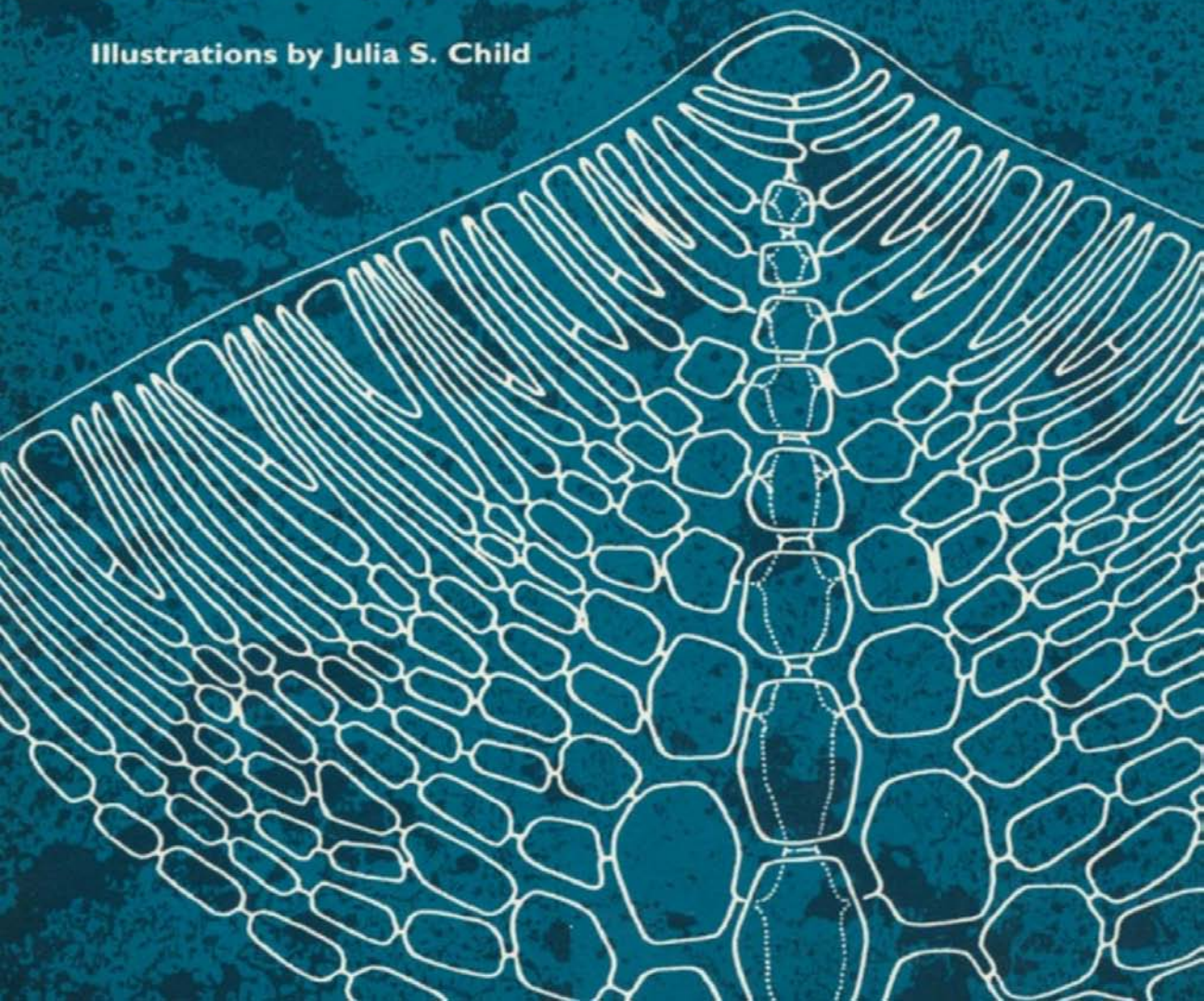


**SEAWEEDS
OF THE
SOUTHEASTERN
UNITED STATES**

CAPE HATTERAS TO CAPE CANAVERAL

Craig W. Schneider and Richard B. Searles

Illustrations by Julia S. Child



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Craig W. Schneider and Richard B. Searles

Trinity College, Hartford, and Duke University, Durham

Illustrations by Julia S. Child

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Dedicated to Ginny and Georgie

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PREFACE

The purpose of this book is to provide a manual for the identification of the seaweeds along the southeastern Atlantic coast of the United States. It is intended as a field guide and laboratory manual for professional and amateur biologists with an interest in the identification of marine plants. The emphasis is therefore on keys, descriptions, and illustrations. Many of the larger, more distinctive seaweeds will be recognizable simply from the illustrations; more difficult taxa will require study of the keys and descriptions. Background and practical information are included in the introductory sections.

The genesis of this book was a joint effort by the authors to investigate the seaweed flora of the deep offshore waters of the Carolinas in the early 1970s. One of the joys of our research was the investigation of the offshore "reefs" and shipwrecks by SCUBA diving. The opportunity to collect while swimming over rock outcroppings never seen before by phycologists or, in most cases, any divers was a unique opportunity that allowed us to explore a special wilderness at our doorstep. At the beginning of our collaboration the only comprehensive report of the seaweeds for the Carolinas was Hoyt's 1920 publication on the marine algae of Beaufort, N.C. During the course of our studies Donald Kapraun published his accounts of the nearshore flora of the Carolinas, but the richness of the offshore waters indicated to us that a comprehensive account of both inshore and offshore seaweeds was needed. At the same time, we began to collect plants in Georgia and realized that with a few additions we could extend the geographic coverage of our book throughout the natural biogeographic region defined by Cape Hatteras and Cape Canaveral. Included in the flora are over 300 species of green, golden brown, brown, and red seaweeds. Faced with the scope of this project and our own limitations of time, energy, and expertise, we chose not to incorporate the Cyanobacteria and vascular flowering plants that grow in the marine and estuarine waters of the region.

The coastal waters of the southeastern United States are a valuable resource, both regionally and nationally. In order to safeguard that resource, we need to know the biological components of the region and understand their interactions. The seaweeds are one of the critical elements in the biological communities in the estuaries and ocean waters of the region, and we hope that this book will make people more aware of these plants, make the plants easier to identify, and stimulate additional studies of them for years to come.

ACKNOWLEDGMENTS

In our preparation of this book and the study of the seaweeds described here we have had the assistance of numerous friends and colleagues, and, at the risk of leaving some out, we thank a few of them: Chuck Amsler, David Ballantine, Dick Barber, Steve Blair, John Brauner, Dan Duerr, Sherry Epperley, Chris van den Hoek, Bill Kirby-Smith, Max Hommersand, Eric Houston, Bill Johansen, Donald Kapraun, Geoff Leister, Paulette Peckol, Joe Ramus, Richard Reading, Steve Ross, Tony Scheer, Susan Vlamynck, James Willis, and Reid Wiseman. Special thanks are due to Paul Silva and Mike Wynne, who, in addition to other kinds of help, each read the rough draft of the manuscript and offered many crucial, critical, and constructive suggestions. Our editor was amazed at the detailed and careful work that they did. Errors of commission and omission have surely crept in since their reading, and for these we accept all responsibility. At the penultimate moment, Geoff Leister came forward to assist with the conversion of the manuscript to the software required for publication.

We are also grateful to the curators and keepers of the herbaria that have made collections available to us. These include the Agardh Herbarium, Lund, Sweden; Allan Hancock Foundation; Botanical Museum, University of Copenhagen; Farlow Herbarium, Harvard University; Muséum National d'Histoire Naturelle, Paris; Harbor Branch Foundation; New York Botanical Garden; Smithsonian Institution; University of Georgia; University of Michigan; University of North Carolina, Chapel Hill; University of North Carolina, Wilmington; and the University of Puerto Rico, Mayagüez.

During the course of the studies leading to the writing of this book we have been supported by grants from the National Science Foundation, the National Oceanographic and Atmospheric Administration, the state of Georgia, and the state of North Carolina. The Duke University Marine Laboratory has been an important base for much of our fieldwork, and without its logistical support our task would have been much more difficult. Our home institutions—Trinity College and Duke University—have been very generous with funds for both research and illustrating the book. Most of the illustrations are the work of a gifted scientific illustrator, Julia S. Child, whom we were fortunate to involve in the project. A few of the illustrations are our own or those of former students at Trinity College, Wendy A. Pillsbury, Richard Reading, Margaret Soltysik, and Shelby Tupper. Charles D. Amsler contributed his expertise on the local species of the Ectocarpaceae by preparing the taxonomic treatment of that family.

The study of the seaweeds in this region has occupied a combined total of over forty years of the authors' lives. During this time our wives, Ginny and Georgie, have provided both the emotional and practical support needed, and we want them to know that it has been appreciated and crucial to the completion of this work.

INTRODUCTION

The coast of the southeastern United States appears barren of seaweeds, but in fact it supports a great diversity of them. In an early account of the seaweeds of the region Harvey (1852) noted that the comparable coast of Europe had more kinds of seaweeds. He attributed the lower diversity here to the prevalence of sandy shores, as contrasted with the rocky coast of Europe. With hundreds of miles of open, sandy beaches, the coast appeared to Harvey as it appears to others: a region mostly devoid of suitable habitats for seaweeds. Investigations going back over 100 years have shown, however, that the waters between Cape Hatteras and Cape Canaveral have a rich and interesting flora of more than 300 seaweed species, even though on some of its shores, particularly the open beaches, seaweeds are few in number. The increase in our knowledge of the flora is reflected graphically in figure 1, which indicates an initial flurry of activity in the mid-nineteenth century, a period of inactivity, and then a steady increase in knowledge through most of the present century, beginning with W. D. Hoyt's notable publication in 1920.

The diversity of seaweeds reflects to some degree the diversity of habitats in the region. Because of the system of barrier islands that fringe the coast and enclose the shallow-water sounds, there are actually many more miles of shore than the distance between the two capes defining the region suggests. Natural rocky shores are almost nonexistent, but in many places jetties, seawalls, groins, bridge supports, and other semipermanent hard structures have been erected that may support algal growth (Hay and Sutherland 1988). Furthermore, large expanses of sheltered, intertidal, and shallow subtidal wetlands lie protected inside barrier islands. Seaweeds are often plentiful in such habitats; they are anchored to shells, worm tubes, or other animal remains, and they grow on or tangled among the marsh grasses and subtidal flowering plants that cover extensive areas in the sounds. These shallow sounds produce large quantities of some seaweeds—enough *Gracilaria*, for instance, to support an agar industry during World War II. In addition, there are areas on the continental shelf offshore where sedimentary rocks emerge through the mantle of sandy sediment to provide a habitat within reach of sunlight that supports a substantial growth of seaweeds.

The seaweeds in the region are of great importance to their marine communities because they provide much of the three-dimensional structure. Along with the vascular plants of the estuaries and the phytoplankton, the seaweeds are the source of the primary production which fuels the abundant populations of herbivores, carnivores, omnivores, detritivores, commensals, and parasites in these waters.

The geographic extent of the flora covered in this work corresponds with the warm temperate waters of the southeastern United States (Searles 1984a). The greatest diversity of seaweeds in this region occurs in North Carolina between

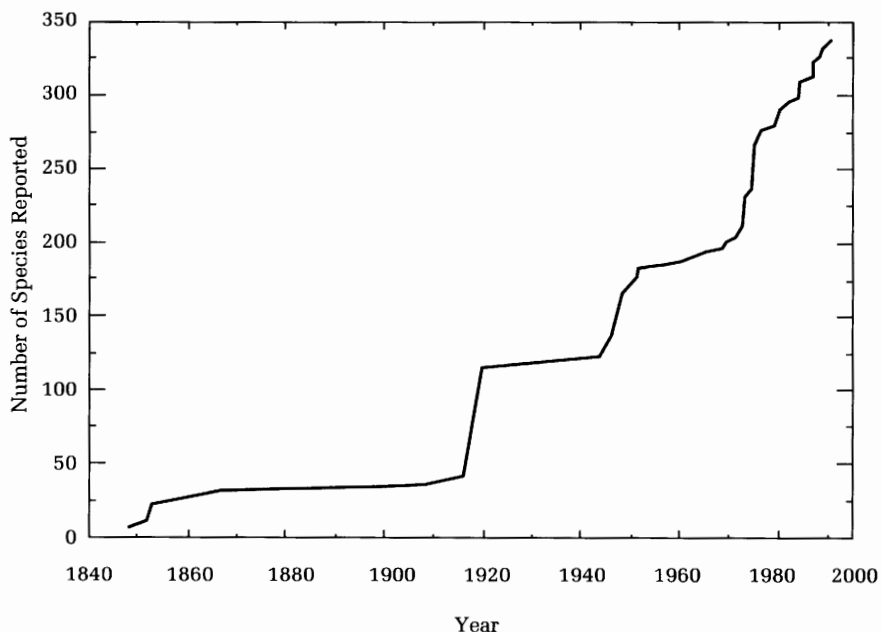


Figure 1. Changes in the number of species reported in the region since the 1840s.

Cape Lookout and Cape Fear. A few additional species appear in the waters south of Cape Fear, but no marked change in the flora is observed until the more tropical waters and seaweeds of southern Florida are reached; conversely, north of Cape Hatteras the characteristic species have centers of distribution in cool, northern waters.

Harvey (1852, 1853, 1858), in his three-part treatise on the seaweeds of North America, listed 28 species from the southeastern United States. By the early part of this century, Hoyt (1920) was able to list 123 species and varieties (excluding Cyanobacteria), mostly from North Carolina. At present, 337 taxa are known, and it seems an appropriate time to bring together the increased knowledge of seaweeds into a single volume.

The marine multicellular representatives of four divisions of eukaryotic algae are included in this flora: the Chlorophyta, the Phaeophyta, the Chrysophyta, and the Rhodophyta. Prokaryotic algae (Cyanobacteria or Cyanophyta) have not been included. For identification of marine Cyanobacteria we suggest reference to Humm and Wicks (1980). For identification of the marine and brackish-water flowering plants we suggest Godfrey and Wooten (1979, 1981).

**SEAWEEDS OF
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HISTORY OF PHYCOLOGY IN THE REGION

Study of the seaweed flora of the mid-Atlantic region began in the mid-1800s when local naturalists sent specimens to experts, most of whom were in Europe. Some of these experts also visited the region, including the noted phycologist William H. Harvey from Trinity College, Ireland. In addition, information came from reports by people responsible for general surveys of the total flora. The situation began to change in the early 1900s as local colleges began to develop into major universities; phycologists were added to their faculties and they gradually developed the diversity of expertise in marine botany we now enjoy.

The first records of seaweeds in the region were published by Jacob W. Bailey (1848, 1851), a member of the faculty at West Point. He reported on plants sent to him from Charleston, South Carolina, by Lewis R. Gibbes and plants he himself collected on a trip to South Carolina and Florida. Bailey corresponded with several of the phycologists in Europe, with Harvey in particular.

Harvey was an oddity among the phycologists of his era, for he actually traveled abroad, personally making many of the collections on which he reported. Most of his colleagues, in contrast, remained in Europe and only processed plants collected and sent to them by resident overseas naturalists or those who were accompanying the voyages of exploration and commerce that were characteristic of the times. In 1850 Harvey traveled along the coast collecting seaweeds between Halifax, Nova Scotia, and Key West, Florida. In January, and again in March, he visited Charleston, South Carolina. There he collected seaweeds with Lewis Gibbes, a local collector who had previously sent specimens to him in Dublin. Harvey also received Charleston specimens from H. W. Ravenel and specimens from North Carolina from C. Congdon. The results of his observations on these plants were published in 1852, 1853, and 1858 as his *Nereis Boreali-Americana; or Contributions to a History of the Marine Algae of North America* under the auspices of the Smithsonian Institution. In this three-part tome he listed twenty-eight species from the region: two from North Carolina, twenty-four from South Carolina, and two not specifically from the region but from all parts of the American coast. One of the South Carolina plants was described as the new species *Grateloupia gibbesii* Harvey, the epithet honoring its collector.

The Reverend Mr. M. A. Curtis (1867) was the first local botanist to publish on the seaweeds of the region; he listed thirty-six species of red, brown, and green seaweeds as well as four blue-green algae in his catalogue of indigenous and naturalized plants of North Carolina. Some of the specimens remain from this early collection, and those that have not been found are readily assignable to common members of the flora. Sixteen of his collections were new records for the region.

J. Cosmo Melvill (1875) published a short account of collections he made in the Charleston area and in Key West, Florida, but within the region these included only three species not previously listed by Harvey.

Duncan S. Johnson of Johns Hopkins University visited the U.S. Fish Commission Laboratory in Beaufort, North Carolina, in June 1899. Based on observations he made there, he published (1900) an account of the algae of the adjacent sounds, listing fifteen species of seaweeds.

The single most illuminating account of the seaweeds in the region in those early days came from a professor of biology at Washington and Lee University, W. D. Hoyt. He collected plants primarily in the region surrounding Beaufort, North Carolina, in the years 1903–1909, but he also visited sites from Okracoke, North Carolina, through South Carolina to Tybee, Georgia. His description of 133 species, varieties, and forms of seaweeds and Cyanobacteria (1920) was more comprehensive than previous accounts for the region and indicated a diverse and interesting flora. Hoyt described the seasonality of North Carolina seaweeds and the overlap of tropical and temperate species that occurs just south of Cape Hatteras. In addition to working along the shore, Hoyt made two dredge collections from offshore in deep water; these were a preview of the rich collecting that would follow at offshore locations in later years.

A further contribution by Hoyt was his study of the reproduction and life history of local populations of *Dictyota* (Hoyt 1907, 1927). With cultured plants he demonstrated the alternation of their generations and observed a monthly periodicity in the formation of gametes in which eggs and sperm are released at the time of the full moon at flood tides. This pattern contrasted with the twice-monthly release of gametes in what was considered to be the same species, *D. dichotoma*, in European waters. Hoyt therefore recognized a new variety, *menstrualis*, which has only recently (Schnetter et al. 1987) been elevated as a separate species, in part on the basis of the differences noted by Hoyt. In addition to that variety, Hoyt described alone (1920) or together with M. A. Howe of the New York Botanic Gardens (1916) ten new species of algae based on plants from the region, most of them small and obscure epiphytic or endophytic plants.

In 1904 James J. Wolfe, a biologist who had studied algae for his Ph.D. at Harvard, was hired on the staff at Trinity College in Durham, North Carolina (later to become Duke University). A native South Carolinian, he was the first resident specialist on the algae in the region. At Beaufort, North Carolina, he followed up Hoyt's study of *Dictyota* with similar studies of the local species of *Padina*, *P. gymnospora* (as *P. variegata*). He demonstrated its alternation of generations and the genetic determination of male and female sexuality while disproving the suggestion that eggs developed parthenogenetically (1918). He died at an early age in 1920, leaving unfinished a monograph on the marine diatoms of the region.

Wolfe was followed at Duke University by the first chairman of its new Department of Botany, Hugo L. Blomquist, an eclectic systematist who published ex-

tensively on bryophytes and flowering plants as well as seaweeds. He authored a series of papers, mostly on ectocarpalean algae (Blomquist 1954, 1955, 1958a, 1958b), but started with an initial account (Blomquist and Pyron 1943) of seaweeds which drifted up on the beach near Beaufort, North Carolina, following a major hurricane in 1940; that account was followed by a listing of additions to the local flora of Beaufort (Blomquist and Humm 1946).

One of Blomquist's students, Louis G. Williams, made reciprocal transplant studies of local *Codium* "species," demonstrating that plants reported as *C. tomentosum* were ecophenic variants of *C. decorticans* (1948b). Williams's greatest contribution (1948a, 1949) was a detailed study of the seasonal changes in the flora at the Cape Lookout jetty in North Carolina. These observations on seasonality expanded those made by Hoyt at nearby Beaufort. In an investigation of the algae on the "Black Rocks" off the North and South Carolina coast, Williams (1951) also published the first report of seaweeds in the region collected by divers.

During this same general time T. A. and Anne Stephenson were conducting the North American part of their worldwide descriptive investigation of intertidal communities. In 1952 they published an account of intertidal plants and animals of Charleston, South Carolina, and Beaufort, North Carolina, complementing Williams's intertidal studies.

Harold J. Humm, another student of Blomquist's at Duke University, later became part of the faculty. Humm demonstrated a variety of interests. During the 1940s he became involved in the wartime effort to find substitutes for the agar products which had previously been imported from Japan. He and others published a series of papers describing agar, local seaweed resources, and the suitability and characteristics of extracts from *Hypnea musciformis* and *Gracilaria verrucosa* (as *G. confervoides*; Humm 1942, 1944, 1951; Humm and Wolf 1946; Micara 1946; Causey et al. 1946; DeLoach et al. 1946a, 1946b). During the war a viable agar industry was centered in Beaufort, North Carolina, using locally collected *Gracilaria* as well as plants brought in from elsewhere along the East Coast.

In 1952 Humm described the flora on the intertidal rocks at Marineland, Florida, the only account of seaweeds from the coast of Florida north of Cape Canaveral since the visit of Bailey to Saint Augustine more than 100 years earlier. Several papers followed, written by or with students about the seaweeds of North Carolina (Aziz and Humm 1962; Earle and Humm 1964; Humm and Cerame-Vivas 1964; Aziz 1967).

William Randolph Taylor published two landmark books on the floras of the western Atlantic Ocean which in part covered the waters of the southeastern United States. The first, published in 1937 (revised in 1957), covered the sea-

weeds of the northeastern United States, and the second, published in 1960, concerned the seaweeds of the tropical and subtropical coasts from Cape Hatteras to Brazil. The mid-Atlantic coast of the United States lies at the edges of these two regions, and Taylor's books were therefore the greatest stimulus and aid to study of the local seaweeds since the publication of Hoyt's 1920 report.

In the early 1960s the University of North Carolina at Chapel Hill added Max H. Hommersand to its staff, and he trained a number of students who contributed to the knowledge of the seaweeds of North Carolina and the region. Donald W. Ott investigated the marine representatives of the xanthophycean genus *Vaucheria* in North Carolina (Ott and Hommersand 1974); Carol Aregood (1975) studied the red alga *Nitophyllum medium* and placed it in a new genus, *Calonitophyllum*; Gayle I. Hansen (1977a, 1977b) completed a morphological and cultural study of another red algal genus, *Cirrulicarpus*, and in particular the local species *carolinensis*; Charles F. Rhyne (1973) investigated the biology of the local species of the green alga, *Ulva*, discovering that most plants belonged to two species not previously recognized as part of the flora; Joy F. Morrill (1976) included local Rhodomelaceae in her study of the dorsiventral members of that group; Joseph P. Richardson resolved questions about the ecology of the seasonal seaweeds *Dictyota menstrualis* (as *D. dichotoma*; 1979), *Dasya baillouviana* (1981), and *Bryopsis plumosa* (1982), which disappear during parts of the year; and Paul W. Gabrielson included regional members of the Solieriaceae in his extensive study of species in that family (Gabrielson 1983; Gabrielson and Hommersand 1982a, 1982b).

Humm moved on to the University of South Florida, and Richard B. Searles came to Duke University and trained several students who studied the local flora. Two of these—D. Reid Wiseman and James Fiore—began their studies with Humm. Wiseman's studies included a survey of the algae from South Carolina (1966, 1978); Fiore (1969, 1977) investigated the life histories of several brown algae, naming the new genus *Hummia* on the basis of some of those studies (1975). Nancy J. Alexander (1970) investigated the genus *Enteromorpha* on the jetty at Fort Macon; John F. Brauner (1975) made a seasonal investigation of the epiphytic algae on seagrasses in the Beaufort, North Carolina, area; and, somewhat later, Mitsu M. Suyemoto (1980) studied the crustose coralline red algae in the offshore waters of Onslow Bay.

Working with Searles, initially as a student, Craig W. Schneider began an investigation of the seaweeds in offshore waters, continuing the work started by Hoyt. Schneider, Searles, and their students combined to publish a series of papers expanding and refining the knowledge of the flora (Reading and Schneider 1986; Schneider 1974, 1975a, 1975b, 1975c, 1980, 1984, 1988, 1989; Schneider and Eiseman 1979; Schneider and Searles 1973, 1975, 1976; Searles 1972, 1984b,

1987; Searles, Hommersand, and Amsler 1984; Searles and Leister 1980; Searles and Lewis 1982; Searles and Schneider 1990; Wiseman and Schneider 1976). Schneider also published monographic studies of the genera *Audouinella* (1983) and *Peyssonnelia* (Schneider and Reading 1987) from the region and described two new genera of red algae, *Searlesia* and *Calliclavula*. Searles described the endophytic brown algal genus *Onslowia* and the red algal genus *Nwynea*. Between them they described twenty-five new species of green, brown, and red seaweeds and with others expanded the known flora from the offshore waters of the region by ninety-nine species. In the process they provided the data for an analysis of the biogeographic relationships of the flora within the region and between neighboring regions and for the productivity of the offshore waters (Schneider 1975d, 1976; Schneider and Searles 1979; Searles and Schneider 1980; Searles 1984a).

Another Searles student, Paulette Peckol, conducted descriptive and experimental ecological studies of the deep-water algal communities on a rock ledge off Cape Lookout (Peckol 1982; Peckol and Searles 1983, 1984). She also made comparative physiological studies of deep-water and shallow-water seaweeds (Peckol 1983; Peckol and Ramus 1985).

In Georgia, Russell L. Chapman (1971, 1973) published accounts of the marine algae of that coast, and Stephen M. Blair and Margaret O. Hall (1981) described a collection of plants from offshore South Carolina and Georgia waters. Searles, stimulated by the establishment of a small rocky area off the coast of Georgia as the Gray's Reef National Marine Sanctuary, published several papers (Searles 1981, 1983, 1987; Searles and Ballantine 1986) and a field guide (1988) describing the offshore flora and several new species. Joseph Richardson, having joined the faculty at Savannah State University, published two papers (Richardson 1986, 1987) on the seaweeds of the near-shore waters of Georgia.

With the appointment of Donald F. Kapraun to the faculty of the University of North Carolina at Wilmington in the mid-1970s there was for the first time a marine phycologist who was a full-time resident at the coast. Kapraun turned much of his attention to the local flora and produced a series of papers clarifying the taxonomic concepts in difficult genera such as *Polysiphonia*. He used controlled culture conditions to study the physiological, cytological, and morphological characteristics of the plants (1977a, 1977b, 1978a, 1978b, 1978c, 1979; Kapraun and Freshwater 1987; Kapraun and Luster 1980; Kapraun and Martin 1987). He also used data from his cultural studies, which related temperature and light conditions to growth and reproduction, in a floristic analysis of the region (1980b). Kapraun and Zechman (1982) made a study of the phenology and vertical distribution of the seaweeds on the jetty at Masonboro Inlet. Kapraun's observations of the seaweeds along the coast and in the sounds of North Carolina

were brought together in a two-volume work (Kapaun 1980a, 1984) describing that flora, the first such work since the pioneering publication of Hoyt. One of Kapaun's students, Charles D. Amsler, investigated the ectocarpalean algae of the region (Amsler 1983, 1984a, 1984b, 1985; Amsler and Kapaun 1985), comparing plants in culture with field-collected plants. He has contributed the section on the Ectocarpaceae in this book.

Work on the local seaweeds continues as a new generation of phycologists brings new techniques and insights to the study of seaweeds. Taxonomic studies are giving way to, or are being supplemented by, ecological, physiological, genetic, and cytological investigations using the wealth of species available. These investigations will ultimately lead to a clearer taxonomic and floristic understanding of the seaweeds of the region.

THE GEOLOGICAL ENVIRONMENT

The region between Cape Hatteras and Cape Canaveral (figure 2) is almost exclusively a region of sandy shores. The nearest natural rocky coastlines to the north are in Long Island Sound. The sandy shore extends south from there, interrupted occasionally by capes and inlets, to southern Florida, where rocky outcroppings reappear as the limestone remains of coral formations. The most prominent cape on the mid-Atlantic coast of the United States is Cape Hatteras, which marks the northern boundary of the region covered in this flora. The only natural rocky shores within the region are very small outcroppings of sedimentary rock at Marineland, Florida, and Fort Fisher, just north of Cape Fear, North Carolina.

The mainland is drained by rivers that originate either in the mountains, the piedmont foothills, or within the coastal plain. The rivers deposit their sediments in the sounds behind the barrier islands. The sands of the outer coast beaches are not recent deposits; they are relict sediments incorporated into the beaches and islands as the shoreline moved inland.

Sea level retreated beyond the edge of the continental shelf more than 20,000 years ago; 18,000 years ago it began to rise and move inland; in the last 5,000 years sea level has risen only a few meters, but the rate at which it has been rising has been increasing in the present century and is currently reflected in high rates of erosion and island migration along many parts of the coast.

The characteristic features of the coast are the barrier islands which front the shallow-water sounds. At the northern end of the region the sounds stretch almost unimpeded up the coastal plain where they form the broad, shallow, highly productive waters of the Pamlico Sound and Neuse River estuary. Along much of the coast to the south the sounds push up against relict barrier islands and are long and narrow. Along the Georgia coast the new barrier islands have fused with old barrier islands to form the relatively broad Georgia Sea Islands. In Florida, like the Carolinas, the sounds are again long and narrow. In North Carolina and northeastern Florida, where tidal ranges are small, the barrier islands are long and inlets are infrequent. In the middle of the region (South Carolina and Georgia) tidal ranges double, increasing the volume of water that enters and exits the sounds twice each day. As a result, inlets tend to occur more frequently, making the islands shorter.

The continental shelf off the barrier islands varies in width. At Cape Hatteras it is about 35 km wide and forms Diamond Shoals. The continental shelf becomes progressively wider to the south until, off Georgia, it is 135 km wide; it then narrows along the Florida coast to 55 km off Cape Canaveral. On the continental shelf, sedimentary rocks are generally covered by a thin layer of shell and sand or muddy sediment unsuitable for anchoring most seaweeds. Rocks emerge through the sediments in some areas across the width of the shelf, and there is an almost continuous band of exposed rock along the outer margin of the continen-

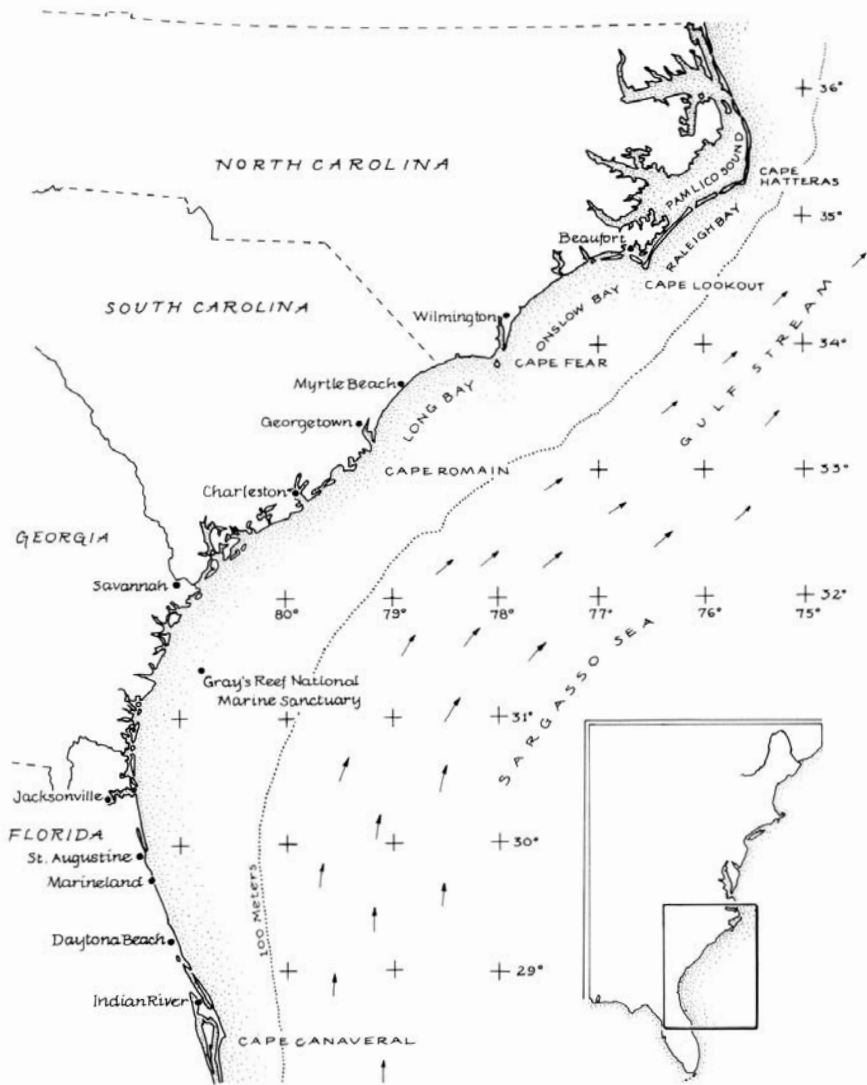


Figure 2. Coastline of the southeastern United States from Cape Hatteras to Cape Canaveral. For additional localities not shown, see the list of collection sites on page 509.

tal shelf. When these outcroppings lie within photic depths, they may support abundant seaweed populations. Such a situation occurs in Onslow Bay, North Carolina, into which no major sediment-carrying rivers empty. In Georgia, one of the outcrop areas with its associated wealth of plants and animals has been designated as the Gray's Reef National Marine Sanctuary.

THE HYDROGRAPHIC ENVIRONMENT

CURRENTS, TIDES, AND WAVES

The Florida Current, or Gulf Stream, originates in the Florida Straits from waters of the Gulf of Mexico. As it flows northward it is joined by the Antilles Current, which moves northward outside the Bahama Islands. The Florida Current usually lies offshore and parallel to the edge of the continental shelf as it moves along the coast to Cape Hatteras; there it leaves the coast and moves out to sea to become the Gulf Stream proper. The position of the Florida Current changes seasonally; in the winter it is driven offshore by the dominant northerly wind. When this happens, the cold waters of the Virginia Coastal Current may move into the northern part of the region, slipping around Cape Hatteras and along the North Carolina coast (Gray and Cerame-Vivas 1963; Stefansson et al. 1971). In summer the Florida Current moves inshore and brings warm, clear water to the continental shelf. This allows more sunlight to reach the bottom, which during the winter may have been below the compensation depth for seaweed photosynthesis. Inshore currents south of Cape Hatteras are variable. South-flowing geostrophic currents are periodically interrupted by inshore movement of the Florida Current, causing northward flow.

Tidal currents can be very strong, particularly adjacent to and inside the inlets through which the sounds empty and fill. Tidal ranges vary from a little more than 1 m near Cape Hatteras and Cape Canaveral, where the continental shelf is narrow, to over 2 m along the Georgia coast. The average height of waves is 1.7 m at Cape Lookout, North Carolina, and 0.8 m at Jacksonville, Florida.

LIGHT

Within the sounds, where tidal currents suspend large quantities of sediment and phytoplankton abundance can be high, light penetration is limited and seaweeds do not generally grow more than 1–2(–4) m below the low tide line. Water clarity can be much greater across the continental shelf, with seaweeds growing as deep as 90 m at the edge of the shelf (Schneider 1976). Water clarity can change markedly, however, in relatively short periods of time. In fall and winter, clarity decreases as storm waves suspend sediment particles and phytoplankton exhibits increased growth. In spring and summer, intrusions of clear “Gulf Stream” water allow increased light penetration, which is correlated with a seasonal increase in the biomass of seaweeds on the continental shelf (Schneider and Searles 1979). The episodic nature of the changes in light availability on the continental shelf are shown in the data of Peckol and Searles (1984) for a mid-shelf station off Cape Lookout, North Carolina.

TEMPERATURE

There are three different temperature transitions of importance within the region. From north to south there is the abrupt temperature change off Cape Hatteras, where the warm waters of the Gulf Stream meet Virginia coastal water (Gray and Cerame-Vivas 1963). A north-south temperature transition of less magnitude occurs at Cape Canaveral (Parr 1933).

There are also transitions in temperature from offshore to inshore and from season to season. In the sounds of North Carolina water temperatures can exceed 30°C in summer and drop to 0°C in winter or spring. In summer, bottom temperatures offshore are in the mid to upper 20s on the inner and middle shelf and down to 10°C at the edge of the shelf at depths where light becomes limiting for algal growth. In winter, bottom temperatures on the middle shelf remain in the middle teens; temperatures decrease toward the edge of the shelf and toward shore (Stefansson and Atkinson 1967). Seasonal temperature changes may therefore exceed 30°C in the sounds but vary only 15°C to 18°C on the inner and mid-shelf and 8°C to 9°C at the shelf edge. The central Florida coast also has high summer temperatures similar to those in the Carolinas (30°C), but these drop only to 14°C in the winter (Mook 1980).

WATER CHEMISTRY

Salinity ranges in ocean waters do not vary enough from 36 percent to affect seaweed growth. In the estuaries there is a full range of salinities from near oceanic values at the inlets to fresh water near the heads of the estuaries (Hoyt 1920; Kapraun and Zechman 1982; Litaker et al. 1987). The abundance of dissolved nutrients of importance to seaweed growth can vary drastically, particularly in the estuaries where there are large changes in the course of a day (Litaker et al. 1987; Ramus and Venable 1987). In offshore waters the changes recorded are tied more closely to the seasons, with relatively high nutrient concentrations in winter contrasted with low summer levels. Ramus and Venable (1987) have demonstrated marked differences in the ability of local seaweed species to utilize short-term, episodic increases in available nutrients. They found that ephemeral weedy plants such as *Ulva* can rapidly take up available nutrients; more persistent long-lived plants such as *Codium* are relatively unaffected by pulses of nutrients in the environment.

BIOGEOGRAPHY AND ECOLOGY

CHARACTERISTICS AND LIMITS OF THE REGION

Hoyt (1920) listed a large percentage of species in the Carolinas that were at their northern or southern limits of distribution. The Stephenson (1952) studied intertidal communities at Marineland, Florida; Charleston, South Carolina; and Beaufort, North Carolina. On the basis of the species of plants and animals present and the average monthly temperatures at these locations they characterized the region as warm temperate. They identified four elements within the flora: (1) eurythermic tropical species, (2) eurythermic cold-water species, (3) eurythermic cosmopolitan species, and (4) mid-Atlantic species with distributions centered in the region.

Humm (1969), instead of considering the region a distinct entity, viewed it as a long transition zone between a Caribbean-centered tropical flora and a North Atlantic-centered cool/cold temperate flora. He said that elements of each flora extended different distances into or across the region, but he recognized no species with a distribution centered in the region.

Van den Hoek (1975) agreed with the Stephenson in recognizing the region as warm temperate and was more specific and quantitative in describing its relationships with other floras. Searles (1984a) discussed the boundaries of the region. The northern boundary at Cape Hatteras is relatively distinct: north of the cape the flora is characterized by the gradual disappearance from north to south of northern species that reach their southern limit of distribution but are not replaced by southern species. Humm (1979) listed only 141 species, exclusive of the blue-green algae, in the Virginia flora. South of Cape Hatteras there is a marked increase in the number of species. Of the 338 taxa reported in the region, almost half (49 percent) are warm-water species at their northern limit of distribution, and most of these extend all the way to the waters of North Carolina. A smaller percentage (13 percent) are northern species that spill south around Cape Hatteras, mostly ending their distribution in North Carolina, with a small number extending on into South Carolina, Georgia, or northern Florida.

The southern boundary of the region is less distinct. Searles (1984a) reported that the waters just to the south of Cape Canaveral have a distinctly more tropical composition, with 42 percent of the species reported there being at their northern limit of distribution. In the less diverse flora north of Cape Canaveral at Marineland only 9 percent of the species are at their northern limit of distribution. The pattern of distribution is complicated by the presence of a number of temperate-water species in the northeastern Gulf of Mexico that are evident in winter (Earle 1969). Taylor (1955) characterized the flora in the northern and northeastern part of the gulf as an impoverished Caribbean flora rather than a temperate flora.

INSHORE AND OFFSHORE FLORAS

The differences between the flora of inshore shallow waters and that of the offshore continental shelf in the Carolinas have been emphasized by Searles and Schneider (1980). The offshore flora is dominated by tropical species, 37 percent of which are at their northern limit of distribution and only 1 percent at their southern limit. The shallow-water flora, on the other hand, is more evenly distributed between northern (10 percent) and southern (21 percent) elements. In both inshore and offshore floras most species have ranges extending north and south beyond the region.

Approximately one-third of the flora (36 percent) is restricted to shallow water, and one-third (38 percent) to deep water, with the remaining 26 percent represented in both environments.

Peckol and Ramus (1985) compared the photosynthetic abilities of different populations of *Sargassum filipendula*, a dominant species in both the shallow subtidal zone on jetties and in deep offshore waters, and demonstrated physiological differences between the populations suggestive of genetic divergence. Other species, such as *Dasya baillouviana*, show morphological and color variations between shallow-water and deep-water populations.

ENDEMIC AND DISJUNCT SPECIES

Van den Hoek (1975) recognized only five endemic species for the region. Searles (1984a) listed thirty-one species that are known only from the region or have distributions centered in the region but spill across the southern boundary at Cape Canaveral. The present twenty-five species restricted to the region (table 1, p. 510) constitute 7 percent of the total flora. Table 1 lists twelve other species whose ranges also extend farther into Florida or to Bermuda. An additional fifteen species with disjunct distributions are listed in table 2 (p. 510); these species are restricted in North America to the Cape Hatteras–Cape Canaveral region.

SEASONALITY

The observations on the seasonality of seaweeds made by Hoyt (1920) have been augmented in North Carolina by Williams (1948a, 1949), Richardson (1978), and Kapraun and Zechman (1982) for the intertidal and near-shore subtidal communities; by Schneider (1976), Peckol (1982), and Peckol and Searles (1983) for deep-water communities in the Carolinas; and by Searles (1987) for Georgia's offshore waters.

Seasonal changes in the shallow-water flora of southern North Carolina were

described by Kapraun and Zechman (1982). A winter-spring flora disappears in May–June and is replaced by a summer flora that reaches a peak in species number in July–August and then slowly declines in the fall. These seasonal species are superimposed on a large group of species that are present throughout the year. Kapraun and his students have experimentally investigated the responses of a variety of plants from shallow water to combinations of light and temperature (Kapraun 1977b, 1978a, 1978b, 1979; Amsler 1984b, 1985; Amsler and Kapraun 1985), relating the results to the seasonal abundance of the species. Richardson (1979, 1981, 1982) demonstrated the ability of species of *Dasya*, *Dicotyota*, and *Bryopsis* to survive as protonemalike or holdfast stages prior to their seasonal appearance as macroscopic plants on the jetties in North Carolina.

There is no distinct winter flora in the offshore waters. There are only a few perennial plants which persist through the winter and begin to renew growth in the spring. Beginning in the spring and extending through the summer, there is a gradual increase in the number of species and the biomass of plants; a peak in both parameters occurs in July–August (Schneider 1976, Schneider and Searles 1979; Searles 1987). In North Carolina this summer flora disappears gradually during the fall; at Gray's Reef in Georgia it disappears precipitously in late August or September (Searles 1987). A number of species (e.g., *Dasya baillouviana* and *Grinnellia americana*) that are restricted to the winter-spring flora in shallow waters are members of the summer flora offshore.

PHYSIOLOGICAL ECOLOGY

In addition to the studies listed above related to seasonality, several investigators have studied a variety of plants from the shallow-water sounds and from offshore waters in attempts to understand the photosynthetic, nutrient uptake, and growth characteristics of the species (Coutinho and Zingmark 1987; Duke, Lapointe, and Ramus 1986; Peckol 1983; Ramus and Rosenberg 1980; Ramus and Venable 1987; Rosenberg and Ramus 1982a, 1982b, 1984). Local species of seaweeds have also been used in refutation of Engelmann's theory of complementary chromatic adaptation as an explanation for the distribution of seaweeds along the gradients of light quality associated with increasing depth (Ramus 1983; Ramus and van der Meer 1983).

BIOLOGICAL INTERACTIONS

In their studies of the intertidal, Kapraun and Zechman (1982) observed seasonal changes in the vertical distribution of some species that they attributed to competition and narrow tolerance for some seasonally changing physical fac-

tors. Hay and Sutherland (1988) suggested that the major factors controlling the composition of the algal communities are desiccation during low tide and grazing by fish during high tide. Although the herbivorous parrotfish and surgeonfish of the tropics are absent or not important in the region, there are omnivorous fishes (e.g., the sheepshead, *Archosargus probatocephalus*) that prefer some intertidal algae and invertebrates (Ogburn 1984). Hay (1986) noted that genera such as *Ulva* and *Enteromorpha*, which are palatable to spottail pinfish (*Diplodus holbrooki*), tend to occur subtidally in the winter when these fish are rare or absent from the jetties. In the warm months, when pinfish are common around the jetties, these algae are mostly restricted to the refuge of the intertidal.

Richardson (1978) studied some aspects of subtidal colonization in the presence and absence of herbivores on a jetty in North Carolina where he excluded grazers with cages. His studies indicated that in the absence of large grazers (fish and sea urchins), hard surfaces were dominated by tube-building polychaete worms, bivalve molluscs, and serpulid worms, whereas seaweeds decreased in abundance. Peckol and Searles (1983) made similar studies of the seaweeds and invertebrates on a rock outcrop offshore on the continental shelf. Their studies suggested that the interactions controlling community structure are complex; there is competition for space when grazers are excluded, and the composition of the community that develops in part reflects the season in which space becomes available. In the absence of large grazers, the dominant organisms in that community appeared to be barnacles rather than algae; in the presence of those grazers, seaweeds were dominant and barnacles were rare. In both studies there were no experimental controls for the smaller grazers such as amphipod and polychaete crustaceans, which are capable of consuming large quantities of larger organisms (Hay et al. 1987, 1988).

Competition between species of seaweeds results in decreased rates of growth in understory plants associated with larger plants such as *Sargassum filipendula* (Hay 1986). Chemical defenses against herbivory have been demonstrated in a number of seaweeds, and Hay (1986) presented data from North Carolina suggesting that the common sea urchin *Arbacia punctulata* preferentially selected or avoided some species of seaweeds on a coastal jetty and specifically demonstrated a low preference for the brown alga *Dictyota menstrualis* (as *D. dichotoma*; Hay et al. 1987).

COLLECTION, PRESERVATION, AND MICROSCOPIC EXAMINATION OF SEAWEED SPECIMENS

COLLECTION

Along the coastline, seaweeds grow on hard surfaces such as seawalls, jetties, pilings, and the rare rock outcroppings. A diverse assemblage of seaweeds also grows epiphytically on the subtidal and intertidal plants of the estuaries. Species of genera such as *Vaucheria*, *Bachelotia*, *Caloglossa*, and *Bostrychia* grow on stable mud or peat deposits in sheltered habitats. Many drift plants are found cast up on the beaches and tangled among the stems of the marsh plants, particularly after storm activity.

Most seaweeds can be collected by wading or, in the subtidal of seawalls and jetties, by surface diving with mask and swimfins. Because of low water clarity near shore, the seaweeds there do not grow below the depths accessible by easy surface diving. To ensure that the whole plant is removed, the collector should use a putty knife or similar instrument to scrape plants from the points of attachment. In rare instances of tightly appressed calcareous algae, a chisel and hammer are necessary. Because hard surface habitats, and therefore seaweeds, are limited along this coast, collectors should be especially careful to remove only the minimum amount of plant material required for study.

The two practical methods for obtaining seaweeds in offshore waters are SCUBA diving and dredging. Dredging demands a sturdy geological rock dredge capable of breaking off pieces of rock or scraping plants and animals from smooth rock, thus requiring a large vessel with a winch and steel cable. Because some of the plants live in the cracks between rocks and are missed by dredges, and because some seaweeds are soft and delicate, SCUBA diving is the preferred method of sampling in all but the deepest locations.

In offshore waters macroscopic seaweeds grow attached to exposed rock along the edges of low ledges and on areas of bare rock on the flats behind the ledges, or more typically emerge through a light covering of shell and sand. Occasionally they grow on large pieces of shell. The latter are often found on the lower levels in front of the ledges where smaller sand particles appear to have winnowed away, perhaps due to the swirling of the currents as they pass over the ledges. Crustose fleshy and coralline red algae may adhere tightly to the rock, and a chisel and hammer may be required to break off pieces; they may also be found on shells and coral fragments.

The only special collecting item required when diving is a mesh bag to hold the specimens. It is useful to have a large bag for the big specimens and one or more small fine-mesh bags into which one can separate the smaller plants. In addition to obvious large algae, one should also collect sessile marine inverte-

brates (bryozoans, hydrozoans, gorgonian corals, molluscs) that have small algae growing on them.

PRESERVATION

Living specimens can be returned to the lab in coolers at ambient temperatures as long as they are not crowded. Specimens can be killed and the tissues fixed with a variety of reagents; the specifics depend on the use intended. For routine purposes specimens are killed and fixed in formalin-seawater in a ratio of 1:10. This is a noxious reagent, and when opening collections in the lab you are advised to wear gloves and work in a ventilated chemical hood. Specimens in formalin-seawater should be stored in the dark, where they will retain most of their color for long periods of time. After the initial killing and fixing, the plants can be transferred to 1:20 formalin-seawater for storage.

MICROSCOPY

Identification of specimens often requires microscopic examination. Small plants can be placed on slides under a coverslip and examined directly. Larger specimens may require sectioning. Coarse, sturdy plants such as *Gracilaria blodgettii* can be sectioned freehand with a single-edged razor blade. Small or membranous plants can be sandwiched between two glass slides and thin pieces cut off with a razor blade drawn against the end of the top slide as it is moved to expose the plant material. The secret in these hand-sectioning techniques is to cut a large number of sections; usually only a few out of two or three dozen are thin enough to be useful, but only one or two of these are necessary to see the diagnostic characteristics of the species.

Sections can be cut more accurately with a freezing microtome. The specimens are oriented and frozen on a mechanical stage in a few drops of water, or water and a solute such as gum arabic, and then cut with a microtome knife or razor blade as the block of tissue is moved into the path of the blade in small increments by the microtome. The sections are transferred to slides using a wet watercolor paintbrush.

Material can be viewed unstained using bright-field optics. The image may be enhanced with phase optics, differential interference-contrast (Nomarski) optics, or, most commonly, by stains. A frequently used stain is aniline blue (cotton blue). One of its advantages is that it is water soluble and the specimens do not have to be transferred to a nonaqueous medium. The stain is prepared as a 1 percent solution in water. Pieces of plant may be stained on a slide for a minute or more, depending on the bulk of the tissue. Excess stain is then removed using

a pipette and the dye is fixed in the cells with a weak acid solution (1% HCl).

Slides may be made permanent by mounting them in a 1:1 corn syrup:water solution, covering with a coverslip, and then periodically replacing the water lost by evaporation with additional corn syrup solution until an equilibrium is established. The process is accelerated by placing the slide mounts on a warming table. The stock corn syrup solution is dilute enough to allow a growth of fungi, so a few drops of phenol per 100 cc of solution are recommended as a fungicide. After the slides have lost all excess water, the coverslip should be ringed with fingernail polish.

TAXONOMIC TREATMENT

LIST OF SPECIES

The following list of species shows the sequence in which the taxa are presented. Natural keys are provided in the text for all taxa, and there is an artificial key to the genera at the end of the taxonomy section.

The accepted name is given for each species, accompanied by the basionym if the species is based on an earlier name. These are followed by the species descriptions. The descriptions are intended to be complete enough to differentiate each species from others in the region. Because we have not necessarily observed all of the variation that has been described for each species, the descriptions of locally collected plants have been augmented with information from the literature. Where we know that the local populations differ significantly from the species as it has been described, the differences are noted at the end of each species treatment together with any problems of classification or historical notes of interest.

Previous records of each species from the region are listed as literature citations, first under the accepted name, followed by synonyms and misapplied names. Misapplied names are followed by the term "sensu" prior to the references using those names.

Habitat and seasonal data are provided for each species. The distribution of each species is listed beginning with the range from north to south in the western Atlantic. If a species occurs in other regions, these are listed sequentially starting in the northeastern Atlantic and continuing south along the coasts of Europe, the Mediterranean, West Africa, southern Africa, the Indian Ocean, Australia, the tropical Pacific islands, the western Pacific, and ending with the distribution north to south along the western shores of the Americas. For widely distributed species the listings are intended to indicate only the general range; we do not attempt to indicate distributional limits with any precision. Distributions have been determined from many sources, but chief among these are South and Tittley (1986), Taylor (1960), Oliviera F. (1977), Lawson and John (1982), Seagriff (1984), Scagel et al. (1986), Abbott and Hollenberg (1976), and Dawson's series of papers on the Marine Algae of Pacific Mexico.

CHLOROPHYTA

Ulvophyceae

Ulotrichales

Ulotrichaceae

Gomontia polyrhiza (Lagerheim) Bornet et Flahault

Monostroma oxyspermum (Kützing) Doty

Ulothrix flacca (Dillwyn) Thuret

Ulvales

Ulvellaceae

- Entocladia viridis* Reinke
- Phaeophila dendroides* (P. Crouan et H. Crouan) Batters
- Pringsheimiella scutata* (Reinke) Marchewianka
- Ulvella lens* P. Crouan et H. Crouan

Ulvaceae

- Blidingia marginata* (J. Agardh) P. Dangeard
- Blidingia minima* (Kützing) Kylin
- Enteromorpha clathrata* (Roth) Greville
- Enteromorpha compressa* (Linnaeus) Nees
- Enteromorpha flexuosa* subsp. *flexuosa* J. Agardh
- Enteromorpha flexuosa* subsp. *paradoxa* (C. Agardh) Bliding
- Enteromorpha intestinalis* (Linnaeus) Nees
- Enteromorpha linza* (Linnaeus) J. Agardh
- Enteromorpha prolifera* (O. F. Müller) J. Agardh
- Enteromorpha ramulosa* (J. E. Smith) Carmichael
- Enteromorpha torta* (Mertens) Reinbold
- Pseudoclonium submarinum* Wille
- Ulva curvata* (Kützing) De Toni
- Ulva fasciata* Delile
- Ulva rigida* C. Agardh
- Ulva rotundata* Bliding

Cladophorales

Cladophoraceae

- Chaetomorpha aerea* (Dillwyn) Kützing
- Chaetomorpha brachygona* Harvey
- Chaetomorpha crassa* (C. Agardh) Kützing
- Chaetomorpha gracilis* Kützing
- Chaetomorpha linum* (O. F. Müller) Kützing
- Chaetomorpha minima* Collins et Hervey
- Cladophora albida* (Nees) Kützing
- Cladophora dalmatica* Kützing
- Cladophora hutchinsiae* (Dillwyn) Kützing
- Cladophora laetevirens* (Dillwyn) Kützing
- Cladophora liniformis* Kützing
- Cladophora montagneana* Kützing
- Cladophora pellucidoidea* van den Hoek
- Cladophora prolifera* (Roth) Kützing
- Cladophora pseudobainesii* van den Hoek et Searles

Cladophora ruchingeri (C. Agardh) Kützing
Cladophora sericea (Hudson) Kützing
Cladophora vadorum (Areschoug) Kützing
Cladophora vagabunda (Linnaeus) van den Hoek
Rhizoclonium riparium (Roth) Harvey
Valoniaceae
Valonia utricularis (Roth) C. Agardh
Anadyomenaceae
Anadyomene saldanhae Joly et Oliveira Filho
Microdictyon boergesenii Setchell
Boodleaceae
Struvea pulcherrima (J. E. Gray) Murray et Boodle
Chaetosiphonaceae
Blastophysa rhizopus Reinke
Caulerpales
Codiaceae
Codium carolinianum Searles
Codium decorticatum (Woodward) Howe
Codium fragile subsp. *tomentosoides* (van Goor) Silva
Codium isthmocladum Vickers
Codium taylorii Silva
Udoteaceae
Avrainvillea longicaulis (Kützing) Murray et Boodle
Boodleopsis pusilla (Collins) Taylor, Joly et Bernatowicz
Udotea cyathiformis Decaisne
Udotea flabellum (Ellis et Solander) Lamouroux
Caulerpaceae
Caulerpa mexicana Kützing
Caulerpa prolifera (Forsskål) Lamouroux
Caulerpa racemosa var. *laetevirens* (Montagne) Weber-van Bosse
Bryopsidaceae
Bryopsis pennata Lamouroux
Bryopsis plumosa (Hudson) C. Agardh
Derbesia marina (Lyngbye) Solier
Derbesia turbinata Howe et Hoyt
Ostreobiaceae
Ostreobium quekettii Bornet et Flahault

CHRYSOPHYTA

Xanthophyceae

Vaucheriales

Vaucheriaceae

- Vaucheria acrandra* Ott et Hommersand
- Vaucheria adela* Ott et Hommersand
- Vaucheria arcassonensis* Dangeard
- Vaucheria coronata* Nordstedt
- Vaucheria erythrospora* Christensen
- Vaucheria litorea* C. Agardh
- Vaucheria longicaulis* Hoppaugh
- Vaucheria minuta* Blum et Conover
- Vaucheria nasuta* Taylor et Bernatowicz
- Vaucheria velutina* C. Agardh

PHAEOPHYTA

Phaeophyceae

Ectocarpales

Ectocarpaceae

- Acinetospora crinita* (Harvey) Kornmann
- Bachelotia antillarum* (Grunow) Gerloff
- Botrytella micromora* Bory
- Ectocarpus elachistaeformis* Heydrich
- Ectocarpus fasciculatus* Harvey
- Ectocarpus siliculosus* (Dillwyn) Lyngbye
- Herponema solitarium* (Sauvageau) Hamel
- Hincksia granulosa* (J. E. Smith) Silva
- Hincksia irregularis* (Kützing) Amsler
- Hincksia mitchelliae* (Harvey) Silva
- Hincksia onslowensis* (Amsler et Kapraun) Silva
- Hincksia ovata* (Kjellman) Silva
- Phaeostroma pusillum* Howe et Hoyt
- Streblonema invisibile* Hoyt
- Streblonema oligosporum* Strömfelt

Ralfsiaceae

- Pseudolithoderma extensum* (P. Crouan et H. Crouan) Lund

Chordariales

Myrionemataceae

- Hecatonema floridanum* (W. R. Taylor) W. R. Taylor

- Hecatonema foecundum* (Strömfelt) Loiseaux
- Hecatonema maculans* (Collins) Sauvageau
- Myrionema magnusii* (Sauvageau) Loiseaux
- Myrionema strangulans* Greville
- Leathesiaceae
 - Leathesia difformis* (Linnaeus) Areschoug
 - Myriactula stellulata* (Harvey) Levring
- Chordariaceae
 - Cladosiphon occidentalis* Kylin
- Spermatochneaceae
 - Nemacystus howei* (W. R. Taylor) Kylin
 - Stilophora rhizodes* (Turner) J. Agardh
- Dictyosiphonales
 - Striariaceae
 - Hummia onusta* (Kützing) Fiore
 - Striaria attenuata* (C. Agardh) Greville
 - Punctariaceae
 - Asperococcus fistulosus* (Hudson) Hooker
 - Punctaria latifolia* Greville
 - Punctaria tenuissima* (C. Agardh) Greville
- Scytosiphonales
 - Scytosiphonaceae
 - Colpomenia sinuosa* (Roth) Derbès et Solier
 - Petalonia fascia* (O. F. Müller) Kuntze
 - Rosenvingea orientalis* (J. Agardh) Børgesen
 - Scytosiphon lomentaria* (Lyngbye) Link
 - Scytosiphon lomentaria* var. *complanatus* Rosenvinge
- Sphacelariales
 - Choristocarpaceae
 - Onslowia endophytica* Searles
 - Sphacelariaceae
 - Sphacelaria rigidula* Kützing
 - Sphacelaria tribuloides* Meneghini
- Dictyotales
 - Dictyotaceae
 - Dictyopteris delicatula* Lamouroux
 - Dictyopteris hoytii* Taylor
 - Dictyopteris membranacea* (Stackhouse) Batters
 - Dictyota cervicornis* Kützing
 - Dictyota ciliolata* Kützing

Dictyota menstrualis (Hoyt) Schnetter, Hörnig et Weber-Peukert
Dictyota pulchella Hörnig et Schnetter
Lobophora variegata (Lamouroux) Womersley
Padina gymnospora (Kützing) Sonder
Padina profunda Earle
Spatoglossum schroederi (C. Agardh) Kützing
Zonaria tournefortii (Lamouroux) Montagne

Sporochnales

Sporochnaceae

Sporochnus pedunculatus (Hudson) C. Agardh

Desmarestiales

Arthrocladiaceae

Arthrocladia villosa (Hudson) Duby

Fucales

Fucaceae

Ascophyllum nodosum (Linnaeus) Le Jolis

Fucus vesiculosus Linnaeus

Sargassaceae

Sargassum filipendula C. Agardh

Sargassum filipendula var. *montagnei* (Bailey) Collins et Hervey

Sargassum fluitans Børgesen

Sargassum natans (Linnaeus) Gaillon

RHODOPHYTA

Rhodophyceae

Bangiophycidae

Porphyridiales

Porphyridiaceae

Chroodactylon ornatum (C. Agardh) Basson

Stylonema alsidii (Zanardini) Drew

Compsopogonales

Erythropeltidaceae

Erythrocladia irregularis Rosenvinge

Erythrocladia endophloea Howe

Erythrotrichia carnea (Dillwyn) J. Agardh

Erythrotrichia vexillaris (Montagne) Hamel

Porphyropsis coccinea (Areschoug) Rosenvinge

Sahlingia subintegra (Rosenvinge) Kornmann

Bangiales

- Bangiaceae
Bangia atropurpurea (Roth) C. Agardh
Porphyra carolinensis Coll et Cox
Porphyra leucosticta Thuret
Porphyra rosengurtii Coll et Cox
- Florideophycidae
- Acrochaetiales
- Acrochaetiaceae
Audouinella affinis (Howe et Hoyt) C. W. Schneider
Audouinella bispora (Børgesen) Garbary
Audouinella botryocarpa (Harvey) Woelkerling
Audouinella corymbifera (Thuret) Dixon
Audouinella dasyae (Collins) Woelkerling
Audouinella daviesii (Dillwyn) Woelkerling
Audouinella densa (Drew) Garbary
Audouinella hallandica (Kyllin) Woelkerling
Audouinella hoytii (Collins) C. W. Schneider
Audouinella hypneae (Børgesen) Lawson et John
Audouinella infestans (Howe et Hoyt) Dixon
Audouinella microscopica (Nägeli) Woelkerling
Audouinella ophioglossa C. W. Schneider
Audouinella saviana (Meneghini) Woelkerling
Audouinella secundata (Lyngbye) Dixon
- Nemaliales
- Helminthocladiaceae
Helminthocladia andersonii Searles et Lewis
- Galaxauraceae
Galaxaura obtusata (Ellis et Solander) Lamouroux
Scinaia complanata (Collins) Cotton
- Gelidiales
- Gelidiaceae
Gelidium americanum (W. R. Taylor) Santelices
Gelidium pusillum (Stackhouse) Le Jolis
- Bonnemaisoniales
- Bonnemaisoniaceae
Asparagopsis taxiformis (Delile) Trevisan
- Naccariaceae
Naccaria corymbosa J. Agardh
- Corallinales
- Corallinaceae

(Articulated Corallines)

- Amphiroa beauvoisii* Lamouroux
- Corallina officinalis* Linnaeus
- Haliptilon cubense* (Kützing) Garbary et Johansen
- Jania adhaerens* Lamouroux
- Jania capillacea* Harvey
- Jania rubens* (Linnaeus) Lamouroux

(Crustose Corallines)

- Fosliella farinosa* (Lamouroux) Howe
- Leptophytum* sp.
- Lithophyllum intermedium* (Foslie) Foslie
- Lithophyllum subtenellum* (Foslie) Foslie
- Lithothamnion occidentale* (Foslie) Foslie
- Mesophyllum floridanum* (Foslie) Adey
- Neogoniolithon accretum* (Foslie et Howe) Setchell et Mason
- Neogoniolithon caribaeum* (Foslie) Adey
- Phymatolithon tenuissimum* (Foslie) Adey
- Pneophyllum lejolisii* (Rosanoff) Chamberlain
- Pneophyllum* sp.
- Titanoderma pustulatum* (Lamouroux) Nägeli

Gigartinales

Peyssonneliaceae

- Peyssonnelia atlantica* C. W. Schneider et Reading
- Peyssonnelia conchicola* Piccone et Grunow
- Peyssonnelia inamoena* Pilger
- Peyssonnelia simulans* Weber-van Bosse
- Peyssonnelia stoechas* Boudouresque et Denizot

Dumontiaceae

- Dudresnaya crassa* Howe
- Dudresnaya georgiana* Searles
- Dudresnaya puertoricensis* Searles et Ballantine

Gymnophloeaceae

- Predaea feldmannii* Børgesen
- Predaea masonii* (Setchell et Gardner) De Toni fil.

Sebdeniaceae

- Sebdenia flabellata* (J. Agardh) Parkinson

Halymeniaceae

- Cryptonemia luxurians* (C. Agardh) J. Agardh
- Grateloupia cunefolia* J. Agardh
- Grateloupia filicina* (Lamouroux) C. Agardh

Grateloupia gibbesii Harvey
Halymenia bermudensis Collins et Howe
Halymenia floresia (Clemente y Rubio) C. Agardh
Halymenia floridana J. Agardh
Halymenia hancockii W. R. Taylor
Halymenia trigona (Clemente y Rubio) C. Agardh
 Kallymeniaceae
 Cirrulicarpus carolinensis Hansen
 Kallymenia westii Ganesan
 Plocamiaceae
 Plocamium brasiliense (Greville) Howe et W. R. Taylor
 Sarcodiaceae
 Trematocarpus papenfussii Searles
 Cystocloniaceae
 Craspedocarpus humilis C. W. Schneider
 Solieriaceae
 Agardhiella ramosissima (Harvey) Kylin
 Agardhiella subulata (C. Agardh) Kraft et Wynne
 Eucheuma isiforme var. *denudatum* Cheney
 Meristiella gelidium (J. Agardh) Cheney et Gabrielson
 Meristotheca floridana Kylin
 Sarcoditheca divaricata W. R. Taylor
 Solieria filiformis (Kützing) Gabrielson
 Hypneaceae
 Hypnea cervicornis J. Agardh
 Hypnea musciformis (Wulfen) Lamouroux
 Hypnea valentiae (Turner) Montagne
 Hypnea volubilis Searles
 Phylloporaceae
 Gymnogongrus griffithsiae (Turner) Martius
 Petroglossum undulatum C. W. Schneider
 Gigartinaceae
 Gigartina acicularis (Wulfen) Lamouroux
 Petrocelidaceae
 Mastocarpus stellatus (Stackhouse) Guiry
 Gracilariales
 Gracilariaceae
 Gracilaria blodgettii Harvey
 Gracilaria curtissiae J. Agardh
 Gracilaria cylindrica Børgesen

Gracilaria mammillaris (Montagne) Howe
Gracilaria tikvahiae McLachlan
Gracilaria verrucosa (Hudson) Papenfuss
Gracilariopsis lemaneiformis (Bory) Dawson, Acleto et Foldvik

Rhodymeniales

Rhodymeniaceae

Agardhinula browneae (J. Agardh) De Toni
Botryocladia occidentalis (Børgesen) Kylin
Botryocladia pyriformis (Børgesen) Kylin
Botryocladia wynnei Ballantine
Chrysomenia agardhii Harvey
Chrysomenia enteromorpha Harvey
Gloioderma atlanticum Searles
Gloioderma blomquistii Searles
Gloioderma rubrisporum Searles
Halichrysis peltata (W. R. Taylor) P. Huvé et H. Huvé
Leptofauchea brasiliensis Joly
Rhodymenia divaricata Dawson
Rhodymenia pseudopalmata (Lamouroux) Silva

Champiaceae

Champia parvula (C. Agardh) Harvey
Champia parvula var. *prostrata* L. Williams

Lomentariaceae

Lomentaria baileyana (Harvey) Farlow
Lomentaria orcadensis (Harvey) W. R. Taylor

Ceramiales

Ceramiaceae

Anotrichium tenue (C. Agardh) Nägeli
Antithamnion cruciatum (C. Agardh) Nägeli
Antithamnionella atlantica (Oliveira F.) C. W. Schneider
Antithamnionella elegans (Berthold) Price et John
Antithamnionella flagellata (Børgesen) Abbott
Calliclavula trifurcata C. W. Schneider
Callithamniella silvae Searles
Callithamniella tingitana (Bornet) Feldmann-Mazoyer
Callithamnion cordatum Børgesen
Callithamnion pseudobyssoides P. Crouan et H. Crouan
Centroceras clavulatum (C. Agardh) Montagne
Ceramium byssoideum Harvey
Ceramium diaphanum (Lightfoot) Roth

Ceramium fastigiatum (Roth) Harvey
Ceramium fastigiatum f. *flaccidum* H. Petersen
Ceramium floridanum J. Agardh
Ceramium leptozonum Howe
Ceramium rubrum (Hudson) C. Agardh
Compothamnion thuyoides (Smith) Schmitz
Griffithsia globulifera Kützing
Lejolisia exposita C. W. Schneider et Searles
Nwynea grandispora Searles
Pleonosporium boergesenii (Joly) R. Norris
Pleonosporium flexuosum (C. Agardh) De Toni
Ptilothamnion occidentale Searles
Rhododictyon bermudense W. R. Taylor
Spyridia clavata Kützing
Spyridia hypnoides (Bory) Papenfuss

Delesseriaceae

Acrosorium venulosum (Zanardini) Kylin
Apoglossum ruscifolium (Turner) J. Agardh
Branchioglossum minutum C. W. Schneider
Branchioglossum prostratum C. W. Schneider
Calloseris halliae J. Agardh
Caloglossa leprieurii (Montagne) J. Agardh
Calonitophyllum medium (Hoyt) Aregood
Grinnellia americana (C. Agardh) Harvey
Haraldia lenormandii (Derbès et Solier) J. Feldmann
Hypoglossum hypoglossoides (Stackhouse) Collins et Hervey
Hypoglossum tenuifolium (Harvey) J. Agardh
Myriogramme distromatica Boudouresque
Searlesia subtropica (C. W. Schneider) C. W. Schneider et Eiseman

Dasyaceae

Dasya baillouviana (Gmelin) Montagne
Dasya ocellata (Grateloup) Harvey
Dasya rigidula (Kützing) Ardissonne
Dasya spinuligera Collins et Hervey
Dasysiphonia concinna C. W. Schneider
Dasysiphonia doliiformis C. W. Schneider
Heterosiphonia crispella var. *laxa* (Børgesen) Wynne

Rhodomelaceae

Acanthophora spicifera (Vahl) Børgesen
Bostrychia radicans (Montagne) Montagne

Bryocladia cuspidata (J. Agardh) De Toni
Bryocladia thyrigera (J. Agardh) Schmitz
Bryothamnion seaforthii (Turner) Kützing
Chondria atropurpurea Harvey
Chondria baileyana (Montagne) Harvey
Chondria curvilineata Collins et Hervey
Chondria dasyphylla (Woodward) C. Agardh
Chondria floridana (Collins) Howe
Chondria littoralis Harvey
Chondria polyrhiza Collins et Hervey
Chondria tenuissima (Goodenough et Woodward) C. Agardh
Dipterosiphonia reversa C. W. Schneider
Herposiphonia delicatula Hollenberg
Herposiphonia tenella (C. Agardh) Nägeli
Laurencia corallopsis (Montagne) Howe
Laurencia pinnatifida (Gmelin) Lamouroux
Laurencia poiteaui (Lamouroux) Howe
Micropeuce mucronata (Harvey) Kylin
Polysiphonia atlantica Kapraun et J. Norris
Polysiphonia binneyi Harvey
Polysiphonia breviararticulata (C. Agardh) Zanardini
Polysiphonia denudata (Dillwyn) Harvey
Polysiphonia ferulacea J. Agardh
Polysiphonia flaccidissima Hollenberg
Polysiphonia gorgoniae Harvey
Polysiphonia harveyi Bailey
Polysiphonia harveyi var. *olneyi* Harvey
Polysiphonia havanensis Montagne
Polysiphonia howei Hollenberg
Polysiphonia nigrescens (Hudson) Greville
Polysiphonia pseudovillum Hollenberg
Polysiphonia scopulorum var. *villum* (J. Agardh) Hollenberg
Polysiphonia sphaerocarpa Børgesen
Polysiphonia subtilissima Montagne
Polysiphonia tepida Hollenberg
Polysiphonia urceolata (Dillwyn) Greville
Pterosiphonia pennata (C. Agardh) Falkenberg
Wrightiella tumanowiczii (Harvey) Schmitz

CHLOROPHYTA

Plants of marine and fresh waters; unicellular, colonial, multicellular, or acellular; cells uninucleate or multinucleate; acellular plants include large, macroscopic individuals formed from interwoven filaments; pigmented with chlorophylls *a* and *b*, alpha, beta, and gamma carotene, and the xanthophylls lutein, violaxanthin, zeaxanthin, antheraxanthin, and neoxanthin; plastids delimited by two membranes, thylakoids in stacks of two to five, often with one or more pyrenoids; cell walls present except in some unicells and contain some combination of cellulose, hydroxyproline glycosides, xylan, mannan, or calcium carbonate; storage compounds alpha-linked glucose (starch); motile cells commonly with two or four flagella, but uniflagellate and multiflagellate cells also characterize particular taxa; flagella naked, or less frequently with organic scales or hairs; sexual life histories either haplontic, diplontic, or diplohaplontic, the latter isomorphic or heteromorphic; asexual reproduction by fragmentation, asexual spores, or parthenogenesis.

The intertidal is often locally dominated by green algae, particularly members of the Ulotrichales (*Enteromorpha*, *Monostroma*, and *Ulva*), Cladophorales (*Chaetomorpha* and *Cladophora*), and Caulerpales (*Bryopsis* and *Codium*). In subtidal waters the Caulerpales are also conspicuously represented by species of *Avrainvillea*, *Caulerpa*, *Codium*, and *Udotea*.

ULVOPHYCEAE

Plants filamentous, parenchymatous, or siphonous; cell division with a persistent, closed, interzonal centric spindle, cytokinesis centripetal with neither phycoplast nor phragmoplast; motile cells scaly or naked, flagellar bases with 180-degree rotational symmetry and counterclockwise absolute orientation; life histories haplontic, diplohaplontic, and diplontic; predominantly marine.

The ordinal classification is based on O'Kelly and Floyd (1984).

Key to the orders

1. Plants acellular, quadriflagellate zoospores absent, cell walls containing mannan or xylan Bryopsidales
1. Plants cellular, quadriflagellate zoospores present, walls containing mannan or cellulose 2
2. Motile cells with scales, terminal cap of flagellar base simple and overlapping, sporangial exit not papillate Ulotrichales
2. Motile cells lacking scales, terminal cap of flagellar base absent or bilobed, sporangial exit papillate 3
3. Cells uninucleate, terminal cap of flagellar base bilobed, sporangial exit papilla without plug Ulvales

3. Cells coenocytic, terminal cap of flagellar base lacking, sporangial exit papilla with plug Cladophorales

ULOTRICHALES

Plants composed of uniseriate branched or unbranched filaments, or monostromatic blades; branched filaments may form pseudoparenchyma; cells uninucleate or multinucleate; motile cells scaly; gametes biflagellate, zoospores quadri-flagellate; flagellar bases with simple, overlapping terminal caps; life history mostly an alternation of a multicellular gametophyte and a unicellular sporophyte, or more rarely with isomorphic phases.

A single family is included in the order here.

Ulotrichaceae

Key to the genera

- 1. Plants with blades Monostroma
- 1. Plants without blades 2
- 2. Branched, growing in shell or wood Gomontia
- 2. Unbranched, not growing in shell or wood Ulothrix

Gomontia Bornet et Flahault 1888

Plants growing in shell or wood; cells near surface irregular, those deeper in the substratum narrower and of more uniform diameter; asexual reproduction by zoospores.

Gomontia polyrhiza (Lagerheim) Bornet et Flahault 1888, p. 164.

Codiolum polyrhizum Lagerheim 1885, p. 22.

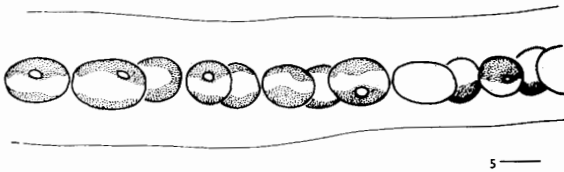
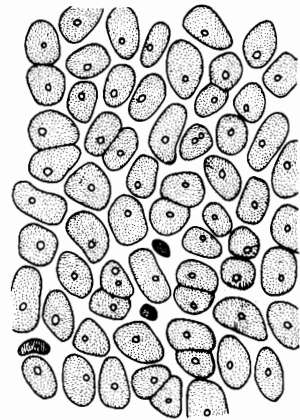
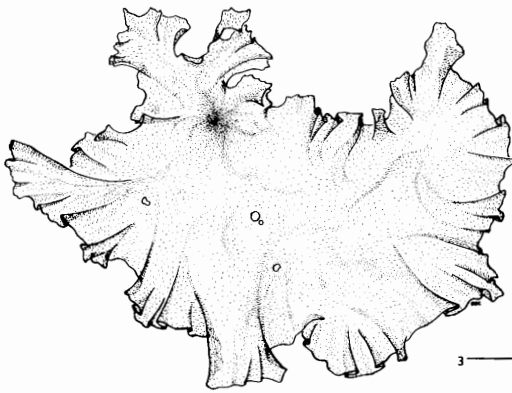
Filaments irregularly branched; cells 4–10 µm diameter, 2–6 times as long (20–50 µm); sporangia 30–40(–150) µm diameter, 150–250 µm long.

Hoyt 1920; Williams 1948a; Taylor 1957, 1960.

Found boring in shells, spring and summer.

Distribution: Canadian Arctic to Virginia, North Carolina, Bermuda, southern Florida, Caribbean, USSR to Portugal, Indian Ocean, Japan, Alaska to California.

Kornmann (1962) found *Codiolum*-like shell-boring stages similar to *Gomontia polyrhiza* in the life history of *Monostroma grevillei* (Thuret) Wittrock, an alga subsequently separated by Gayral (1964) into the genus *Ulvopsis*. Wilkinson and Burrows (1972) studied *Gomontia polyrhiza*-like algae in the British Isles and concluded that six different taxa, including *Eugomontia sacculata* Kornmann, *Entocladia perforans* (Huber) Levring, and *Codiolum* stages in the



Figures 3–5.

Monostroma oxyspermum. 3. Habit, scale 1 cm. 4. Surface cells of blade, scale 10 μm . 5. Cross section of blade, scale 10 μm .

life histories of *Codiolum polyrhizum* Lagerheim and *Monostroma grevillei* (Thuret) Wittrock, were confused under the designation *Gomontia polyrhiza*. Hoyt's report of this alga from North Carolina indicated plants with filaments 4–8 μm diameter, sporangia 30–40 μm diameter, zoospores of two kinds (10–12 μm and 5–6 μm diameter, or 5 μm long and 3.5 μm diameter), and aplanospores 4 μm diameter. The status of this alga will be unclear until the local representatives are isolated and studied in culture.

***Monostroma* Thuret 1854**

Plants monostromatic blades, developing from a discoid or filamentous germling.

Monostroma oxyspermum (Kützing) Doty 1947, p. 12.

Ulva oxysperma Kützing 1843, p. 296.

Figures 3–5

Plants light green, flat or ruffled sheets, to 10(–60) cm tall; attached basally by rhizoids or free floating; cells irregularly arranged or in groups of two or four, in surface view 7–18(–26) μm diameter, rounded angular to round or oval, walls thick; blade 20–40(–60) μm thick, cells in section rounded rectangular with lumens 14–21 μm tall; sexual reproduction unknown.

Chapman 1971. As *Ulvaria oxysperma*, Kapraun 1984; Richardson 1986, 1987.

On mud in marshes and on shells and seawalls in sounds, winter and spring.
Distribution: Canadian Arctic to Virginia, North Carolina, South Carolina, Georgia, Bermuda, southern Florida, Brazil, USSR to Portugal, Alaska to California.

The genus was placed in the Ulotrichales on the basis of flagellar ultrastructural characteristics (O'Kelly and Floyd 1984), but the generic placement of *oxy-spermum* remains uncertain. This species reproduces only asexually and, based on studies of populations in different parts of the world, there is disagreement about the method of spore release (Gayral 1965; Tatewaki 1969; Golden and Garbary 1984) which makes the generic placement in *Monostroma* rather than *Ulvaria* arbitrary.

Ulothrix Kützing 1833

Plants filamentous, unbranched, usually attached by elongate basal cells; cells cylindrical, length equal to width or shorter, uninucleate; plastids single parietal bands completely or incompletely circling the cells, with one to several pyrenoids.

Ulothrix flacca (Dillwyn) Thuret in Le Jolis 1863, p. 56.

Conferva flacca Dillwyn 1809, p. 53, pl. 49.

Figure 6

Filaments 10–25 μm diameter, 0.25–0.75 diameters long, plastids incomplete bands covering entire length of inner walls with one to three pyrenoids; sporangial cells swollen to 50–60(–80) μm .

Blomquist and Humm 1946; Williams 1948b; Chapman 1971; Kapraun and Zechman 1982; Kapraun 1984.

Epiphytic and on intertidal rocks in winter and spring, rare in summer.

Distribution: Canadian Arctic to Virginia, North Carolina, South Carolina, Georgia, USSR to Portugal, Azores, Japan.

Although some species assigned to *Ulothrix* have symmetrical, chlorophycean flagellar bases and phycoplast-type cell division and are more appropriately placed in the Chlorophyceae, Sluiman et al. (1983) indicated that *Ulothrix flacca* is probably a member of the Ulvophyceae and should be retained in the

Figure 6. *Ulothrix flacca*, portion of filament, scale 5 μm .



genus *Ulothrix*. Perrot (1972) studied "*Ulothrix flacca*" in France and demonstrated that collections from Roscoff consisted of two species, one with isogametes and isomorphic phases, the other with anisogametes and heteromorphic phases.

Local specimens have a single pyrenoid in each plastid.

ULVALES

Plants with branched, uniseriate filaments, sometimes united in pseudoparenchymatous discs, or plants forming single- or two-layered blades or tubes; cells typically uninucleate; bases of all flagella with a bilobed terminal cap and proximal sheath consisting of two equal subunits; exit pore of gametangia and sporangia papillate, producing a more or less rounded pore after motile cell release; life history diplohaplontic with isomorphic phases.

Key to the families

- 1. Plants filamentous and in some cases pseudoparenchymatous; rhizoplasts lacking in motile cells Ulvellaceae
- 1. Plants parenchymatous or pseudoparenchymatous; rhizoplasts present in motile cells Ulvaceae

Ulvellaceae

Plants filamentous, uniseriate, branched, heterotrichous or creeping, plant or base of plant sometimes discoid and erect filaments pseudoparenchymatous; colorless hairs (setae) sometimes present; motile cells without rhizoplasts.

Generic concepts in this group are not clear (Nielsen 1972; South 1974; Yarish 1975). The disposition of *Phaeophila* was not indicated by O’Kelly and Floyd (1984), but it is included here with the genera with which it is traditionally placed.

Key to the genera

- 1. Plants discoid 2
- 1. Plants not discoid 3
- 2. Cells of disc with aseptate setae Pringsheimiella
- 2. Cells of disc without aseptate setae Ulvella
- 3. Pyrenoids one, or rarely more than one per cell, cleavage of sporangia sequential Entocladia
- 3. Pyrenoids more than one per cell, cleavage of sporangia simultaneous Phaeophila

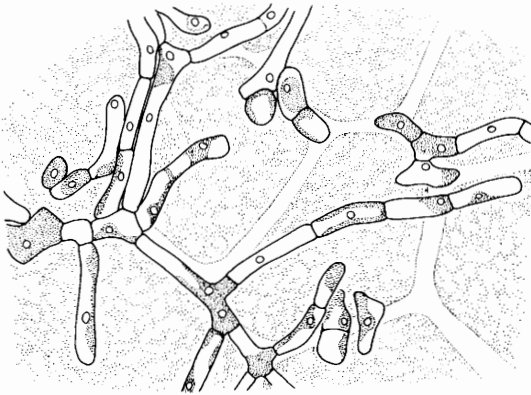
Entocladia Reinke 1879

Plants epiphytic or endophytic, creeping on surface or penetrating outer walls of host; filamentous, irregularly branched, with or without free erect filaments, but sometimes becoming pseudoparenchymatous in center of radiating filaments; plastids single, parietal, with one or more pyrenoids; cells uninucleate, with or without aseptate setae; zoospores quadriflagellate, division of sporangium sequential, spore release explosive; gametes biflagellate, isogamous.

Entocladia viridis Reinke 1879, p. 476.

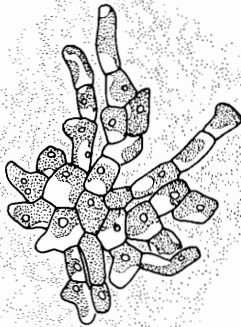
Figures 7 and 8

Filaments much branched, without central pseudoparenchymatous region; cells 3.5–7(–10) μm diameter, 1–4(–6) diameters long, cylindrical, swollen, or ir-



7 —

Figures 7, 8.
Entocladia viridis. 7. Epi-
phytic filaments, scale
10 μm . 8. Crust growing
on glass, scale 15 μm .



8 —

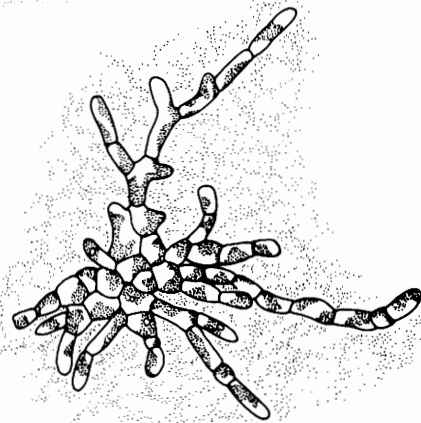
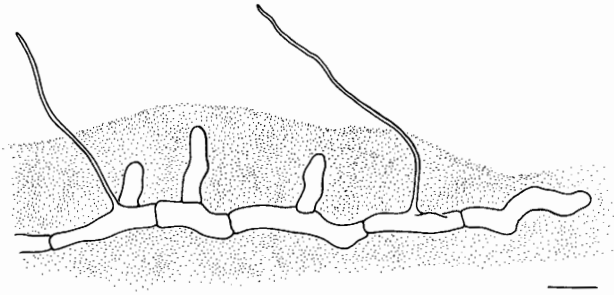


Figure 9. *Phaeophila dendroides*, growing in shell, scale 25 μm .



regular; plastids with usually one, though sometimes up to four, pyrenoids; with or without septate setae.

Williams 1948a, 1951; Taylor 1960. As *Endoderma viride*, Hoyt 1920; Humm 1952.

Growing in the cell walls of *Cladophora*, *Calonitophyllum*, *Hypoglossum*, and *Rhodymenia*, summer.

Distribution: Canadian Arctic to Virginia, North Carolina, northeastern Florida, Caribbean, Brazil, Norway to Portugal; elsewhere, widespread in temperate and tropical seas.

O'Kelly and Yarish (1980) used the differences in sporangial ontogeny given here in the generic descriptions to distinguish *Entocladia* from *Phaeophila*. They also (1981) distinguished *Entocladia* from *Acrochaete* as circumscribed by Nielsen (1979) by the absence of the erect filaments that characterize the latter genus.

Phaeophila Hauck 1876

Plants epi-endophytic or boring in carbonate shell; cells of branched, uniseriate filaments bearing one to three, long, aseptate hairs; hair cytoplasm not separated from cell by wall, hair bases not swollen; plastids lobed, parietal, with several pyrenoids; zoospores quadriflagellate, sporangial mother cells multinucleate, cleavage simultaneous.

Phaeophila dendroides (P. Crouan et H. Crouan) Batters 1902, p. 13.

Ochlochaete dendroides P. Crouan et H. Crouan 1852, no. 346.

Figure 9

Plants frequently and widely branched; cells 9–40 μm diameter; 15–50(–80) μm long, generally cylindrical, partly of irregular diameters; setae occasional to frequent, one to three per cell, their bases often spirally twisted; zoosporangia intercalary or terminal on short branches, often swollen, 16–40 μm diameter, 30–85 μm long.

Aziz and Humm 1962.

On *Dictyota menstrualis*, summer.

Distribution: Newfoundland to Virginia, North Carolina, Bermuda, southern Florida, Caribbean, Brazil, Norway to Portugal; elsewhere, widespread in temperate and tropical seas.

Pringsheimiella v. Höhnel 1920

Plants discoid, single layered, the filaments laterally closely united, cells in center of disc somewhat taller than those toward margins, which are radially elongate; growth marginal; young cells sometimes bear colorless hairs; plastids parietal, platelike, with single pyrenoids; zoospores and gametes quadriflagellate.

Pringsheimiella scutata (Reinke) Höhnel ex Marchewianka 1924, p. 42.

Pringsheimia scutata Reinke 1889, p. 33, pl. 25.

Plants discoid, 0.1–0.2 mm diameter, cells variable in size and shape, marginal cells horizontally elongate, laterally branched; central cells vertically elongate, to 12 μm diameter; zoosporangia oval to subpyriform, 15–22 μm diameter, 28–38 μm high, zoospores 15 μm diameter, gametes 4 μm diameter.

Aziz and Humm 1962.

On *Sargassum filipendula* and *Cladophora* spp., June and October.

Distribution: Canadian Arctic to Connecticut, North Carolina, Bermuda, Caribbean, Brazil, Norway to Spain, southern Africa, Japan, Washington.

Ulvella H. Crouan et P. Crouan 1859

Plants epiphytic, endophytic, or on rock; discoid, disc cells compressed and disc more than one cell thick in center, more clearly filamentous toward margins, and some marginal cells showing precocious branching (Y-shaped cells); without hairs or setae; cells uni- to multinucleate; plastids parietal, with or without pyrenoids; reproduction by biflagellate zoospores; zoosporangia formed by central cells of disc; sexual reproduction unclear.

Ulvella lens H. Crouan et P. Crouan 1859, p. 288, pl. 22, figs 25–28.

Figure 10

Discs 1–5 mm diameter, margins single layered, centers two to three layered; central cells 5–10(–20) μm diameter, irregularly polygonal, marginal cells elongate, 3–4(–15) μm diameter by 15–30 μm long, some peripheral cells forked; multinucleate; central cells forming four, eight, or sixteen zoospores.

Hoyt 1920; Williams 1948a, 1949, 1951; Humm 1952; Taylor 1960; Amsler and Searles 1981.

On shells, hydroids, and *Codium* and other algae, summer.

Distribution: Canadian Arctic, Massachusetts, North Carolina, South Carolina, northeastern Florida, southern Florida, Caribbean, Norway to Spain, Azores.

Kapraun (1984) pointed out that *Pseudulvella* Wille differs from *Ulvella* in having quadriflagellate zoospores. Since the zoospores of the local plants have not been observed, the generic identity of the local plants is not certain.

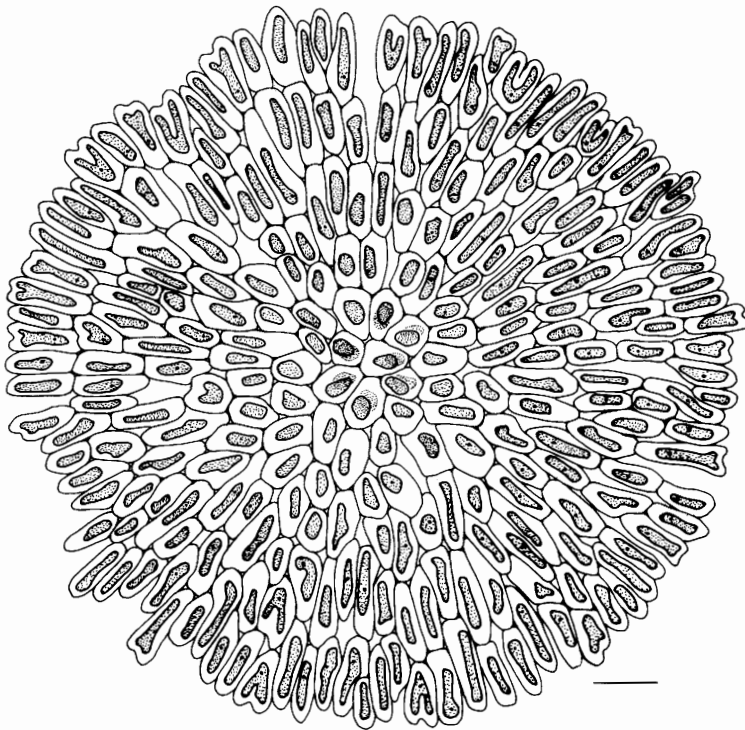


Figure 10. *Ulvella lens*, scale 10 μm .

Ulvaceae

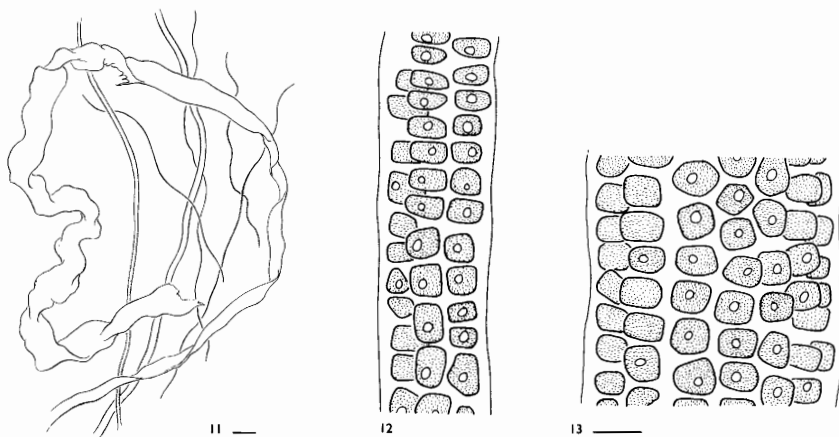
Plants pseudoparenchymatous discs, single or two layered blades, or tubular; motile cells with rhizoplasts.

Key to the genera

1. Plants filamentous, pseudoparenchymatous, sometimes discoid, but not erect or tubular *Pseudendoclonium*
1. Plants not pseudoparenchymatous; erect and tubular or membranous 2
2. Plants tubular or if partly membranous the base of the blade tubular 3
2. Plants membranous throughout *Ulva*
3. Plastids stellate, erect plant originating from a disc without rhizoids
 *Blidingia*
3. Plastids not stellate, erect plant attached by rhizoids *Enteromorpha*

Blidingia Kylin 1947

First cell of germling receiving all of zoospore cytoplasm; germling closely branched, discoid, becoming two layered; mature plant erect, tubular, *Enteromorpha*-like; plastids one per cell, stellate, parietal, with one pyrenoid; asexual reproduction by quadriflagellate zoospores; sexual reproduction unknown.



Figures 11–13. *Blidingia marginata*. 11. Young, slender, tubular filaments, and older, irregular, collapsed filaments, scale 25 μm . 12, 13. Surface cells of young filaments, scale 10 μm .

Key to the species

- 1. Plants simple, or with little proliferous branching, cells in longitudinal series, especially along blade margins, blades 12–100 μm thick *B. marginata*
- 1. Plant branched or unbranched, cells not in linear series, wall of tubular branches 8–10 μm thick or thicker *B. minima*

Blidingia marginata (J. Agardh) P. Dangeard 1958, p. 347.

Enteromorpha marginata J. Agardh 1842, p. 16.

Figures 11–13

Plants simple or rarely with a few marginal proliferations, cylindrical when young, becoming flattened with age, 2–5 cm high; to 15–20 cells, 100–200 μm wide; 12–100 μm thick; cells to 10 μm long, sometimes in longitudinal series, particularly in young branches; attached by basal discs; blades narrow toward bases and tips, otherwise of constant diameter, sometimes slightly inflated; long, narrow threads forming tangled masses.

Chapman 1971; Kapraun 1984; Richardson 1987.

In salt marshes, winter–spring.

Distribution: Canadian Arctic to Virginia, North Carolina, Georgia, Bermuda, ?Caribbean, Norway to Portugal, Australia, British Columbia to California.

Parke and Burrows (1976) suggested that *Blidingia minima* and *B. marginata* may be conspecific.

Blidingia minima (Nägeli ex Kützing) Kylin 1947, p. 8.

Enteromorpha minima Nägeli ex Kützing 1849 p. 482.

Figure 14

Plants deep green or yellowish, simple or branched, 1–24 cm tall, bases of

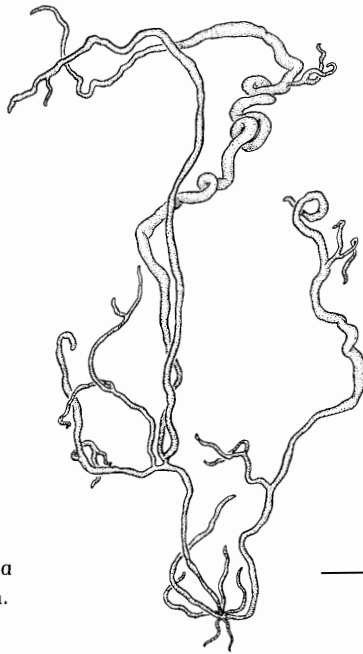


Figure 14. *Blidingia minima*, scale 2 mm.

fronds slender, one or more attached to basal discs; blades expanded above bases, linear, sometimes torulose and more or less tubular, 1–2(–5) mm broad; cells angular, (3–)5–7(–10) μm diameter, in no apparent order, almost cuboidal in section; walls thin; stellate plastids covering the exposed face of the cells.

Stephenson and Stephenson 1952; Kapraun 1984; Richardson 1987. As *Enteromorpha minima*, Williams 1948a; Taylor 1960.

On intertidal jetties and seawalls in sounds and on outer coast, winter–spring.

Distribution: Canadian Arctic to Virginia, North Carolina, South Carolina, Georgia, Bermuda, Iceland, British Isles to Portugal, southern Africa, Australia, Japan, Alaska to Pacific Mexico, Chile.

Enteromorpha Link 1820, nom. cons.

Plants in part hollow and tubular, walls of tubes one cell thick, lower part of plant always hollow, upper parts tubular or becoming filamentous in many species, flattened and bladelike in others; simple or branched, attached by non-septate rhizoidal outgrowth of cells, sometimes free floating; cells uninucleate, plastids parietal, platelike, cup shaped, or tubular, with one or more pyrenoids; asexual reproduction by quadriflagellate zoospores or fragmentation; sexual reproduction by isogamous or anisogamous, biflagellate gametes.

Key to the species and subspecies

1. Plants filiform, unbranched, consisting of four to ten cell rows, 30–60 μm in diameter; central cavity 10–15 μm diameter *E. torta*
1. Plants filiform or not, branched or unbranched; central cavity greater than 15 μm diameter 2
2. Pyrenoids one to two in majority of cells 3