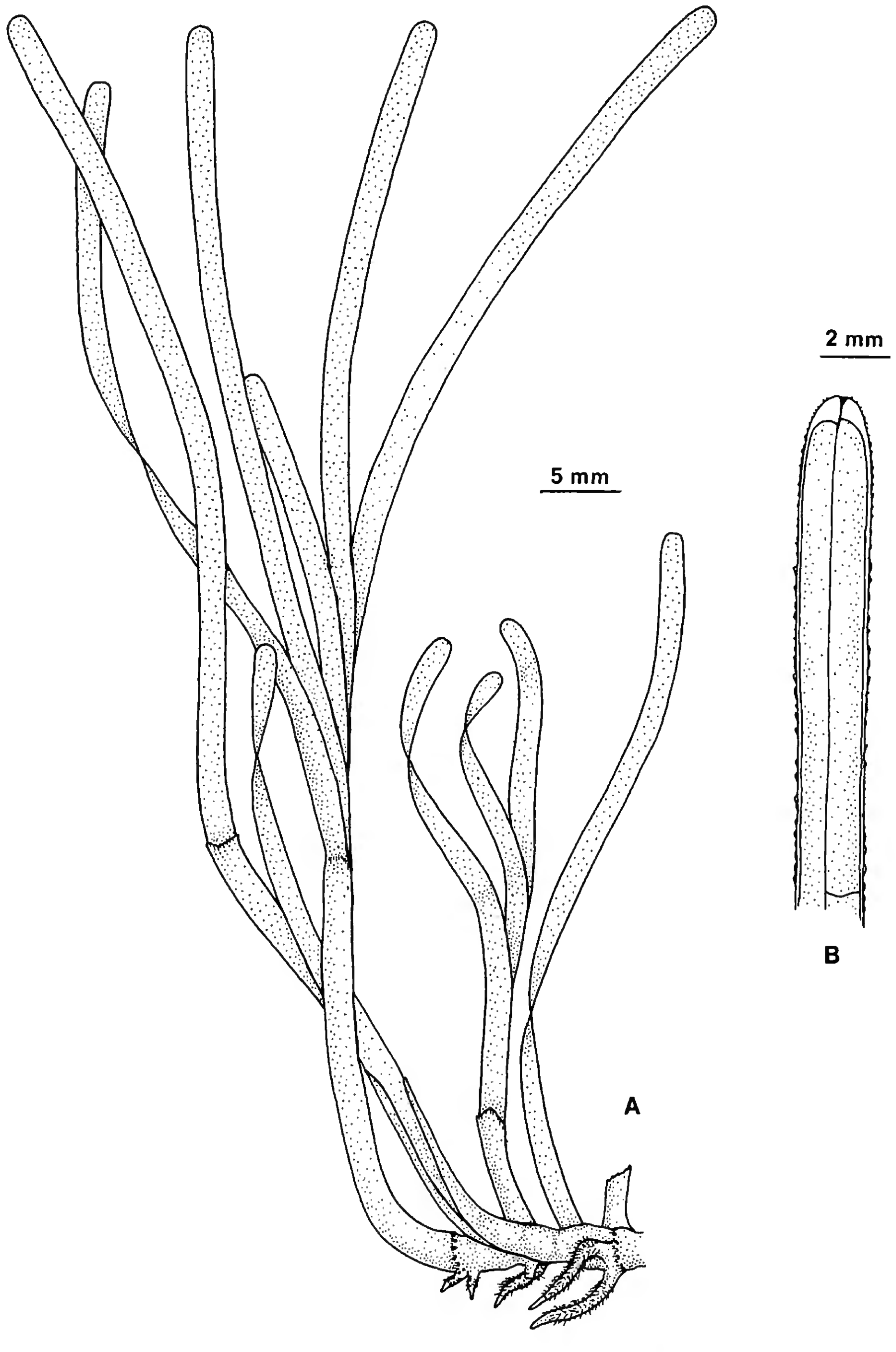

FIGURE 18.—*Phyllospadix japonicus:* A, habit of plant; B, leaf tip.

NATURAL HISTORY.—The species is distributed from the lower intertidal zone to the shallow subtidal on surf-beaten coasts. It can withstand extremely high energy wave action.

DISTRIBUTION.—Plants occur from Sitka, Alaska, south to the Tropic of Cancer on Baja California. The species is particularly abundant north of Monterey, California (Map 11).

Phyllospadix serrulatus Ruprecht ex Ascherson

FIGURE 20

CHARACTERISTICS.—Rhizome internodes each with 2 roots; older part of rhizome covered with yellowish brown fibers; internodes 3–10 mm long. Leaf sheath 3.5–18 cm long. Leaf

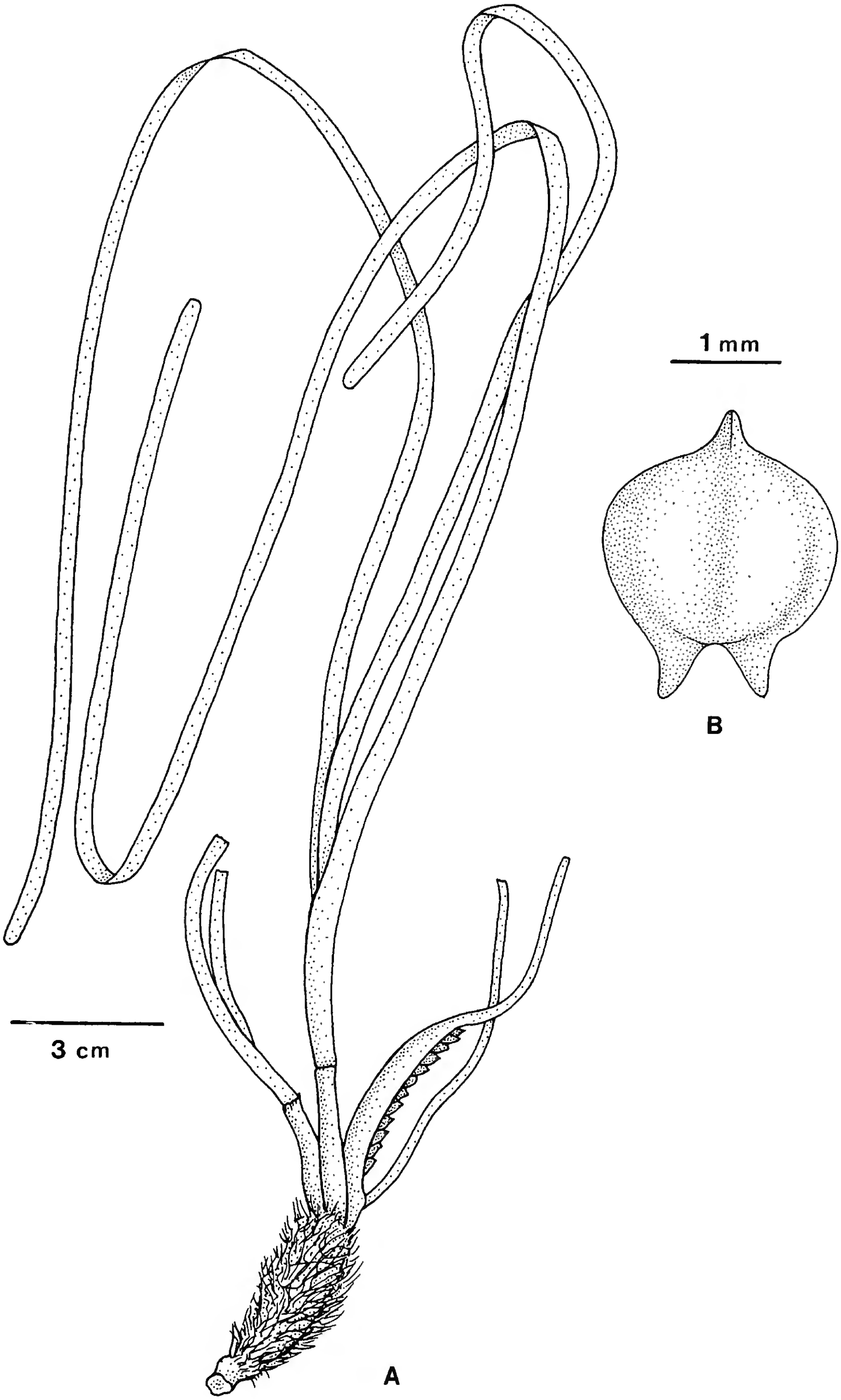

FIGURE 19.—*Phyllospadix scouleri:* A, habit of plant; B, fruit.

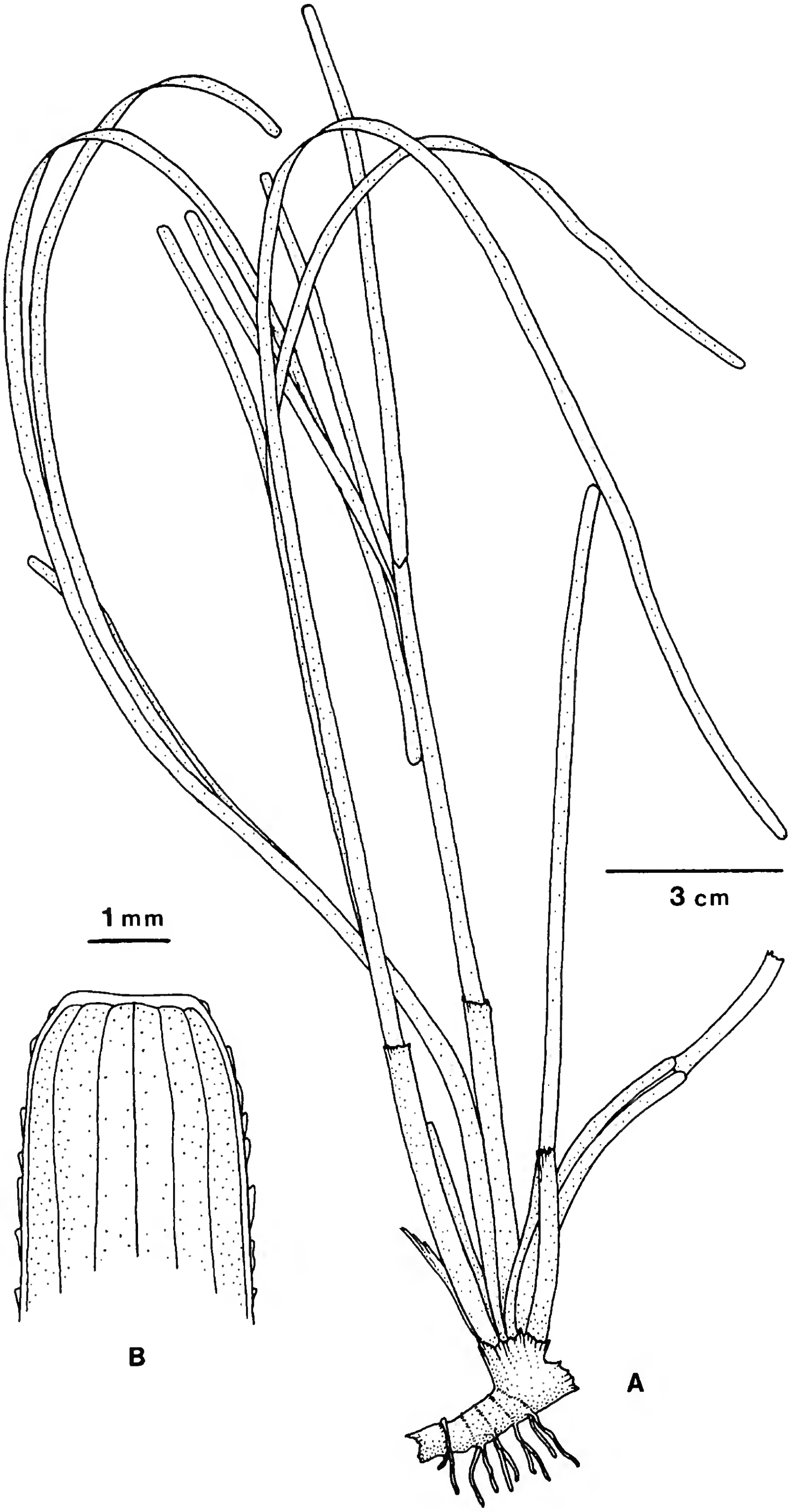

FIGURE 20.—*Phyllospadix serrulatus*: A, habit of plant; B, leaf tip.

blade up to 1 m long and 2.0–8.3 mm wide; veins 5–7; tip truncate. Reproductive shoot with one spathe. Spathal sheath 4 cm long and 5 mm wide. Female spadix linear-lanceolate with 8–10 flowers; retinacula linear-lanceolate, apex obtuse, truncate or retuse.

NATURAL HISTORY.—The species grows in Washington from +1.5 m to mean lower low water, but was once found in a large subtidal meadow from −1.5 m to −6 m deep. Plants occur on rocks on surf-beaten coasts but seem to avoid the most exposed sites. The plants in the subtidal meadow occurred on a muddy sediment. Where the 3 species co-occur, *P. serrulatus* is at a level higher than the other two species.

DISTRIBUTION.—Plants are found from Cape Arago, southern Oregon, to the Chirikof Islands, southwest of Kodiak Island, in the Gulf of Alaska (Phillips, 1979; Map 12).

Phyllospadix torreyi S. Watson

FIGURE 21

CHARACTERISTICS.—Rhizome internodes each with 2 groups of 3–5 roots; older part of rhizome covered with pale yellow to grey fibers which may be 2–5 cm long; internodes 7–10 mm long and 5 mm wide. Leaf sheath 7–55 cm long. Leaf blade 0.5–2 m long and 0.5–1.5 mm wide; veins 3; tip obtuse, slightly emarginate. Reproductive shoot 50–60 cm long, branched; each of the upper 2–4 nodes bears 1–4 pedunculate spathes; spathes arranged in a pseudo-whorl or rarely in a distinct rhipidium. Spathal sheath 15–65 mm long and 2–4 mm wide. Spadix linear-lanceolate. Male spadix with 14–20 flowers; retinacula broadly lingulate, obtuse. Female spadix with 14–20 flowers; retinacula long elliptic to spatulate. Fruit 3 mm long and 3 mm wide. Seed ovoid, 3 mm long; testa brown.

NATURAL HISTORY.—The species occurs on surf-beaten rocky coasts but seems to avoid the most exposed sites. It grows from the lower intertidal down to about 15 m deep (reported by Dawson, Neushul and Wildman, 1960, in California). Where *P. torreyi*, *P. scouleri*, and *P. serrulatus* occur on the same reef, *P. torreyi* grows at a level lower than the other two.

DISTRIBUTION.—Plants occur from the north tip of Vancouver Island south to the Tropic of Cancer on Baja California. The species is particularly abundant south of Monterey, California (Map 13).

Genus *Heterozostera*

Heterozostera tasmanica (Martens ex Ascherson) den Hartog

FIGURE 22

CHARACTERISTICS.—Rhizome 0.75–1.5 mm wide, with 2 roots at each node; internodes 5–45 mm long. Erect stems arise at irregular intervals, 20–30 cm long, red, purplish, or black; with a cluster of 7–10 leaves at the top which is shed in autumn. Leaf sheath 1–4 cm long, 1 mm wide. Leaf blade 5–25 cm long, 1–2.5 mm wide; veins 3; tip obtuse with a central triangular notch. Reproductive shoot 15–25 cm long with up to 20 spathes. Spathal sheath 12–25 mm long, 3.5–4 mm wide. Spadix lanceolate or spathulate with 3–6 female flowers and 3–6 male flowers; retinacula linear-lanceolate. Fruit ovoid to ellipsoid, 3–4 mm long, 2 mm wide; pericarp reddish brown. Seed with a testa with longitudinal ribs.

NATURAL HISTORY.—The species occurs slightly above mean low water spring tide to the shallow subtidal in sheltered locations.

DISTRIBUTION.— Plants are found from Western Australia to Jervis Bay in New South Wales, Australia. The species is found in Tasmania and at Coquimbo, Chile (Map 14).

Genus *Posidonia*

Recently, Kuo and Cambridge (1984) described four more new species of *Posidonia* in Australia, using characters of leaf morphology and anatomy as primary determinants. Leaf width was a secondary emphasis, but they acknowledged that widths overlapped among the 4 species. As a conservative measure, we do not recognize these 4 new species in this treatment, in the belief that to be useful, taxonomy should include macroscopic as well as microscopic characters that can be recognized in the field.

Key to Species of *Posidonia*

1. Leaf sheath bicuspidate with a bow-shaped, short ligula; higher bracts of inflorescence with blades larger than or as large as their sheath; testa without a membranous ventral wing . . . . ***P. oceanica***
   Leaf sheath auriculate with a well-developed ligule; higher bracts of inflorescence with blades as large as or shorter than their sheath; testa with a membranous ventral wing 2
2. Leaves 1–3.5 (–5) mm wide, with predominantly 5–7 veins . . . . . ***P. ostenfeldii***
   Leaves wider, veins more 3
3. Leaf sheaths brown and remaining membranaceous when old, splitting into strips when dry . . . . ***P. sinuosa***
   Leaf sheaths disintegrating into pale fibers with age 4
4. Leaves narrow, 4–7 mm wide, with 7–11 veins . . . . ***P. angustifolia***
   Leaves broad, (6–) 10–15 (–20) mm wide with 14–21 veins . . . . . . ***P. australis***

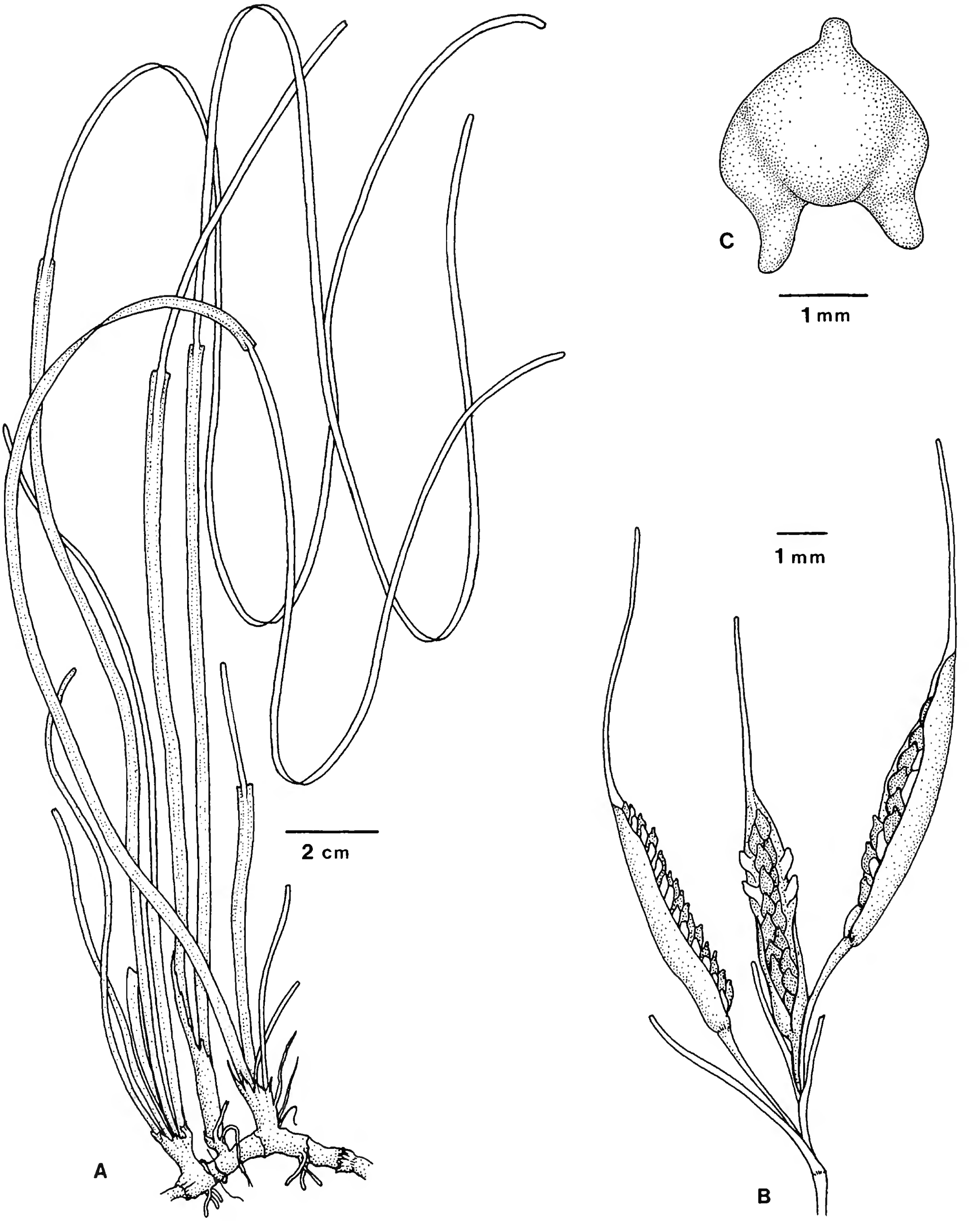

FIGURE 21.—*Phyllospadix torreyi:* A, habit of plant; B, fertile plant showing spadices; C, fruit.

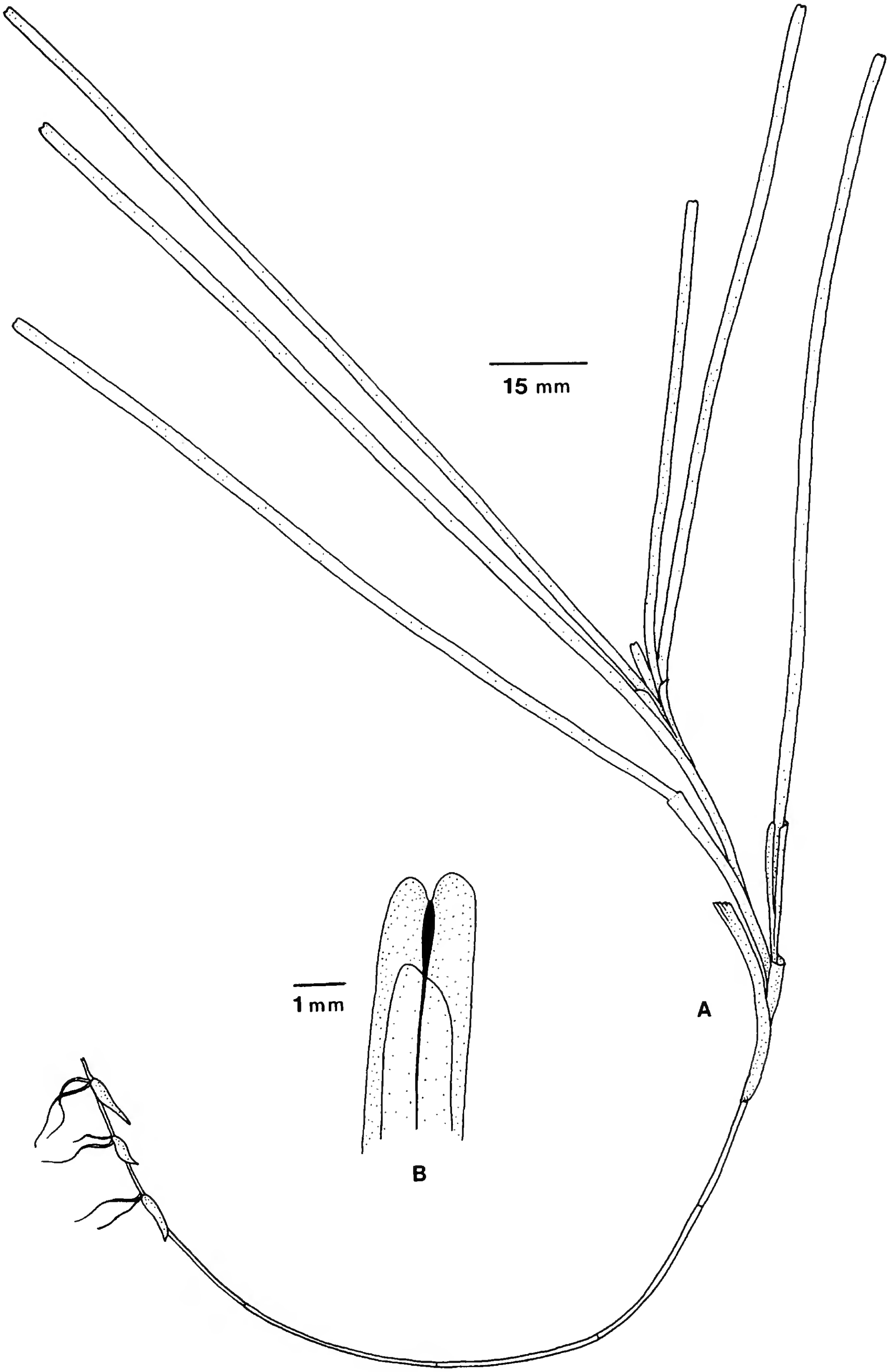

FIGURE 22.—*Heterozostera tasmanica:* A, habit of plant; B, leaf tip.

Posidonia angustifolia Cambridge and Kuo

FIGURE 23

CHARACTERISTICS.—Rhizome 4–6 mm wide; internodes 1–60 mm long. Leaf sheath 5–12 cm long, 4–6 mm wide, shallowly semi-lunar, auricles 2 mm long; disintegrating to fine straw-like fibers. Leaf blade (10–) 20–75 cm long, 4–6 mm wide; 7–11 veins; tip obtuse. Inflorescence 10–15 cm long; spikes 2–4, each consisting of 3–4 (–6) hermaphroditic flowers. Stamens 3. Fruit 2.5 cm long, 1–1.2 cm wide.

NATURAL HISTORY.—Plants are found on open nearshore habitats from 2–35 m deep.

DISTRIBUTION.—The species occurs from Houtmans Abrolhos, Western Australia, to St. Vincent Gulf, South Australia.

Posidonia australis Hooker

FIGURE 24

CHARACTERISTICS.—Rhizome 5–8 mm wide; roots 7–20 (–32) cm long, 1–2 mm wide, richly branched; internodes 5–10 (–48) mm long. Leaf sheath 6–12 (–19) cm long, 9–12 (–15) mm wide; biauriculate; when old torn into longitudinal pieces and finally into bundles of straw-like fibers. Leaf blade 30–60 cm long, 6–20 mm wide; 11–21 veins; tip obtuse or truncate. Inflorescence 5–12 cm long; spikes 2–7, each consisting of 3–6 hermaphroditic flowers. Stamens 3. Fruit 15–30 mm long; oblong–ellipsoid, often acuminate, falcate. Seed up to 20 mm long.

NATURAL HISTORY.—Plants occur in sheltered bays from low tide to 10 m deep. They are tolerant to salinity fluctuations from dilute to hyperhaline conditions.

DISTRIBUTION.—The species is widely distributed in Australia from Shark Bay in Western Australia to Macquarie on the east coast. It also occurs in Tasmania (Map 15).

Posidonia oceanica (Linnaeus) Delile

FIGURE 25

CHARACTERISTICS.—Rhizome up to 1 cm wide; roots up to 15 cm long and 4 mm wide, richly branched; internodes 1–10 mm long. Leaf sheath 3–5 cm long and 10–12 mm wide, bicuspidate and without auricles; when old torn into longitudinal pieces which persist as bundles of stiff fibers, giving the base of the shoot the appearance of a shaving brush. Leaf blade 40–50 cm long, 5–9 mm wide; 13–17 veins; tip obtuse to emarginate. Inflorescence 2.5–4.5 cm long; spikes 1–4, each consisting of 3 (–5) hermaphroditic flowers. Stamens 3. Fruit about 10 mm long, ovoid.

NATURAL HISTORY.—Plants grow along exposed to moderately sheltered localities on open coasts and at heads of bays. The optimum substrate is a rather coarse sand with good water circulation. The species occurs from low water down to 40 m deep. Plants are not tolerant of salinity or temperature fluctuations, and do not occur in anoxic water. Leaves show a high mortality at water temperatures above 20°–22°C, and plants are not found where temperatures fall below 10°C.

DISTRIBUTION.—Plants are widely distributed in the Mediterranean (Map 16).

Posidonia ostenfeldii den Hartog

FIGURE 26

CHARACTERISTICS.—Rhizome 1–4 mm wide; internodes with 2 long ones (2–8.5 cm) alternating with 1–4 short ones (0.1–0.5 cm). Leaf sheath 4–20 cm long, 2–5 mm wide, biauriculate; when old torn into longitudinal pieces that persist as bundles of entangled, very fine fibers. Leaf blade 40–100 cm long, 1–3.5 (–5) mm wide; 5–9 veins; tip obtuse. Inflorescence 5–10 cm long; spikes 6–14, each consisting of 3–5 hermaphroditic flowers. Stamens 3. Fruit 16–26 mm long, falcate, acuminate. Seed up to 20 mm long.

NATURAL HISTORY.—Plants occur on sand platforms in high energy locations (Cambridge and Kuo, 1979).

DISTRIBUTION.—The species occurs from Carnarvon, Western Australia, to Beachport, South Australia (Map 17).

Posidonia sinuosa Cambridge and Kuo

FIGURE 27

CHARACTERISTICS.—Rhizome 5–8 mm wide; roots 7–20 (–40) cm long, 0.1–2 mm wide, richly branched; internodes 1–50 mm long. Leaf sheath 6–12 cm long, 4–11 mm wide, biauriculate; remains membranaceous when old. Leaf blade (2–) 30–70 (–120) cm long, 4–11 mm wide; 8–13 veins; tip obtuse, emarginate or truncate. Inflorescence generally 10 cm long; spikes 2–4, each consisting of 3–4 (–6) hermaphroditic flowers. Stamens 3. Fruit up to 20 mm long; lanceolate.

NATURAL HISTORY.—Plants are found in embayments and coastal areas from low water to 15 m deep.

DISTRIBUTION.—The species occurs from Shark Bay, Western Australia, to Kingston, South Australia.

Genus *Halodule*

Den Hartog (1964, 1970) used leaf tip characteristics to separate species. Field work done by Phillips (1967) in Florida indicated that leaf tips varied from bicuspidate to tridentate on shoots on the same rhizome.

Field collection and culture of *Halodule* from diverse locations throughout the Indo-Pacific resulted in plants with leaf tips ranging from bicuspidate to tridentate (McMillan, 1983a; McMillan, Williams, Escobar, and Zapata, 1981). Isozyme analyses of diverse collections of *Halodule* throughout the western tropical Atlantic, some with bicuspidate and some with tridentate leaf tips, showed uniform patterns. The same was true for plants from diverse locations throughout the Indo-Pacific. McMillan (1983a) found that genetic differences exist between the species of the two ocean systems, but there

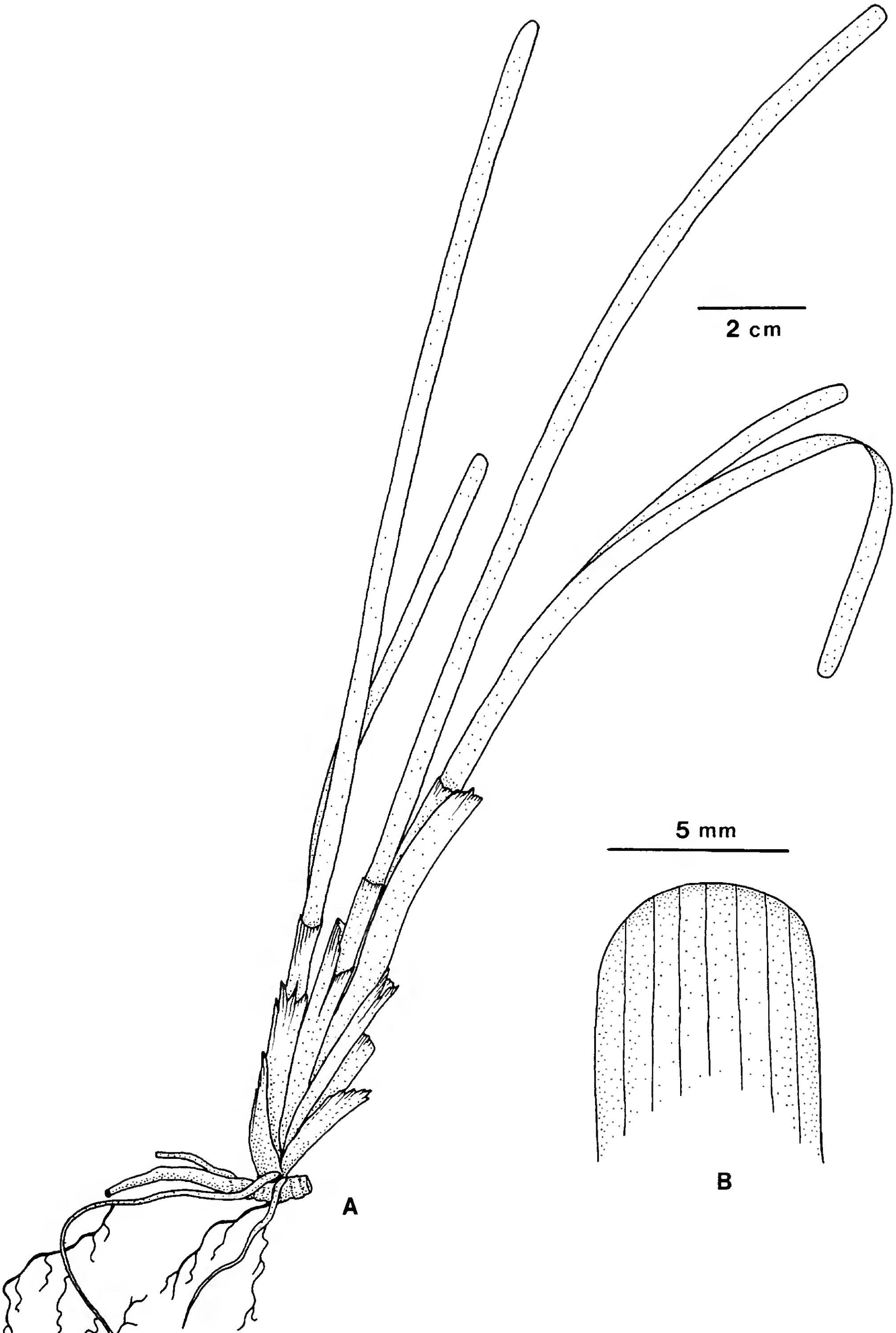

FIGURE 23.—*Posidonia angustifolia:* A, habit of plant; B, leaf tip.

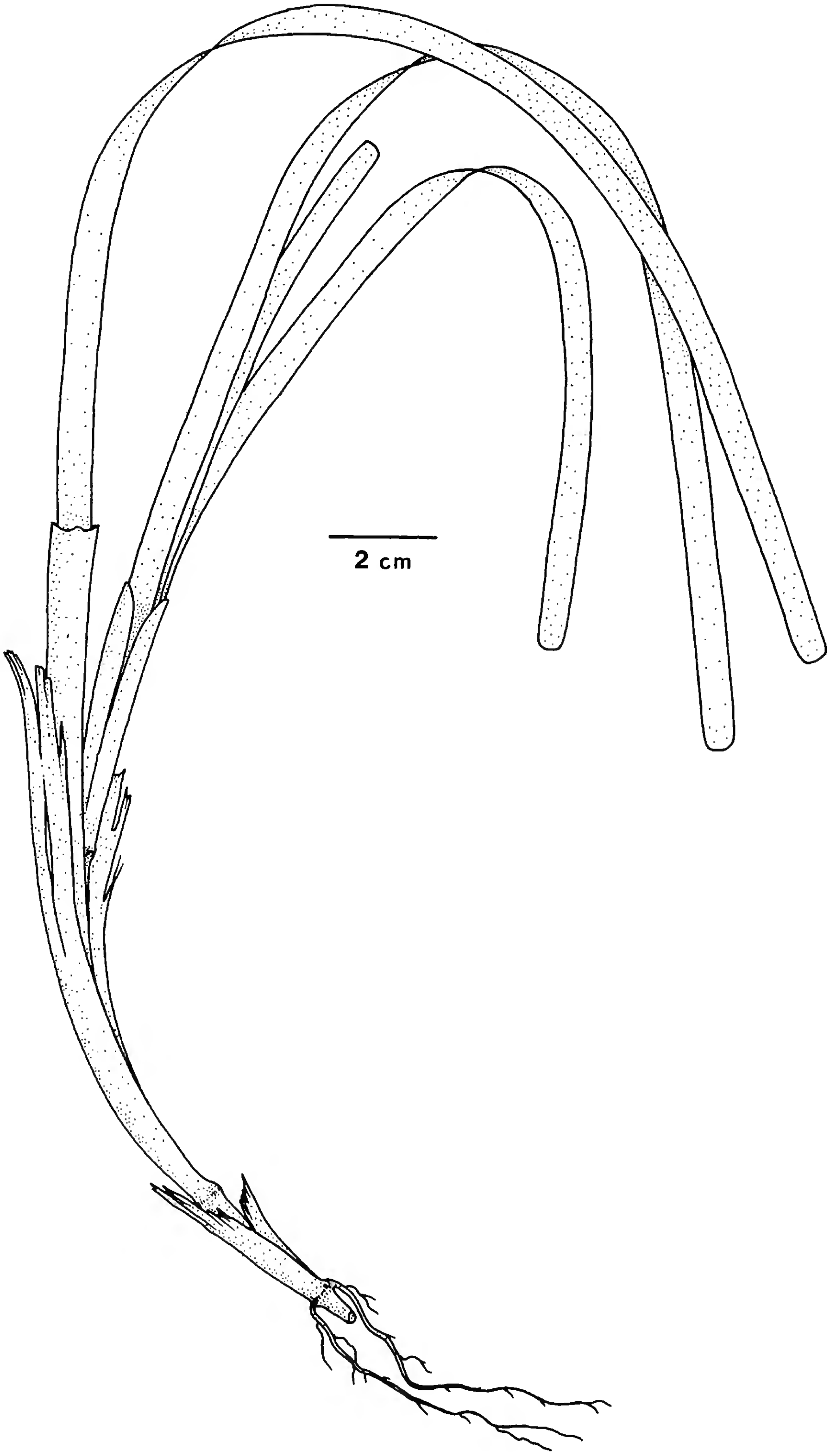

FIGURE 24.—*Posidonia australis:* habit of plant.

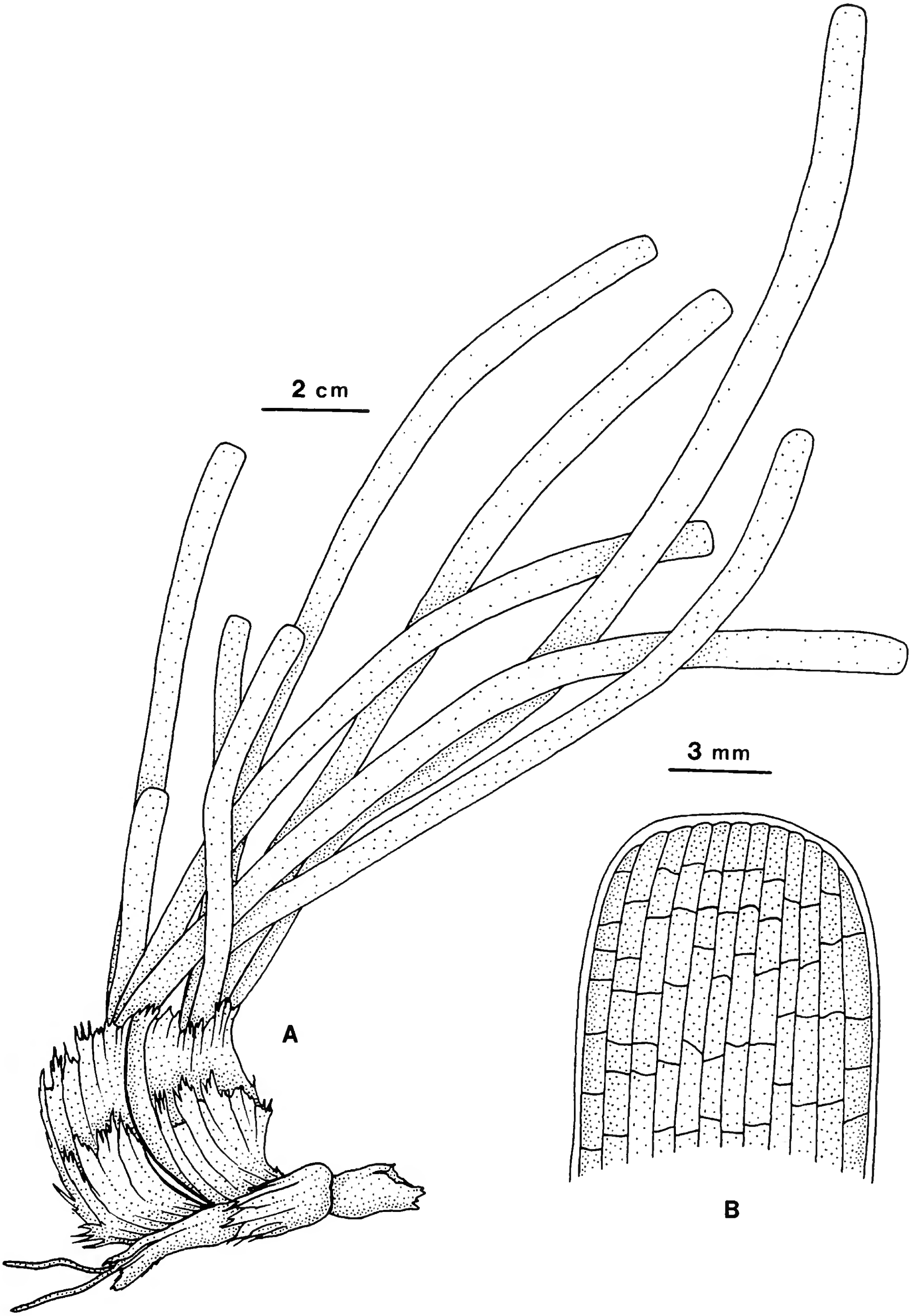

FIGURE 25.—*Posidonia oceanica:* A, habit of plant; B, leaf tip.

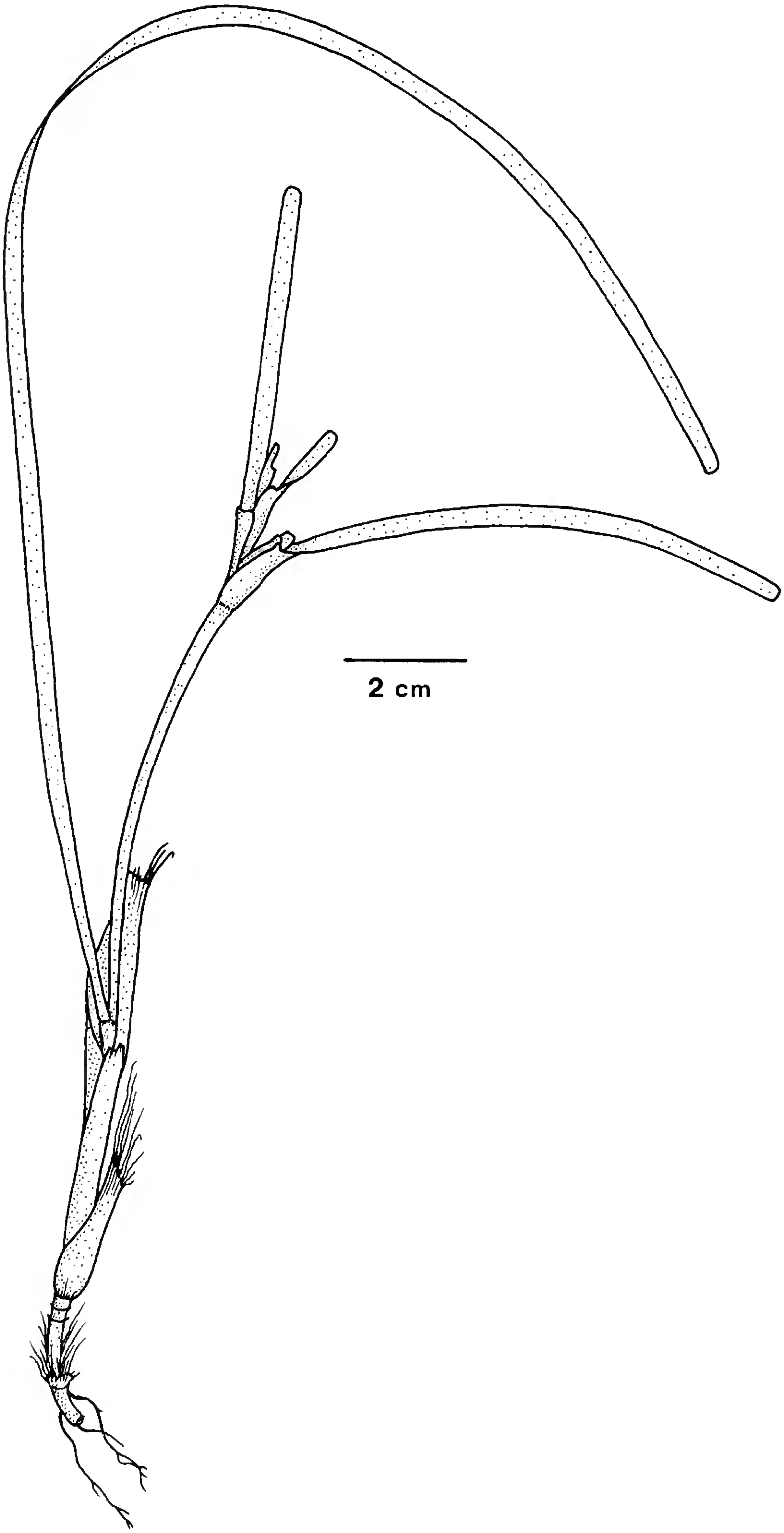

FIGURE 26.—*Posidonia ostenfeldii:* habit of plant.

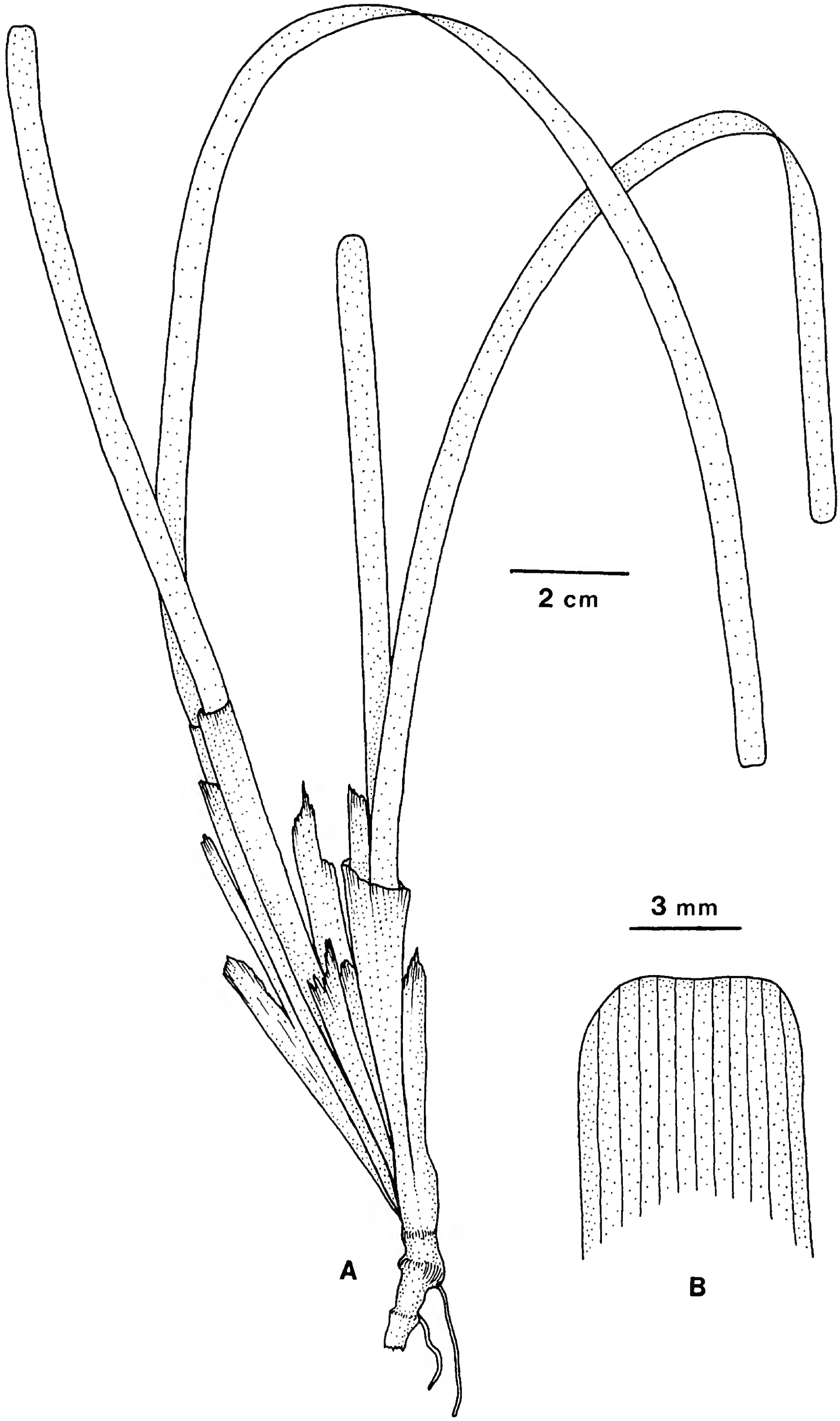

FIGURE 27.—*Posidonia sinuosa:* A, habit of plant; B, leaf tip.

is uniformity among populations of a species in each of the two ocean systems. Thus, we conclude that *Halodule* in the western tropical Atlantic is *H. wrightii,* while that in the Indo-Pacific is *H. uninervis.*

McMillan, Williams, Escobar, and Zapata (1981) concluded on the basis of experimental culture that leaf tips of *Halodule* are environmentally modifiable. McMillan (1983a) suggested that leaf tip variability was related to nutrient availability.

A third species, *H. pinifolia,* in the western tropical Pacific, shows rounded leaf tips that are more or less serrulate. McMillan (pers. comm., 1982) concluded that *H. pinifolia* is a valid species since it retained the apical "teeth" in experimental culture.

Thus, it appears that only three species of *Halodule* can be used with confidence at this time, viz., *H. wrightii* from the western tropical Atlantic (including those plants from the Atlantic coast of Africa) and *H. uninervis* and *H. pinifolia* from the Indo-Pacific. For the latter two species, if leaf tips are bicuspidate or tridentate, the species is *H. uninervis;* if leaf tips are rounded and serrulate, the species is *H. pinifolia.*

Halodule species are highly eurybiontic and form pioneering growths on newly formed or disturbed substrates.

Key to Species of *Halodule*

1. Leaf tip rounded, more or less serrulate . . . . ***H. pinifolia***
   Leaf tip with well-developed "teeth" 2
2. Tips of mature leaves tridentate . . . . ***H. uninervis***
   Tips of mature leaves bidentate . . . . ***H. wrightii***

Halodule pinifolia (Miki) den Hartog

FIGURE 28

CHARACTERISTICS.—Rhizome internodes 1–3 cm long; nodes each with 2–3 roots and a leafy shoot. Leaf sheath 1–4 cm long. Leaf blade 5–20 cm long, 0.6–1.2 mm wide. Male flower on a stalk 1.0 cm long; anthers 2.5–3 mm long. Female flower with an ovoid ovary, 1.0 mm long; style 13 mm long. Fruit ovoid, 2–2.5 mm long.

NATURAL HISTORY.—Plants occur from the lower intertidal to the upper subtidal on sandy and muddy substrates in sheltered bays, on coral platforms, and in high energy locations. Plants may occur in creeks and in mangrove swamps.

DISTRIBUTION.—The species is widely distributed in the western tropical Pacific from Taiwan and the Ryukyu Islands (southern Japan) to Queensland, Australia (Map 18).

Halodule uninervis (Forsskål) Ascherson

FIGURE 29

CHARACTERISTICS.—Rhizome internodes 0.5–4 cm long; nodes each with 1–6 roots and a leafy shoot. Leaf sheath 1–3.5 cm long. Leaf blade 6–15 cm long, 0.25–3.5 mm wide. Male flower on a stalk 6–20 mm long, anthers 2–3 mm long. Female flower with an ovoid ovary, 1.0 mm long; style 28–42 mm long. Fruit 2–2.5 mm × 1.75–2.0 mm.

NATURAL HISTORY.—Plants occur from the intertidal to 30 m deep on firm sand and soft mud in extremely sheltered to exposed locations on coral reefs and in creeks in mangrove swamps.

DISTRIBUTION.—The species is widely distributed throughout the Indo-Pacific from the eastern coast of Africa to the northern Philippines and Queensland, Australia (Map 19).

Halodule wrightii Ascherson

FIGURE 30

CHARACTERISTICS.—Rhizome internodes 0.75–3.5 cm long; nodes each with 2–5 roots and a leafy shoot. Leaf sheath 1.5–4 cm long. Leaf blade 3.5–32 cm long, 0.3–2.2 mm wide. Male flower on a stalk 12.5–23 mm long, anthers 3.5–5 mm long. Female flower with a globose to ellipsoid ovary, 1.5–2 mm long; style 10–28 mm long. Fruit ovoid or globose, 1.5–2 mm long.

NATURAL HISTORY.—Plants are widely distributed in the lower intertidal and upper subtidal zones on sandy and muddy substrates in sheltered as well as exposed locations. Plants may also occur on coral reefs and in creeks in mangrove swamps. In places populations are found from 8–12 m deep.

DISTRIBUTION.—The species is found throughout the western tropical Atlantic and from the Atlantic coast of Africa (Map 20).

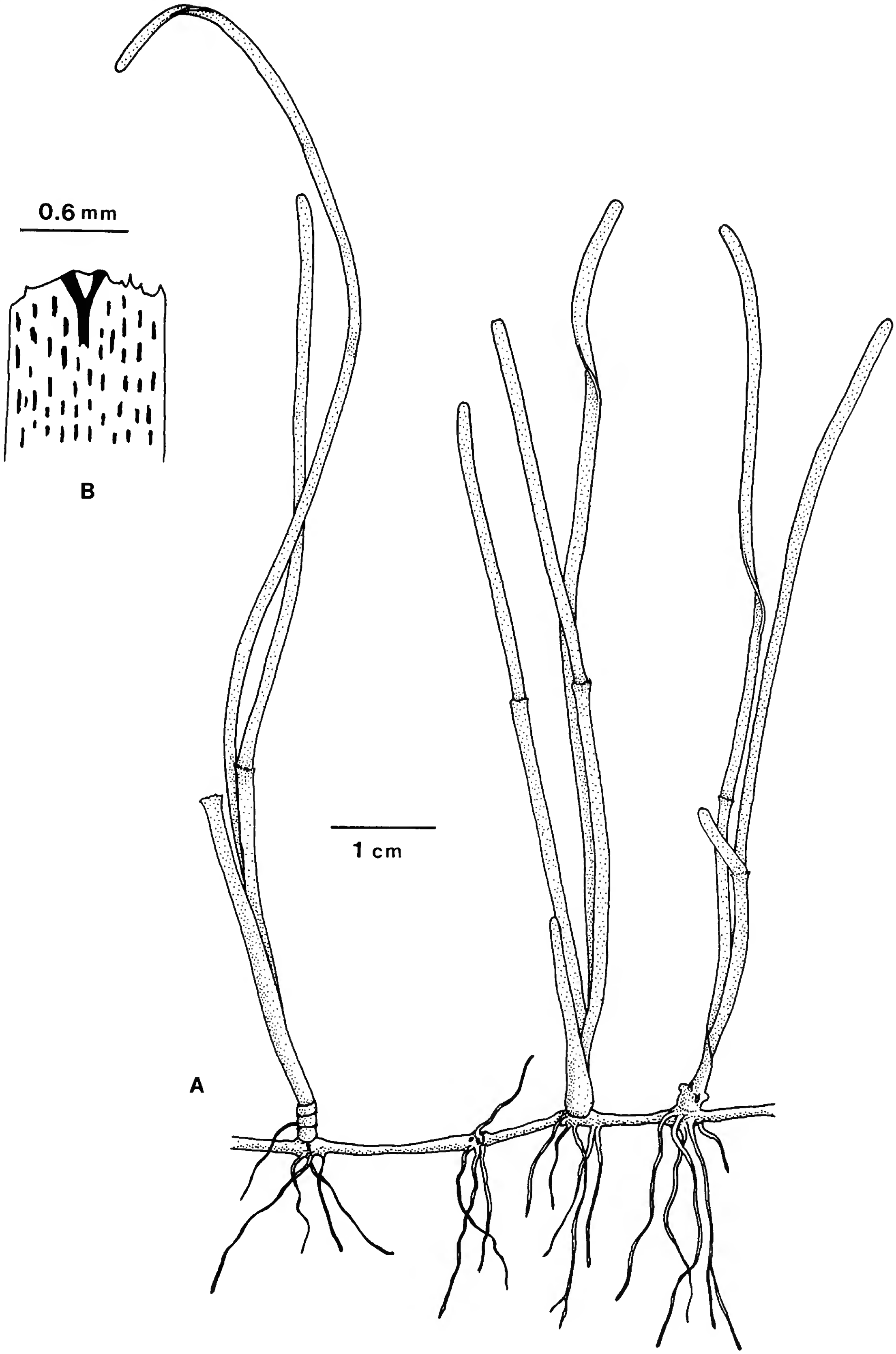

FIGURE 28.—*Halodule pinifolia:* A, habit of plant; B, leaf tip.

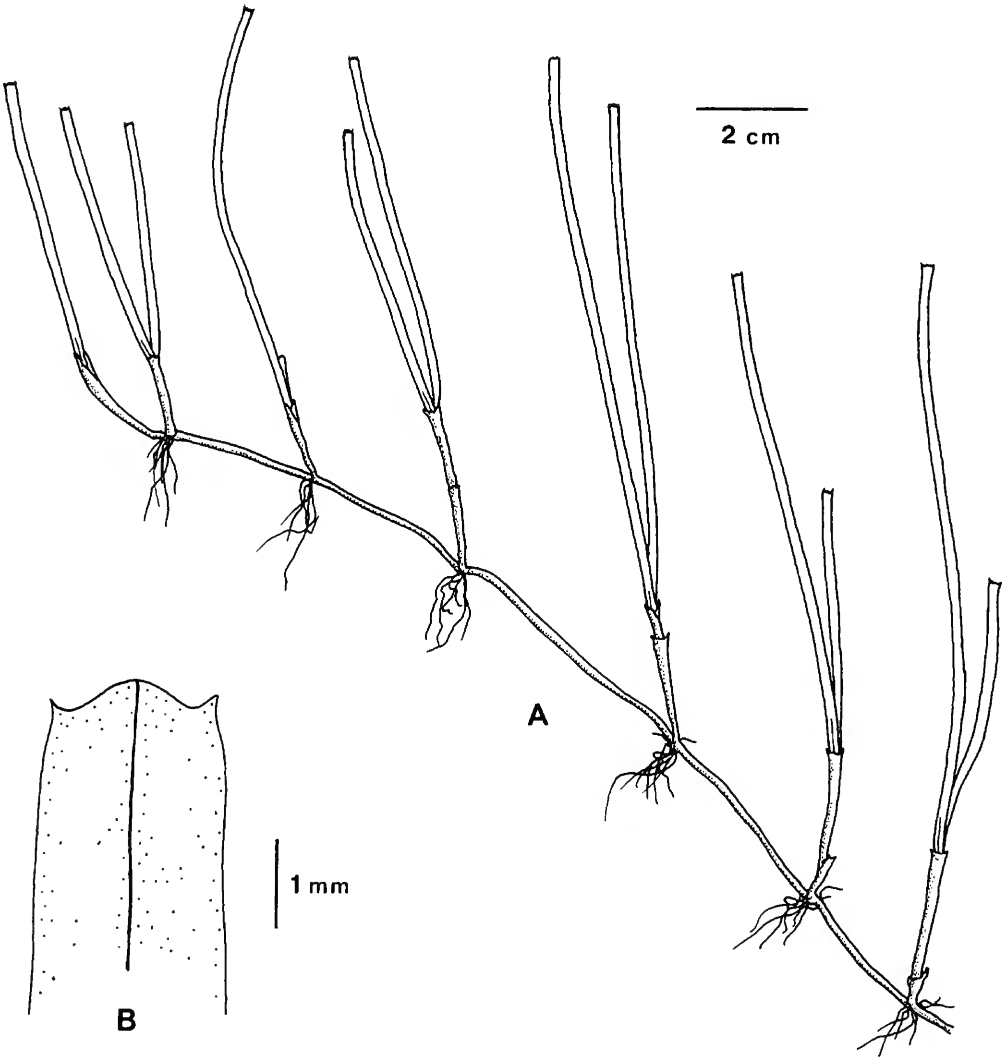

FIGURE 29.—*Halodule uninervis:* A, habit of plant; B, leaf tip.

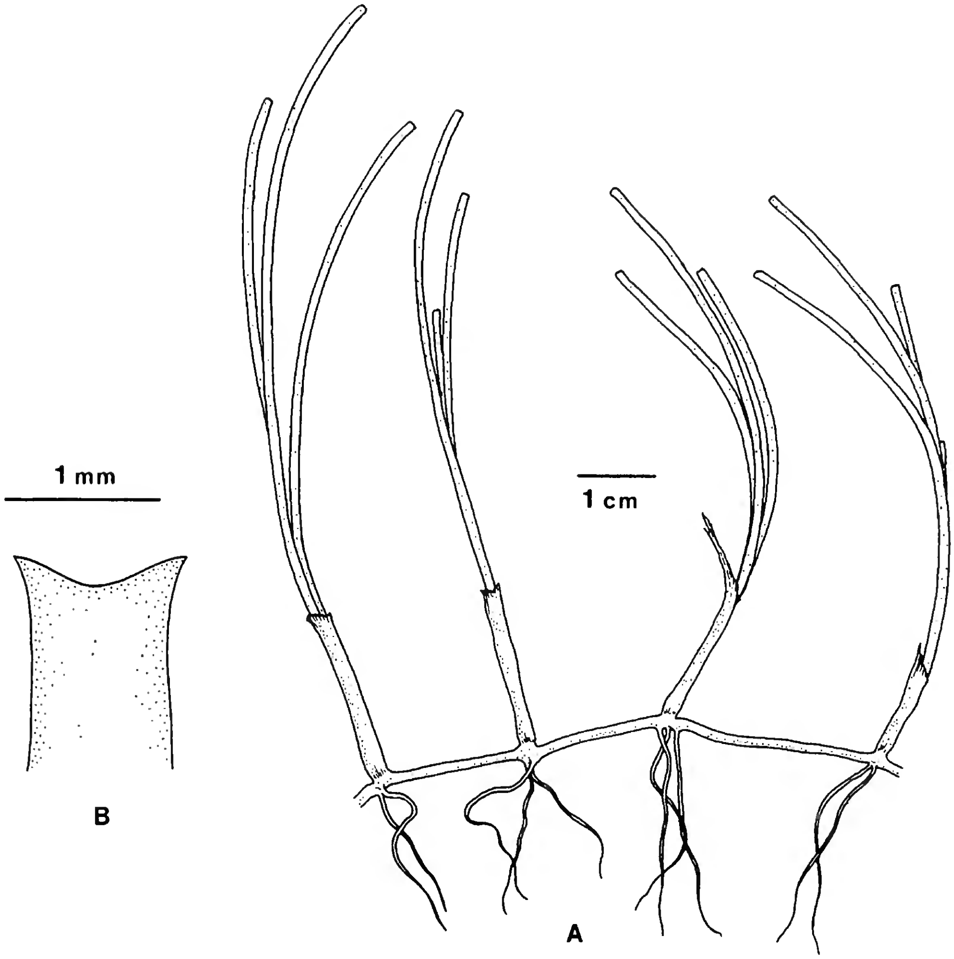

FIGURE 30.—*Halodule wrightii:* A, habit of plant; B, leaf tip.

Genus *Cymodocea*

Key to Species of *Cymodocea*

1. Leaf scars closed 2
   Leaf scars open 3
2. 7–9 veins in leaf; old sheaths entire when shed; fruit with smooth dorsal ridges . . . . *C. nodosa*
   9–15 veins; old sheaths forming a scarious mass at the base of each shoot; fruit with dentate dorsal ridges . . . . *C. rotundata*
3. 13–17 veins; leaves 4–9 mm wide . . . . *C. serrulata*
   9–13 veins; leaves 3–6 mm wide . . . . *C. angustata*

Cymodocea angustata Ostenfeld

FIGURE 31

CHARACTERISTICS.—Rhizome internodes 1.5–2 cm long; nodes each with 1 root and a leafy shoot. Leaf sheath 3–4 cm long and 4–6 mm wide. Leaf blade 15–20 cm long, 3–6 mm wide; 9–13 veins. Male flower unknown. Female flower with an ovoid ovary, 2.5 mm long, style short and 2 very long stigmas. Fruit subcircular, compressed, at least 6 mm long.

NATURAL HISTORY.—Plants have only been found washed ashore.

DISTRIBUTION.—The species is only found on the northwestern coast of Australia.

Cymodocea nodosa (Ucria) Ascherson

FIGURE 32

CHARACTERISTICS.—Rhizome internodes 1–6 cm long; nodes each with 1 root and a leafy shoot. Leaf sheath 2.5–7 cm long; shed entire which leaves a circular scar on the stem. Leaf blade 10–30 cm long, 2–4 mm wide; 7–9 veins. Male flower on a stalk 7–10 cm long; anthers 11–15 mm long. Female flower with an ovoid ovary, 3.0 mm long; style 2–3 mm long. Fruit semicircular, laterally compressed, 8 mm long, 6 mm wide, 1.5 mm thick with 3 entire to slightly crenulate ridges.

NATURAL HISTORY.—The species is a pioneering one. Plants can colonize unvegetated sediments or recently disturbed sediments that supported *Posidonia oceanica*. Plants can grow on sand or mud.

DISTRIBUTION.—The species is widely distributed in the Mediterranean, and occurs along the Atlantic coast of Africa and southern Spain (Map 21).

Cymodocea rotundata Ehrenberg and Hemprich ex Ascherson

FIGURE 33

CHARACTERISTICS.— Rhizome internodes 1–4.5 cm long; nodes each with 1–3 roots and a leafy shoot. Leaf sheath 1.5–4 cm long, shed entire which leaves a circular scar on the stem. Leaf blade 7–15 cm long and 2–4 mm wide; 9–15 veins. Male flower with anthers 11 mm long. Female flower with a very small ovary; ovary and style only 5 mm long, stigmata 30 mm long. Fruit semicircular, laterally compressed, 10 mm long, 6 mm wide, 1.5 mm thick, with 3 dorsal ridges (central ridge has 6–8 acute teeth; one ventral ridge has 3–4 teeth).

NATURAL HISTORY.—Plants are most common at the lowest low water mark. It seems to occur commonly on platforms with coral sand, but is abundant on extensive mud flats in sheltered areas. It grows in estuaries of small rivers, in pools on coral reefs, and in creeks running through mangrove swamps.

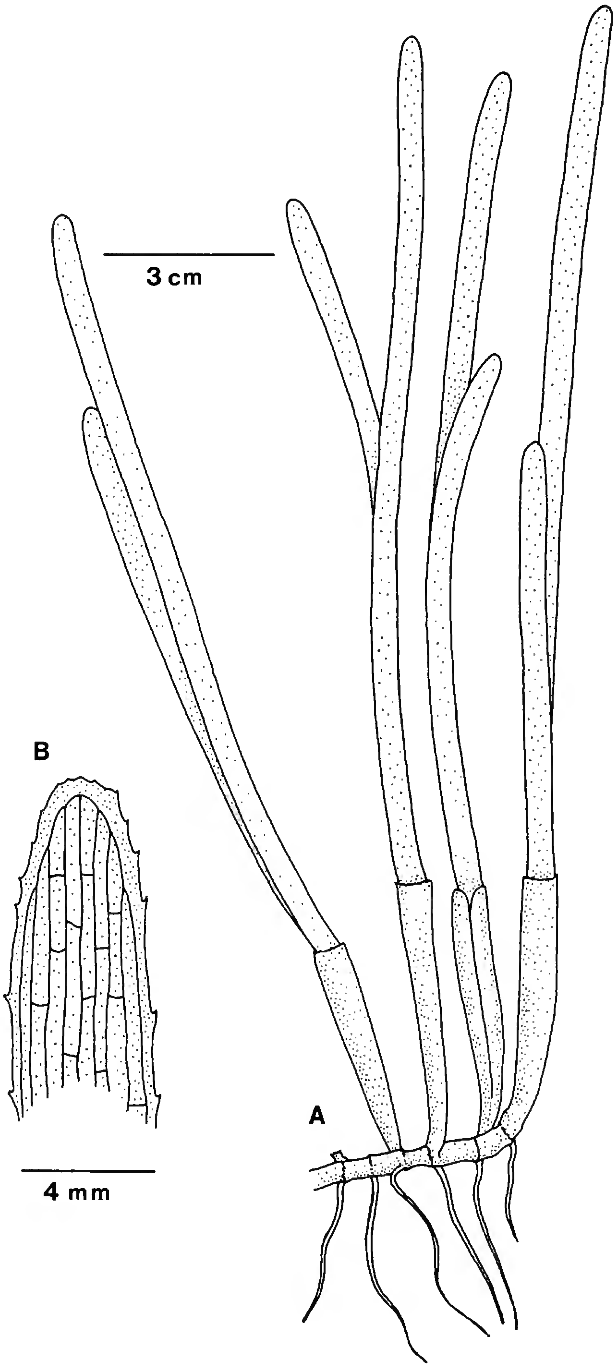

FIGURE 31.—*Cymodocea angustata:* A, habit of plant; B, leaf tip.

DISTRIBUTION.—The species is widely distributed in the Indian Ocean from the east coast of Africa to the western Pacific from the Ryukyu Islands to Queensland, Australia (Map 22).

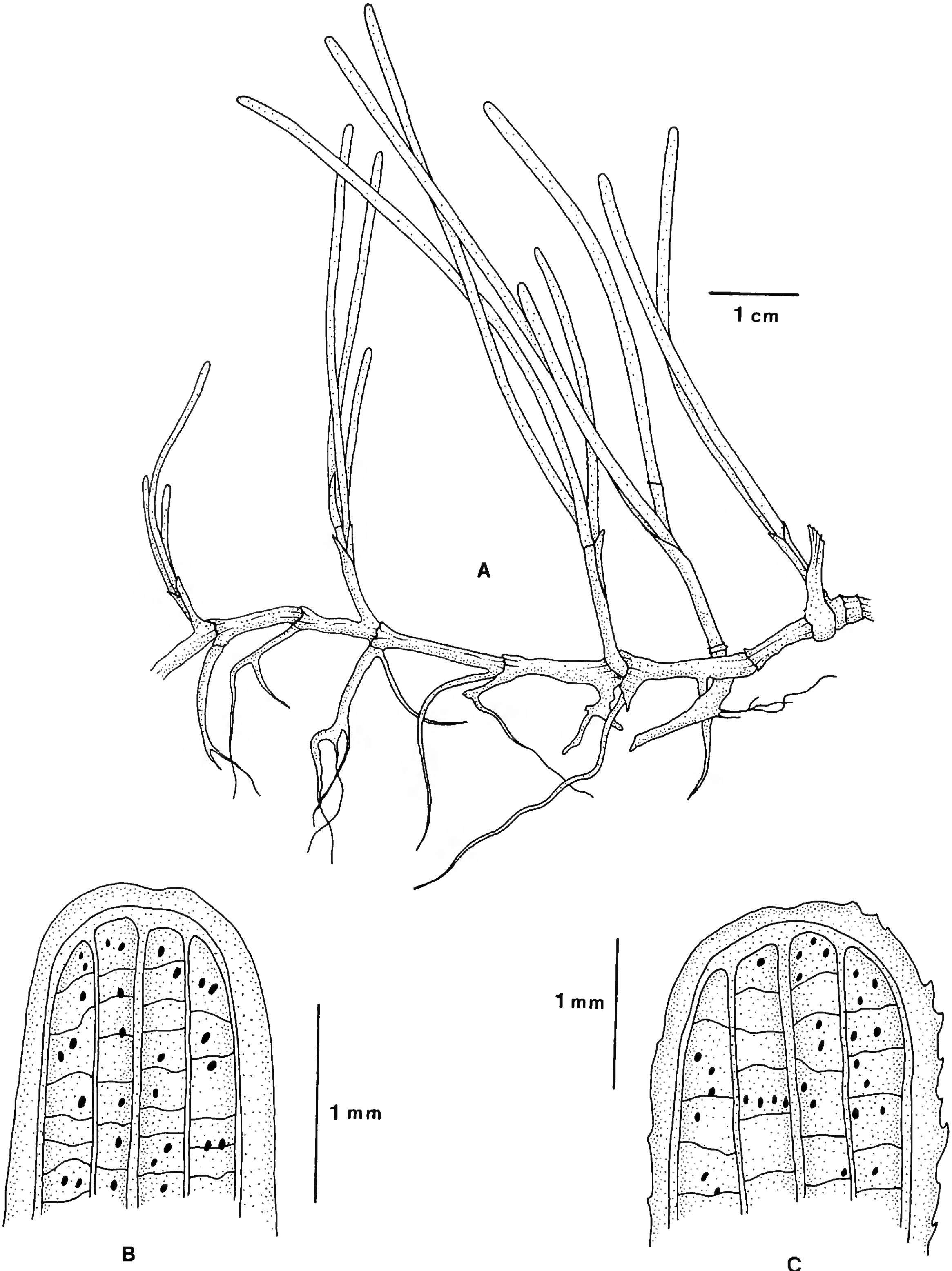

FIGURE 32.—*Cymodocea nodosa:* A, habit of plant; B, C, leaf tip.

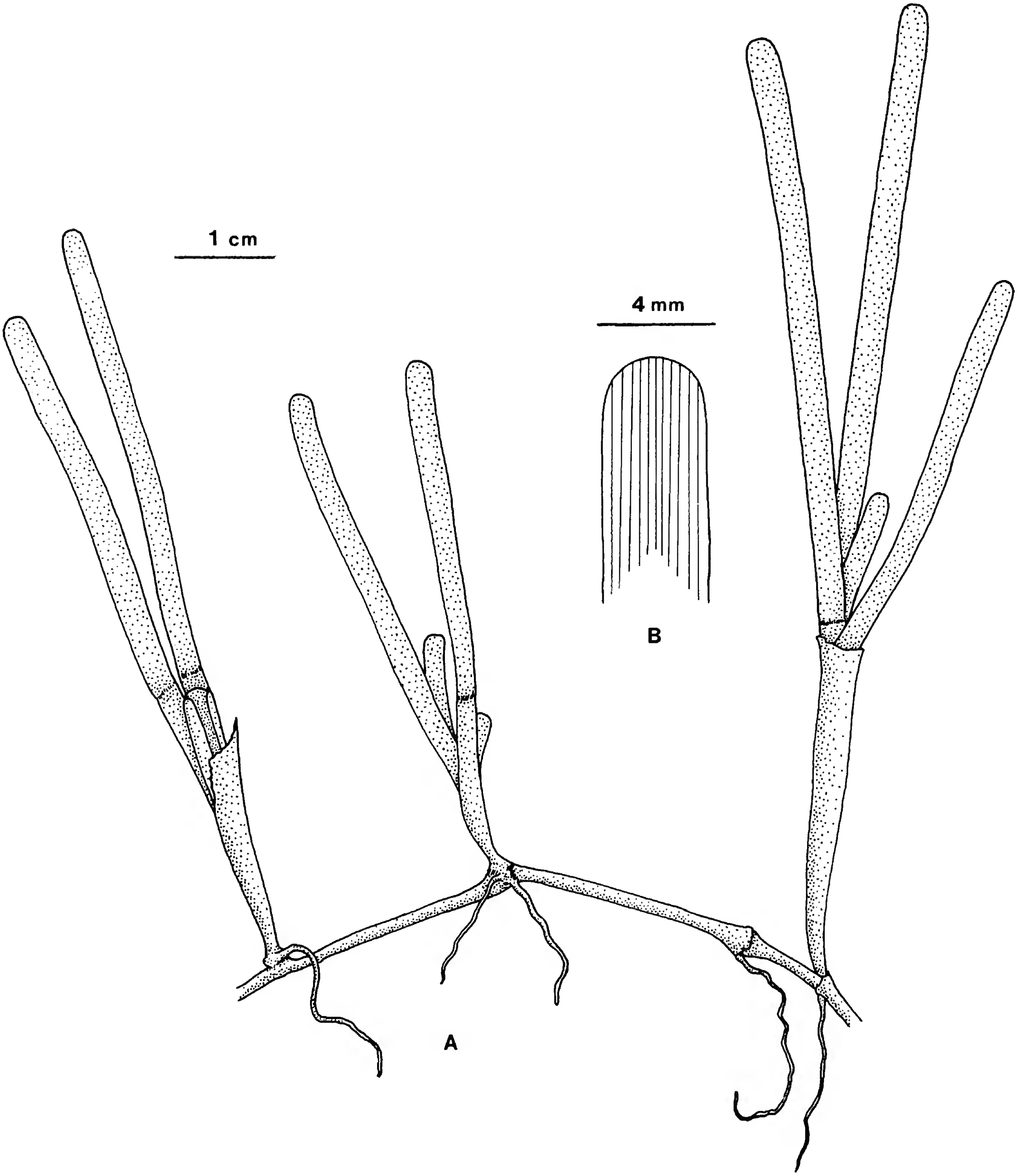

FIGURE 33.—*Cymodocea rotundata:* A, habit of plant; B, leaf tip.

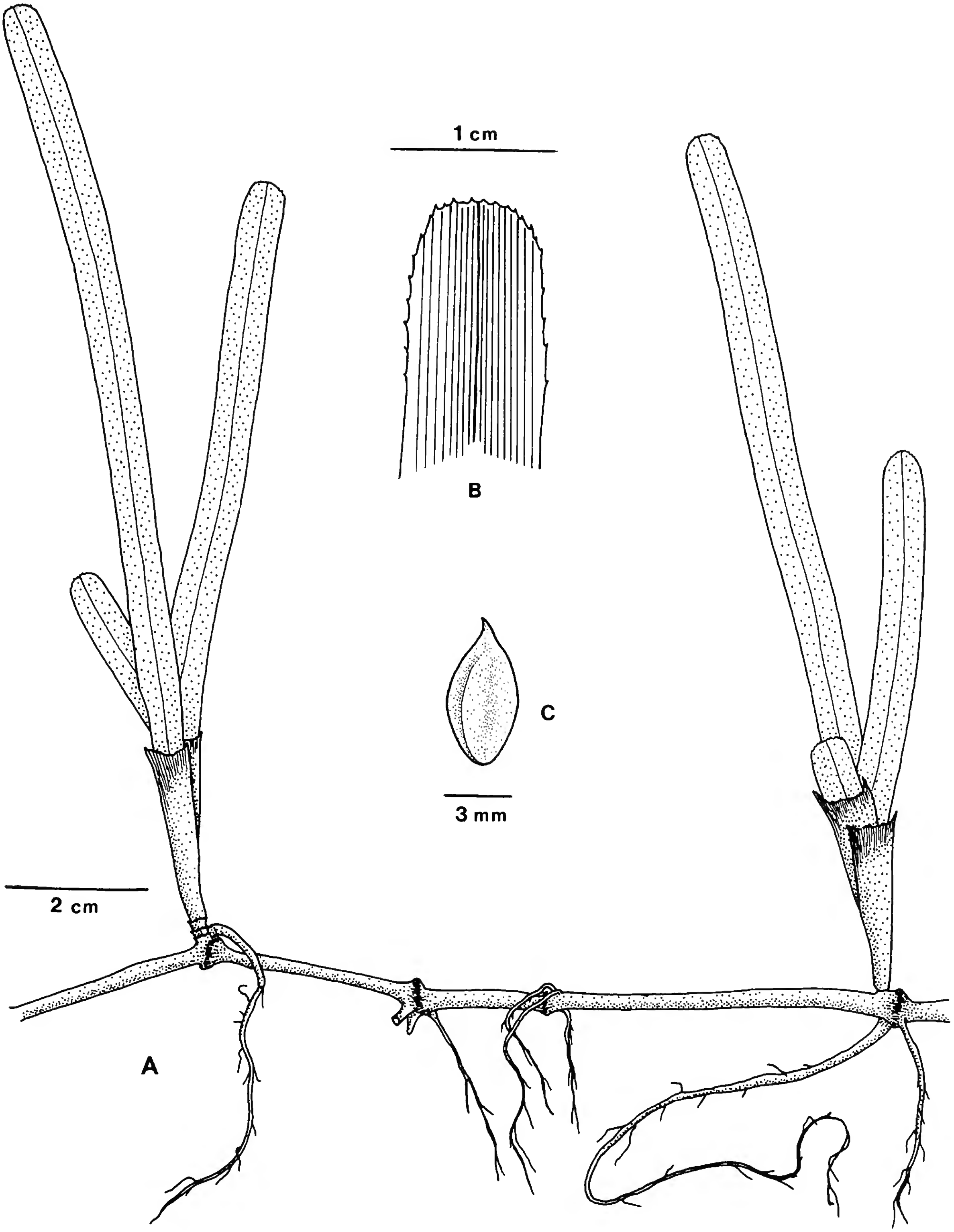

FIGURE 34.—*Cymodocea serrulata:* A, habit of plant; B, leaf tip.

Cymodocea serrulata (R. Brown) Ascherson and Magnus

FIGURE 34

CHARACTERISTICS.—Rhizome internodes 2–5.5 cm long; nodes each with 2–3 roots and a leafy shoot. Leaf sheath 1.5–3 cm long, shed entire which leaves a circular scar on the stem. Leaf blade 6–15 cm long, 4–9 mm wide; 13–17 veins. Male flower unknown. Female flower with an ovary 1.5 mm long; style 2–4 mm long; stigmata 23–27 mm long. Fruit elliptic, laterally compressed, 7–9 mm long, 3.75–4.5 mm wide, 2 mm thick; 3 dorsal blunt ridges.

NATURAL HISTORY.—Plants occur below mean low water spring tide levels on mud and coral sand substrates. On coarse sand substrates the species is poorly developed. Plants do not tolerate a dilution in salinity.

DISTRIBUTION.—The species is common in the Red Sea and along the coasts of East Africa eastward in the Indian Ocean to the western Pacific (Ryukyu Islands to Queensland, Australia; Map 23).

Genus *Syringodium*

Key to Species of *Syringodium*

Leaf blade with 7–10 pericentral veins . . . . *S. isoetifolium*
Leaf blade with 2 pericentral veins . . . . *S. filiforme*

Syringodium filiforme Kützing

FIGURE 35

CHARACTERISTICS.—Rhizome internodes 1–5 cm long; nodes each with a short shoot and 2–4 roots. Leaf sheath 2.5–6 cm long. Leaf blade 10–30 cm long, 0.8–2 mm wide; 2 pericentral veins. Male flower on a 5–10 mm long stalk; anthers ovate to elliptic, 3–4 mm long, 2 mm wide. Female flower sessile; ovary ellipsoid; stigmata 4–6 mm long. Fruit obliquely obovoid, 6–7 mm long, 3.5–5 mm wide.

NATURAL HISTORY.—The species is restricted to the subtidal. It often occurs mixed with *Thalassia testudinum* from low tide down to 10 m, but occasionally forms monospecific stands down to 18 m. It is most luxuriant at a depth from 0.7–.5 m.

DISTRIBUTION.—Plants are found throughout the western tropical Atlantic, the Gulf of Mexico, up to Cape Canaveral on the east coast of Florida, and in Bermuda (Map 24).

Syringodium isoetifolium (Ascherson) Dandy

FIGURE 36

CHARACTERISTICS.—Rhizome internodes 1.5–3.5 cm long; nodes each with a short shoot and 1–3 roots. Leaf sheath 1.5–4 cm long. Leaf blade 7–30 cm long, 1–2 mm wide; 7–10 pericentral veins. Male flower on a 7 mm long stalk; anthers ovate, 4 mm long. Female flower sessile; ovary ellipsoid; stigmata 4–8 mm long. Fruit obliquely ellipsoid, 3.5–4 mm long, 1.75–2 mm wide.

NATURAL HISTORY.—Plants occur mainly on mud substrates in the subtidal and from low water to 6 m deep. The species may occur in the intertidal in shallow pools on tidal flats or coral reefs, but it can tolerate air exposure for only a very short time.

DISTRIBUTION.—The species is widely distributed in the Indian Ocean from the Red Sea down to Madagascar, Mauritius, and the Seychelles, in the Persian Gulf eastward into the western Pacific. It is found south to Perth in Western Australia, east to Fiji, Tonga, and north to the Ryukyu Islands (Map 25).

Genus *Thalassodendron*

Key to Species of *Thalassodendron*

Roots 1–5, 0.5–2 mm thick, strongly branched and coiled. Leaf tip with acute teeth . . .
. . . . *T. ciliatum*
Roots in pairs, 3–5 mm thick, unbranched and straight. Leaf tips and margins with square to trapezoid appendages . . . . *T. pachyrhizum*

Thalassodendron ciliatum (Forsskål) den Hartog

FIGURE 37

CHARACTERISITCS—Rhizome internodes 1.5–3 cm long. Stems 1–2, 10–65 cm long. Roots 1–5, little or much branched, coiled, 0.5–2 mm wide. Leaf sheath 15–30 mm long; ligula 2–2.5 mm long; leaf scars 2–8 mm apart. Leaf blade 6–13 mm wide; veins 17–27; teeth along margin form an irregular serration. Female flower: style 4 mm long; false fruit 3.5–5 cm long.

NATURAL HISTORY.—The species occurs in the upper subtidal from mean low water spring tides down to at least 10 m deep.

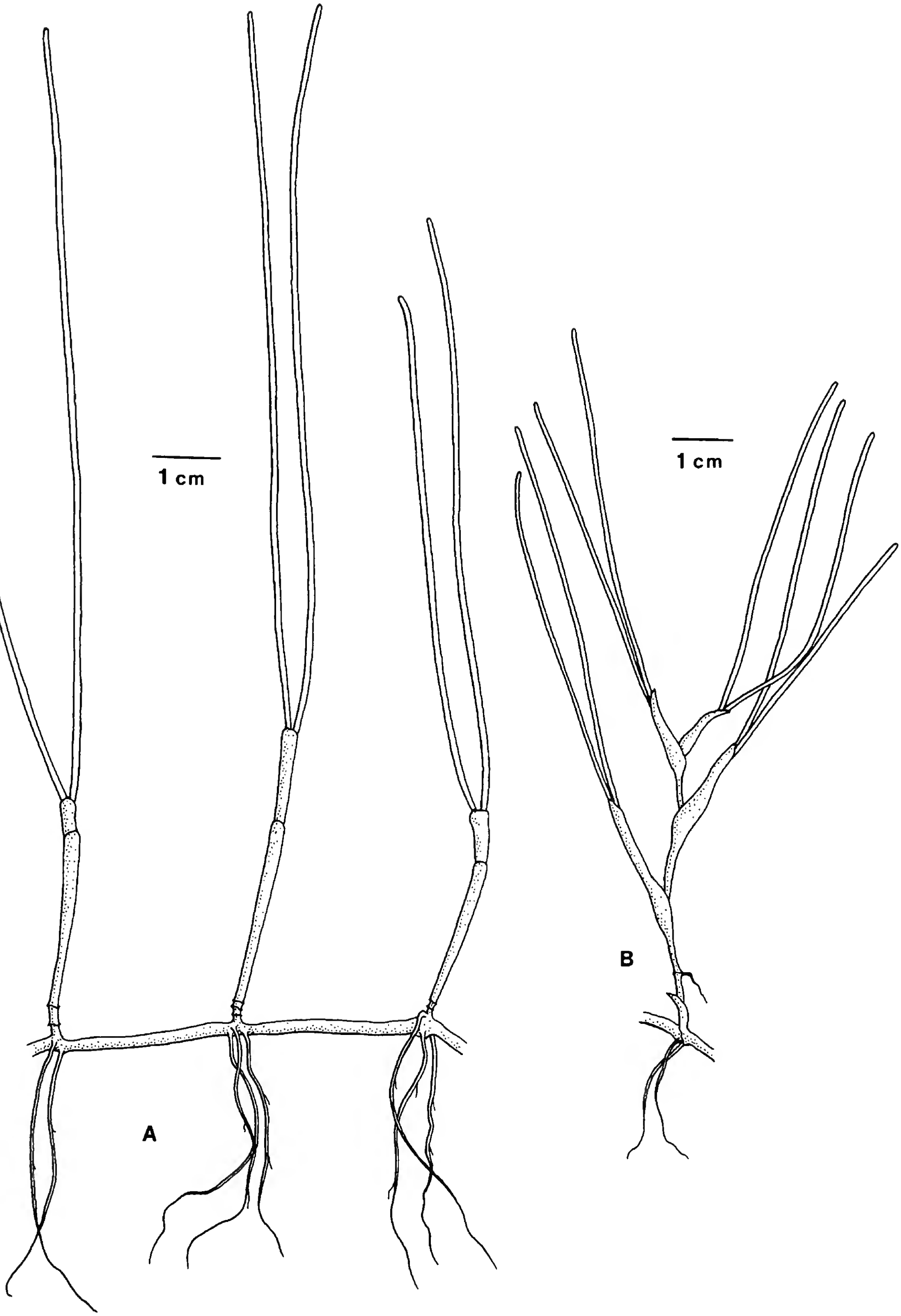

FIGURE 35.—*Syringodium filiforme:* A, habit of sterile plant; B, habit of fertile plant.

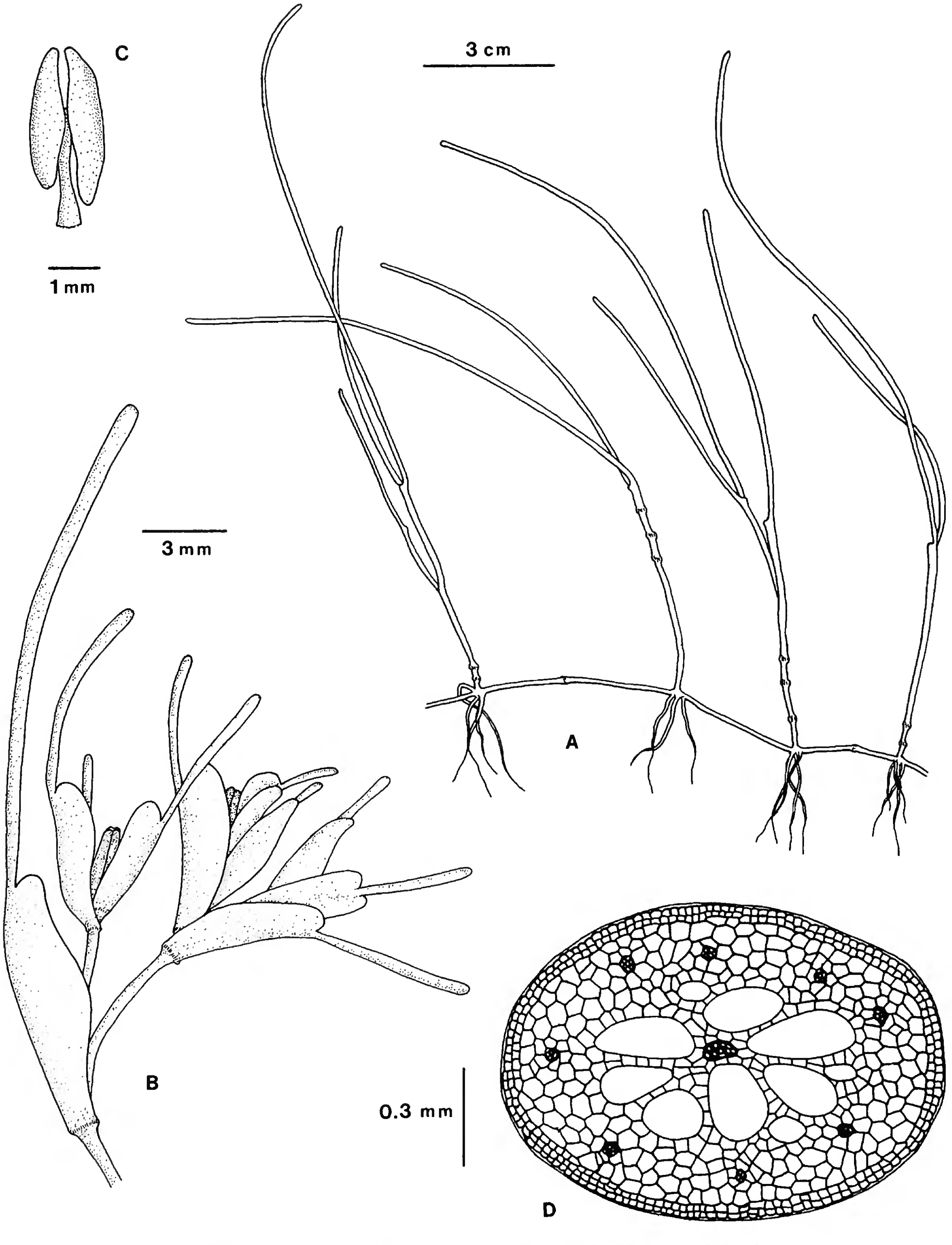

FIGURE 36.—*Syringodium isoetifolium:* A, habit of plant; B, portion of a male plant; C, staminate of flower; D, section of leaf blade showing central vascular bundle and air channels.

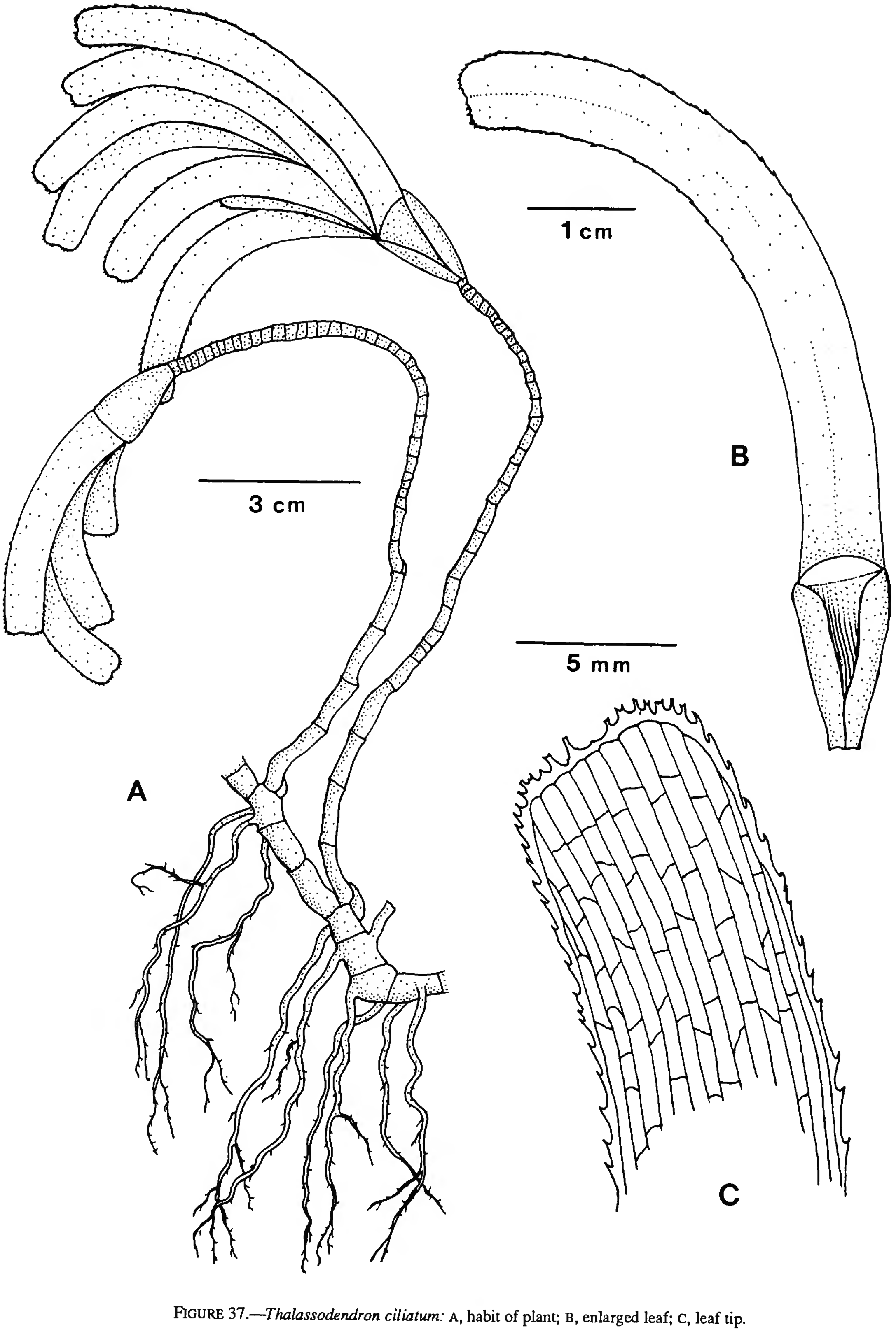

FIGURE 37.—*Thalassodendron ciliatum:* A, habit of plant; B, enlarged leaf; C, leaf tip.

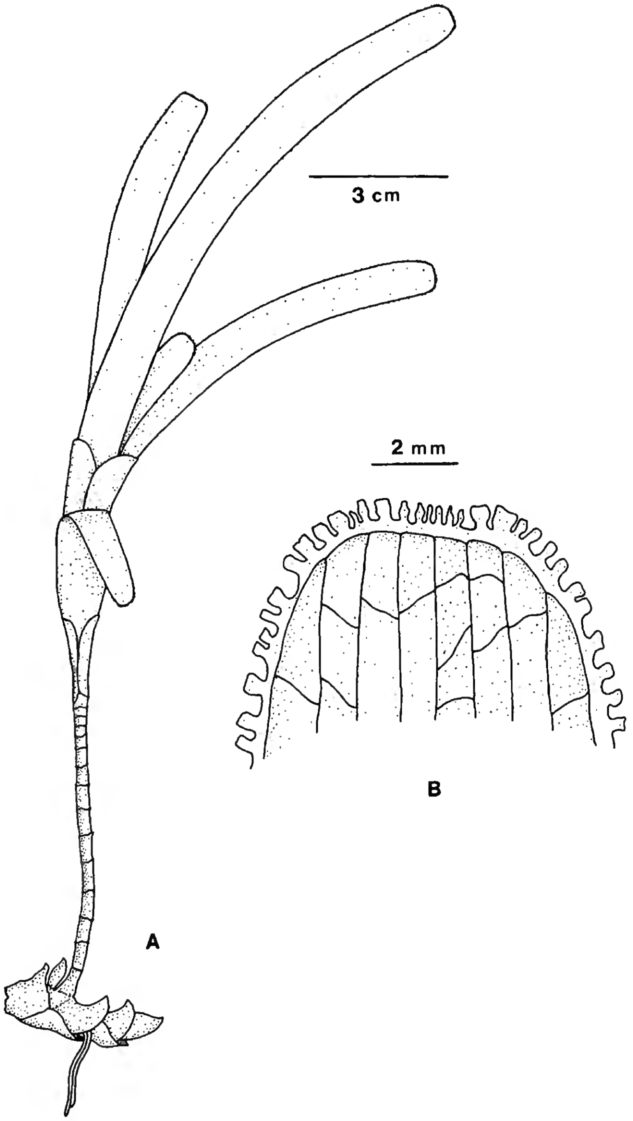

FIGURE 38 (above).—*Thalassodendron pachyrhizum:* A, habit of plant; B, leaf tip.

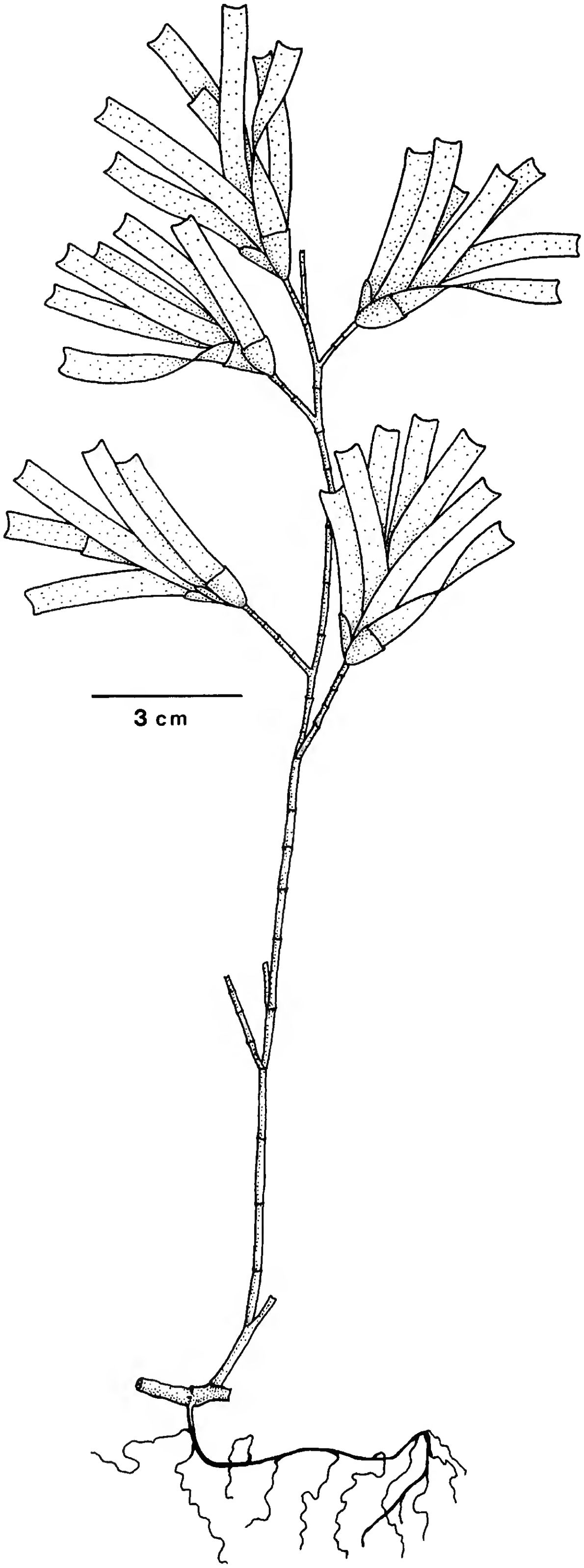

FIGURE 39 (right).—*Amphibolis antarctica:* habit of plant.

Plants may occur in patches in shallow water, but may occur in extensive meadows over coral reefs and sand-covered rocks.

DISTRIBUTION.—The species is common in the Red Sea and the western Indian Ocean. It occurs south to Zululand and eastward to Malaysia, the Solomon Islands, and Queensland (Map 26).

Thalassodendron pachyrhizum den Hartog

FIGURE 38

CHARACTERISTICS.—Rhizome internodes 3–5 mm long. Stems one at each fourth internode, 10–20 cm long. Roots 2, almost unbranched, little curved. Leaf sheath 30–44 mm long; ligula 1 mm long; leaf scars 1.5–18 mm apart. Leaf blade 7–10 mm wide; veins 13–19. Leaf tip set with 0.5–1 mm long square to trapezoid appendages; leaf margin set with similar appendages. Female flower with style 1 mm long or shorter; false fruit 5.5–7 cm long.

NATURAL HISTORY.—Plants have only been found washed ashore.

DISTRIBUTION.—Warm-temperate coast of Western Australia.

Genus *Amphibolis*

Key to Species of *Amphibolis*

Leaf sheath wide (1.2–1.8 times as long as wide). Auriculae acute, longer than the ligula. Sheathing flaps narrow, overlapping near the base only. Leaf blade 2.5–10 times as long as wide . . . . *A. antarctica*

Leaf sheath narrow (2.5–3.6 times as long as wide). Auriculae broadly obtuse, shorter than the ligula. Sheathing flaps wide, overlapping over their entire length. Leaf blade 12–15 times as long as wide . . . . *A. griffithii*

Amphibolis antarctica (Labillardiere) Sonder and Ascherson

FIGURE 39

CHARACTERISTICS.—Rhizome 2–4.5 mm wide. Roots up to 20 cm long. Leaf sheath wide, short, 6–14 mm long by 4–9.5 mm, 1.2–1.8 times as long as wide; auriculae acute; ligula 1.2–2 mm long. Leaf blade 20–52 cm long, 4–10 mm wide, 2.5–10 times as long as wide, 8–21 veins. Female flower with an involucre of 4 or more scales.

NATURAL HISTORY.—The species is confined to the subtidal on sand, on sand-covered rocks, and occasionally on compact clay where the water moves by currents or wave action.

DISTRIBUTION.—The species is widely distributed from Shark Bay in Western Australia to a point east of Melbourne. It is also found in northern Tasmania (Map 27).

Amphibolis griffithii (J.M. Black) den Hartog

FIGURE 40

CHARACTERISTICS.—Rhizome 1.5–2.5 mm wide. Roots up to 10 cm long. Leaf sheath narrow, relatively long, 12–20 mm by 3.5–7 mm, 2.5–3.6 times as long as wide; auriculae broadly obtuse; ligula obtusely rounded, 1 mm long. Leaf blade 32–76 mm long, 2.5–5 mm wide, 12–15 times as long as wide. Female flower with no involucre.

NATURAL HISTORY.—Plants are subtidal and live in locations which experience more hydroturmoil than *A. antarctica.*

DISTRIBUTION.—The species occurs in Western and South Australia (Map 28).

Family HYDROCHARITACEAE

Genus *Enhalus*

Enhalus acoroides (Linnaeus f.) Royle

FIGURE 41

CHARACTERISTICS.—Rhizome up to 1.5 cm wide, densely clothed with the persistent fibrous strands of decayed leaves. Roots numerous, not branched, 10–20 cm long, 3–5 mm wide. Leaves 30–150 cm long, 1.25–1.75 cm wide. Male flower: sepals white, about 2 mm long; petals white, about 1.75 mm long; stamens white; pollen grains spherical. Female flower: peduncle 40–50 cm long, coiled and contracted after anthesis, uncoiled in fruiting stage; sepals reddish; petals white, 4–5 cm long, 3–4 mm wide. Fruit 5–7 cm long. Seeds 1–1.5 cm long.

NATURAL HISTORY.—Plants occur along sheltered coasts on sandy and muddy bottoms. The species grows best just above the level of mean low water springs and grows to generally 4 m deep. Flowering occurs where plants are uncovered briefly during spring low tides or where the flowers can reach the water surface.

DISTRIBUTION.—The species has a broad distribution from the east coast of Africa to the Ryukyu Islands south and east to the Solomon Islands, New Caledonia, to the Torres Strait, North Queensland, Australia (Map 29).

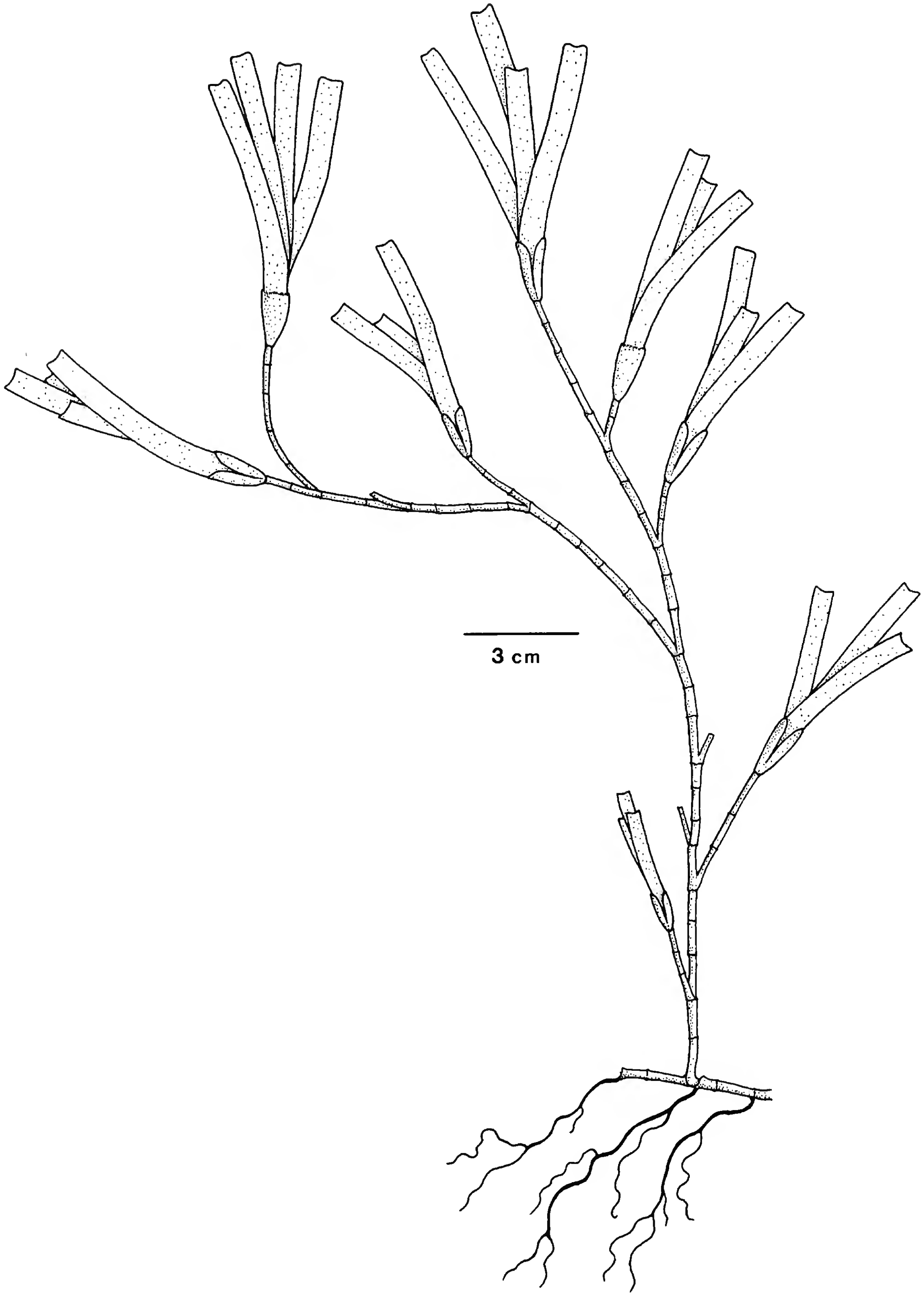

FIGURE 40.—*Amphibolis griffithii:* habit of plant.

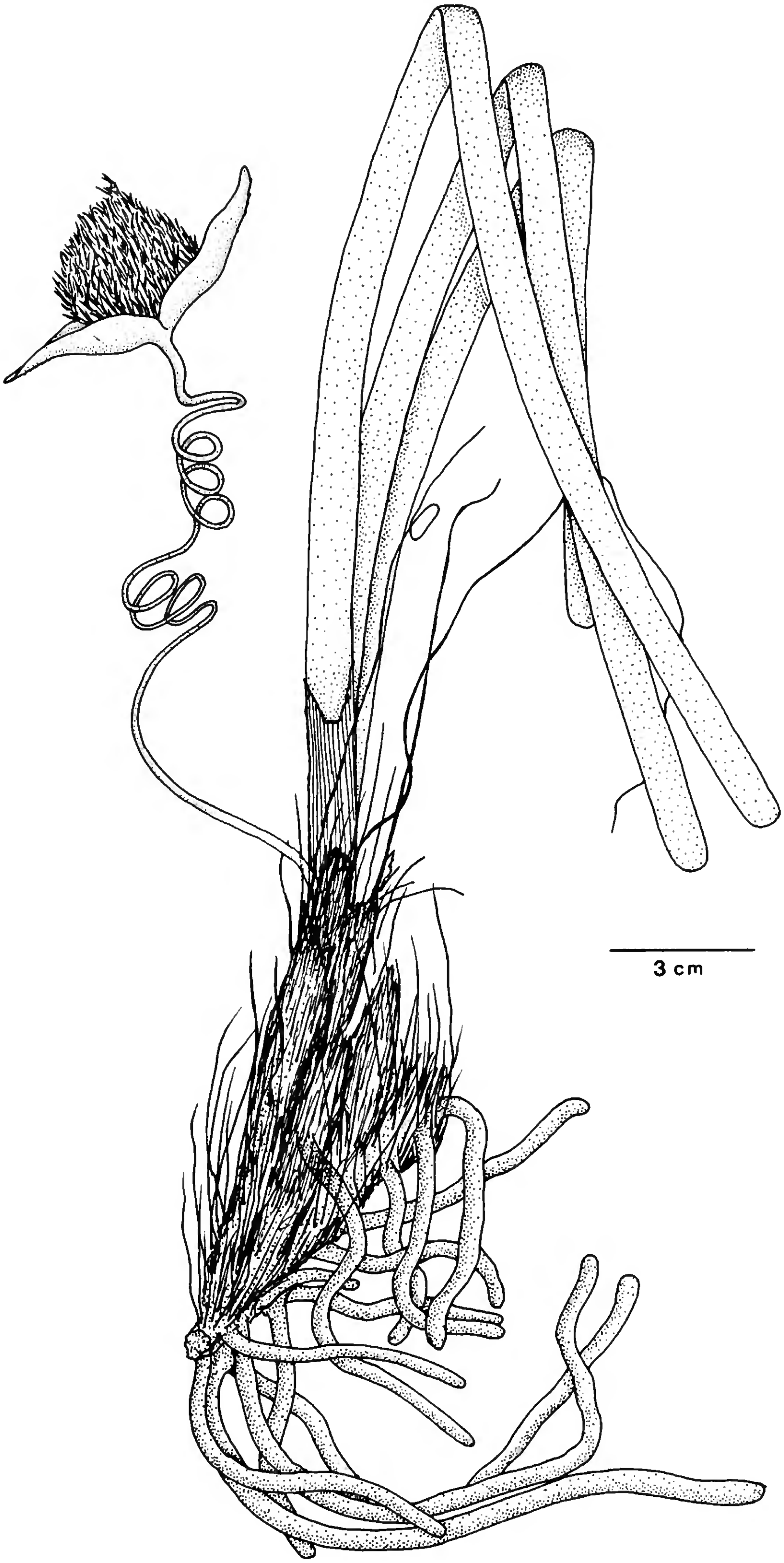

FIGURE 41.—*Enhalus acoroides:* habit of plant.

Genus *Thalassia*

Key to Species of *Thalassia*

Margin of spathe serrulate. Tepals 10–12 mm long, 4.4.5 mm wide. Stigmatic branches 5–6 times as long as the style. Fruit with a 4–7 mm long beak . . . . . ***T. testudinum***

Margin of spathe entire. Tepals 7–8 mm long, 3 mm wide. Stigmatic branches 2 times as long as the style. Fruit with a 1–2 mm long beak . . . . ***T. hemprichii***

Thalassia hemprichii (Ehrenberg) Ascherson

FIGURE 42

CHARACTERISTICS.—Male flower: peduncle about 3 cm long; stamens 3–12, mostly 6–9. Female flower: 1–1.5 cm long; styles 6, 5–7 mm long. Fruit splits into 8–20 irregular valves, beak 1–2 mm long. Seeds 3–9.

NATURAL HISTORY.—The species is dominant on dead reef platforms and subtidal flats whose substrate is clean coral sand or coral debris. Plants may occur on mixed mud and sand or soft mud substrates. The species principally occurs in the subtidal from low tide to 5 m deep. It may grow in the intertidal up to the mangrove fringe.

DISTRIBUTION.—The species is widely distributed from the east coast of Africa, through the Indian Ocean, up to the Ryukyu Islands, down to Queensland, and east to Micronesia (Map 30).

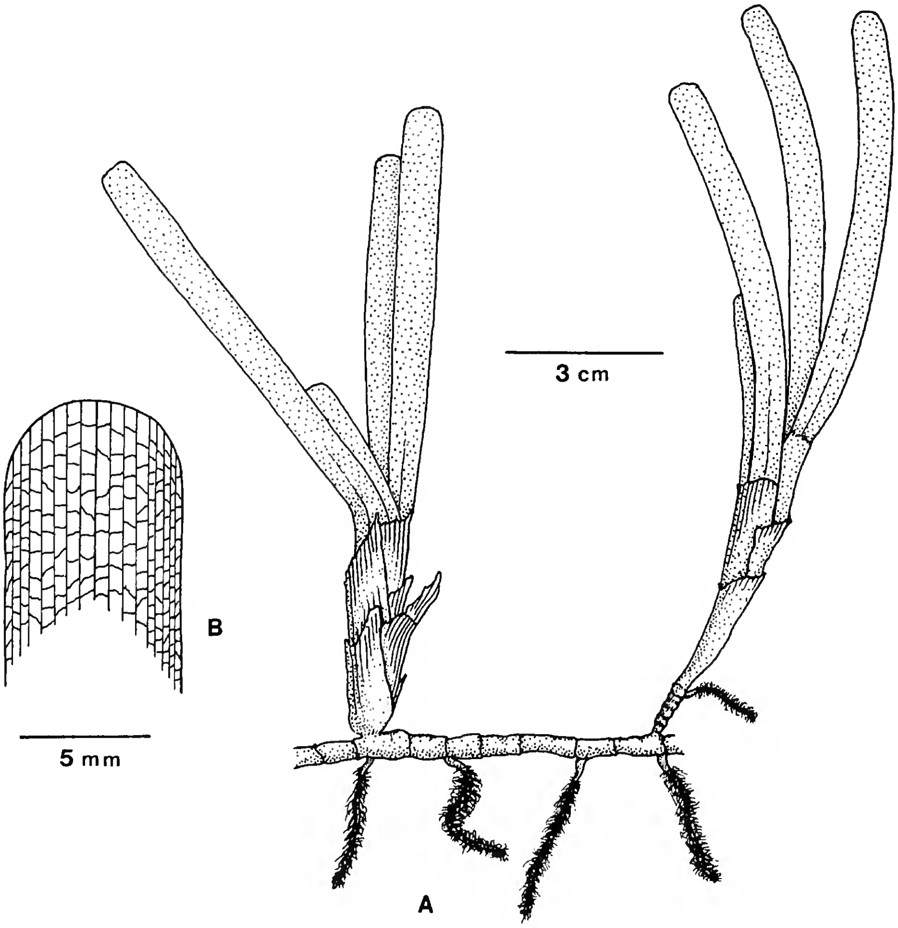

FIGURE 42.—*Thalassia hemprichii:* A, habit of plant; B, leaf tip.

Thalassia testudinum Banks ex König

FIGURE 43

CHARACTERISTICS.—Male flower: peduncle 3–7.5 cm long, pedicel 1.25–2.5 cm long; stamens 9. Female flower: peduncle 3–4 cm long; styles 7–8, 1.5–2.5 mm long. Fruit splits into 5–8 irregular valves, beak 4–7 mm long. Seeds 3.

NATURAL HISTORY.—The species occurs in the subtidal from low tide to 10 m deep, but may occur to 30 m deep where the water is clear. Plants occur mainly on mud and/or sand in relatively sheltered locations. Dense meadows are relatively unaffected by the erosive effects of hurricanes.

DISTRIBUTION.—The species is widely distributed in the tropical western Atlantic from Venezuela to Cape Canaveral, Florida, and also in Bermuda (Map 31).

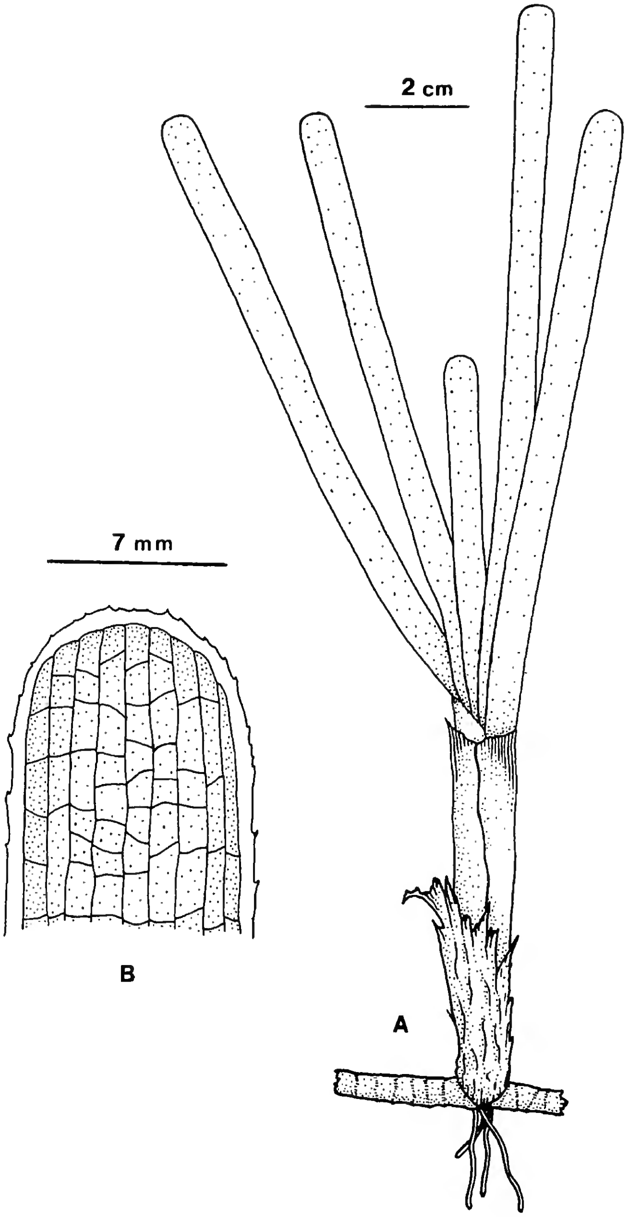

FIGURE 43.—*Thalassia testudinum:* A, habit of plant; B, leaf tip.

Genus *Halophila*

Key to Species of *Halophila*

1. Erect lateral shoots with 2 scales at the base, 2 other scales about halfway up, and a pseudowhorl of 4–8 leaves at the top 2
   Erect lateral shoots with 2 scales only at the base 3
2. Leaves subsessile or very shortly petiolate, acute, with 6–8 pairs of cross-veins . . . . *H. engelmannii*
   Leaves distinctly petiolate, obtuse, with 3–5 pairs of cross-veins . . . *H. baillonis*

3. Erect lateral shoots with 10–20 pairs of sessile, distichously arranged leaves . . . . *H. spinulosa*
   Erect lateral shoots with at most 5 pairs of petiolate leaves at the top 4
4. Lateral shoots 1–2 cm long, bearing a pseudowhorl of 6–10 leaves . . *H. beccarii*
   Lateral shoots variable in length, bearing 1 pair of leaves or several pairs of leaves, 1 pair at each node 5
5. Lateral shoots up to 18 cm long; no cross-veins in leaves . . . . . . *H. tricostata*
   Lateral shoots rarely exceeding 0.5 cm long; leaves with ascending cross-veins . 6
6. Leaves elliptic or ovate 7
   Leaves linear 10
7. Leaves with serrulate margins . . . . *H. decipiens*
   Leaves with entire margins 8
8. Leaves 0.5–1.5 cm long . . . . *H. minor*
   Leaves 1–5.5 cm long 9
9. Blades decurrent-petiolate; veins usually forked; cross-veins 5–8 pairs . . . . *H. hawaiiana*
   Blades rounded, obtuse, truncate, or cuneate; veins usually unbranched; cross-veins 10–25 pairs . . . . *H. ovalis*
10. Leaves with serrulate margins; petioles sheathing . . . . *H. stipulacea*
    Leaves with entire margins; petioles not sheathing . . . . *H. johnsonii*

Halophila baillonis Ascherson

FIGURE 44

CHARACTERISTICS.—Rhizome thin. Leaf blades 0.5–2.2 cm long, 2–8 mm wide; margins finely spinulose; apex obtuse; base cuneate; cross veins 3–8 pairs ascending at 60–80 degree angles. Petioles 2–5 mm long. Dioecious.

NATURAL HISTORY.—Plants occur in soft mud and in fine and coarse sand. They grow in sheltered sites from low spring tide level to 30 m deep.

DISTRIBUTION.—The species is widely distributed in the western tropical Atlantic southward to Brazil. It was found on the Pacific side of Panama (Map 32).

Halophila beccarii Ascherson

FIGURE 45

CHARACTERISTICS.—Rhizome thin. Leaf blades 6–13 mm long, 1–2 mm wide; margin entire or occasionally spinulose; apex broadly acute; base cuneate; cross veins absent. Petiole 1–2 cm long; sheathing. Dioecious.

NATURAL HISTORY.—Plants occur in the lower littoral and occasionally in the upper fringe of the subtidal. It grows in sheltered sites on muddy and sandy substrates.

DISTRIBUTION.—The species is widely distributed in the South China Sea and the Bay of Bengal (Map 33).

Halophila decipiens Ostenfeld

FIGURES 46, 47

CHARACTERISTICS.—Rhizome thin, fragile. Leaf blades 1–2.5 cm long, 3–6 mm wide; margin finely serrulate; apex obtuse or rounded; base cuneate; cross veins 6–9 pairs, ascending. Petiole 3–15 mm long. Monoecious.

NATURAL HISTORY.—Plants grow from water level to 85 m deep. They usually occur between 10–30 m deep. The species appears to be euryhaline.

DISTRIBUTION.—The species is the only truly pantropic seagrass species. It is widely distributed in the Indian Ocean and tropical parts of the Pacific and western Atlantic Oceans. Exceptions include Sydney, Australia, Florida, and Bermuda (Map 34).

Halophila engelmannii Ascherson

FIGURES 48, 49

CHARACTERISTICS.—Rhizome thin. Leaf blades 1–3 cm long, 3–6 mm wide; margins finely serrulate; apex obtuse, occasionally apiculate; base cuneate; cross veins 6–8 pairs, ascending at 30–45 degree angles. Petiole 2 mm long. Dioecious. Male flower unknown.

NATURAL HISTORY.—The species is found in sheltered sites from low spring tide level to 90 m deep on sandy and muddy substrates. It may also occur on a shell-hash substrate.

DISTRIBUTION.—Plants are widely distributed in the northern Gulf of Mexico, from southern Florida, from Cuba, and the Bahamas (Map 35).

Halophila hawaiiana Doty and Stone

FIGURE 50

CHARACTERISTICS.—Leaf blade 2.0–3.0 cm long, 2.5–6 mm wide; margin entire; elongate and very narrowly cuneate and gradually decurrent-petiolate. Petiole up to 3.5 cm long, sheathing. Cross veins ascending, 5–8 pairs. Male flowers unknown.

NATURAL HISTORY.—Plants grow on firm sand, muddy sand, or on coral sand from low tide to 5 m deep.

DISTRIBUTION.—The species occurs on Kauai, Oahu, Molokai, and Maui in the Hawaiian Islands.

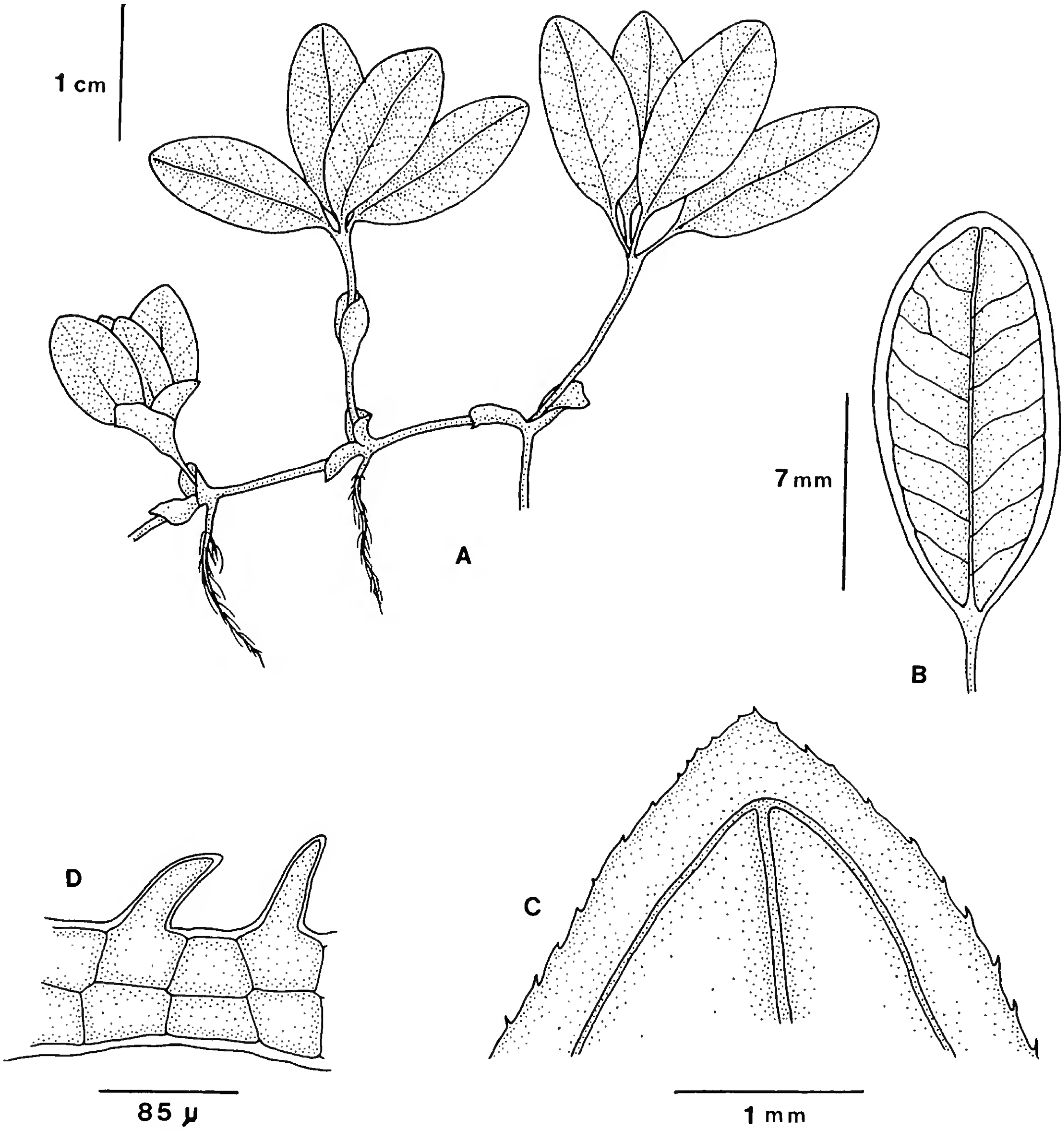

FIGURE 44.—*Halophila baillonis:* A, habit of plant; B, enlarged leaf; C, leaf tip; D, cross-section of blade showing hairs.

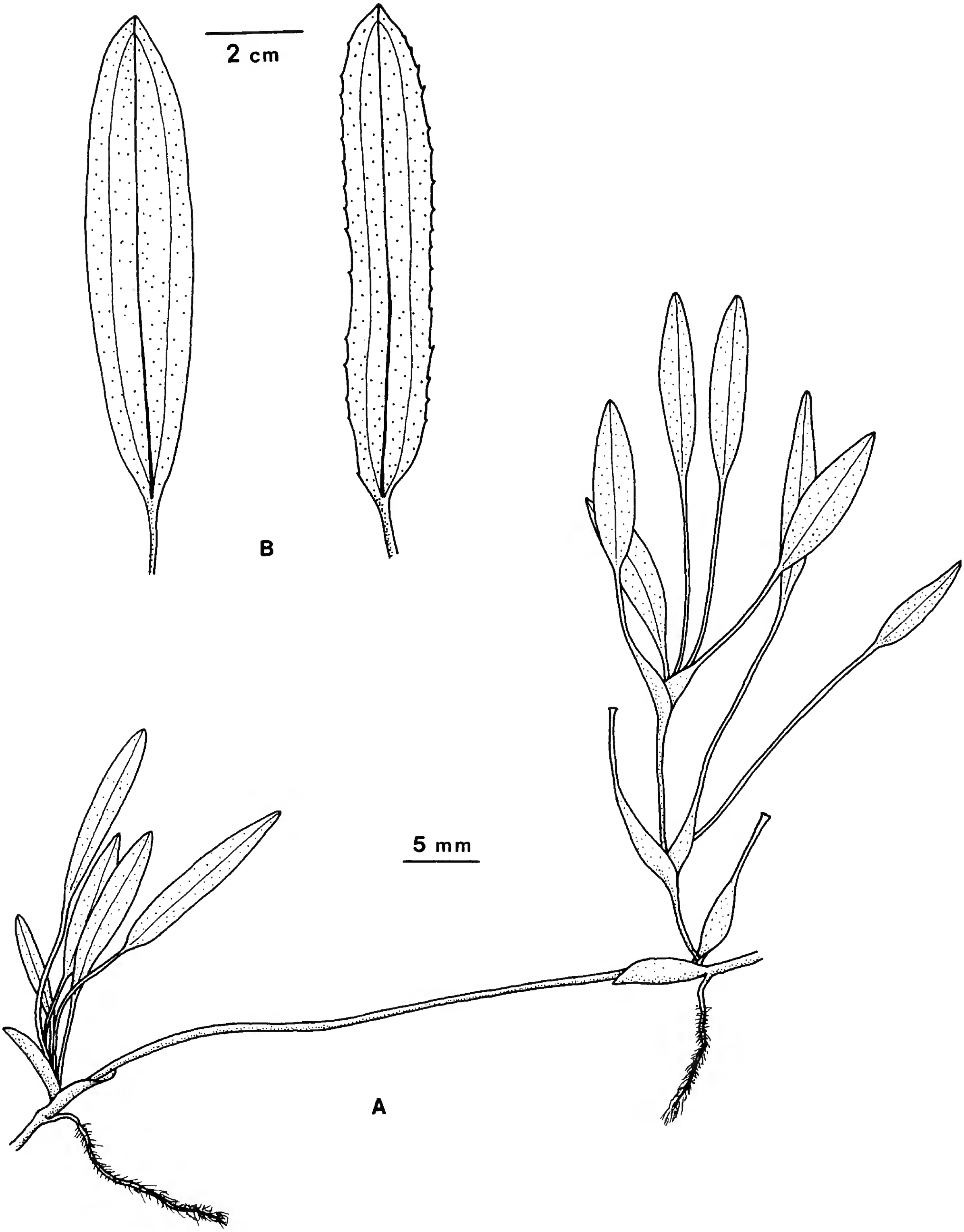

FIGURE 45.—*Halophila beccarii:* A, habit of plant; B, enlarged leaves showing entire and spinulose margins.

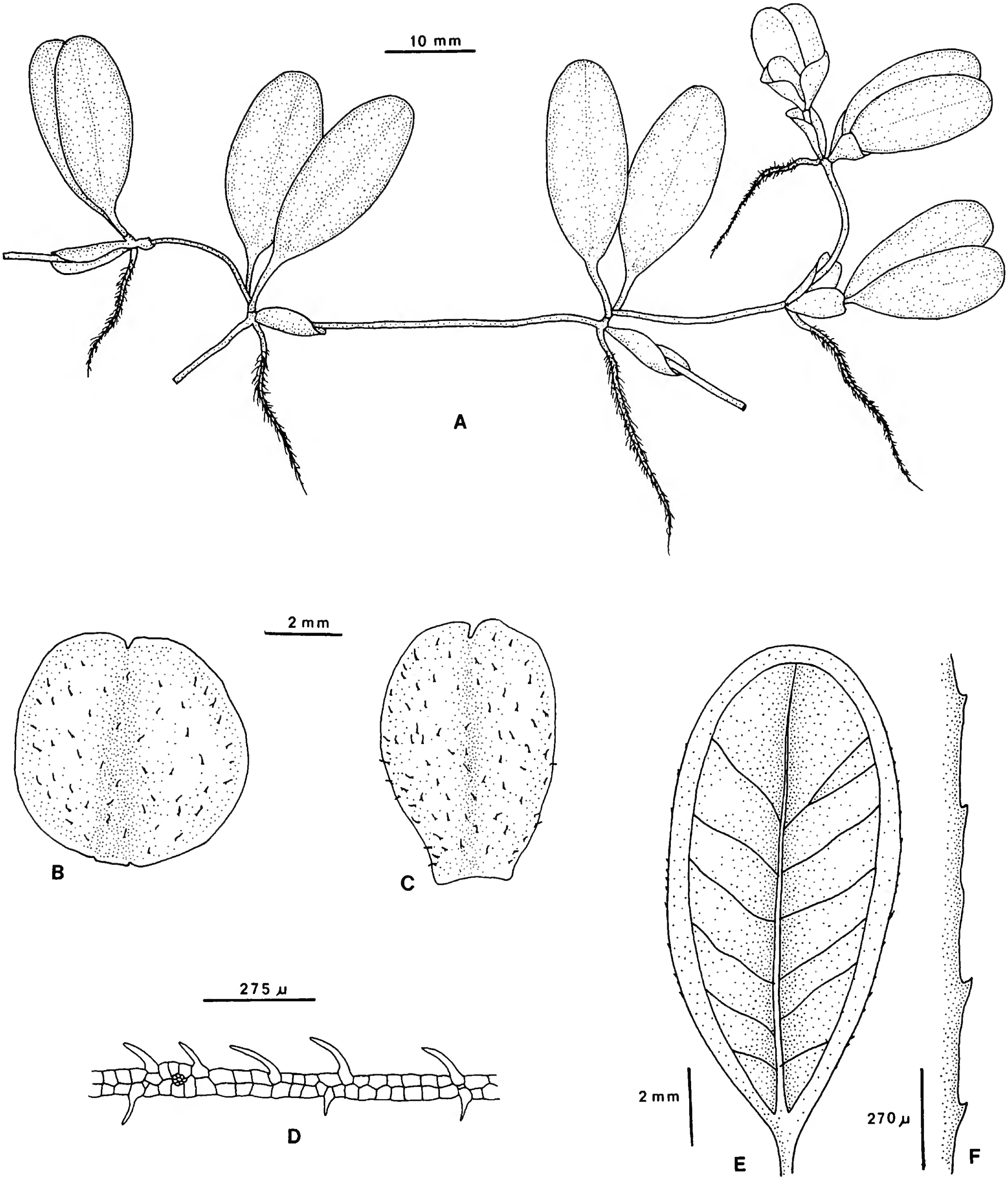

FIGURE 46.—*Halophila decipiens:* A, habit of a sterile plant; B,C, scales, with hairs on dorsal surface; D, cross-section of leaf showing hairs on both surfaces; E, leaf, showing lateral veins and serrate margins; F, magnified serrate margin of a leaf.

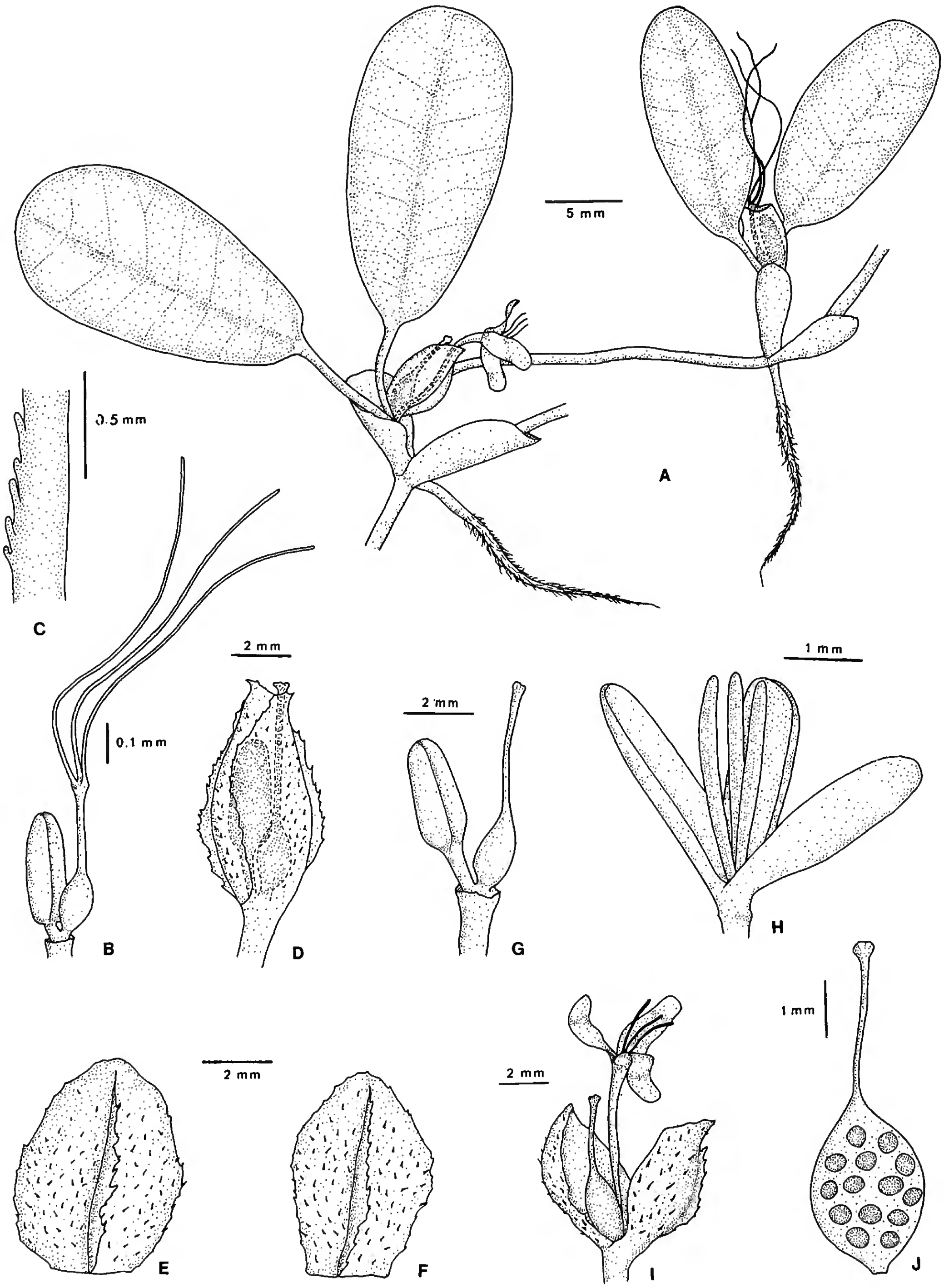

FIGURE 47.—*Halophila decipiens:* A, habit of fertile plant with male and female flowers; B, male and female flowers without the spathe; C, magnified portion of a style with papillae; D, male and female flowers enclosed by spathe; E,F, spathes with keels and hairs; G, mature flowering stage, showing female flower after the styles have fallen off and a male flower; H, male flower with three perianth segments; I, spathe enclosing beaked fruit and male flower after anthesis, the latter showing long pedicel, perianth segments, and persistent connective tissues; J, beaked fruit, showing subglobose seeds.

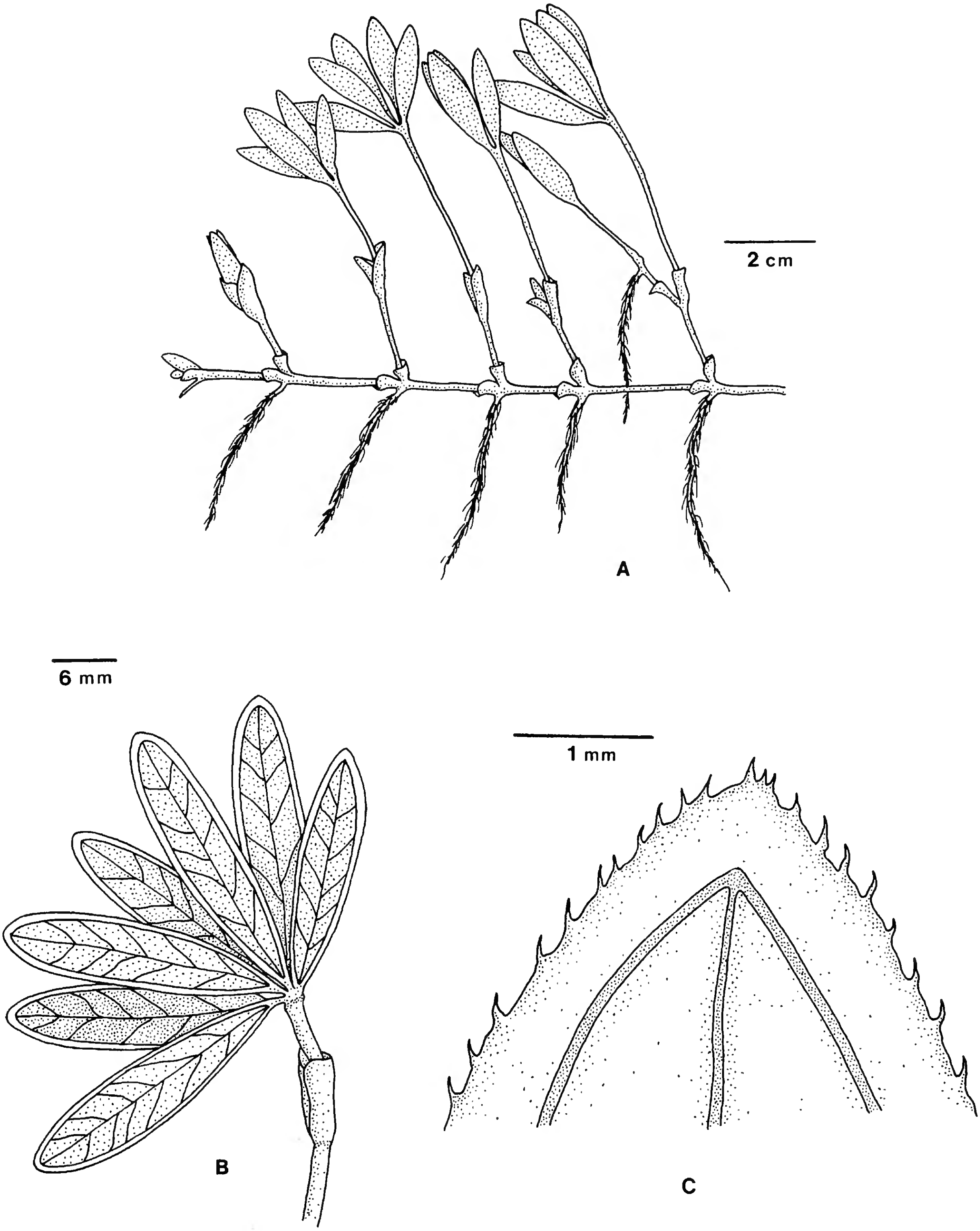

FIGURE 48.—*Halophila engelmannii:* A, habit of a sterile plant; B, enlarged portion of an erect shoot; C, leaf tip.

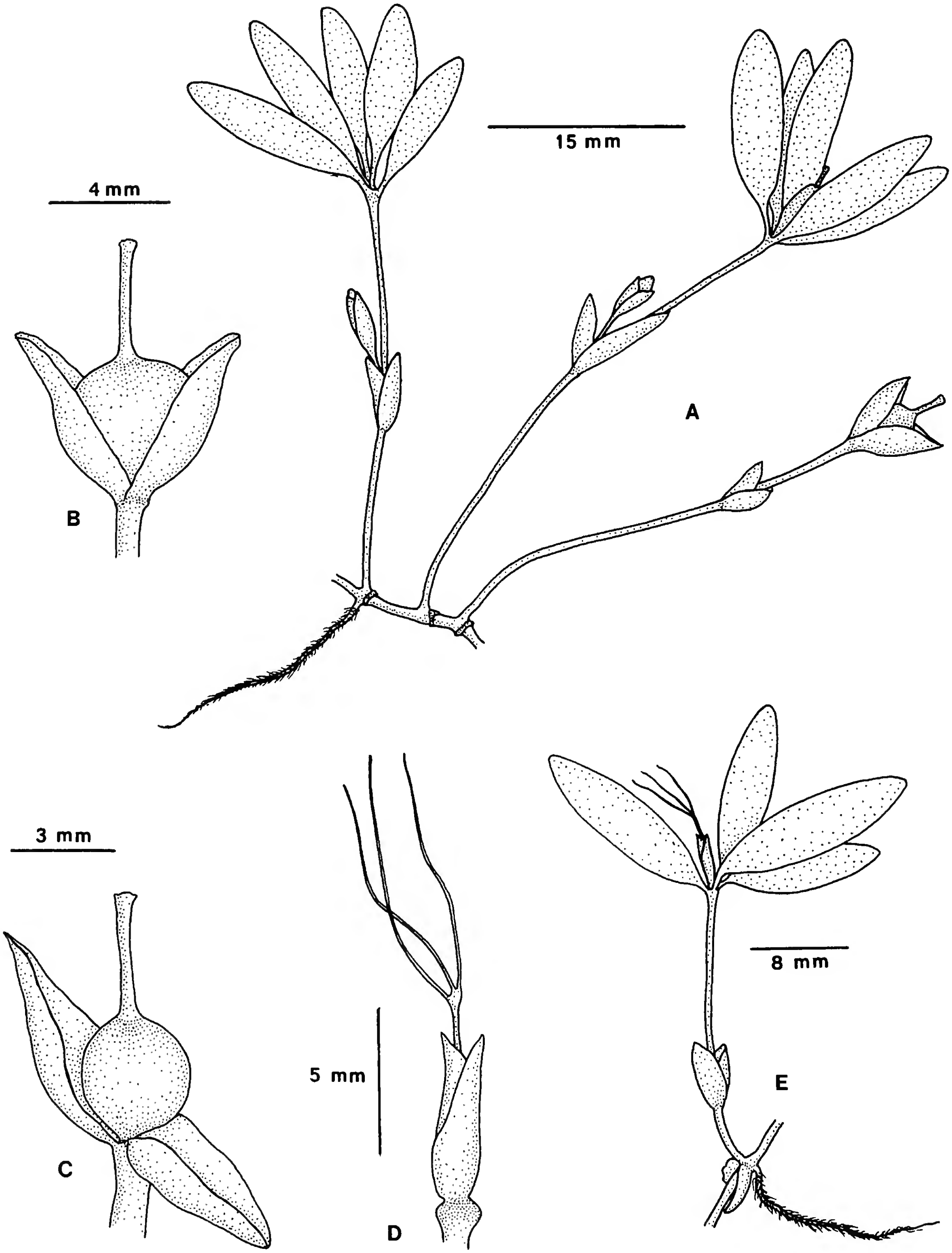

FIGURE 49.—*Halophila engelmannii:* A, habit of a female plant; B,C, beaked fruit enclosed by spathe; D, pistillate flower enclosed in spathe; E, portion of a plant with pistillate flower.

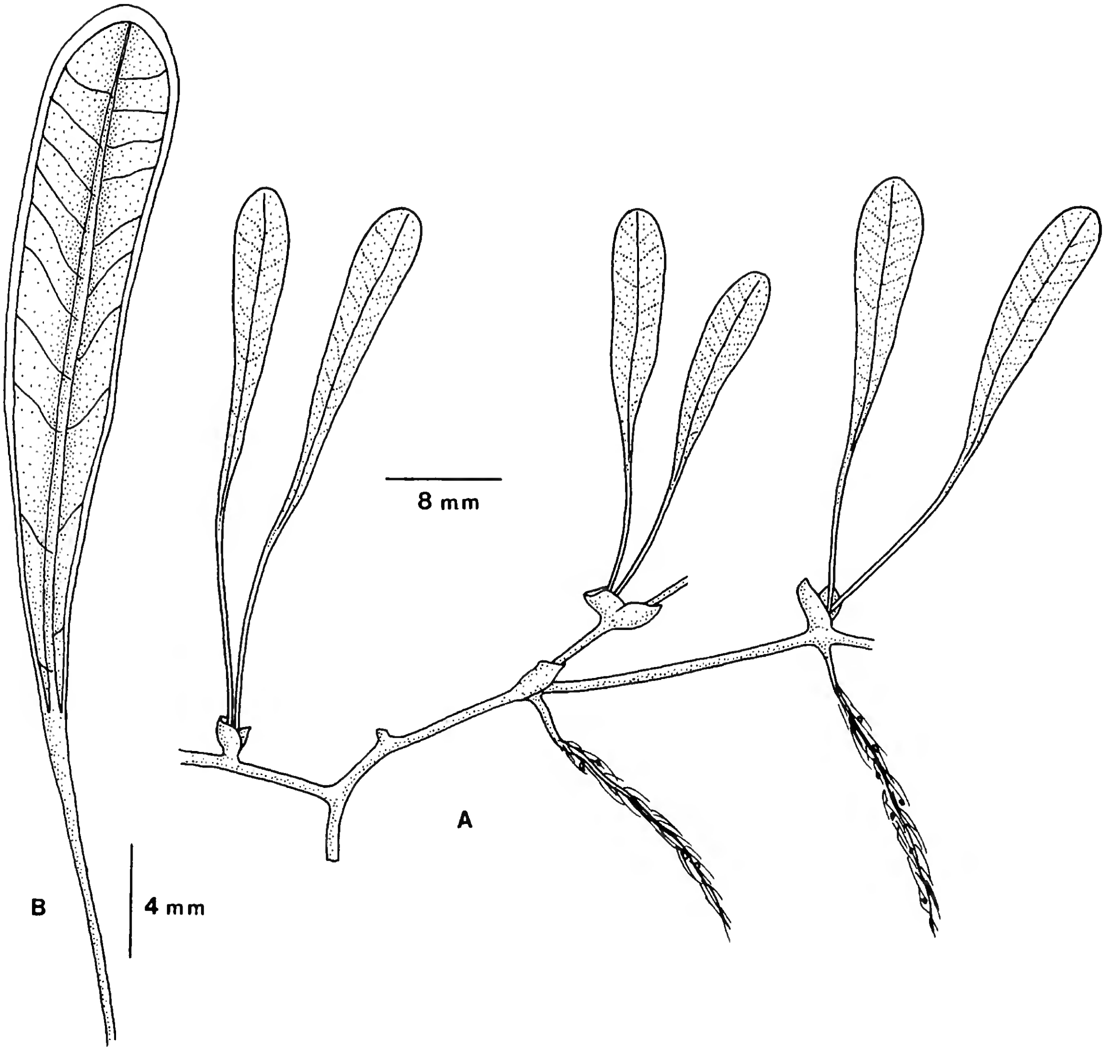

FIGURE 50.—*Halophila hawaiiana:* A, habit of plant; B, enlarged leaf.

Halophila johnsonii Eiseman

FIGURE 51

CHARACTERISTICS.—Rhizome 1 mm wide. Leaf blades 0.5–2.5 cm long, 1–4 mm wide; margin entire; base elongate-cuneate, gradually decurrent-petiolate. Petiole 1.0–2.0 cm long, not sheathing. Cross veins unequally alternate at 45 degree angles to nearly opposite, 5–10 pairs. Male flowers unknown.

NATURAL HISTORY.—The species has only been found in coastal lagoons. It is an intertidal species and occurs on fine sand.

DISTRIBUTION.—The species occurs in southeastern Florida from Sebastian Inlet to Virginia Key, Biscayne Bay.

Halophila minor (Zollinger) den Hartog

FIGURE 52

CHARACTERISTICS.—Rhizomes thin, fragile. Leaf blades 0.7–1.4 cm long, 3–5 mm wide; margin entire; apex obtuse or cuneate; cross veins 3–8 pairs, ascending at angles of 70–90 degrees. Petiole 0.5–2 cm long. Dioecious.

NATURAL HISTORY.—The species lives in sheltered areas on sandy and muddy substrates in the lower littoral and upper subtidal to 2 m deep. Plants tolerate heavy sedimentation.

DISTRIBUTION.—Plants occur from Kenya on the east coast of Africa, on the southern tip of India, eastward and north to Hong Kong, throughout the Philippines, throughout Malaya and Indonesia, to Queensland, Australia (Map 36).

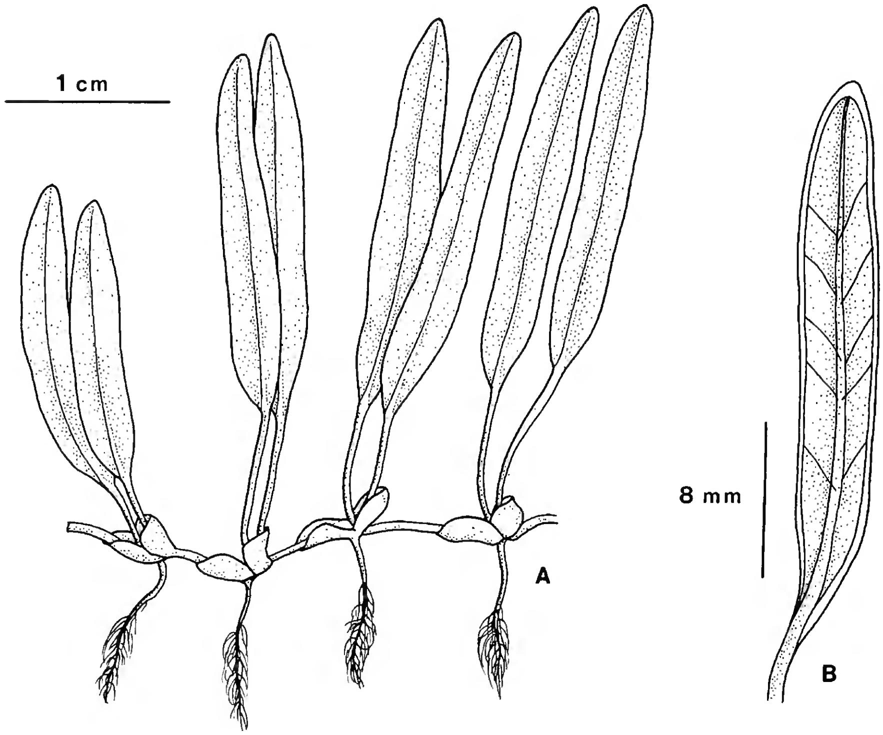

FIGURE 51.—*Halophila johnsonii:* A, habit of plant; B, enlarged leaf.

Halophila ovalis (R. Brown) Hooker f.

FIGURE 53

CHARACTERISTICS.—Rhizomes up to 2 mm wide. Leaf blades 1–4 (rarely to 7) cm long, 0.5–2 cm wide; margin entire; apex rounded; base variable, from rounded to cuneate; cross veins 10–25 pairs, ascending at angles of 45–60 degrees. Petiole 1–4.5 cm (rarely to 12 cm) long. Dioecious.

NATURAL HISTORY.—Species is extremely eurybiontic, extending from the intertidal level to 10–12 m deep. Plants grow on coarse coral rubble to soft mud. The species is the most eurythermic of all seagrasses, occurring from the tropics to the warm temperate.

DISTRIBUTION.—The species occurs from the eastern coast of Africa, throughout the Indian Ocean, north to Japan, throughout Australia, and east to Samoa and Tonga (Map 37).

Halophila spinulosa (R. Brown) Ascherson

FIGURES 54, 55

CHARACTERISTICS.—Leaf blades 1–2.6 cm long, 2–5 mm wide; margin serrulate; apex rounded; cross veins 4–5 pairs, almost perpendicular to the midrib. Dioecious.

NATURAL HISTORY.—Plants are found from low spring tide level to 45 m deep on sand, mud or substrates consisting of foraminiferans and coral fragments.

DISTRIBUTION.—The species is widely distributed in Melanesia, along the northeast and west coasts of Australia, in the Philippines, Malaya, and Indonesia (Map 38).

Halophila stipulacea (Forsskål) Ascherson

FIGURE 56

CHARACTERISTICS.—Rhizome 0.5–2 mm wide. Leaf blades 3–6 cm long, 2.5–8 mm wide; margin serrulate; apex obtuse; base cuneate or gradually decurrent-petiolate; cross veins ascending at 45–60 degrees. Petiole 0.5–1.5 cm long, sheathing lopsidedly at base. Dioecious.

NATURAL HISTORY.—Plants occur in shallow water on sand and on mud, in deep pools and on sediment-covered coral platforms. Plants may occur in the intertidal, but are most common in the upper subtidal to 7 m deep.

DISTRIBUTION.—The species is restricted to the western part of the Indian Ocean. It is common in the Red Sea, has been collected in Kenya and in Tanzania, the Persian Gulf, from India and Madagascar. It migrated to the Mediterranean via the Suez Canal (Map 39).

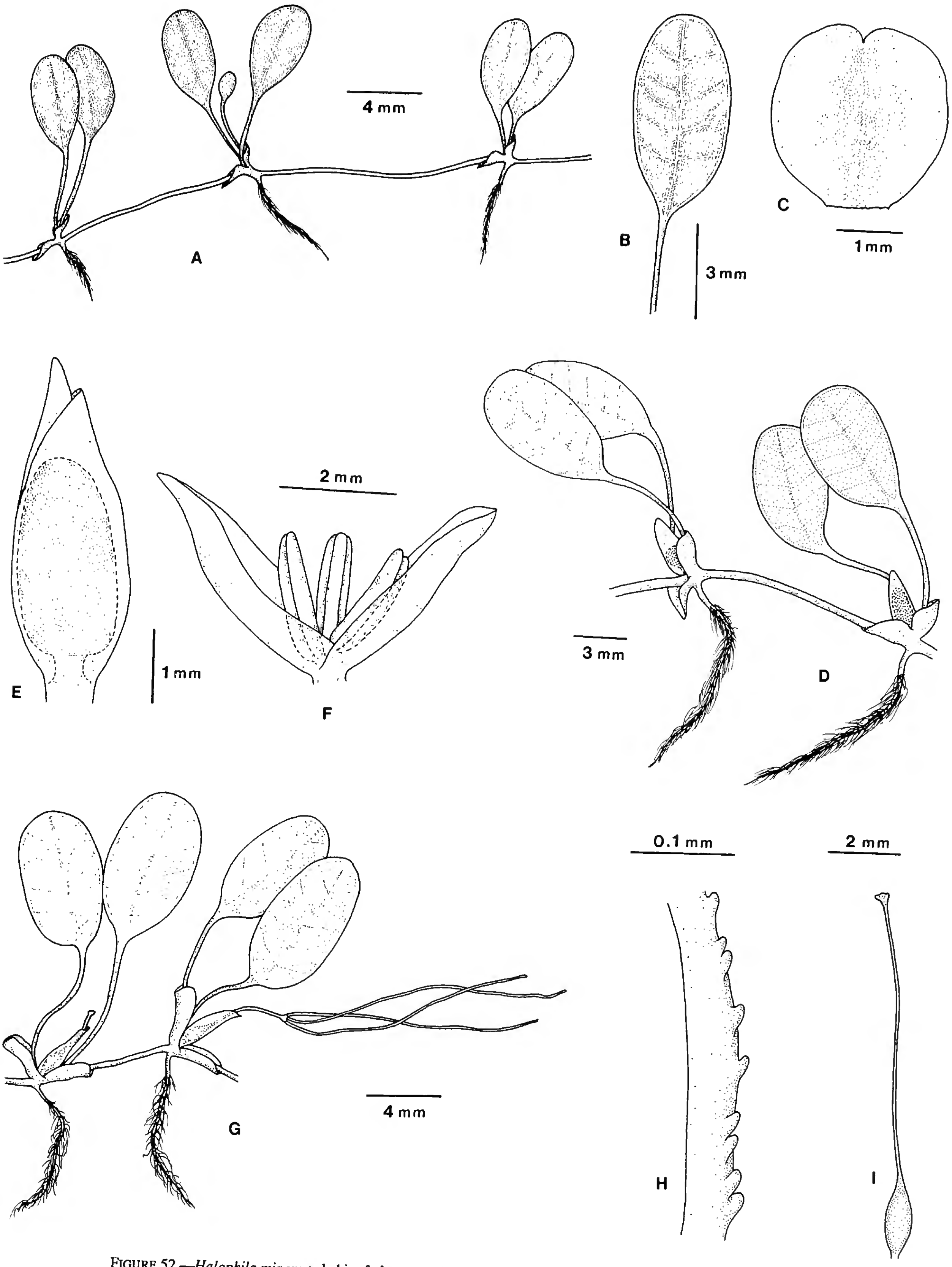

FIGURE 52.—*Halophila minor:* A, habit of plant; B, enlarged leaf; C, scale; D, portion of plant showing staminate flowers; E,F, enlarged staminate flowers enclosed by spathes; G, portion of plant showing pistillate flowers; H, enlarged portion of style with papillae; I, beaked fruit.

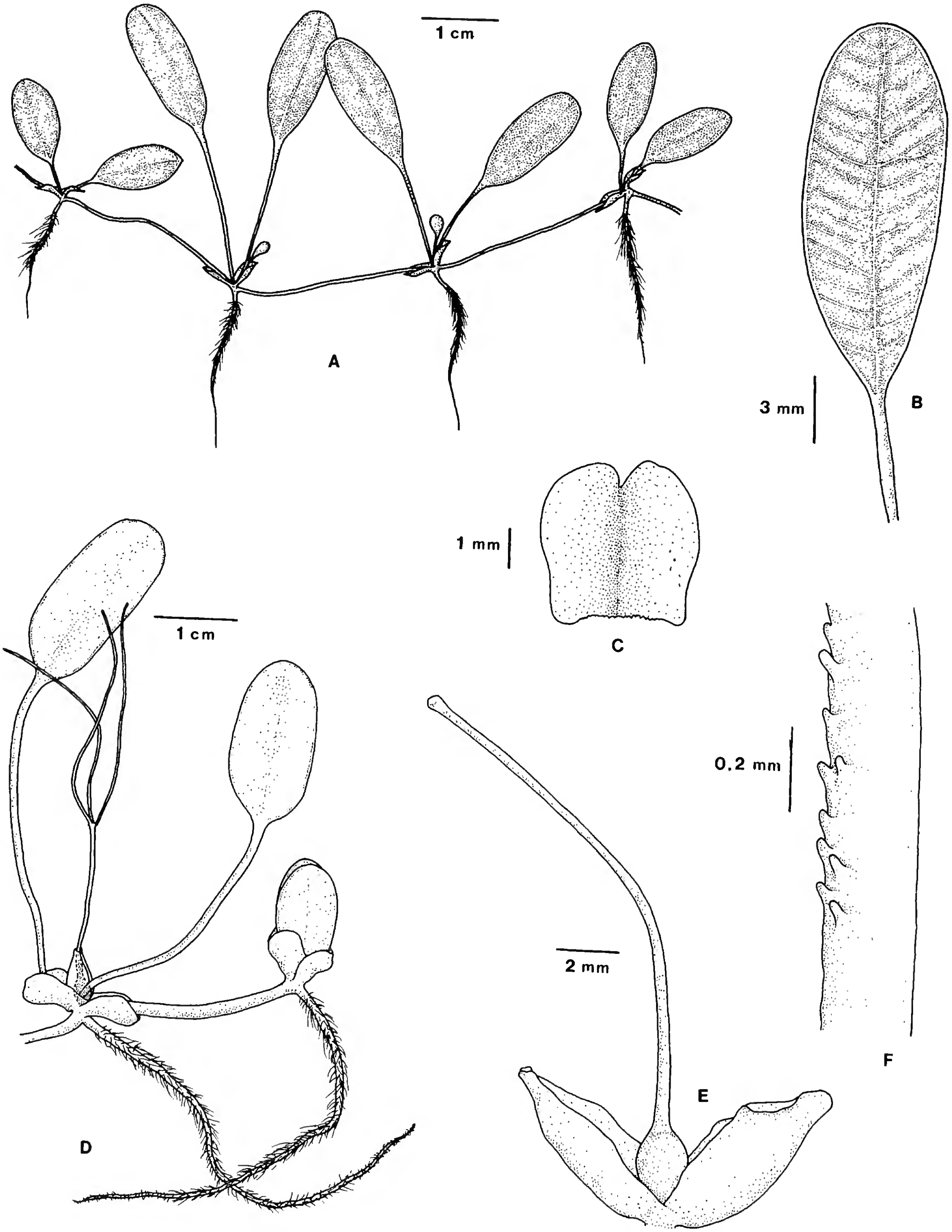

FIGURE 53.—*Halophila ovalis:* A, habit of plant; B, enlarged leaf; C, enlarged scale; D, habit of plant with pistillate flower; E, spathe enclosing beaked fruit; F, enlarged portion of a style with papillae.

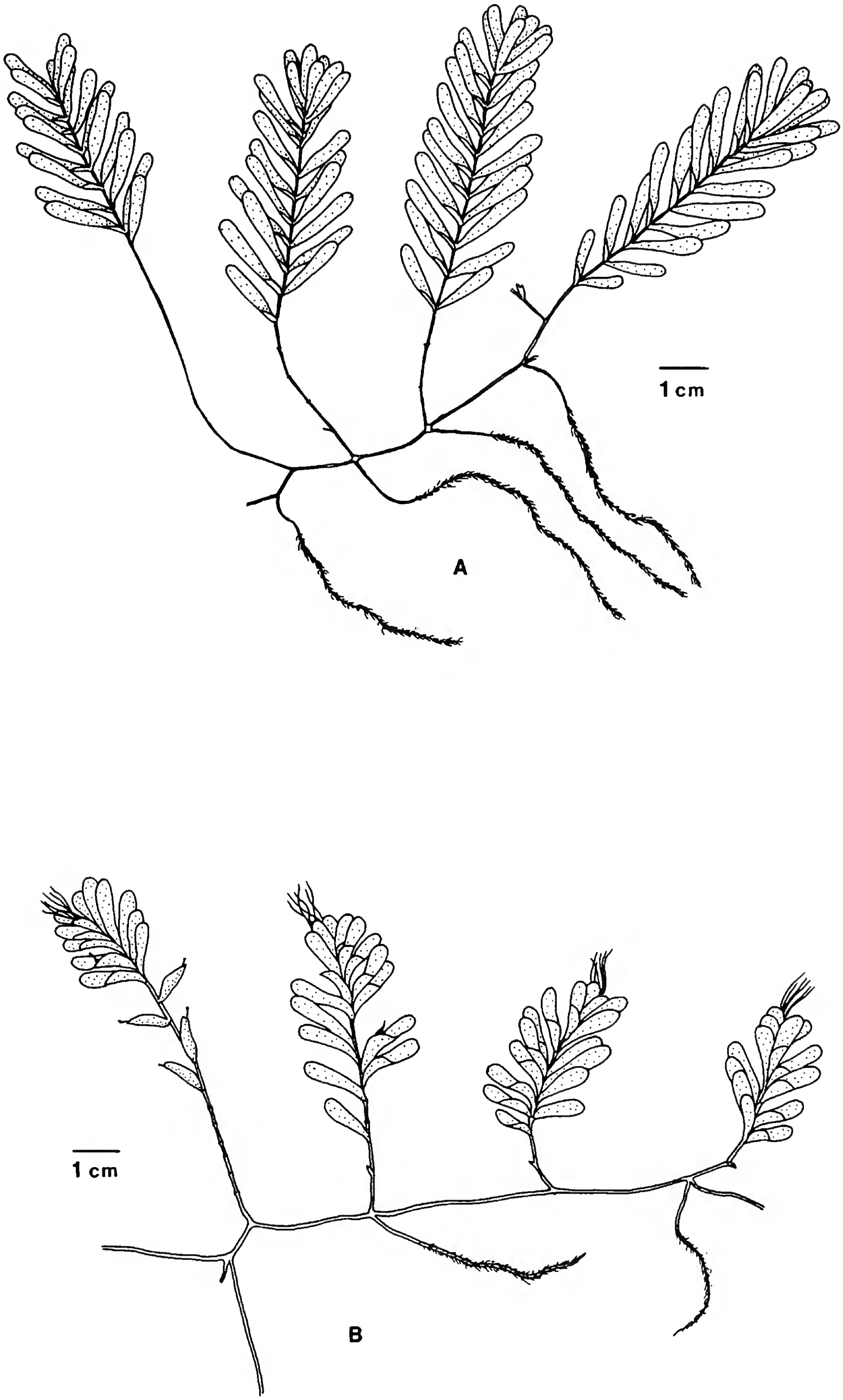

FIGURE 54.—*Halophila spinulosa:* A, habit of sterile plant; B, habit of female plant.

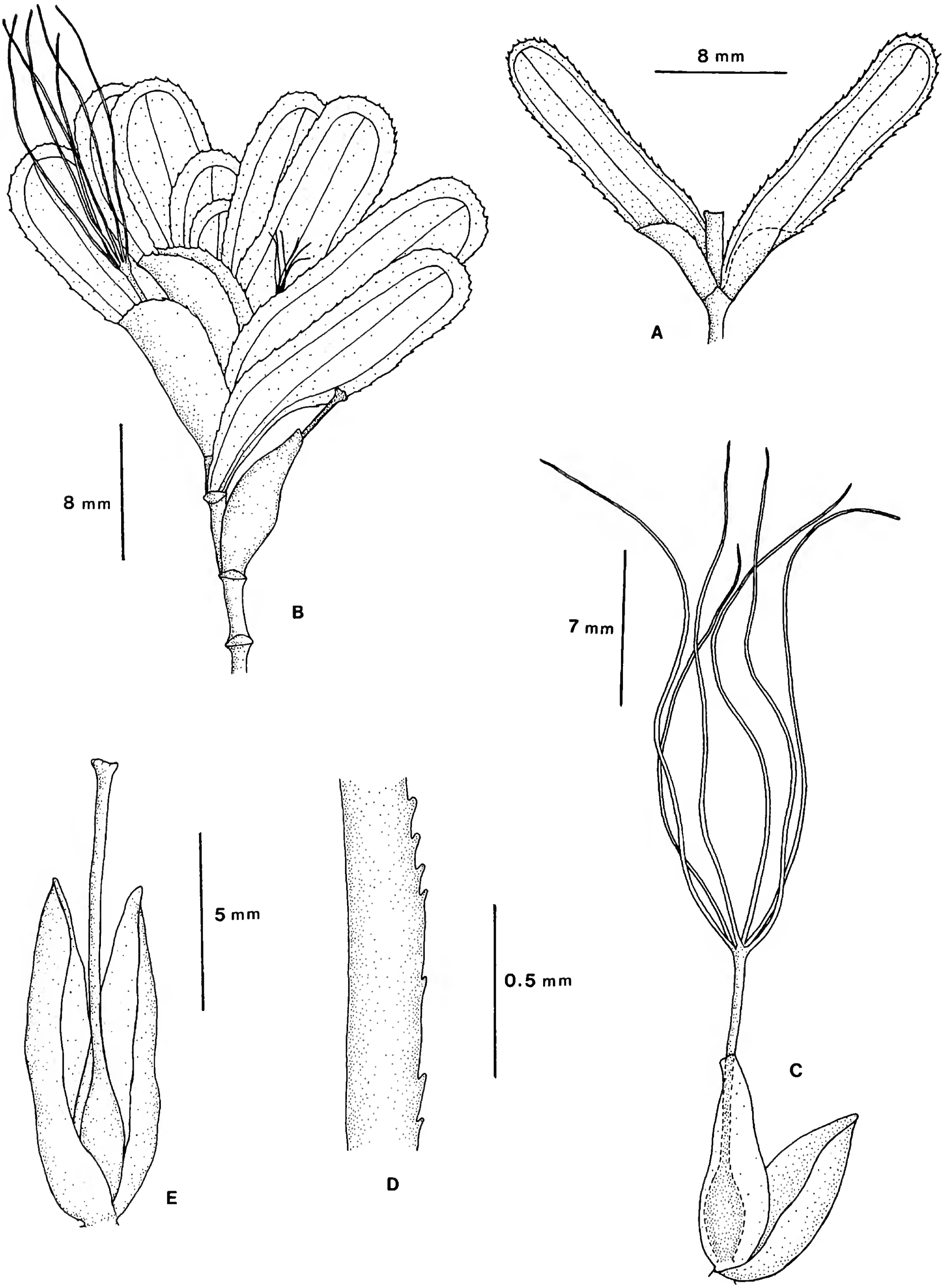

FIGURE 55.—*Halophila spinulosa:* A, portion of an erect shoot with two amplexicaulous leaves, showing folded basal end; B, shoot bearing pistillate flowers; C, pistillate flower enclosed in spathe; D, magnified portion of a style with papillae; E, spathe enclosing beaked fruit.

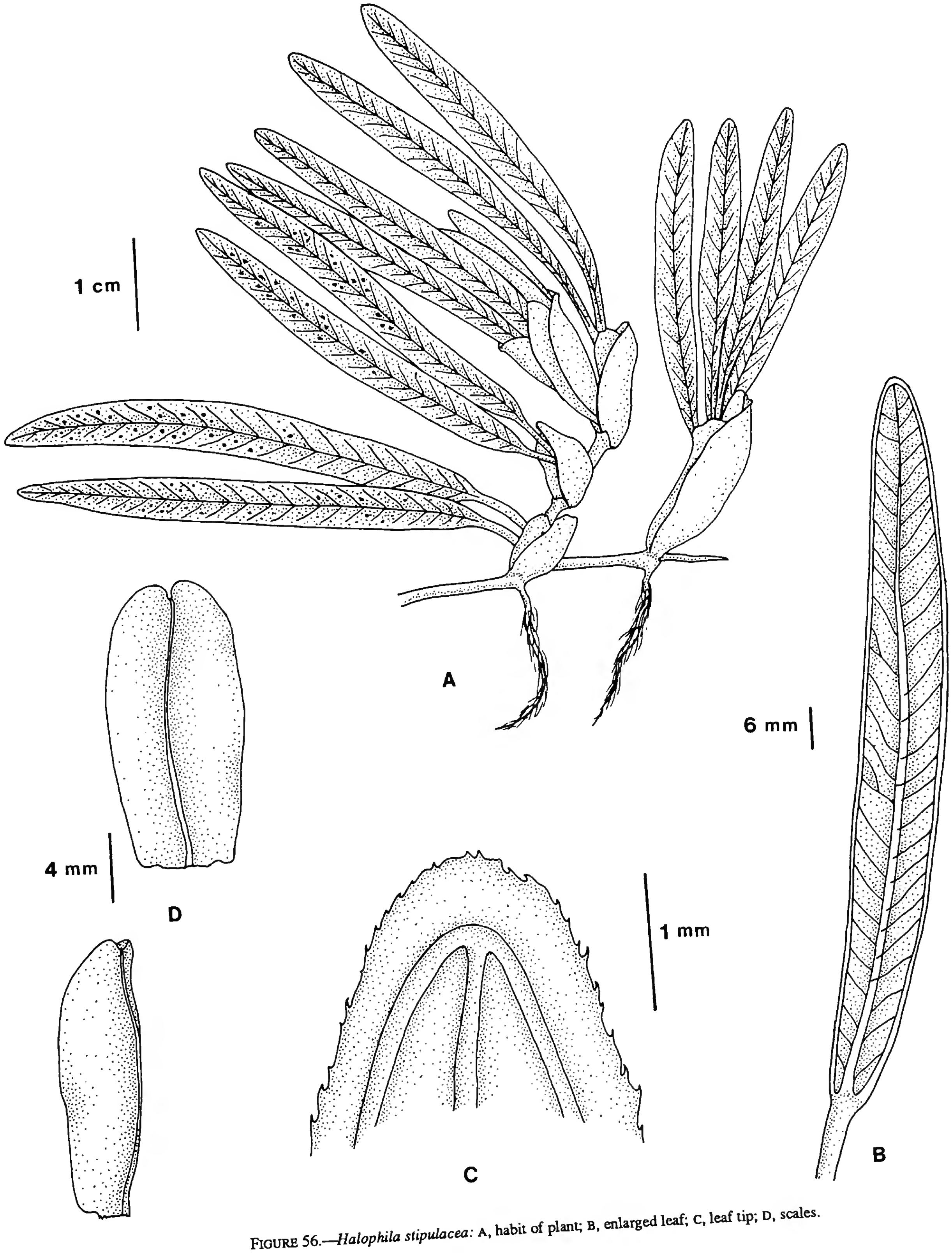

FIGURE 56.—*Halophila stipulacea:* A, habit of plant; B, enlarged leaf; C, leaf tip; D, scales.

Halophila tricostata Greenway

FIGURE 57

CHARACTERISTICS.—Rhizome 1 mm wide. Leaf blades 1.2–2.0 cm long, 2–4 mm wide, margins serrulate; base cuneate-sheathing. Erect shoots 8–18 cm long, 2–3 leaves on each node, 6–18 nodes on each shoot shoot. No cross veins in leaf; there are only 3 primary parallel veins in each blade. Dioecious.

NATURAL HISTORY.—Plants were found between 15–30 m deep on a substrate of coarse coral sand, shell fragments, and foraminiferans.

DISTRIBUTION.—Plants were collected at Lizard and Magnetic Islands, Great Barrier Reef, Queensland, Australia.

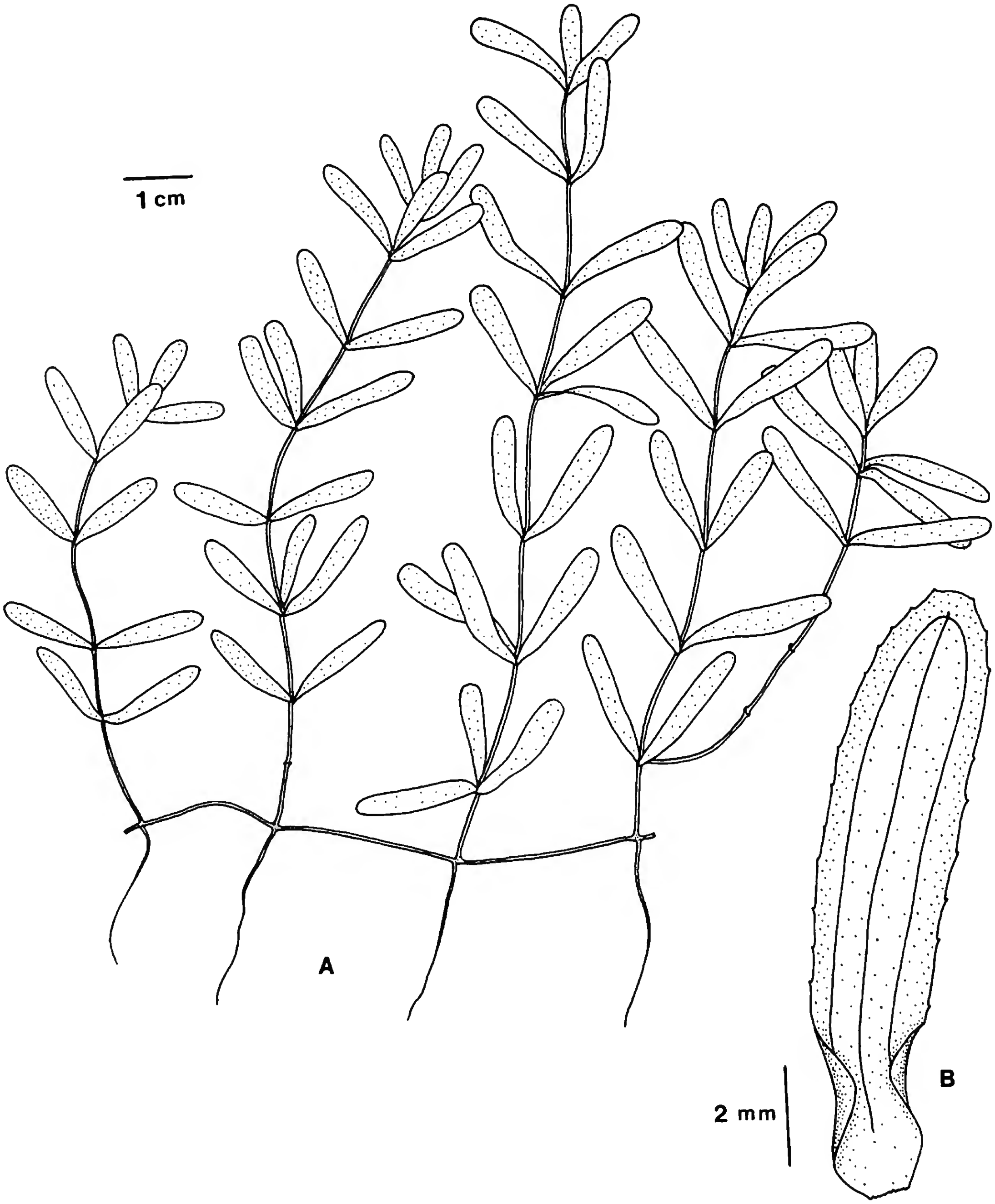

FIGURE 57.—*Halophila tricostata:* A, habit of plant; B, enlarged leaf.

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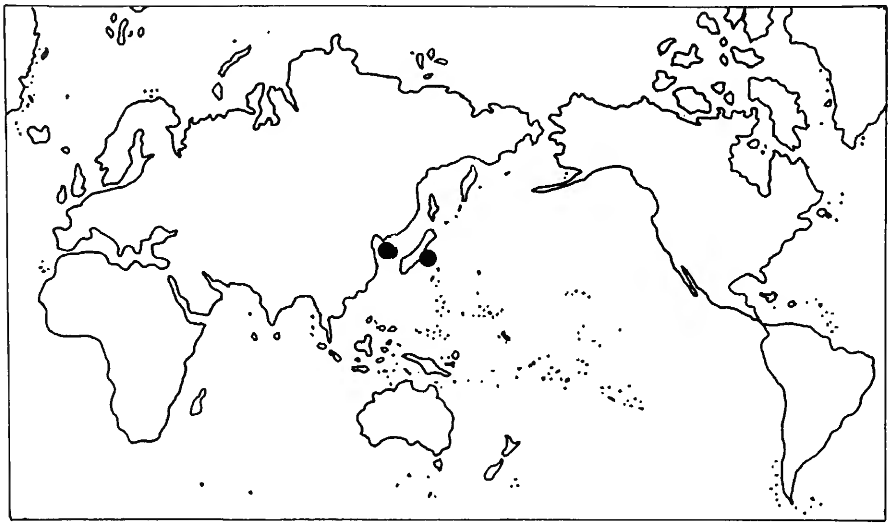
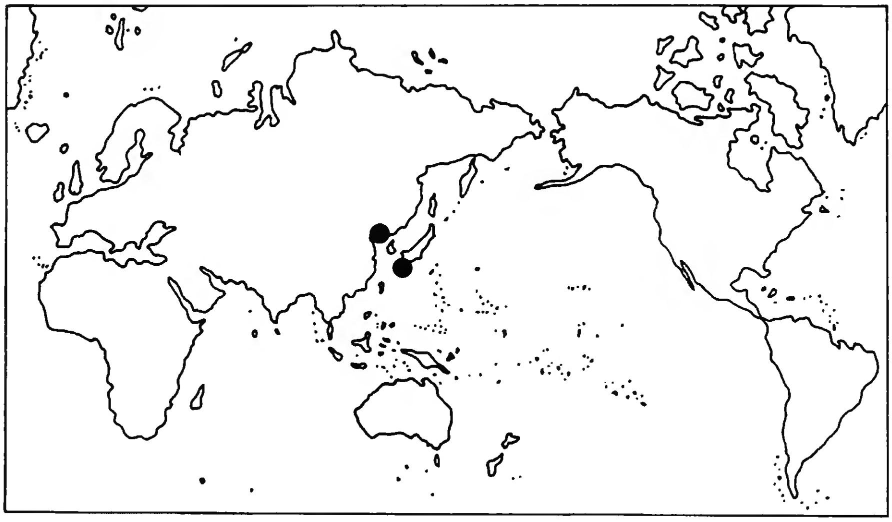
Worldwide Distribution Maps

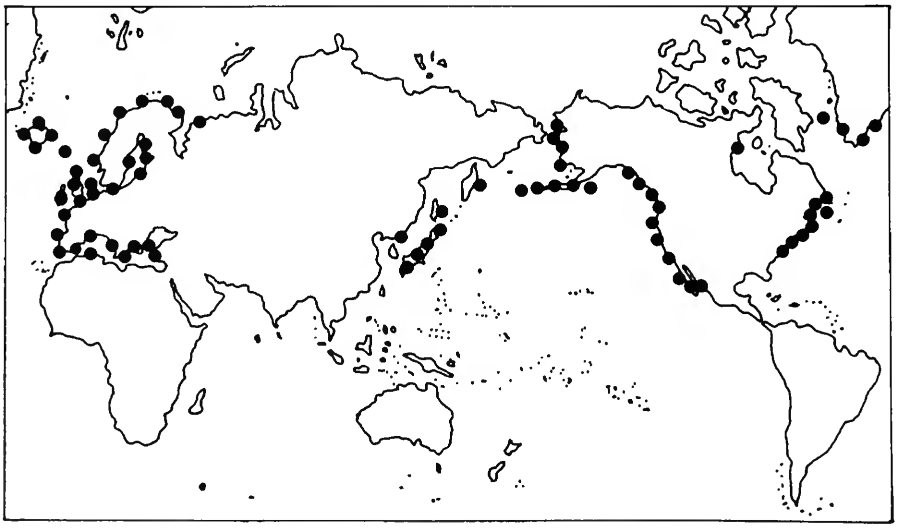
MAP 1
Zostera asiatica



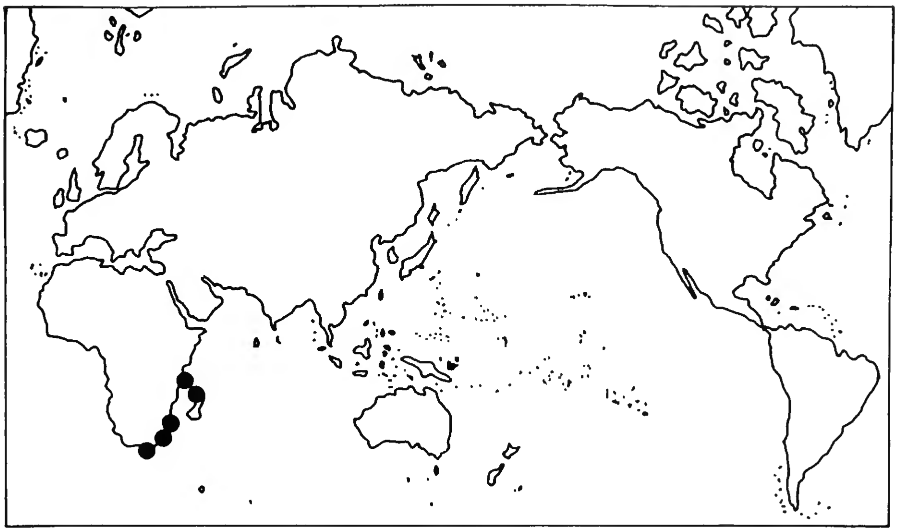
MAP 2
Zostera caulescens



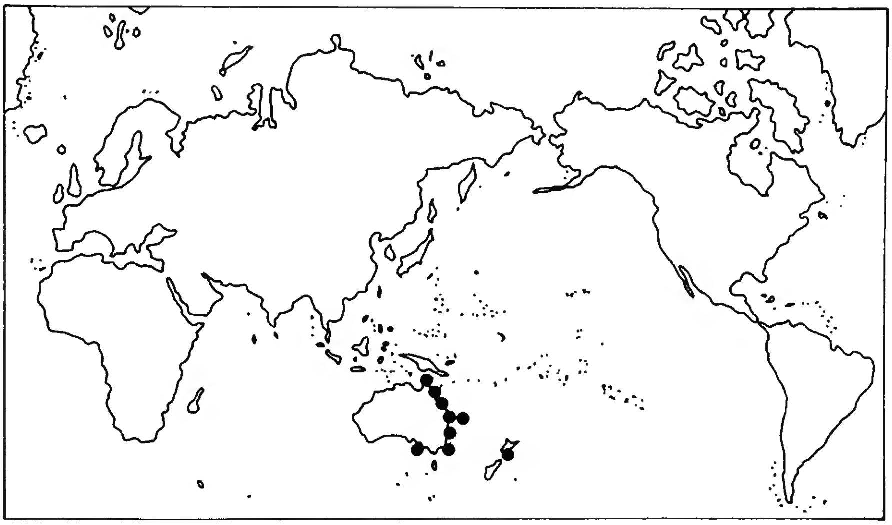
MAP 3
Zostera marina



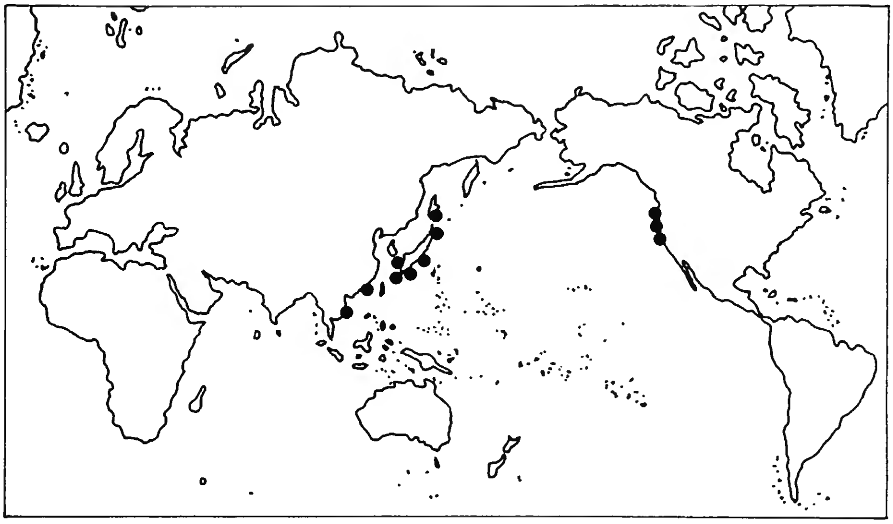
MAP 4
Zostera capensis



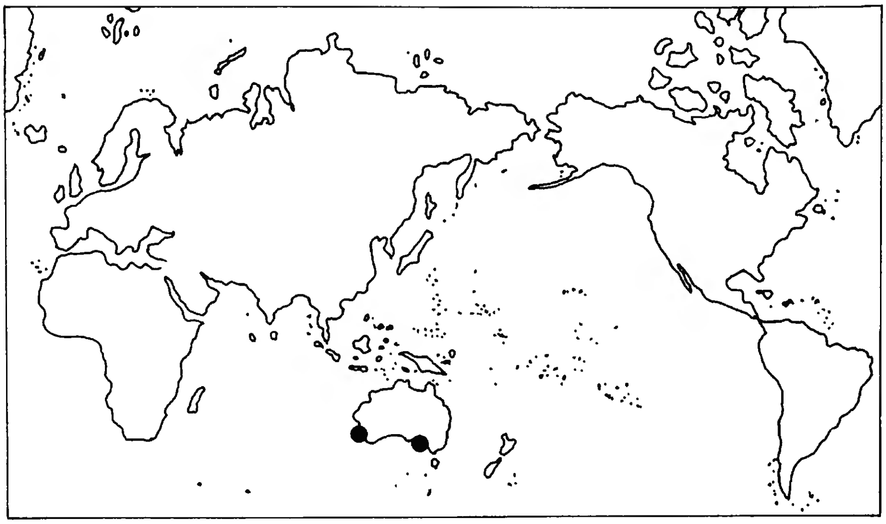
MAP 5
Zostera capricorni



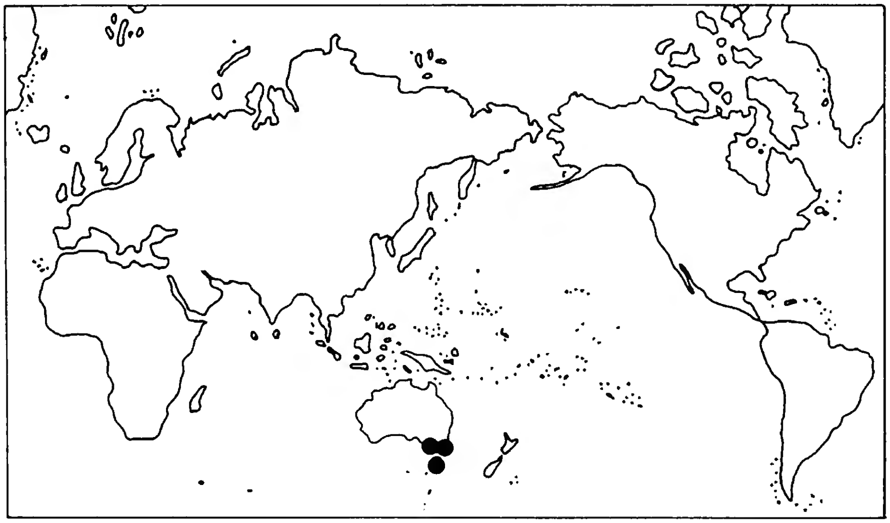
MAP 6
Zostera japonica



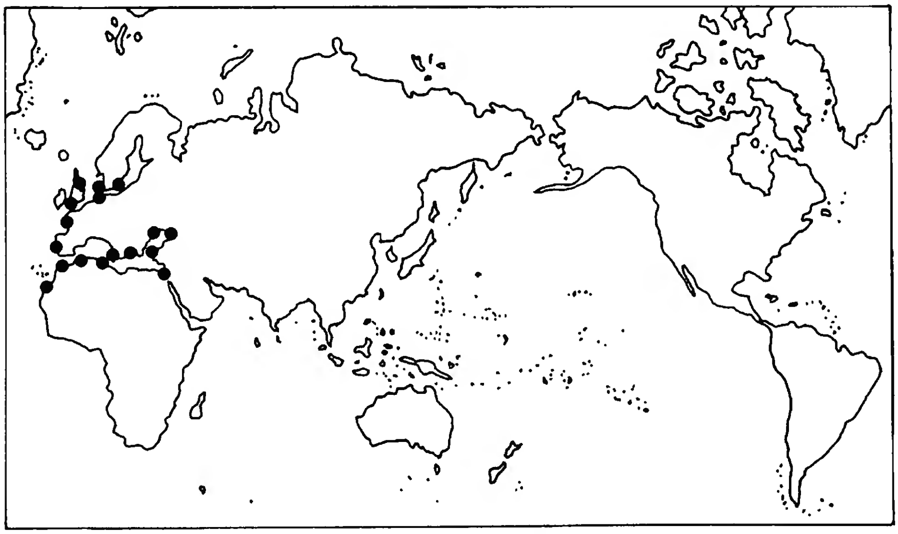
MAP 7
Zostera mucronata



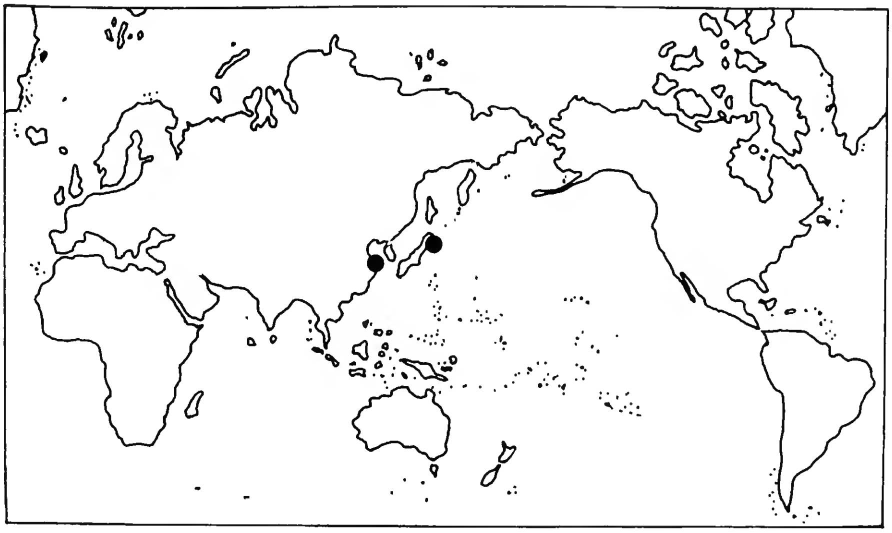
MAP 8
Zostera muelleri



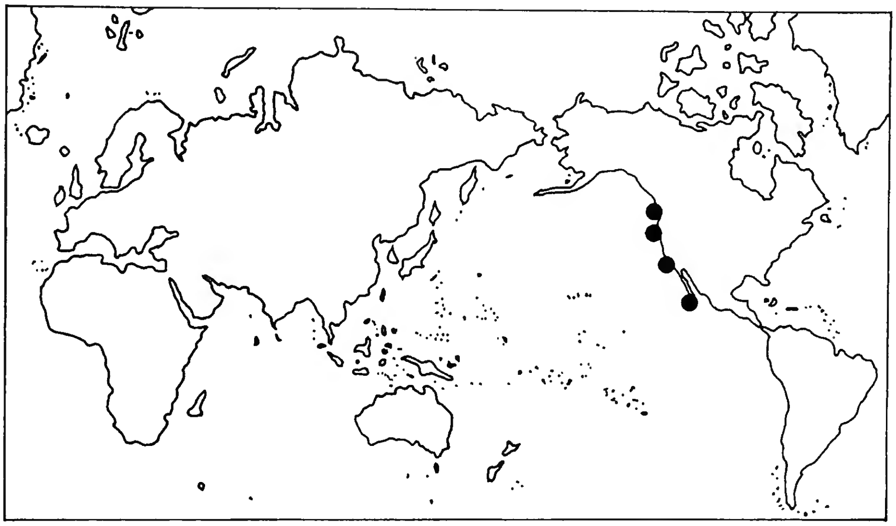
MAP 9
Zostera noltii



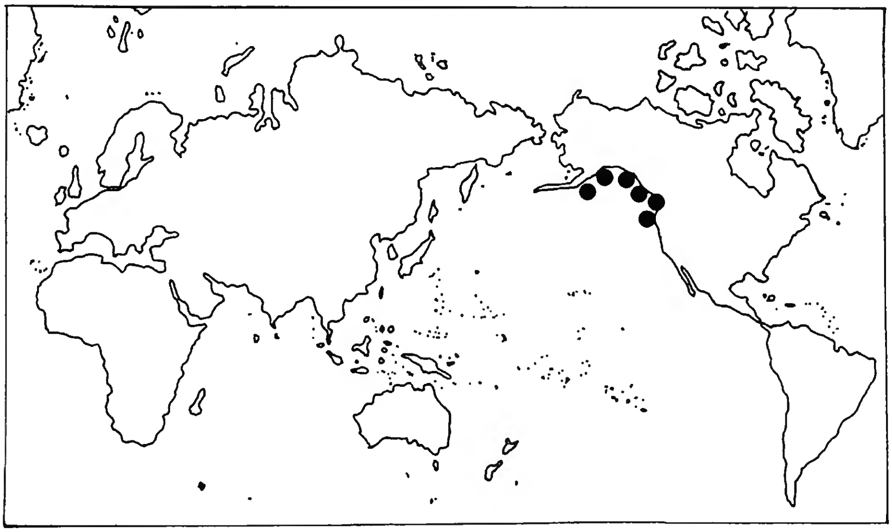
MAP 10
Phyllospadix iwatensis



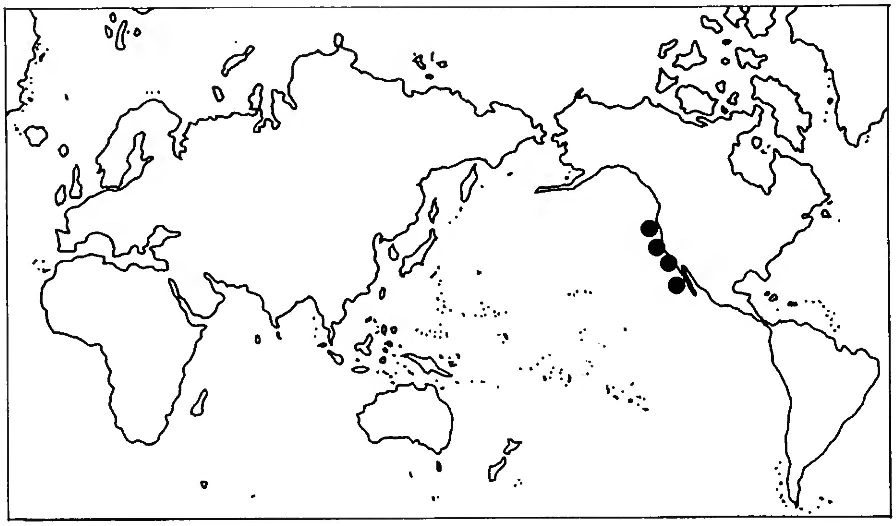
MAP 11
Phyllospadix scouleri



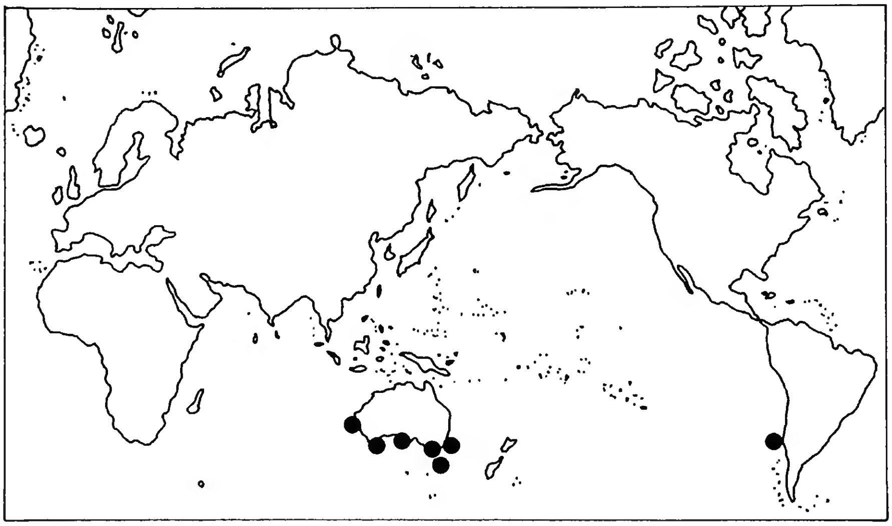
MAP 12
Phyllospadix serrulatus



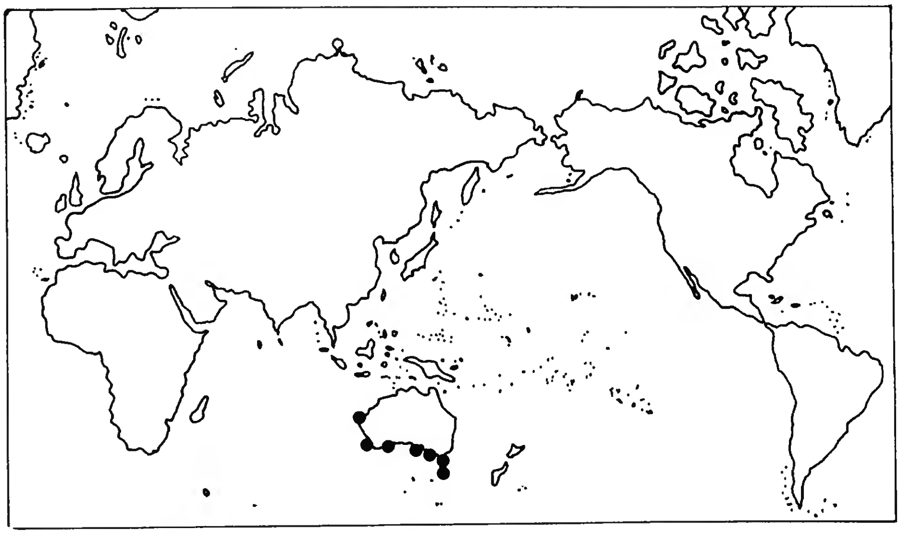
MAP 13
Phyllospadix torreyi



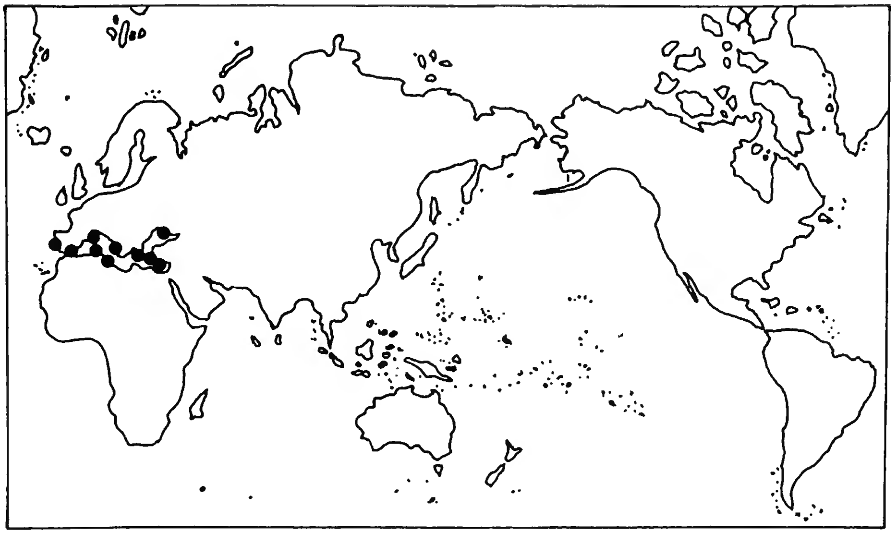
MAP 14
Heterozostera tasmanica



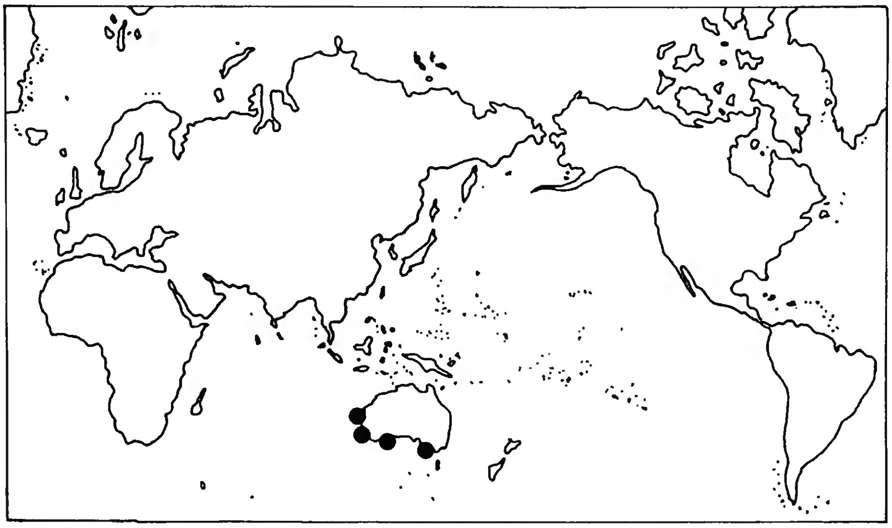
MAP 15
Posidonia australis



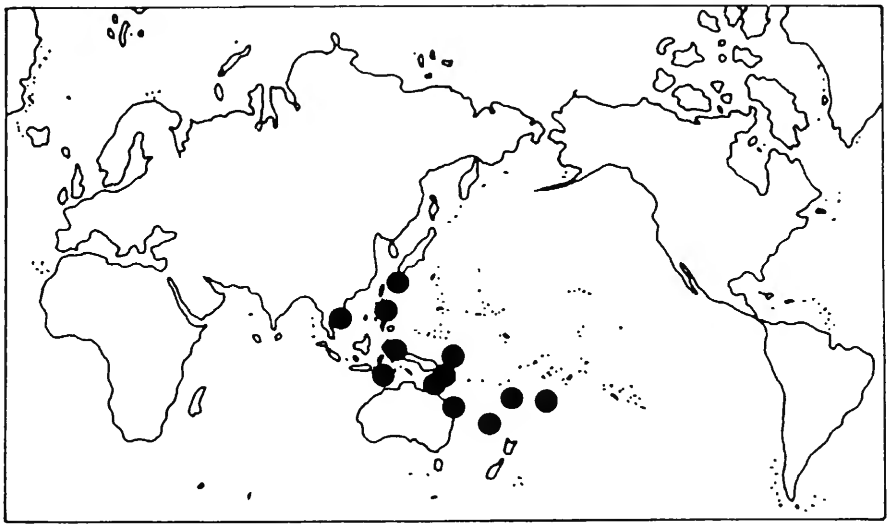
MAP 16
Posidonia oceanica



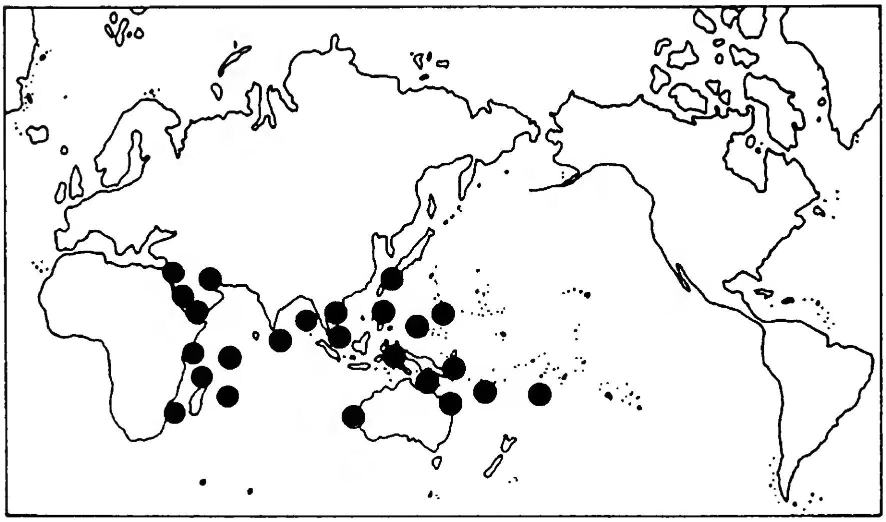
MAP 17
Posidonia ostenfeldii



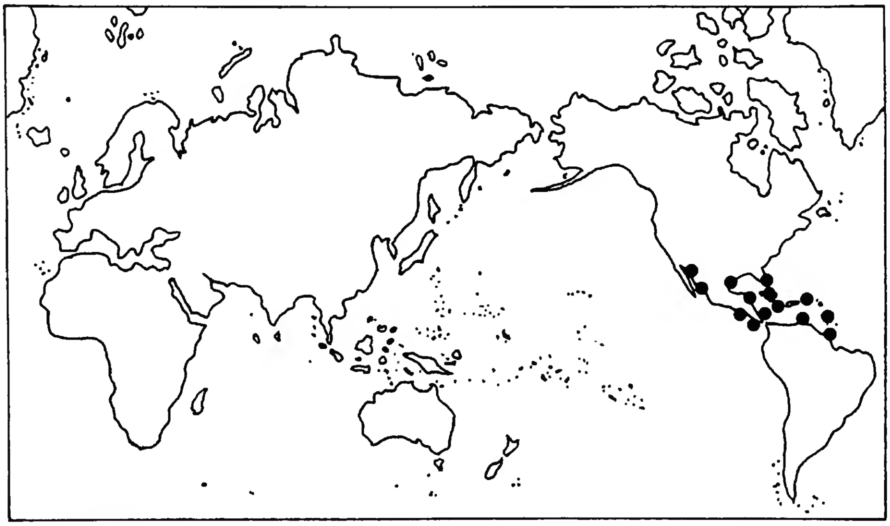
MAP 18
Halodule pinifolia



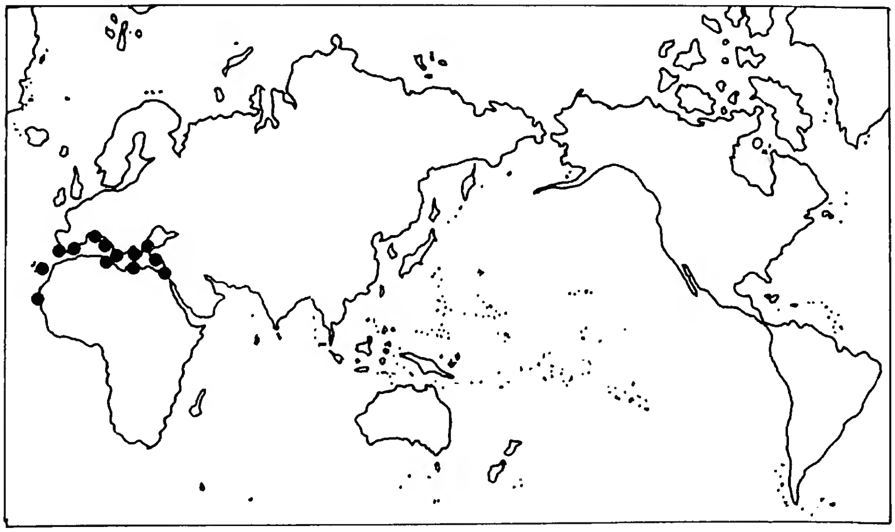
MAP 19
Halodule uninervis



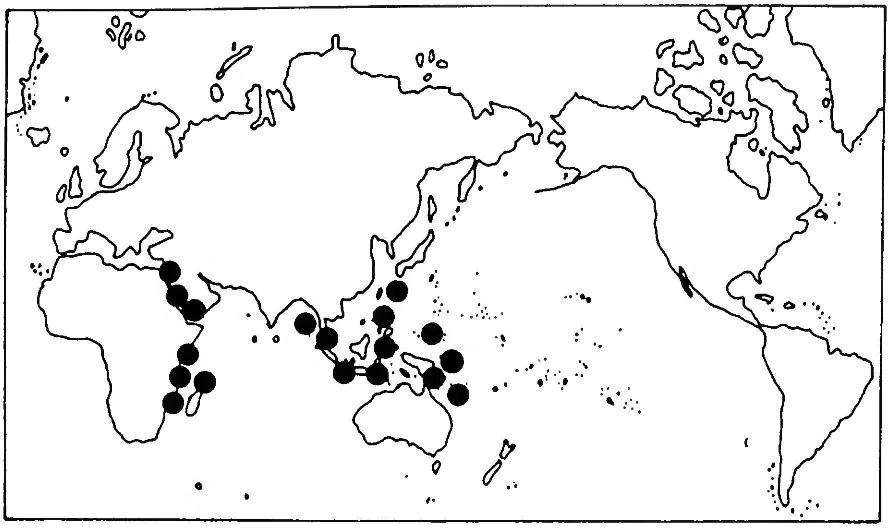
MAP 20
Halodule wrightii



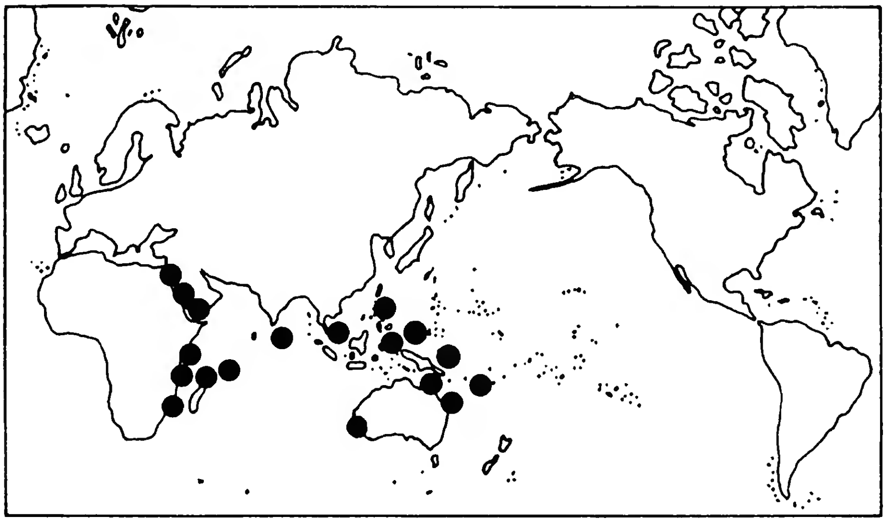
MAP 21
Cymodocea nodosa



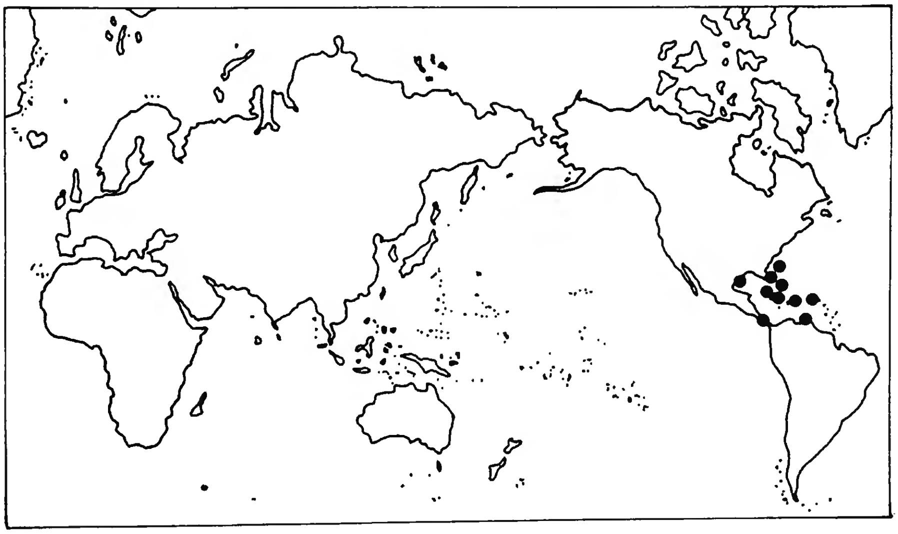
Map 22
Cymodocea rotundata



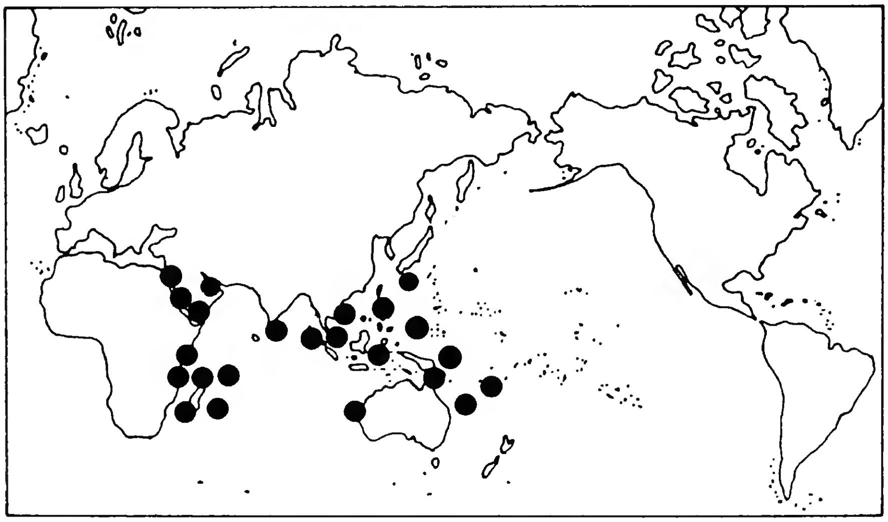
Map 23
Cymodocea serrulata



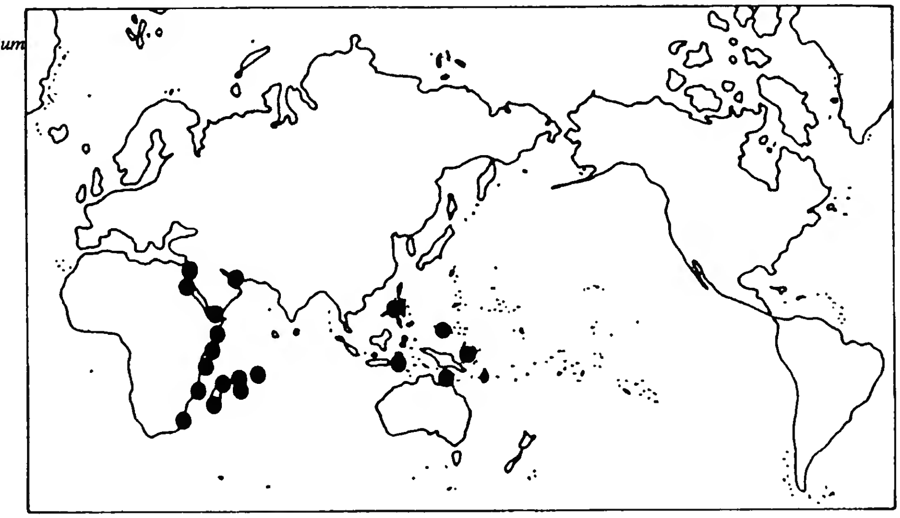
Map 24
Syringodium filiforme



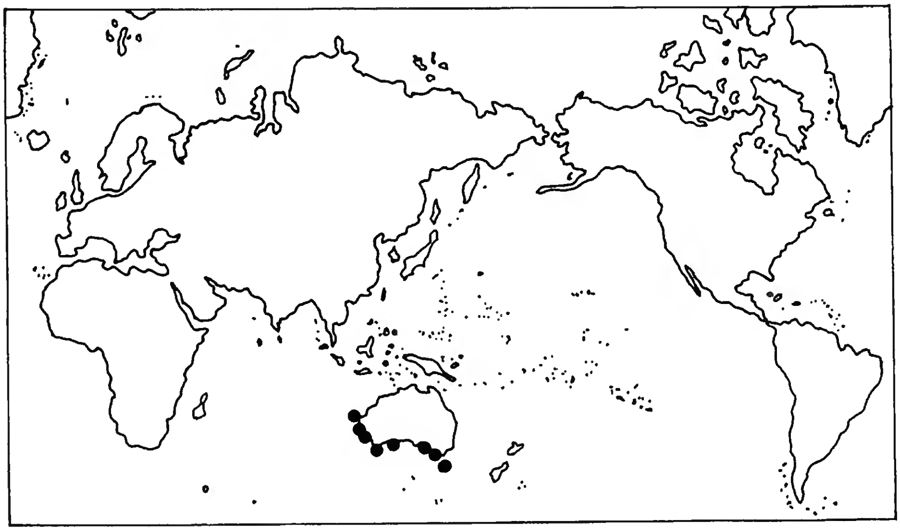
MAP 25
Syringodium isoetifolium



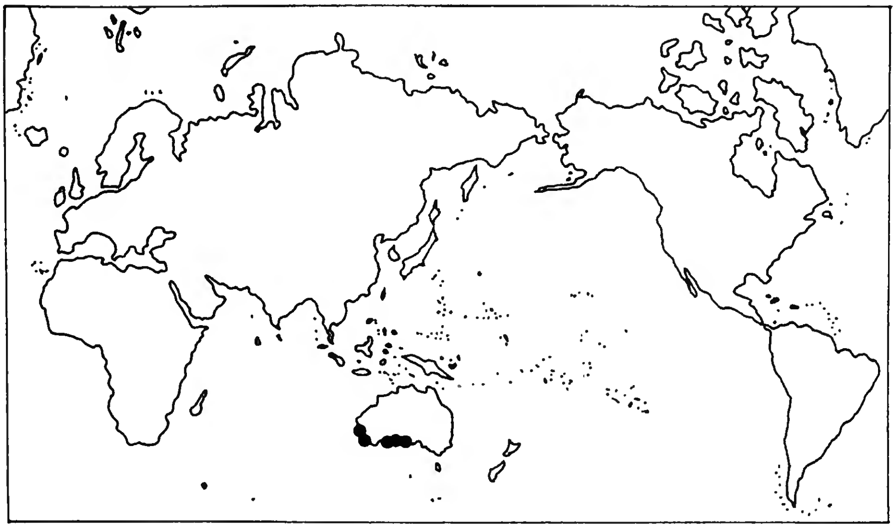
MAP 26
Thalassodendron ciliatum



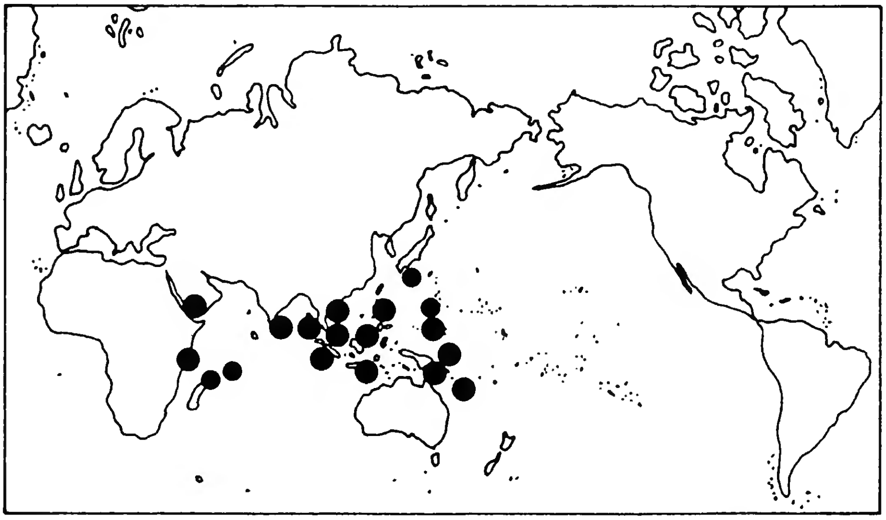
MAP 27
Amphibolis antarctica



MAP 28
Amphibolis griffithii

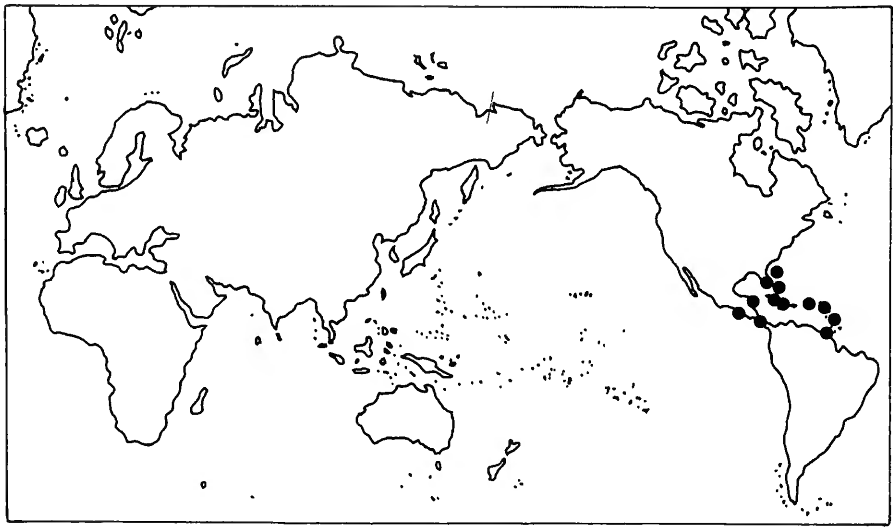


MAP 29
Enhalus acoroides

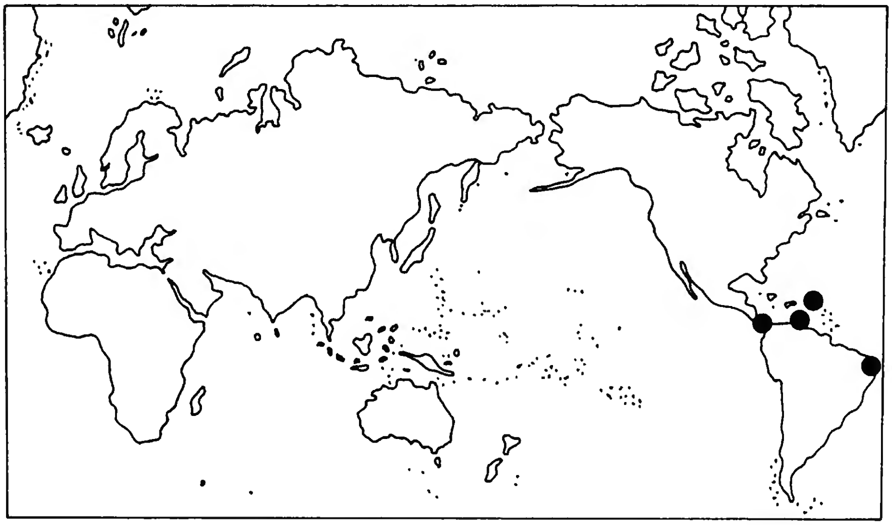


MAP 30
Thalassia hemprichii

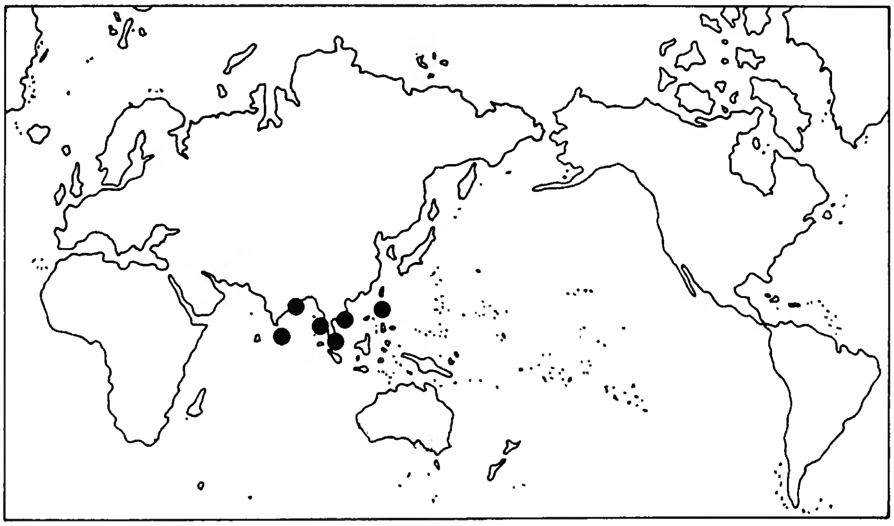
MAP 31
Thalassia testudinum



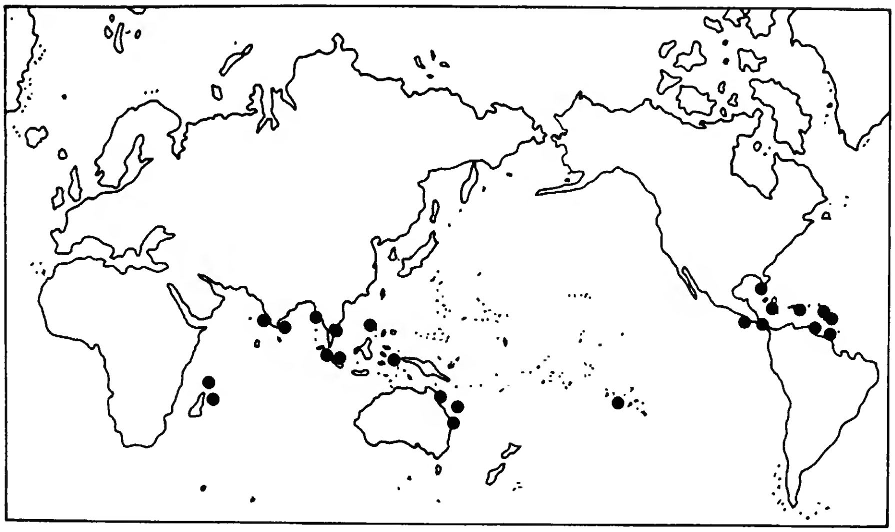
MAP 32
Halophila baillonis



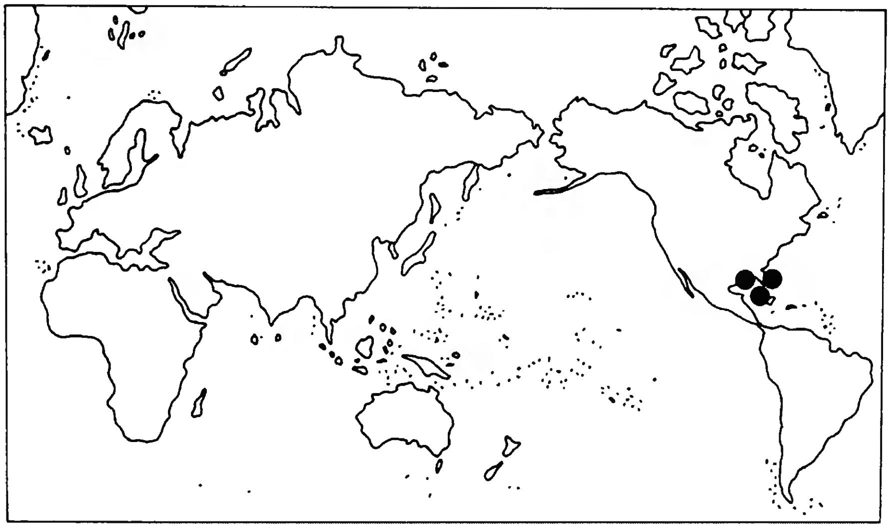
MAP 33
Halophila beccarii



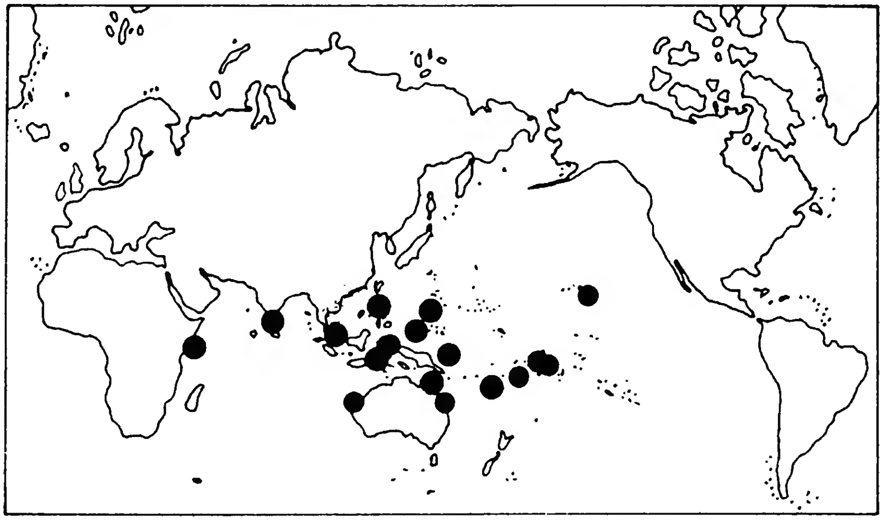
MAP 34
Halophila decipiens



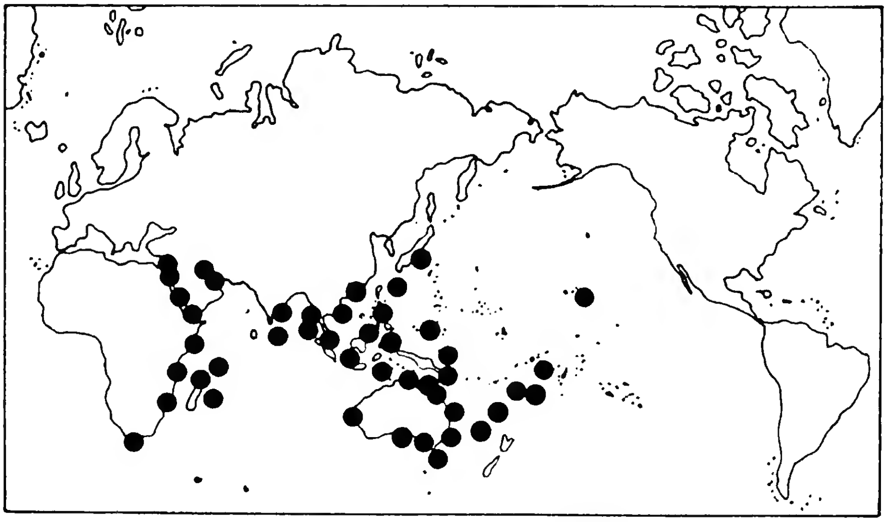
MAP 35
Halophila engelmannii



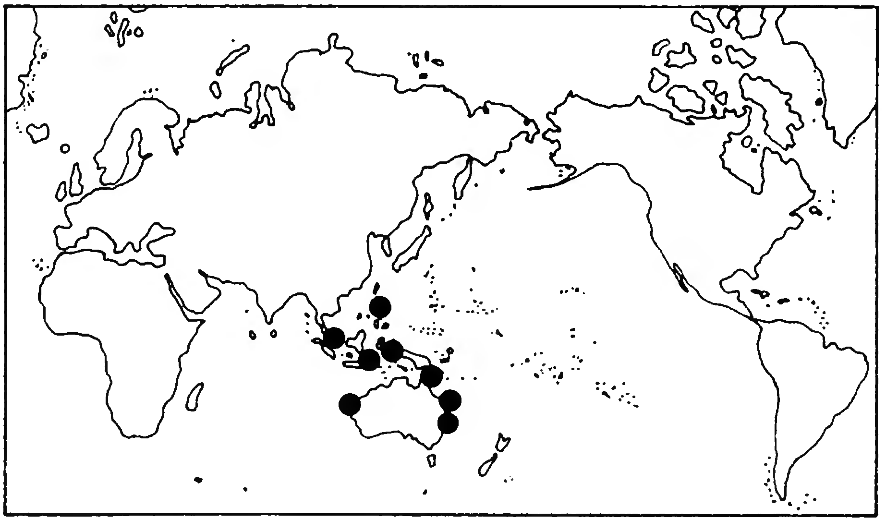
MAP 36
Halophila minor



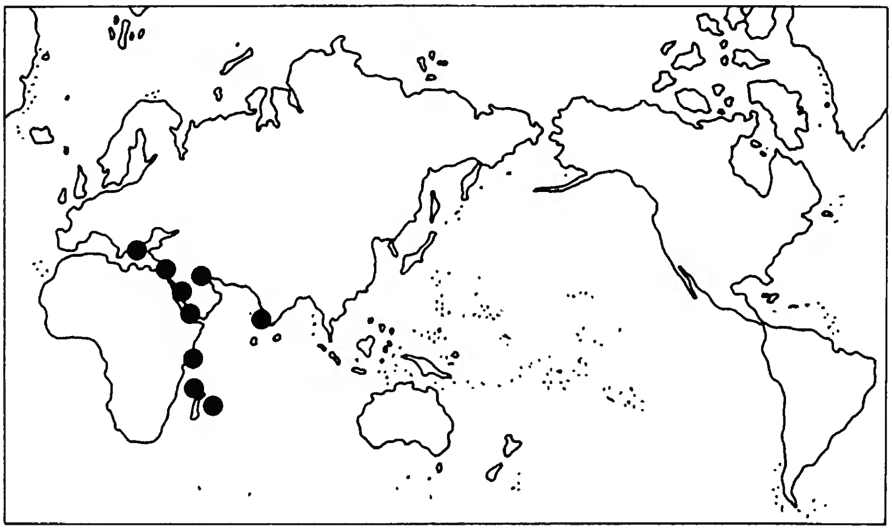
MAP 37
Halophila ovalis



MAP 38
Halophila spinulosa



MAP 39
Halophila stipulacea



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Tabulations within text (lists of data, often in parallel columns) can be typed on the text page where they occur, but they should not contain rules or numbered table captions.

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Synonymy in zoology must use the short form (taxon, author, year:page), with full reference at the end of the paper under "Literature Cited." For botany, the long form (taxon, author, abbreviated journal or book title, volume, page, year, with no reference in "Literature Cited") is optional.

Text-reference system (author, year:page used within the text, with full citation in "Literature Cited" at the end of the text) must be used in place of bibliographic footnotes in all Contributions Series and is strongly recommended in the Studies Series: "(Jones, 1910:122)" or ". . . Jones (1910:122)." If bibliographic footnotes are required, use the short form (author, brief title, page) with the full citation in the bibliography.

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