



The Marine Benthic Algal Flora of Puerto Rico, I. Ochrophyta Phaeophyceae, Pelagophyceae, and Xanthophyceae

*David L. Ballantine, James N. Norris,
and Hector Ruiz*

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Flora of Puerto Rico,
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ABSTRACT

Ballantine, David L., James N. Norris, and Hector Ruiz. *The Marine Benthic Algal Flora of Puerto Rico, I. Ochrophyta: Phaeophyceae, Pelagophyceae, and Xanthophyceae*. Smithsonian Contributions to Botany, number 114, vi + 111 pages, 78 figures, 2021. — This treatment is a taxonomic study of the benthic species of Ochrophyta known from Puerto Rico, Caribbean Sea. In all, 3 classes, 10 orders, 16 families, 33 genera, and 77 species occur in the benthic marine communities in Puerto Rico. Of these, three species of *Sargassum* are found only as unattached and free-floating. A brief summary of phycological studies in Puerto Rico and ecological descriptions of the most common marine habitats are presented. Along with date, place, and author(s) of valid publication for all genera and species, type locality information and descriptive accounts of vegetative morphological and reproductive anatomy are provided. Distribution of each species is given, and where relevant, comments on their habitat and their taxonomic and nomenclatural status are discussed. A key to the genera and keys to species within genera are included. Either an in situ or other illustration accompanies most species. Two new geographical distribution records for Puerto Rico and a description of one new species, *Lobophora brooksii* D. L. Ballant. et J. N. Norris, are included.

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Cover images, from left: *Dictyota friabilis*, *Padina gymnospora*, *Turbinaria turbinata*.

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The Marine Benthic Algal Flora of Puerto Rico, I. Ochrophyta

Phaeophyceae, Pelagophyceae, and Xanthophyceae

David L. Ballantine,^{1*} James N. Norris,¹ and Hector Ruiz²

INTRODUCTION

A BRIEF PHYCOLOGICAL HISTORY OF PUERTO RICO

Studies of Puerto Rican benthic marine algae date to the latter part of the nineteenth century. Perhaps the first professional botanist to collect algae in Puerto Rico was German botanist Paul Sintenis (1847–1907), who spent three years between 1884 and 1887 on the island and collected both marine and terrestrial plants. Regrettably, the first set of his Puerto Rican collections was mostly destroyed at Dahlem (Berlin) during World War II. Another European botanist, Ferdinand Hauck, originally from the Czech Republic and later a post office official in Trieste, Italy, provided the first published account of Puerto Rican algae (Hauck 1888). That work listed 90 algal species based on his collections made from 1886 to 1889 in Puerto Rico, with specific locales at Manatí, Fajardo, Yabucoa, Guánica, and Cabo Rojo. Some of these records were subsequently treated as “uncertain records” by Taylor (1960). Many of these species have not been collected again in Puerto Rico, and the specimens as reported were probably misapplied names, which are herein noted as excluded taxa.

Notable botanist Marshall Avery Howe (1867–1936; Figure 1B) was a specialist in liverworts and algae and curator at the New York Botanical Garden (NYBG) beginning in 1906 and later became its director in 1935. Howe made several collecting trips to Puerto Rico. His engaging accounts (Howe 1903, 1915) of travel from New York to Puerto Rico by steamer from New York and then conveyance by stagecoach from the port of San Juan across Puerto Rico to Guánica make for interesting reading. Howe (1903, 1907, 1915) published his observations and descriptions of Puerto Rican algae and deposited his specimens, including type specimens, at NYBG. Howe also worked extensively in the broader Caribbean, publishing on the algae of the Bahamas, Jamaica, Cuba, and Barbados, in addition to Brazil and Uruguay. These studies established NYBG as a historically important repository of Caribbean algal specimens (duplicates of many were deposited in the U.S. Algal Collection). Many of the species that Howe described are included in this flora. His collaboration with the Norwegian phycologist Mikael Heggelund Foslie (1855–1909; Figure 1A) resulted in publication of two new coralline algae from Culebra Island (Foslie and Howe 1906): *Goniolithon acropetum* Foslie et M. Howe 1906 [= *Neogoniolithon acropetum* (Foslie et M. Howe) W. H. Adey 1970] and *Lithophyllum antillarum* Foslie et M. Howe 1906 [= *Porolithon antillarum* (Foslie et M. Howe) Foslie et M. Howe 1909 (in Foslie 1909)]. Later, a third coralline species was added from Culebra Island (Foslie 1907): *Goniolithon affine* Foslie et M. Howe [= *Neogoniolithon*

¹ Department of Botany, National Museum of Natural History, Smithsonian Institution, Washington, D.C. 20560, USA.

² HJR Reefscaping, P.O. Box 1126, Hormigueros, Puerto Rico 00660, USA.

* Correspondence: ballantined@si.edu

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FIGURE 1. Early phycologists who have contributed to the understanding of the Puerto Rican algal flora: (A) Mikael Heggelund Foslie (from Wikipedia), (B) Marshall Avery Howe (from NYBG archives), (C) Hugo M. Blomquist (from Wikipedia), (D) Manuel Diaz-Piferrer (photo credit: John West; note the photographer's left foot in foreground), and (E) Luis R. Almodóvar.

affine (Foslie et M. Howe) Setchell et L. R. Mason 1943]. Foslie appears to have limited his field work to Europe; however, he received collections from colleagues all over the world, including Puerto Rican specimens collected by Marshall Howe. A dozen species and varieties of coralline algae collected in Puerto Rico

are illustrated in his posthumously published *Contributions to a Monograph of the Lithothamnium* (Foslie 1929).

More recent marine algal floristic studies in Puerto Rico have mostly been conducted out of the Department of Marine Sciences (DMS) of the University of Puerto Rico at Mayagüez

(UPRM). At the time of its founding, originally as the Institute of Marine Biology, the DMS began with a faculty of 11 members in 1967, including Puerto Rico's first practicing phycologist, Luis Raúl Almodóvar (1931–1996; Figure 1E), who taught marine botany and made numerous algal collections. During his tenure, Almodóvar supervised an astonishing number (47) of M.S. and Ph.D. students and published several papers on marine algae of the region (cited herein). Another original member of the Institute of Marine Biology faculty, Cuban-born Manuel Díaz-Piferrer (1914–1997; Figure 1D), also taught and published on Puerto Rican marine algae. Unfortunately, Almodóvar and Díaz-Piferrer maintained a long-standing feud, and as a result, the two “split” the flora, with Díaz-Piferrer having dominion on the north coast of Puerto Rico and Almodóvar the south. Duke University professor Hugo L. Blomquist (1888–1964; Figure 1C) visited the marine lab of the UPRM for several years and managed to collaborate on studies of Puerto Rican algae with both Díaz-Piferrer and Almodóvar (Almodóvar and Blomquist 1959, 1961, 1965; Blomquist and Almodóvar 1961; Blomquist and Díaz-Piferrer 1961).

Alida Ortiz Sotomayor was the University of Puerto Rico's first Ph.D. graduate who specialized in marine botany, producing a monograph of the island's *Gracilaria* species (Ortiz Sotomayor 1976). David L. Ballantine (1947–) joined the DMS in 1978 and was the first phycologist in Puerto Rico to regularly employ scuba diving as a means of subtidal collection. Examination of the deepwater marine flora through scuba, dredging, limited submersible diving, and the introduction of technical rebreather diving helped place Puerto Rico at the forefront of Caribbean deepwater phycological research. Nilda E. Aponte (1957–) became a member of the DMS in 1990 and published a series of papers on the red algal family Callithamniaceae and collaborated extensively with Ballantine. More than 120 years of phycological research and intensive collection in Puerto Rico have produced arguably the best-known marine algal flora of any Caribbean island or island group in the region.

As a consequence of the Almodóvar and Díaz-Piferrer feud, collections of Puerto Rican marine algae have historically been housed in two herbaria (as holdings in the same academic department) on the island. The first of these, the Ficoteca Puertorriqueña (FPDB), was established in 1958 and directed by Díaz-Piferrer. The second algal herbarium (MSM) was founded by Almodóvar, also in 1958. Both herbaria were recognized in the *Index Herbariorum* (Holmgren et al. 1990), with the abbreviations FPDB and MSM, respectively, and were housed within the DMS of UPRM. Following the retirements of both Almodóvar and Díaz-Piferrer, the two herbaria were officially combined into a single herbarium, MSM, by Ballantine in 1990. Now known as the Herbario Marino Puertorriqueño (Thiers 2020), the collection contains more than 36,000 specimens. As of this writing, the herbarium is in the process of being transferred to the Department of Biology, UPRM.

The first complete list of the marine benthic algal flora of Puerto Rico was compiled by Almodóvar and Ballantine (1983) and reported 384 species (excluding Cyanophyta). A revision

by Ballantine and Aponte (1997) recognized 473 species, and their second revision, “A Checklist of the Benthic Marine Algae Known to Puerto Rico” (Ballantine and Aponte 2002), recorded 492 species of algae, including macroscopic Chrysophyceae and Xanthophyceae from Puerto Rico, but excluded Cyanophyta.

Collector abbreviations used in text are defined as follows:

DLB	David L. Ballantine
HLB	Hugo L. Blomquist
HR	Hector Ruiz
LRA	Luis Raul Almodóvar
M&DL	Mark and Diane Littler
MAH	Marshall A. Howe
MDP	Manuel Díaz-Piferrer
RJZ	Roger J. Zimmerman

THE GENERAL PHYSICAL SETTING IN PUERTO RICO

Lying between 65.652°W and 67.140°W and between 17.966°N and 18.466°N, Puerto Rico and its smaller islands (Figure 2) are centrally situated in an arc of islands comprising the West Indies. The Greater Antilles, of which Puerto Rico is the easternmost island, define the northern boundary of the Caribbean Sea; thus, the north coast of Puerto Rico abuts the Atlantic Ocean, whereas the remaining coasts are technically Caribbean. Puerto Rico is roughly rectangular in shape, measuring approximately 50 km north to south and 180 km east to west. It possesses an area of 9,104 km² and a coastline of approximately 1,384 km, including the islands of Vieques, Culebra, Desecheo, and Mona. Puerto Rico is a “high island” with an average annual terrestrial temperature of 29°C. Rainfall is unequally distributed because of a combination of factors, including the mountainous terrain, with annual rainfall averages of 155 cm on the east, north, and west coasts and less than 80 cm in the southwest. Puerto Rico possesses a narrow insular shelf, less than 2.0 km broad on the north coast, whereas on the other coasts, the insular shelf is of variable breadth, to approximately 20 km broad off La Parguera, southwest Puerto Rico, and to a maximum of 40 km broad to the east, where it encompasses Vieques Island. The north coast is exposed to greater wave activity generated by swells in the Atlantic, and in contrast, the south coast is less exposed. Because of its proximity to an amphidromic node, diurnal tides in Puerto Rico have a limited amplitude of less than 30 cm.

HABITATS

Figure 3 is a photograph, facing south from a nearshore cliff in La Parguera, that includes marine habitats where a number of the collections reported herein were made. In the foreground to the right lies a portion of Magueyes Island, site of the UPRM Marine Laboratory. The small mangrove-lined embayment on the east end of Magueyes Island was known as Burkholder Bay, named after Paul Burkholder. Anchored to the east of the island is the R/V *Crawford*, the DMS oceanographic research vessel during the 1960s and 1970s. Seaward of Magueyes Island are



FIGURE 2. Map of Puerto Rico showing frequent collection sites: (1) Grappler Bank, (2) Caja de Muertos, (3) shelf edge off Salinas (off Guánica), (4) Punta Brea algal plain, (5) Ballena Bay, (6) Magueyes Island, (7) Media Luna algal plain, (8) Guayacan Island, (9) “Buoy,” (10) Margarita Reef algal plain, (11) Punta Arenas, (12) Bajo de Sico, (13) Isabella, (14) Guajataca, (15) Islote. The depth contour surrounding the island represents a depth of 50 m. The scale bar in the La Parguera inset = 2.0 km.

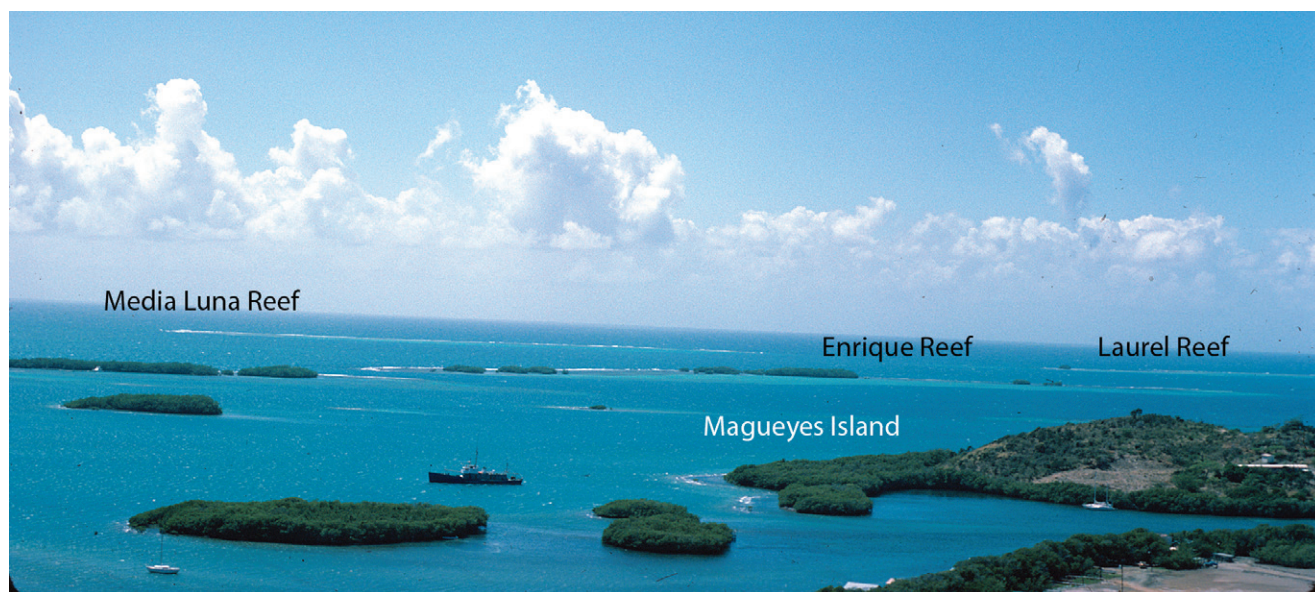


FIGURE 3. La Parguera reef arcs. Photo taken facing south from near shoreline cliff in La Parguera. Magueyes Island, home of the Department of Marine Sciences (DMS) Marine Laboratory, is located in the right foreground. The small embayment east and leeward of Magueyes Island is Burkholder Bay. Just to the east of Magueyes Island is the R/V *Crawford*, an oceanographic research vessel operated by the DMS in the 1960s and 1970s, at anchor. Beyond Magueyes Island two reef arcs are visible. Closest to shore is the arc containing Enrique Reef. Seaward of this arc is another containing Media Luna and Laurel Reefs. A third reef arc is not visible.

three reef arcs, the inner one containing Enrique Reef, a second arc containing Media Luna and Laurel Reefs as well as numerous small mangrove cays, and a third reef arc farther seaward that is not visible in this photo.

Contributing to the high diversity of algal species comprising the Puerto Rican flora are a variety of different intertidal and subtidal habitats: Shorelines of Puerto Rico are characterized by rocky intertidal, depauperate sand shore, and mangrove environments. Offshore environments include seagrass beds, deep and shallow coral reefs, reef flats, and algal plains in addition to pelagic communities.

Rocky Intertidal

FIGURES 4, 5

Despite the physical rigors of the intertidal, wave-exposed rocky environments are among the most diverse algal habitats known and represent the most intensively studied marine environments, in large part because of their accessibility. The intertidal is frequently densely colonized by algae in highly organized communities that demonstrate zonation patterns of different species, often characteristically colored by the dominant organisms

that inhabit the zones and corresponding to different parts of the intertidal zone. Stephenson and Stephenson (1972: 15) in their classic work on intertidal communities noted that “as we proceed from the higher and drier parts of the shore to the lower and wetter parts, the assortment of species presents not only changes, but on the whole increases in number and variety.” The differential wetting and exposure results in different species inhabiting different belts along the shore, one above the other, sometimes sharply differing from adjacent zones.

Zonation patterns may be complex as organism position is controlled by a combination of physical and biological influences. Physical influences include characteristics of the tidal regime (tidal amplitude and breadth, diurnal or mixed diurnal tides) and degree of insolation (greater in tropics than temperate regions). These factors influence the duration of immersion and degree of emersion locally. The ability to withstand desiccation under the tropical sun during emersion limits susceptible species to more frequently wetted portions of the intertidal. Wetting due to wave action prevents desiccation and has the effect of widening the intertidal. Other physical parameters include the slope of the substratum and degree of exposure to wave activity. Intertidal algae must be able to withstand strong surge from waves and thus by necessity are strongly attached. Because of



FIGURE 4. Rocky intertidal: Intertidal rocky platform at entrance to Bahia Sucia, southwest Puerto Rico, close to Cabo Rojo lighthouse (unusually calm conditions).



FIGURE 5. Rocky intertidal: Close-up of rich intertidal algal cover.

the lower tidal amplitude in Puerto Rico, the breadth of the intertidal is typically decreased locally. Zonation is also influenced by biological interactions. These include direct competition between algae or between algae and invertebrate competitors for space and by herbivorous fish and invertebrate grazing. Examples of these interactions are mostly drawn from temperate region examples (e.g., Paine and Vadas 1969; Hodgson 1980; Lubchenco 1980).

Several shallow rocky intertidal communities surround the island, each varying somewhat in their exposure to waves, and are all highly species rich. These include Cabo Rojo (southwestern Puerto Rico), Ballena Bay (south coast to the east of La Parguera) and those along the north coast of the island. Guajataca on the north coast has a rich shallow and intertidal algal community and has served as a productive collection site.

Mangroves

FIGURE 6

Mangroves form unique marine-influenced tropical plant assemblages of trees and shrubs (Hogarth 1999), an ecological association of plants that are not taxonomically related. The Puerto Rican mangrove environment ranges from the intertidal to the supralittoral and is found in areas of reduced wave energy and high sedimentation. It is characteristically inhabited only by those species that have evolved mechanisms to deal with the haline environment. The morphological, anatomical, and physiological adaptations employed by mangroves are reviewed in Dawes (1981) and Tomlinson (1986).

Four species of trees dominate Puerto Rican mangrove communities: *Rhizophora mangle* L., *Avicennia germinans* (L.) L.,



FIGURE 6. Mangrove channel to the lee of Guayacan Island, La Parguera. Note dense stand of *Thalassia testudinum* leeward of the mangrove island and the entangled *Rhizophora mangle* prop roots.

Laguncularia racemosa (L.) C.F. Gaertn., and *Conocarpus erectus* L., commonly known as red, black, white, and buttonwood mangroves, respectively. Much of the southern coast of Puerto Rico is fringed with well-developed mangrove forests and occasional mangrove islets. Mangroves are important for a variety of reasons. In addition to providing shoreline protection and land building, ecologically, they provide a unique habitat to both algae and animals, serve as a nursery for juvenile invertebrate and fish species, have high primary productivity, recycle mineral nutrients through bacterial action, remove terrestrial-based organic materials, and support detrital food chains through export of leaf fall (e.g., Lugo and Snedaker 1974). Golley et al. (1962) reported a gross primary productivity of 8.2 g C/m² per day and an aboveground biomass of 62,850 kg (dry weight)/ha for mangroves at Bahía Fosforescente, La Parguera. There has been a net loss of mangroves in Puerto Rico as well as worldwide due to a variety of causes, including, most prominently, urban development. Puerto Rican legal protection of mangrove environments,

begun in 1972, has resulted in some reforestation (Martinuzzi et al. 2009).

Typically, the most seaward mangrove, *Rhizophora mangle*, is anchored to the bottom by abundant prop roots. The prop roots in shallow water support a varied macroalgal flora [including, among others, the “Bostrichietum” community (see below), plus *Caulerpa* spp., *Acanthophora spicifera* (M. Vahl) Børgesen, *Heterosiphonia* spp., and *Laurencia obtusa* (Hudson) J. V. Lamour]. A particularly well-developed fouling community on mangrove roots lining the intricate mangrove channels is found in the vicinity of Guayacan Island (3.4 km west of Maguëyes Island). Almodóvar and Pagán (1971) described zonation of algae epiphytic on prop roots in the Guayacan channel. One common red algal genus in mangrove epiphytic communities is *Bostrychia*, which forms mosslike growths intertidally on *Rhizophora* prop roots. *Bostrychia* frequently occurs in association with *Murrayella pericladus* (C. Agardh) F. Schmitz, *Catenella caespitosa* (With.) L. M. Irvine, and *Caloglossa leprieurii* (Mont.)

Mart., which are typically associated with the mangrove fouling community. Post (1936) referred to the common tropical worldwide association of these genera as the “Bostrichietum” community. These species generally possess broad tolerances to salinity and temperature. Within mangrove channel environments, peat accumulations are commonly encountered. At Guayacan Island, these commonly support large growths of the green alga *Batophora oerstedii* J. Agardh as well as other mud-inhabiting species such as *Vaucheria* sp. and *Caulerpa verticillata* J. Agardh. Also, floristically unique are the occasional hypersaline lagoons that are found among the mangroves, also in the vicinity of Guayacan Island.

Seagrass Beds

FIGURE 7

Seagrasses are completely submerged flowering plants, angiosperms, that form extremely important habits in shallow

water worldwide. Puerto Rican seagrass beds, for the most part, are best developed along the southern coast of the island and comprise *Thalassia testudinum* König, *Syringodium filiforme* Kütz., *Halodule wrightii* Asch., and *Halophila decipiens* Ostenf. See the excellent treatise on Caribbean seagrasses in Tussenbroek et al. (2010) for concise discussions accompanied by excellent illustrations.

An invasive seagrass species, *Halophila stipulacea* (Forssk.) Asch., was recently reported for the north coast of Puerto Rico by Ruiz et al. (2017). Originally from the Red Sea, *H. stipulacea* represents a trans-Atlantic immigrant that was first reported in the Caribbean Sea from the Grenadines (Caribbean Sea) by Ruiz and Ballantine (2004).

Seagrasses represent foundation species that both moderate the abiotic environment and strongly influence the biotic community. As such, they are ecologically important for a variety of functions that include shoreline protection, sediment stabilization, and providing habitat for a diverse infauna and are the holobiont for a diverse algal epiphytic flora (e.g., Ballantine and

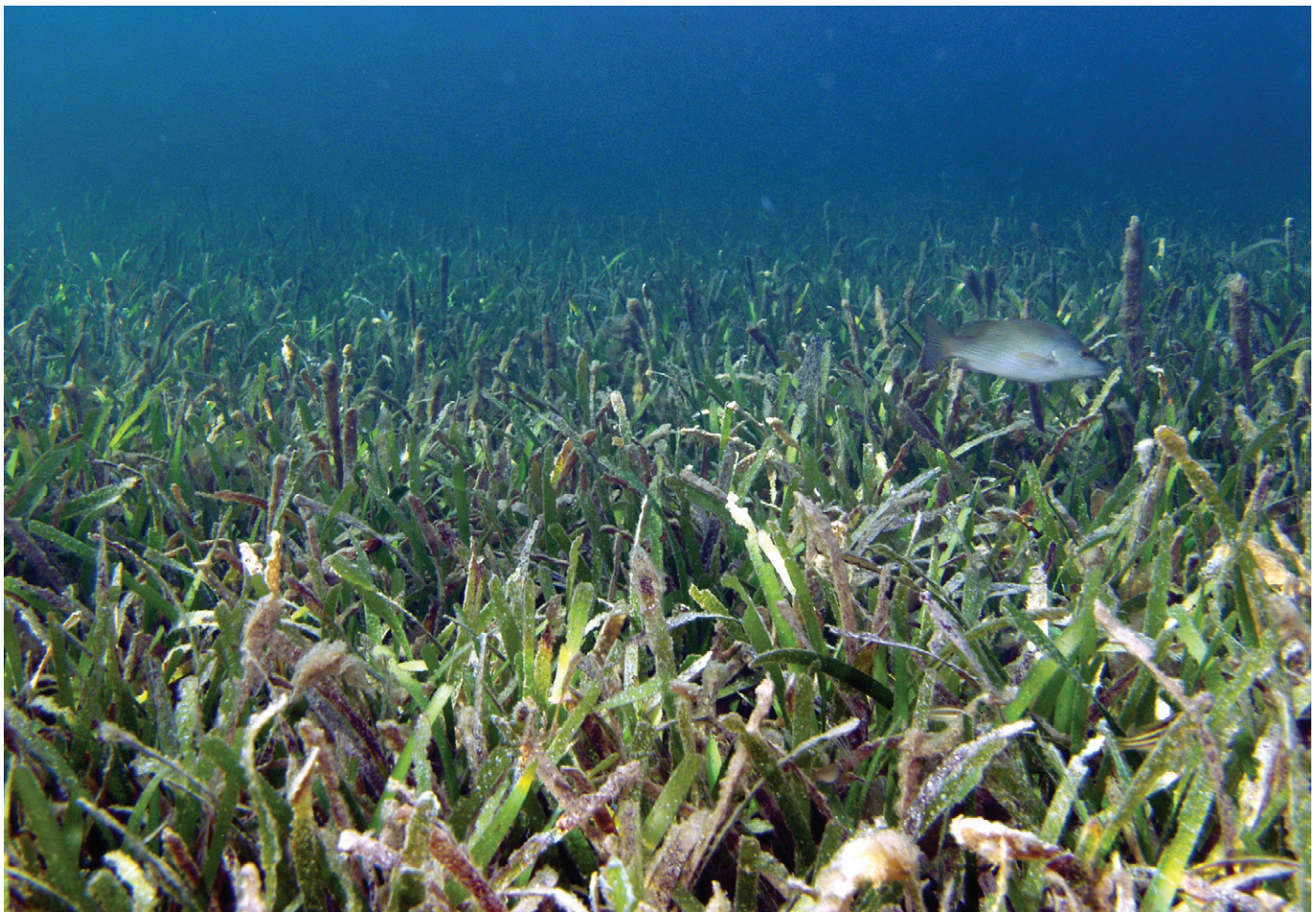


FIGURE 7. *Thalassia testudinum* meadow, seaward Guayacan Island, La Parguera, in shallow water. Field width = approximately 1.0 m.

Humm 1975; Stewart and Meyers 1980; Stoner and Lewis 1985; Garcia and Duarte 2001; Hendriks et al. 2010). Seagrass beds also provide nursery habitat for commercially important fish and invertebrate species, have high primary productivity, and serve as direct food for a variety of fish, sea turtles, manatees, and invertebrates. Seagrass beds provide habitat for a number of algae that are able to anchor in loose or unconsolidated substrata. These include psammophytic species of *Caulerpa*, *Halimeda*, *Avrainvillea*, *Penicillus*, and *Udotea*. An extensive seagrass bed ranging in depth from less than 1.0 to approximately 5.0 m is found seaward of Guayacan Island, extending west toward the Cabo Rojo lighthouse.

Coral Reefs

FIGURES 8, 9

Inshore and shelf edge coral reefs comprise one of the most biologically complex and species-rich ecosystems present on

Earth (Wells 1957; Connell 1978). Oligotrophic tropical waters are known for their low-nutrient concentrations, and coral reefs evolved to live under these conditions. Muscatine and Porter (1977) discussed how symbiotic associations and nutrient recycling allow complex communities to exist in nutrient-poor environments. Algae play extremely important, if not broadly appreciated, roles in coral reefs. Their importance is such that some believe the term coral reef is a misnomer in that it is zoologically chauvinistic, implicitly emphasizing the animal over the algal components. Research done toward the beginning of the previous century (Finckh 1904) indicated that benthic calcified red and green algae were the principal reef-forming organisms at Funafuti Atoll (Pacific Ocean) and corals were only fourth in overall reef-building importance. In terms of aerial surface and biomass, many other Pacific Ocean reefs are dominated by coralline red algae. Although less abundant in the Caribbean, several reef-building coralline algal structures, algal ridges, have also been identified (Adey 1976). Thus, in recognition of the importance of algae to reefs, some prefer the terms bioherm (Adey



FIGURE 8. Coral reef environment: Inshore coral reef, Enrique Reef. Field width = approximately 5.0 m, La Parguera.

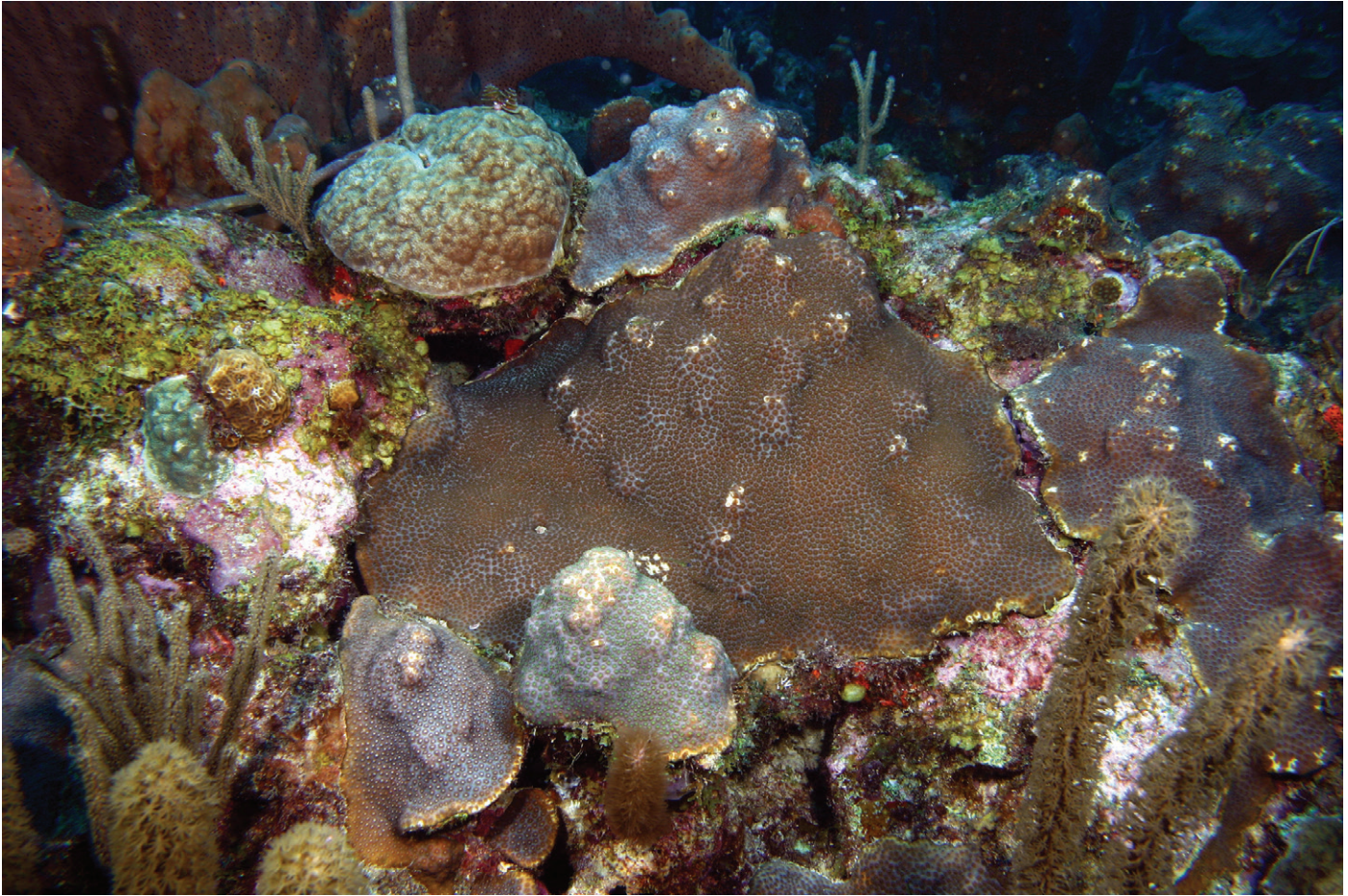


FIGURE 9. Coral reef environment: Shelf edge coral reef environment, 20 m, La Parguera. The bottom is dominated by scleractinian corals, octocorals, and sponges; however, note also crustose coralline algae and *Lobophora* sp.

and Burke 1976) or biotic reef (Littler and Littler 1985) over coral reefs.

Contributions from algae to coral reef communities include physical consolidation (Borowitzka et al. 1974), high species diversity (Hoek et al. 1975; Wanders 1976; Conner and Adey 1977; Littler and Littler 1994a), food for fish and invertebrates (Borowitzka 1981; Carpenter 1981; Hay 1984), contributions to reef sediment and sand (Wray 1977; Bach 1979), primary productivity (Vooren 1981; Hawkins and Lewis 1982; Morrissey 1985), and nitrogen fixation (Mague and Holm-Hansen 1975; Wiebe et al. 1975). Coralline algae also provide a structural framework (Adey 1976, 1978; Wray 1977). In some parts of the world, coralline algae provide the principal reef-building framework of the reefs, although their contribution to reef building is secondary to corals in the Caribbean.

Among the important roles played by crustose coralline algae in coral reef environments is the production of surface chemicals that serve as signals for the metamorphosis of a variety of marine coral reef invertebrate species (Morse et al. 1988).

Given the importance of this function, the relatively recent discovery of crustose coralline algae diseases is a cause for concern. Littler and Littler (1998) found a fungal pathogen, coralline lethal orange disease (CLOD), in Pacific coral reefs. More recently, Ballantine et al. (2005) recognized a pathogenic condition, termed coralline white band syndrome, that kills the coralline species *Neogoniolithon accretum* (Foslie et M. Howe) Setch. et L. R. Mason. We have also observed CLOD in offshore Puerto Rican reefs (unpublished data). Another well-known negative interaction between corals and algae involves endolithic species of Chlorophyta and Cyanobacteria species that weaken reef skeletons. In addition, some algal species may have allelopathic interactions with corals (Jompa and McCook 2003; Titlyanov et al. 2007; Bonaldo and Hay 2014). Finally, epizootic interactions in which Rhodophyta species overgrow and kill corals (Antonius 1999, 2001; Ballantine and Ruiz 2011, 2013; Reyes-Contreras et al. 2016) are increasingly being reported.

“Healthy” reefs normally harbor large numbers of both herbivorous fishes and invertebrates; thus, algae are exposed to

intensive grazing pressure, resulting in their typically not being conspicuous on reefs. Nevertheless, they can be more abundant than they might appear to the casual observer and, in fact, may comprise a higher biodiversity and a higher aerial cover. In the face of high herbivory, algae persist through a number of (not mutually exclusive) adaptations that allow them to exist in an environment of pervasive herbivory (Littler et al. 1983a, 1983b). These include refuge habitats that are physically unfavorable to herbivores, such as areas of very high water turbulence or living in cryptic microhabitats (crevices and among the fine interstices of corals); physical or structural resistance or thallus toughness (species of *Sargassum* or calcification may provide a physical impediment to herbivory); low caloric value (incorporation of calcium carbonate decreases the amount of organic nutrition per foraging effort); and allelopathic substances (e.g., *Asparagopsis* possesses brominated compounds [McConnell and Fenical 1977], and some *Laurencia* species contain phenolics as well as brominated compounds [Young et al. 1980; Davyt et al. 2001], natural products that have been determined to deter grazing). A variety of compounds found in species of *Halimeda* have also been shown to deter herbivory (Paul and Van Alstyne 1988). Other escapes from herbivory include growth habit (prostrate growing algae such as *Peyssonnelia* species and some crustose Corallinales may make them inconspicuous or less desirable to herbivores), life histories with an alternation of heteromorphic generations that include a crustose stage (providing a temporal escape), growth in proximity to toxic or otherwise unpalatable organisms, and rapid growth that replaces vegetative tissues while satiating consumers.

Coral reefs have been in decline globally because of a variety of environmental insults, including rising seawater temperatures, nutrient input and declining water quality, herbivore decline through overfishing and *Diadema* die-off, coral disease and bleaching, algal epizooism on corals, increased sedimentation, and extreme weather events (see specific references in Ballantine et al. 2008). One result, as well as self-reinforcing causation, of coral decline is a well-documented phenomenon known as phase shifts. That is, fleshy algae have become the dominant organisms on coral reefs (e.g., Hughes 1994; Mumby 2009). At the risk of oversimplification, algae may be thought of as being influenced on coral reefs by top-down and bottom-up controls. In the former, algal growth is kept in check by consumption by herbivorous fish and invertebrates. In the latter, algal growth is related to response to nutrient levels. An increase in nutrients may increase because of runoff, one result of poor land use management. When normal environmental conditions are changed that release algae from grazing pressures and encourage growth due to an increase in nutrients, algal growth is largely unchecked, and algae may become the dominant benthic element. Under such circumstances, algae can outcompete corals (Littler and Littler 1994b). Unfortunately, coral reef phase shifts are occurring worldwide. In Puerto Rico at the insular shelf break offshore from La Parguera, a well-developed, vibrant coral reef habitat changed drastically within just a four-year period, 2003–2007

(Ruiz and Ballantine 2009). During this period, algal cover increased from 43% to 75% and from 67% to 82% at two shelf edge sites, and there was a concomitant 53% loss in live coral tissue during this same period (Weil et al. 2009).

Reef Flats

FIGURE 10

Bellwood et al. (2018: 4109) defined a reef flat “as an extensive shallow area of the reef, bounded at the seaward by the reef crest and leeward by the back of the reef.” Water flows across the reef flat as a result of waves breaking on the reef crest and toward the lee. Reef flats have been described as complex habitats whose communities are influenced by heavy herbivore pressure and variable currents and turbulence, depth, temperature, and tidal levels.



FIGURE 10. Reef flat, Enrique Reef, La Parguera. The reef flat extends seaward from mangrove islet. Note coral rubble tossed onto the reef flat by storms.

The habitat imposes some physical challenges, including very high solar exposure and desiccation during low tides. The temperature range due to shallowness is also greater than other benthic habitats. Reef flats typically support corals, coralline algae, algal turfs, and macroalgae. In general, they are recognized as being areas of high primary productivity (Hatcher 1988).

Reef flats in La Parguera are somewhat variable in terms of their dominant benthic characteristics, frequently being heterogeneous. The reef flat immediately behind Enrique Reef (1.0 km seaward of Magueyes Island, La Parguera) is typical of many Caribbean reef flats. Immediately behind the crest are large mats of *Halimeda opuntia* (L.) J. V. Lamour. among living coral. The diminutive *Wrangelia argus* (Mont.) Mont. is variably common at this site. The Enrique Reef flat is mostly colonized by stunted seagrass, *Thalassia testudinum* with large carpets of zoanthids and species of Bryopsidales, including *Penicillus capitatus* J. V. Lamour. and species of *Halimeda*. Although conspicuous when found, *Laurencia obtusa* (Huds.) J. V. Lamour. is intermittently present, presumably avoiding predation through chemical defense (Hay et al. 1987). Coral rubble and large coral fragments tossed up over the reef crests by storms provide substrata for a variety of algal species, principally turf-forming algae. Algal turfs are heterogeneous, multispecies assemblages of often densely placed filamentous algae that are typically close-cropped by herbivores (Hay 1981; Fricke et al. 2011). Turfs are important for a variety of reasons, including productivity and being a site of nitrogen fixation.

Back Reef and Lagoon Environments

Inshore coral reefs in La Parguera have a profile similar to that illustrated by Goreau (1959: fig. 5) for Jamaica. Between the shore and the reef are a lagoon and back reef. The lagoon between La Parguera and Enrique Reef reaches 15–20 m in depth, and much of the lagoon region is barren, with bottom substrata consisting of fine-grained and muddy sediments (Morelock et al. 1977). In portions, it is colonized by *Thalassia testudinum* and calcified chlorophycean species of *Halimeda*, *Penicillus*, and *Udotea*. The back-reef region is made up principally of biogenic sediments and is colonized principally by stunted *Thalassia testudinum*. Large quantities of drift (unattached) algae such as species of *Dictyota* and *Spyridia* may be found behind inshore reefs. Back reefs differ somewhat among La Parguera reefs; for example, nearby Media Luna Reef differs from Enrique Reef in being dominated by rubble. The rubble is colonized seasonally by large quantities of *Liagora* spp. and *Liagorothamnion mucoides* Huisman, D. L. Ballant., et M. J. Wynne. Among the rubble are abundant rhodoliths (Ballantine et al. 2000) comprising *Peyssonnelia imbricans* D. L. Ballant. et H. Ruiz (originally misreported as *Cruoriella* sp. by Ballantine et al. 2000) surrounding nuclei of common coral species (Ballantine et al. 2000; Ballantine and Ruiz 2006). These rhodoliths are somewhat unusual in that the algal component is a peyssonneliacean species, as opposed to usually being a coralline algae (Corallinales).

Algal Plains

FIGURE 11

Offshore subtidal plains dominated by algal growth are common habitats in the Caribbean region. These plains generally have coarse sediments with coral rubble and some limestone hard substrata and are normally situated in 15–25 m depths. Dahl (1973) and Morelock et al. (2001) published observations on these habitats in Puerto Rico, reporting that the substrata of algal plains consisted of coarse biogenic sand, composed of mollusk fragments mixed with *Halimeda* segments and, to a lesser degree, fragments of coralline algae overlying finer sediments. The unconsolidated sediment supports the growth of numerous siphonaceous chlorophyte species of *Caulerpa*, *Halimeda*, *Penicillus*, and *Udotea*, as well as the seagrass *Halophila decipiens*. Hard substrata provided by coral fragments or by larger dead coral outcrops are colonized by large macroalgae, including rhodophytes *Halymenia pseudofloresii* Collins et M. Howe, *Alsidium triquetrum* (S.G.Gmel.) Trevis., and species of *Dasya*, *Laurencia*, *Chondria*, *Agardhiella*, and *Gracilaria*; phaeophyte species of *Sargassum* and *Dictyopteris*; and chlorophytes, including species of *Anadyomene* and *Codium*. Overall, the community supports a dense, highly species-rich algal growth; for example, Ballantine (1977) reported more than 200 algal species, including epiphytes for the Media Luna algal plain alone. Numerous fish and invertebrate species live in association with the algae of these habitats. There are at least four extensive algal plains off the south coast of Puerto Rico: two are offshore from Punta Brea and La Parguera, and they average 17 m in depth; a deeper algal plain, offshore from Margarita Reef, lies at 24 m. The La Parguera algal plain is termed a *rastrial* by local fisherman because of its flat and level nature.

The high species diversity seen in algal plains is at least partially due to intermediate stochastic disturbances, principally due to wave energy causing surge and sediment movement on the bottom. The algal plains are also subjected to periodic mass mortalities caused by hurricanes (Ballantine 1984).

Mesophotic Habitats

FIGURES 12, 13

The term “mesophotic” is somewhat difficult to define precisely, in part because its depth ranges vary geographically. Nevertheless, Hinderstein et al. (2010: 248) characterized mesophotic communities as consisting of light-dependent corals and associated communities “typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. Due to differences in water transparency, the lower depth limit is to about 90 m in the Caribbean and to greater than 150 m in some Pacific Ocean communities. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species.” Because of the



FIGURE 11. Algal plain, seaward Media Luna Reef, 17 m.

decreased light at these depths, these environments have been referred to as “twilight zones” (Fricke et al. 1987; Pyle 1996; Brokovich et al. 2008).

Published accounts of tropical and subtropical western Atlantic deep reef-associated algae are proportionately few, and the benthic flora (>35 m) in the region remains poorly to incompletely known, largely because of logistical difficulties in working in water deeper than is safely accessible by scuba. Scuba collections are limited by decreased bottom time at depth and limits imposed on depth by modern scientific diving safety standards. Submersible diving has provided for an increase in knowledge of the deepwater flora in a relatively limited number of localities in the Caribbean. The high expense associated with submersible diving has limited the intensity and geographical breadth of collections from these platforms. The recently expanding utilization of trimix rebreather (closed-circuit) diving now allows substantially less obstructed access to this environment. The use of trimix rebreather technology in Puerto Rico has greatly enhanced our understanding of these habitats locally.

Thus, deeper-water studies have historically been largely hampered by existing technology.

Ballantine et al. (2016) reported a total of 186 species of Puerto Rican marine algae living below 35 m and summarized deepwater algal exploration of the island’s mesophotic realm. The mesophotic reef habitats at the insular shelf break in southern Puerto Rico are diverse in physical and geomorphic attributes, with the bottom habitat slightly to steeply inclined and, in some locales, nearly vertical. The substrata available for settlement and colonization are mostly hard bottom (primarily dead *Agaricia* plates). Downslope sediment transfer grooves, which are extensions of the spur and groove environment at the shelf break, are generally devoid of macroscopic biological growth. As a result, mesophotic community development is largely restricted to topographical highs (Sherman et al. 2010). Living coral cover is occasionally substantial; however, a high percentage of bottom cover is often dominated by algal and sponge growth. In terms of composition, few foliaceous algal species are present, and the flora is made up of mostly encrusting Corallinales species

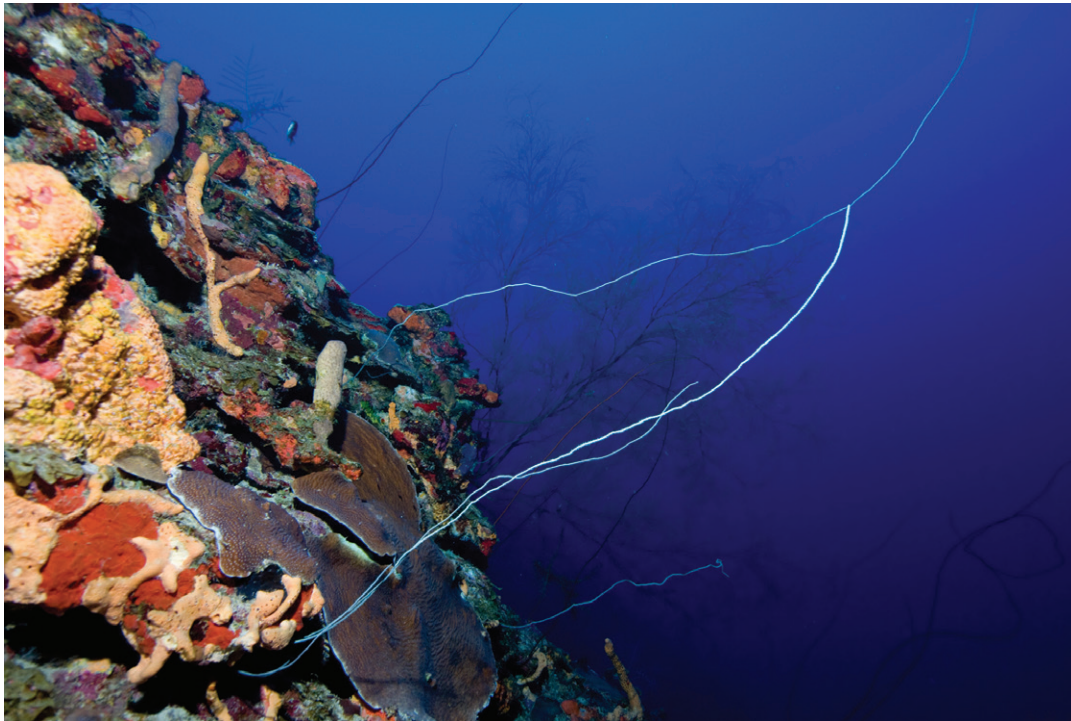


FIGURE 12. Mesophotic reef environment: Near vertical drop-off, near shelf edge, offshore from La Parguera, approximately 50 m depth.

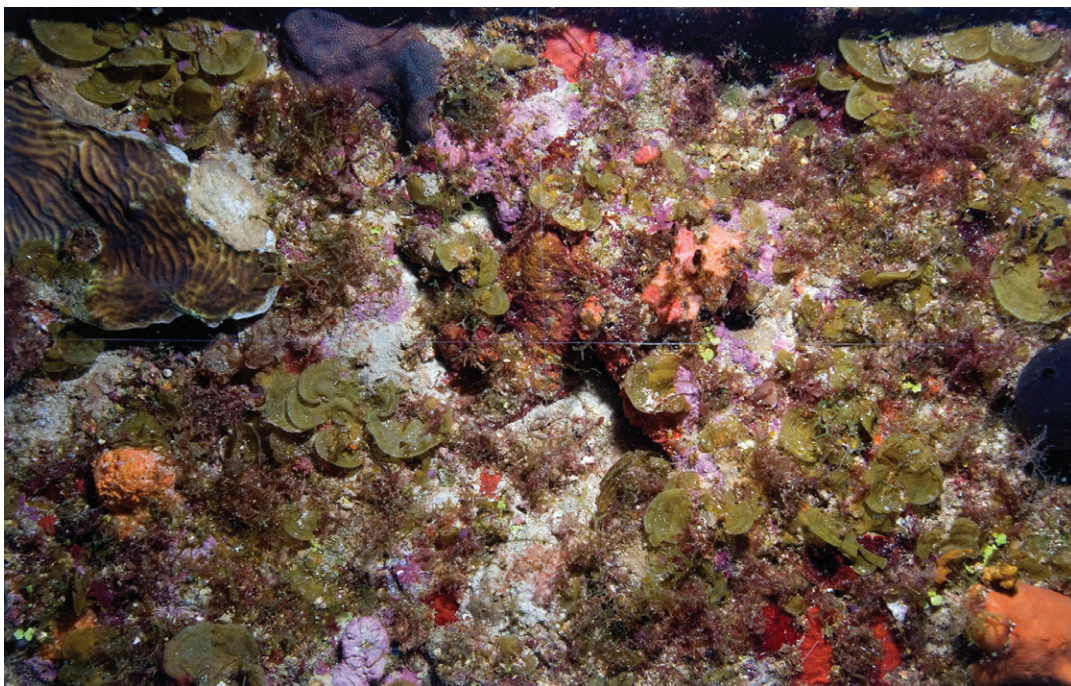


FIGURE 13. Mesophotic reef environment: Close-up of bottom biota in a 0.125 m² quadrat at 56 m depth. Crustose coralline algae, *Lobophora* sp., *Peyssonnelia* spp., and algal turf are the dominant algal elements.

in addition to Peyssonneliaceae species; leafy Phaeophyceae, including *Dictyota* spp. and *Lobophora* spp.; and multispecies turf (Ballantine et al. 2016). The domination of benthic encrusting organisms at a typical bottom habitat at the edge of the southern Puerto Rico insular shelf and at depths of 49 to 76 m is seen in Figure 13. The extensive sand-bottom mesophotic habitats reported in the Pacific by Spalding (2012) have not been seen in Puerto Rico.

Pelagic Environments

FIGURE 14

The Sargasso Sea, a large gyre in the tropical North Atlantic, entrains the largest floating mass of *Sargassum* in the world (Kilar et al. 1992). The community does not have sharp boundaries and stretches from roughly 40°W to 70°W Latitude and from 20°N to 35°N Longitude. Collins (1917) provided early information on the Sargasso Sea and reviewed some of the mythology surrounding it. Recently, other sources of pelagic *Sargassum* and the shifting distribution of the Sargasso Sea itself have been suggested (Gower et al. 2013).

Two species of *Sargassum*, *S. natans* and *S. fluitans*, comprise the bulk of pelagic algae of the Sargasso Sea, with the former being more abundant. Both are unattached and free-floating and have apparently lost the capacity for sexual reproduction.

As would be expected of an organism never attached to the bottom and living in a three-dimensional environment, these algae do not display a basal-apical polar growth habit. Christopher Columbus, who first discovered the floating masses of *Sargassum* in the fifteenth century, is said to have been able to discriminate the (polar versus nonpolar) growth habit and thus recognized that polar growth of floating *Sargassum* indicated that these specimens were once benthically attached and therefore were derived from shallow water. By extension of this logic, the character of growth polarity indicated to him that his ships were close to shore. Pelagic *Sargassum* species also lack cryptostomata that are thought by some to be a relic of sexual reproduction. Thus, vegetative reproduction by the pelagic *Sargassum* species is accomplished through fragmentation. *Sargassum natans* and *S. fluitans* both possess abundant vesicles that maintain them afloat either at the water surface or just below. Another pelagic species, *Sargassum pusillum*, has been reported from Puerto Rico; however, it is extremely rare.

Pelagic *Sargassum* found in offshore coastal areas break free from the gyre as drifting strands to large mats because of a storm or other disturbance. In recent years, huge inshore floating masses of *S. fluitans* and *S. natans* have been reported in the Caribbean (Franks et al. 2016; Sissini et al. 2017). In Puerto Rico, excessive drifts of floating *S. fluitans* are now a regular occurrence at Mona Island, Puerto Rico. These mass accumulations are probably related to multiple factors that may include sources of *Sargassum*



FIGURE 14. Large floating mass of *Sargassum natans*, 8.0 km offshore from Guayanilla.

other than the Sargasso Sea in addition to increased nutrients (Gower et al. 2013; Franks et al. 2016; Sissini et al. 2017).

Hard-Bottom Algal Pavements

FIGURE 15

Hard-bottom pavements are low-relief, consolidated carbonate rock benthic surfaces that are colonized by a number of benthic organisms, including macroalgae, sponges, and scleractinian and alcyonacean corals. These communities are frequently dominated by macroalgae. On the basis of a National Oceanic and Atmospheric Administration benthic mapping program in Puerto Rico, Kendall et al. (2001) determined that an area of approximately 500 km² constituted pavement that was colonized mainly by algae. Overall, this habitat is characterized by a diverse community that supports a dense, species-rich algal cover that includes large macroalgae species, including brown algal species of *Sargassum*, *Padina*, *Dictyoferis*, *Dictyota*, *Stypopodium*

zonale, and *Nereia tropica*; green algal species of *Caulerpa*; and red algal species (of such genera as *Dasya*, *Acanthophora*, and *Amphiroa*). Extensive algal pavements are most common along the north coast of Puerto Rico, principally in the range of 5–30 m depths. The north coast of Puerto Rico is generally subject to high wave energy, strong currents, and, consequently, low sediment accumulations. As a consequence of these conditions, sampling has been limited in Puerto Rico. The limited number of collections that have been accomplished were shore access and ship-based scuba diving in addition to dredging.

ATTRIBUTIONS

Authority names of taxa are abbreviated according to Brummitt and Powell (1992), and herbarium abbreviations follow Thiers (2020). Unless otherwise indicated, in situ photos and herbarium specimen scans are of algae from Puerto Rico. We have followed the taxonomic arrangement of Wynne (2017). Within orders, subordinate taxa are alphabetically arranged.



FIGURE 15. Algal pavement, 300 m offshore from Hatillo (north coast), 15 m depth.

Distributions of algal species listed herein are based on Taylor (1960), Guiry and Guiry (2021), and original literature. Type and type localities are from original publications where possible. Species distributions are mostly culled from Taylor (1960) and Guiry and Guiry (2021). Within distributions, we use, for convenience, “Netherlands Antilles” for records pertaining to Aruba, Bonaire, and Curaçao. As a political entity, the Netherlands Antilles was officially dissolved in 2010.

This work builds on a substantial literature that precedes us. Foremost among these works is William Randolph Taylor’s (1960) *Marine Algae of the Eastern Tropical and Subtropical Coasts of the Americas*, which included 237 genera and 750 species of Chlorophyta, Heterokontophyta (as Phaeophyta), and Rhodophyta. That compilation listed algae from the geographical area from Beaufort North Carolina (North America) southward to southern Brazil (South America). Roughly 36 years later, Wynne began publishing a series of revised checklists of

benthic marine algae of the region (Wynne 1986, 1998, 2005, 2011, 2017), bringing updated nomenclature and distribution and providing a wealth of floristic information. Preparation of our Puerto Rican marine flora would have been substantially more difficult without *AlgaeBase* (Guiry and Guiry 2021).

Keys and species accounts are only partially original as much of the information herein has been assembled from a variety of sources. Portions of keys and taxa accounts are derived from original literature (cited with corresponding taxa) in addition to the compilations of Taylor (1960), Earle (1968), Abbott and Hollenberg (1976), Schneider and Searles (1991), De Clerck (2003), Dawes and Mathieson (2008), Huisman (2015), and Guiry and Guiry (2021).

The following is an artificial key to Ochrophyta genera of Puerto Rico. Users of the key should bear in mind that its use for algae not currently recognized for Puerto Rico may not necessarily result in keying to a correct genus.

KEY TO THE OCHROPHYTA GENERA OF PUERTO RICO

1. Algae are green coenocytic filaments, forming mats in shallow water, frequently in muddy environments *Vaucheria*
Algae not as above 2
2. Algae consisting of uniseriate filaments within a diffuse gelatinous matrix *Chrysonephros*
Algae not as above 3
3. Algae consisting of unicells embedded in a mucilaginous matrix *Chrysocystis*
Algae not as above 4
4. Algae crustose, closely adhering to the substratum across its entire ventral surface or with crustose base and erect filaments 5
Algae erect, not crustose 7
5. Algae with a colorless medullary layer with several layers of cortical cells; growing from a marginal row of cells
. *Lobophora* (in part)
Algae not as above 6
6. Algae forming monostromatic disks or crusts *Kuetzingiella*
Algae forming distromatic disks or crusts with files of cells laterally united; sporangia lateral on ascending filaments . . .
. *Neoralgsia*
7. Algae distinctly filamentous, uniseriate 8
Algae parenchymatous or, if filamentous, then multiseriate, parenchymatous, or multiaxial 15
8. Basal filaments endophytic *Herponema*
Basal filaments epiphytic or epilithic 9
9. Principal erect filaments hair tipped *Myriotrichia*
Filaments not hair tipped 10
10. Repent basal filaments forming spongy mass, erect filaments with short, hook-shaped branchlets *Asteronema*
Algae not as above 11
11. Algae with basal creeping filaments, sporangia borne in an intercalary position *Bachelotia*
With or without creeping basal filaments, sporangia borne terminally 12
12. Algae sparsely branched, short branches positioned at right angles to axial filament *Acinetospora*
Plants without short branches at right angles 13
13. Plastids rod shaped or band shaped, few to many per cell *Ectocarpus*
Plastids discoid, numerous per cell 14
14. Gametangia cylindrical or fusiform *Hincksia*
Gametangia conical *Feldmannia*
15. Plant filamentous with growth from a large apical cell and filaments multiseriate, bearing multicellular propagulae
. *Sphacelaria*
Algae not as above 16

16. Algae of radially oriented filaments internally, nonlaterally united or with large parenchymatous medullary cells . . .	17
Algae not as above	18
17. Algae multiaxial, surface of plants soft, composed of radially oriented filaments that are not laterally united	
.	<i>Cladosiphon</i>
Alga uniaxial, typically with 4 large parenchymatous medullary cells	<i>Stictyosiphon</i>
18. Axes hollow, totally or in part terete or inflated and bladder-like	19
Algae not hollow, with or without hollow vesicles	21
19. Plants branched, tubular	<i>Rosenvingea</i>
Plants not tubular	20
20. Plants saccate, deeply lobed	<i>Colpomenia</i>
Plants clathrate, spongy	<i>Hydroclathrus</i>
21. Axes wiry, branchlets terminating in tufts of pigmented hairs	22
Algae not as above	23
22. Sporangia borne on branched paraphyses localized in special swollen branchlets	<i>Sporochnus</i>
Sporangia on fertile papillae scattered over the plant	<i>Nereia</i>
23. Axes cylindrical, bearing ultimate branchlets that are different from the central axis	24
Algal thallus bladelike	25
24. Algae bearing leaflike branches; spherical hollow vesicles usually present	<i>Sargassum</i>
Foliar organs turbinate or obpyriform with or without a vesicle in the distal end	<i>Turbinaria</i>
25. Blade with midribs	<i>Dictyopteris</i>
Blade without midribs	26
26. Blades narrow, generally less than 1 cm broad	27
Branches fan shaped or strap shaped, more than 1 cm broad	28
27. Branch tips obtuse	<i>Canistrocarpus/Dictyota</i>
Branch tips acute	<i>Chnoospora</i>
28. Thallus of strap-shaped branches	<i>Spatoglossum</i>
Thalli entire, lobed or split	29
29. Apical margin inrolled	<i>Padina</i>
Apical margin not inrolled	30
30. Algae large, erect, thallus generally split into narrow segments, blades zonate, frequently iridescent, sori with paraphyses	<i>Styopodium</i>
Algae fan-shaped, blades not zonate	31
31. Puerto Rican members of the genus with 1–2 medullary cell layers, sori lacking paraphyses	<i>Lobophora</i> (in part)
Medulla in mature portions 4 or more cell layers	32
32. Medulla with 2 cell layers distally and 4 cell layers distally; sori with paraphyses	<i>Taonia</i>
Medulla with up to 6 cell layers; sori lacking paraphyses	<i>Zonaria</i>

The Ochrophyta Species of Puerto Rico

OCHROPHYTA CAVAL.-SM.

PELAGOPHYCEAE R. A. ANDERSEN ET G. W. SAUNDERS

SARCINOCHRYSIDALES GAYRAL ET BILLARD

CHRYSOCYSTACEAE MELKONIAN, H. S. YOON ET R. A. ANDERSEN

Chrysocystis Lobban, D. Honda et Chihara

Chrysocystis Lobban, D. Honda et Chihara in Lobban et al. 1995: 97.

Thalli are colonial and gelatinous with peripherally located cells. Vegetative cells, within the gelatinous matrix, are pyriform or ovoid with 1 or several chloroplasts and 2 laterally inserted flagella. Reproduction is by formation of zoospores or asexually by fragmentation. *Chrysocystis* is a monotypic genus.

Chrysocystis fragilis Lobban, D. Honda et Chihara

FIGURE 16

Chrysocystis fragilis Lobban, D. Honda et Chihara in Lobban et al. 1995: 97, figs. 1–16.

Puerto Rican Record: Ballantine et al. 2009.

Western Atlantic Distribution: Puerto Rico.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Luminao Reef, Guam.

Thalli are fragile globular colonies, 30–50 mm in extent, up to 5.0 mm thick. Vegetative cells are spherical, 10–14 μm in diameter with 4–8 elliptical, peripheral chloroplasts. Algae are pale golden yellow in color.

Habitat and comments: *Chrysocystis fragilis* grows in coral reef habitats, from shallow water to at least 20 m depths. In the western Atlantic, *C. fragilis* is known only from Puerto Rico, where it has been occasionally observed in bloom-like abundance. In describing *C. fragilis*, Lobban et al. (1995) reported similar bloom-like occurrences in

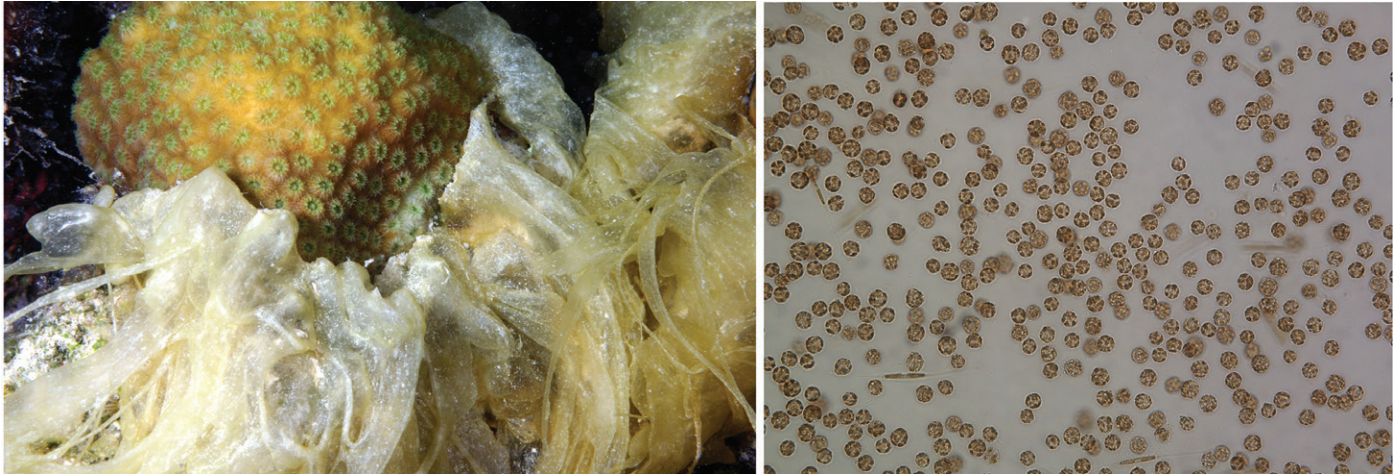


FIGURE 16. *Chrysocystis fragilis*. Left: In situ photograph showing a mucilaginous matrix growing around coral, *Orbicella annularis* Ellis et Solander. Field width = approximately 10 cm. Right: Micrograph of unicells within gelatinous matrix. Cells = 5.0 µm diam.

Guam and speculated that the species may exist nonconspicuously in the microbenthos when it is not blooming.

SARCINOCHRYSIDACEAE GAYRAL ET BILLARD

Chrysonephos W. R. Taylor

Chrysonephos W. R. Taylor 1952: 79.

Thalli are filamentous and dichotomously forked, occurring in clumps, 1.0–4.0 cm tall with inconspicuous holdfasts. Algae consist of few-celled prostrate filaments that develop an erect axis. Filaments are uniseriate, with some oblique divisions causing older axes to become irregularly pluriseriate. The gelatinous filaments are thin walled and cylindrical, measuring 30–48 µm diameter (diam) proximally, tapering to 5.0–12 µm distally. Cells possess 2 to 4, yellowish-brown, oval to band-shaped chloroplasts, each with a bulging pyrenoid. *Chrysonephos* is a monotypic genus.

Chrysonephos lewisii (W. R. Taylor) W. R. Taylor

Chrysonephos lewisii (W. R. Taylor) W. R. Taylor 1952: 79.

Basionym: *Chrysophaeum lewisii* W. R. Taylor 1951: 129, figs. 1–26.

Puerto Rican Records: As *Chrysonephos lewisii*: Almodóvar 1964a; Taylor 1969; Hinds and Ballantine 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Jamaica, Puerto Rico.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Port Royal Bay, Hunt Island, Bermuda.

Thalli, 1.0–3.0 cm tall, are composed of uniseriate or locally pluriseriate filaments, 30–38 µm diam proximally and 4.5–7.7 µm diam distally. Algae are sulfur yellow in color.

Habitat and comments: *Chrysonephos lewisii* can form abundant diffuse filaments over coral sand and seagrasses in shallow, protected environments. Verlaque et al. (2015) noted *C. lewisii* was not recorded in the Mediterranean prior to 1988 and, in reporting it from Corsica to Monaco, considered it an “invasive” introduced species (see also Guiry and Guiry 2021). [Additional illustrations: Taylor 1960: pl. 28: figs. 2–7.]

PHAEOPHYCEAE KJELLM.

DICTYOTALES BORY

DICTYOTACEAE J. V. LAMOUR. EX DUMORT.

Canistrocarpus De Paula et De Clerck

Canistrocarpus De Paula et De Clerck in De Clerck et al. 2006: 1285.

Thalli are erect or prostrate and basally attached by rhizoids and/or by marginal rhizoids. Flattened blades have smooth margins, and apices are obtuse or apiculate. Branching is dichotomous, alternate or cervicorn. Thalli possess a single-layered medulla with a 1-layered cortex on both surfaces. Sporangia are isolated or grouped in sori, borne on 1-celled stalks and surrounded by sterile cells. Three species are currently recognized

in the genus, with one known from Puerto Rico. *Canistrocarpus cervicornis* is included in the *Dictyota* key to species.

***Canistrocarpus cervicornis* (Kütz.)
De Paula et De Clerck**

FIGURE 17

Canistrocarpus cervicornis (Kütz.) De Paula et De Clerck in De Clerck et al. 2006: 1285.

Basionym: *Dictyota cervicornis* Kütz. 1859: 11, pl. 24: fig. II.

Misapplied Name: *Dictyota indica* Sond. ex Kütz. 1859: 8, pl. 17: fig. 1 [non *D. indica* sensu Vickers 1908: 39, pl. 18; =*D. caribaea* Hörnig et Schnetter in Hörnig et al. 1992: 58].

Puerto Rican Records: As *Dictyota cervicornis*: Almodóvar and Blomquist 1961; Almodóvar 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Bal-

lantine and Aponte 1997, 2002; Ballantine et al. 2016. As *Dictyota indica*: Almodóvar and Blomquist 1961; Almodóvar 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 2002.

Western Atlantic Distribution: Belize, Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Dominica, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Panama, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Key West, Florida Keys, Monroe County, Florida, USA.

Thalli, measuring to 20 cm tall, are dichotomously branched and sometimes entangled. Axes are 4.0–6.0 mm wide proximally, 1.0–2.5 mm broad distally, and 180–220 µm thick. Intradichotomy distances are 1.0–4.0 cm. Branching is cervicorn near the

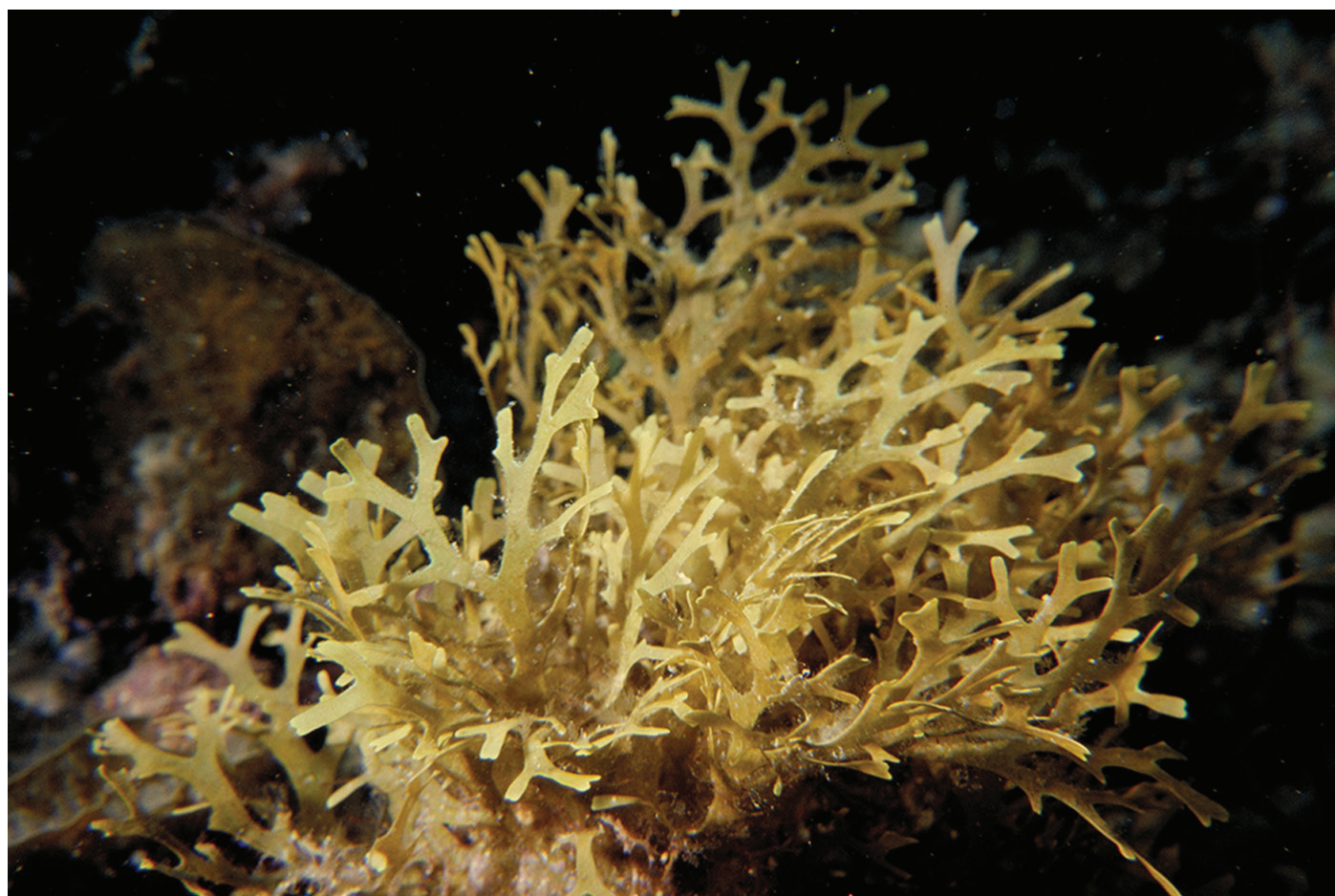


FIGURE 17. *Canistrocarpus cervicornis*. In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field width = approximately 15 cm.

apices, sometimes with spurs or short forks. Branching dichotomies are narrow, and branches may be twisted. Medullary cells are rectangular, 140–180 µm tall.

Habitat and comments: *Canistrocarpus cervicornis* is usually observed in shallow, sheltered habitats, but is also found down to 50 m depths in Puerto Rico (Ballantine et al. 2016). The morphological features that separate *Canistrocarpus* from *Dictyota* are neither clear cut nor easily observable; however, *C. cervicornis* is separable from Puerto Rican *Dictyota* species on the basis of branching morphology.

***Dictyopteris* J. V. Lamour.**

Dictyopteris J. V. Lamour. 1809a: 332.

Thalli are small to large with strap-shaped branches that possess a pronounced midrib and also bear lateral veins in some species. Blades are 2–9 cell layers thick, and growth is from clusters of meristematic cells at branch tips. Five of the 35 currently recognized species of *Dictyopteris* occur in Puerto Rico.

KEY TO THE *Dictyopteris* SPECIES OF PUERTO RICO

- | | |
|--|------------------------|
| 1. Veinlets present | <i>D. plagiogramma</i> |
| Veinlets absent | 2 |
| 2. Blade membrane 1 or 2 cells thick | 3 |
| Blade membranes 4 cells thick or greater | 4 |
| 3. Thalli less than 8 cm tall; less than 5.0 mm broad | <i>D. delicatula</i> |
| Thalli greater than 8 cm tall; greater than 5.0 mm broad | <i>D. jamaicensis</i> |
| 4. Blades 4 cells thick | <i>D. justii</i> |
| Blades 6–9 cells thick | <i>D. jolyana</i> |

***Dictyopteris delicatula* J. V. Lamour.**

FIGURE 18

Dictyopteris delicatula J. V. Lamour. 1809a: 332, pl. 6: fig. 2B.

Puerto Rican Records: Hauck 1888; Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar 1964b, 1964c; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997; Hinds and Ballantine 1987; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Bequia, Cuba, Dominica, Grenadines, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Eustatius, St. Kitts, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Antilles, West Indies.

Thalli measure 2.0–8.0 cm tall and are attached to the substratum at multiple points. Algae are frequently decumbent with axes attached to each other. Branching is dichotomous to irregular with blades, 0.5–5.0 mm broad, having rounded apices. Blades are thin and membranous, 2 cells thick away from midrib and not forming veinlets. Reproductive sori are in single rows on both sides of the midrib. Algae are light to dark brown in color.

Habitat and comments: *Dictyopteris delicatula* is extremely common in shallow-water coral reef environments throughout the Caribbean. In Puerto Rico the species is also encountered in deepwater turf communities, down to 82 m depths (Ballantine et al. 2016). [Additional illustrations: Vickers 1908: pl. 3; Wysor and De Clerck 2003: figs. 1–11; Braune and Guiry 2011: fig. 34.1.]

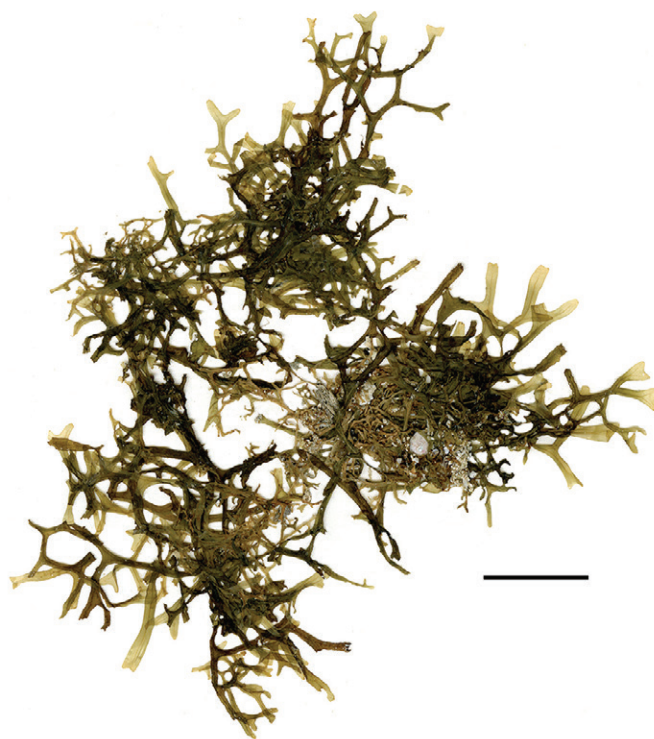


FIGURE 18. *Dictyopteris delicatula*. LRA4438, herbarium specimen: Guayanilla. Scale bar = 2.0 cm.

***Dictyopteris jamaicensis* W. R. Taylor**

FIGURE 19

Dictyopteris jamaicensis W. R. Taylor 1960: 228–229, 631, pl. 32: fig. 2.

Puerto Rican Records: Almodóvar 1970; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Barbados, Cuba, Hispaniola, Jamaica, Panama, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Hellshire Hills, St. Catherine, Jamaica.

Thalli are tall, to 15 cm or greater; the lower axes denuded and stalklike. Branching is in 1–3 degrees, subdichotomously divided proximally, becoming alternately branched distally. Blades are strap shaped with somewhat undulate, minutely dentate margins and measure 7.0–11 mm broad and 42–60 μm thick. Blades are 1 cell thick near growing points, becoming 2 cells thick with maturity. Midribs are conspicuous, and lateral veins are absent. Algae are light brown in color.



FIGURE 19. *Dictyopteris jamaicensis*. DLB2779, herbarium specimen: 1.5 km seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

Habitat and comments: *Dictyopteris jamaicensis* is typically collected in deeper water, 33–73 m depth; Almodóvar (1970) reported the species to 24 m in Puerto Rico.

Dictyopteris jolyana
E. C. Oliveira et R. P. Furtado

FIGURE 20

Dictyopteris jolyana E. C. Oliveira et R. P. Furtado 1978: 760, figs. 1–5.

Puerto Rican Records: Ballantine and Norris 1989; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Martinique, Puerto Rico, St. Eustatius, Brazil, Venezuela.

Type Locality: Ilha de Francês, Espírito Santo (state), Brazil.

Thalli, reaching 20–30(–50) cm tall, are borne on simple or 1–3 times dichotomously branched, 2.0–3.0 cm long stipes. Attachment is by feltlike rhizoids that cover the lower portion of stipes. Strap-shaped blades are oblanceolate, 5.0(–6.0) cm broad and 400 μ m thick. Blade margins are usually torn and possess a smooth to ruffled entire margin. Blades possess conspicuous midribs and lack lateral veins. The medulla comprises 4–7 layers of translucent cells, measuring 38–68 μ m tall and 76–152 μ m long. The medullary cells are bordered by a single cortical



FIGURE 20. *Dictyopteris jolyana*. DLB5905, herbarium specimen: Seaward Margarita Reef, La Parguera, 24 m. Scale bar = 5.0 cm.

cell layer on each surface. Cortical cells are 34 μm tall by 26 μm long. Oogonia are ovoid, 68 μm diam and 164 μm long. Algae are brownish yellow in color.

Habitat and comments: *Dictyopteris jolyana*, considered a deepwater species by Oliveira Filho and Furtado (1978), has since then been encountered in moderately wave-exposed habits in the intertidal to 30 m depths. On the south coast of Puerto Rico, the species occurs from 1.0 to 3.0 m depths at Balena Bay, Guánica, and down to 24 m depths offshore from Margarita Reef, La Parguera.

***Dictyopteris justii* J. V. Lamour.**

FIGURE 21

Dictyopteris justii J. V. Lamour. 1809a: 332, pl. 6: fig. 2A.

Puerto Rican Records: Hauck 1888; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964c; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cuba, Grenadines, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Panama, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

Type Locality: “Hab. in Antilles” (Lamouroux 1809a: 332).

Thalli measure to 40 cm tall or greater. Stipes are denuded below and stalklike. The strap-shaped, dichotomously branched blades are 1.5–8.0 cm broad and possess a prominent midrib. Margins of the blade are entire or irregularly crenulate, and blade tips are obtuse. Blades are approximately 200 μm thick,



FIGURE 21. *Dictyopteris justii*. In situ photograph of a young plant. Field width = approximately 20 cm.

with 2 medullary layers and an outer cortical layer of smaller cells on each surface. Medullary cells are rectangular, 100 μm long, and 30–65 μm high. Algae are dark brown in color and sometimes iridescent.

Habitat and comments: *Dictyopteris justii* is reported as ranging from the intertidal in moderately exposed habitats to 40 m depths (Taylor 1960). In Puerto Rico, it has been collected nearshore at Ballena Bay, at the offshore algal plains, and to depths of 60 m (Ballantine et al. 2016). [Additional illustrations: Vickers 1908: pl. 5; Braune and Guiry 2011: fig. 34.2.]

***Dictyopteris plagiogramma* (Mont.) Vickers**

FIGURE 22

Dictyopteris plagiogramma (Mont.) Vickers 1905: 58.

Basionym: *Haliseris plagiogramma* Mont. 1837: 356.

Puerto Rican Records: As *Dictyopteris plagiogramma*: Hauck 1888; Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.



FIGURE 22. *Dictyopteris plagiogramma*. RJZsn, herbarium specimen: Islote, 17 m. Scale bar = 5.0 cm.

Western Atlantic Distribution: Mexico, North America, Bermuda, Barbados, Cuba, Grenadines, Hispaniola, Martinique, Panama, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Havana, Cuba.

Thalli are up to 25 cm tall with alternately to irregularly branched blades. The blades measure 2.0–7.0(–10) mm broad and possess a prominent midrib and less pronounced pinnate veinlets running obliquely from the midrib toward the margin. Blades are a single layer thick, 35–50 μm , not including the midrib region. Blade margins are entire, smooth, and crenulate. Reproductive sori are irregularly scattered near the midribs, 80–120 μm diam. Algae are brown in color.

Habitat and comments: *Dictyopteris plagiogramma* is found from moderate depths to deeper waters. In Puerto Rico, the species occurs at depths of 10–14 m in offshore habitats on the north coast. [Additional illustration: Vickers 1908: pl. 4.]

Excluded taxon

Dictyopteris polypodioides (DC.) J. V. Lamour. 1809a: 332.

Heterotypic Synonym: *Dictyopteris membranacea* Batters 1902: 54.

The single record of *D. polypodioides* in Puerto Rico by Almodóvar (1970) as *D. membranacea* Batters was from the algal plain, offshore from Punta Brea. As specimens have not been located in MSM, this record cannot be verified.

Dictyota J. V. Lamour.

Dictyota J. V. Lamour. 1809a: 38.

Thalli are erect or decumbent, usually attached by a fibrous holdfast or sometimes by secondary holdfasts on branches in contact with the substratum. Generally, branching is dichotomous or subdichotomous; less commonly, branching is alternate or pinnate. Thalli develop from a single apical cell; the medulla is single celled or 2 or more layers thick, with a single cortical layer on each surface; midribs and veins are absent. Of the 75 currently recognized species of *Dictyota*, 14 occur in Puerto Rico.

KEY TO THE *DICTYOTA* AND *CANISTROCARPUS* SPECIES OF PUERTO RICO

1. Thalli with a stoloniferous base *D. stolonifera*
Thalli not as above (lacking stolon-like basal attachments) 2
2. Thalli with hooklike lateral branches *D. hamifera*
Thalli not as above (without hooklike branches) 3
3. Blade margins dentate 4
Blade margins entire 5
4. Blades up to 12 mm wide *D. ciliolata*
Blades narrower, 3.0–4.5 mm wide *D. jamaicensis*
5. Thalli generally decumbent 6
Thalli generally erect 7
6. Dichotomous to subdichotomously branched, mostly to 1.0 (rarely to 5.0) cm tall; live thalli with bluish-green iridescence *D. humifusa*
Dichotomous to alternately branched, to 3.0 cm tall; live thalli with bluish iridescence and, commonly, noniridescent transverse bands *D. friabilis*
7. Blades very narrow, less than 2.0 mm broad 8
Blades broader (wider than 2 mm) 10
8. Blades frequently twisted *D. caribaea*
Blades not twisted 9
9. Blades becoming much narrower distally; branching angles broad *D. pulchella*
Blades not abruptly narrowing distally; branching angles narrow *D. implexa*
10. Branching alternate 11
Branching dichotomous 13
Branching cervicorn *Canistrocarpus cervicornis*
11. Blade medulla 1 cell throughout *D. mertensii*
Blade medulla near the base 2 or more cells thick 12
12. Blades 0.5–1.5 mm wide; branching mostly in 1 plane *D. guineënsis*
Blades 2.0–4.0 mm wide; branching not conspicuously in 1 plane *D. pinnatifida*
13. Upper sinuses broad; blades 100–140 μm thick *D. bartayresiana*
Upper sinuses narrower; blades 150–250 μm thick *D. menstrualis*

***Dictyota bartayresiana* J. V. Lamour.**

FIGURE 23

Dictyota bartayresiana J. V. Lamour. 1809b: 43.

Homotypic Synonym: *Dictyota bartayresii* J. V. Lamour. 1809a: 311, *nom. illeg.*

Puerto Rican Records: As *Dictyota bartayresiana*: Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016. As *D. bartayresii*: Almodóvar and Blomquist 1959; Almodóvar 1964b; Almodóvar and Pagán 1971; Schwartz and Almodóvar 1971; Ballantine et al. 1987.

Western Atlantic Distribution: Mexico, North America, Bahamas, Antigua, Barbados, Belize, Cuba, Hispaniola, Jamaica, Martinique, Panama, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Antilles, West Indies.

Thalli measure 5.0–20 cm tall and are dichotomously branched with obtuse to rounded apices. Branch angles are broad, (45°–)70°–90°(–100°). Blades are (2.3–)4.0–7.0(–11.8) mm wide and 100–140 µm thick. The medulla consists of a single layer of rectangular medullary cells, 110 × 45 µm (length × height). Marginal rhizoids are produced along blades, attaching them to the substratum as well as to other blades. Spherical sporangia measure 60–110 µm diam. Algae are brown in color and sometimes iridescent.

Habitat and comments: In Puerto Rico *Dictyota bartayresiana* typically grows in shallow, semiprotected habitats and also occurs in deep water down to 61 m depths (Ballantine et al. 2016). [Additional illustration: Braune and Guiry 2011: fig. 35.1.]

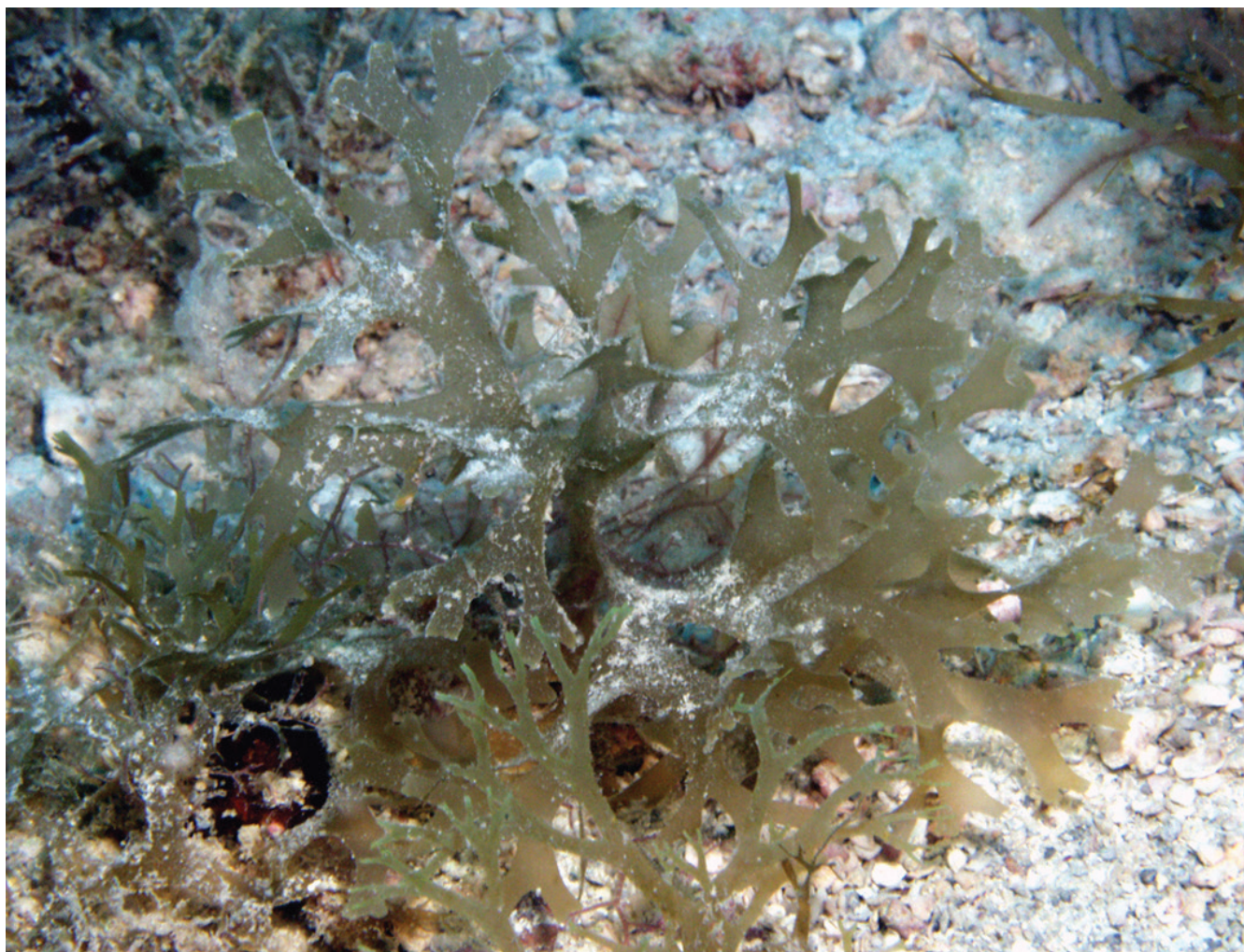


FIGURE 23. *Dictyota bartayresiana*. In situ photograph, 1.5 km seaward Media Luna Reef. Field width = approximately 10 cm.

***Dictyota caribaea* Hörnig et Schnetter**

FIGURE 24

Dictyota caribaea Hörnig et Schnetter in Hörnig et al. 1992: 58.

Heterotypic Synonyms: *Dictyota volubilis* sensu Vickers 1908.

Puerto Rican Records: As *Dictyota volubilis*: Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Antigua, Cuba, Dominica, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Acuario, Isla de San Andrés, Colombia, Caribbean Sea.

Thalli reach to 10(–20) cm tall; branching is cervicorn to dichotomous. Spirally twisted blades are narrow and strap shaped, 0.3–1.5 mm broad, and 200–300 μ m thick. The medulla is a single layer of rectangular cells, 180 μ m tall by 280 μ m long. Algae are yellow-olive brown in color.

Habitat and comments: *Dictyota caribaea* is usually found unattached, in shallow water but also occurs at moderate depths down to 12 m. Wysor and De Clerck (2003) provisionally



FIGURE 24. *Dictyota caribaea*. LRA5442: Punta Brea algal plain, 16 m. Scale bar = 2.0 cm.

referred *Dictyota volubilis* sensu Vickers (Taylor 1928, 1960) to *D. caribaea*. [Additional illustrations: as *D. volubilis*, Vickers 1908: pl. 20: figs. 1–4.]

***Dictyota ciliolata* Sond. ex Kütz.**

FIGURE 25

Dictyota ciliolata Sond. ex Kütz. 1859: 12.

Heterotypic Synonym: *Dictyota dichotoma* sensu Taylor 1960: 218 [non *Dictyota dichotoma* (Huds.) J. V. Lamour. 1809b: 42].

Puerto Rican Records: As *Dictyota dichotoma* sensu Taylor 1960: Almodóvar and Blomquist 1961; Díaz-Piferrer 1963; Almodóvar 1964b, 1964c; Ballantine 1977, 1979; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, North America, Bermuda, Antigua, Barbados, Belize, Cayman Islands, Cuba, Dominica, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Kitts, U.S. St. Eustatius, St. Vincent, Trinidad and Tobago, Virgin Islands, Brazil, Colombia, Venezuela.

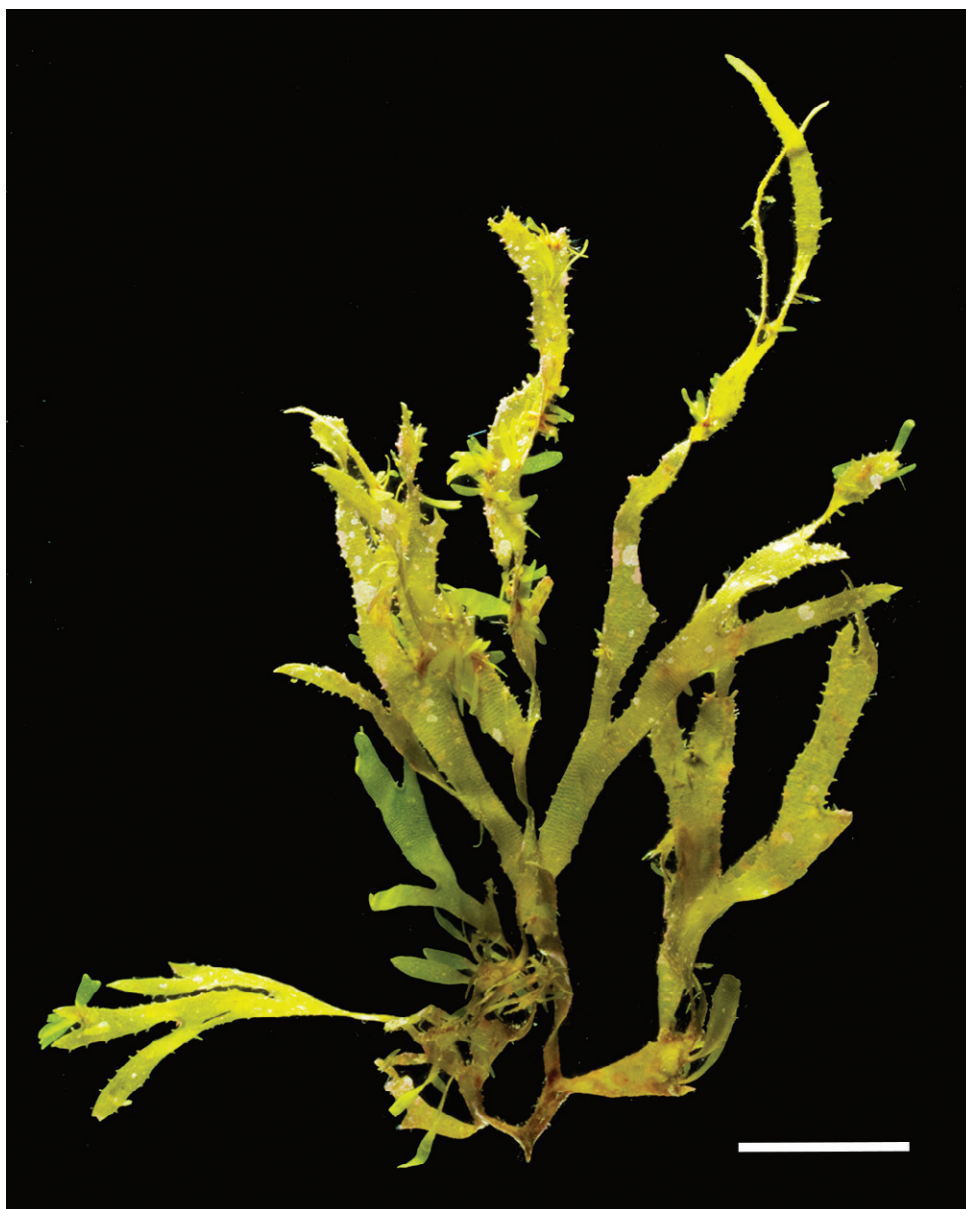


FIGURE 25. *Dictyota ciliolata*. DLB8322: Rincon, 20 m (leg. HR). Scale bar = 2.0 cm.

World Distribution: See Guiry and Guiry 2021.

Type Locality: La Guaira, near Caracas, Venezuela.

Thalli reach to 15 cm tall and are regularly dichotomously or irregularly branched, the dichotomies with narrow branching angles. Blades are frequently spirally twisted, measuring to 12 mm broad below forks and to 7.0 mm above, and are 150 μ m thick. Branches taper terminally and are subacute, and blade margins are sparingly aculeate-dentate, commonly with proliferations. The medulla comprises a single cellular layer, to 125 μ m tall. Oogonia are to 200 μ m diam, occurring in scattered sori. Algae are light brown in color.

Habitat and comments: *Dictyota ciliolata* is generally found on rocks, in tide pools from the low intertidal and down to 24 m depths. In Puerto Rico it has also been collected from deeper habitats at 36–46 m depths (Ballantine et al. 2016). DNA analysis has confirmed the broad distribution of *D. ciliolata* in

warm temperate to tropical waters (Tronholm et al. 2013). [Additional illustrations: Vickers 1908: pl. 17: figs. 1–4; Tronholm et al. 2013: figs. 2–15.]

***Dictyota friabilis* Setch.**

FIGURE 26

Dictyota friabilis Setch. 1926: 91, pl. 13: figs. 4–7, pl. 20: fig. 1.

Heterotypic Synonym: *Dictyota pfaffii* Schnetter 1972: 12, fig. 1.

Puerto Rican Records: As *Dictyota friabilis*: Ruíz and Ballantine 2009; Ballantine et al. 2009. As *Dictyota pfaffii*: Ballantine et al. 2004.

Western Atlantic Distribution: Belize, Cuba, Martinique, Puerto Rico, St. Eustatius, Brazil, Colombia, Venezuela.



FIGURE 26. *Dictyota friabilis*. In situ photograph, edge of insular shelf, offshore from La Parguera, 18 m. Field width = approximately 14 cm.

World Distribution: See Guiry and Guiry 2021.

Type Locality: In pools among rocks; reef at Tafaa Point, Tahiti.

Thalli possess a decumbent habit, being attached at multiple sites. Blades, up to 3.0 cm in length, 3.0–6.0 mm broad, and 100–200 μm thick, have broad sinuses. The species has a single layered medulla, 60–160 μm high. Branching is mostly in one plane, and branches possess short interdichotomies and obtuse branch apices. Tetrasporangia are up to 160 μm in diameter. Algae are light brown to greenish brown, commonly iridescent.

Habitat and comments: In Puerto Rico, *Dictyota friabilis* is commonly present on the south coast at the edge of the insular shelf. In the field when living, it is easily recognized by its distinctive blue and green iridescent bands. Wysor and De Clerck (2003) considered *D. pfaffii* to be conspecific with *D. friabilis*.

***Dictyota guineënsis* (Kütz.)
P. Crouan et H. Crouan**

FIGURE 27

Dictyota guineënsis (Kütz.) P. Crouan et H. Crouan in Mazé and Schramm 1878: 126.

Basionym: *Spatoglossum guineense* Kütz. 1843: 339.

Homotypic Synonym: *Dilophus guineënsis* (Kütz.) J. Agardh 1882: 108.

Puerto Rican Records: As *Dictyota guineënsis*: Ballantine and Aponte 1997, 2002. As *Dilophus guineënsis*: Almodóvar and Blomquist 1961; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Belize, Bequia, Cayman Islands,



FIGURE 27. *Dictyota guineënsis*. DLB6984, herbarium specimen: Ballena Bay. Scale bar = 1.0 cm.

Cuba, Dominica, Grenadines, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: São Tomé [island], São Tomé and Príncipe [nation], Gulf of Guinea, eastern Atlantic Ocean.

Thalli reach 0.5–12(–30) cm tall, with main axes 0.5–4.0 mm broad. First-order branching is alternate, and subsequent branching is mostly dichotomous. Branches possess smooth margins and obtuse to acute apices. Internally, the medulla is 2(–4) layers, except outward toward margins, where the medulla is 1 cell thick. Medullary cells measure up to 80 μ m high.

Habitat and comments: *Dictyota guineënsis* grows on hard substrata in shallow exposed habitats down to 10 m depths. In Puerto Rico, it commonly occurs at Ballena Bay, Guánica. The multilayered medulla of this and some other species was previously a generic character used to separate *Dilophus* from the single-layer medulla of *Dictyota*. Studies of Hörnig et al. (1992)

concluded that the criterion of number of medullary layers was inadequate and considered the two congeneric. [Additional illustration: Vickers 1908: pl. 9: figs. 1–5.]

***Dictyota hamifera* Setch.**

FIGURE 28

Dictyota hamifera Setch. 1926: 92.

Puerto Rican Record: Ballantine et al. 2009.

Western Atlantic Distribution: Bermuda, Panama, Puerto Rico, St. Eustatius, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: “On wave benches” [reef platforms], near Faarapa, Tahiti (Setchell 1926); between Papenu and Huau, Tahiti.

Thalli are up to 3.0(–12) cm long with blades 1.0–2.0 mm broad and 80–125(–290) μ m thick. Branching is dichotomous,

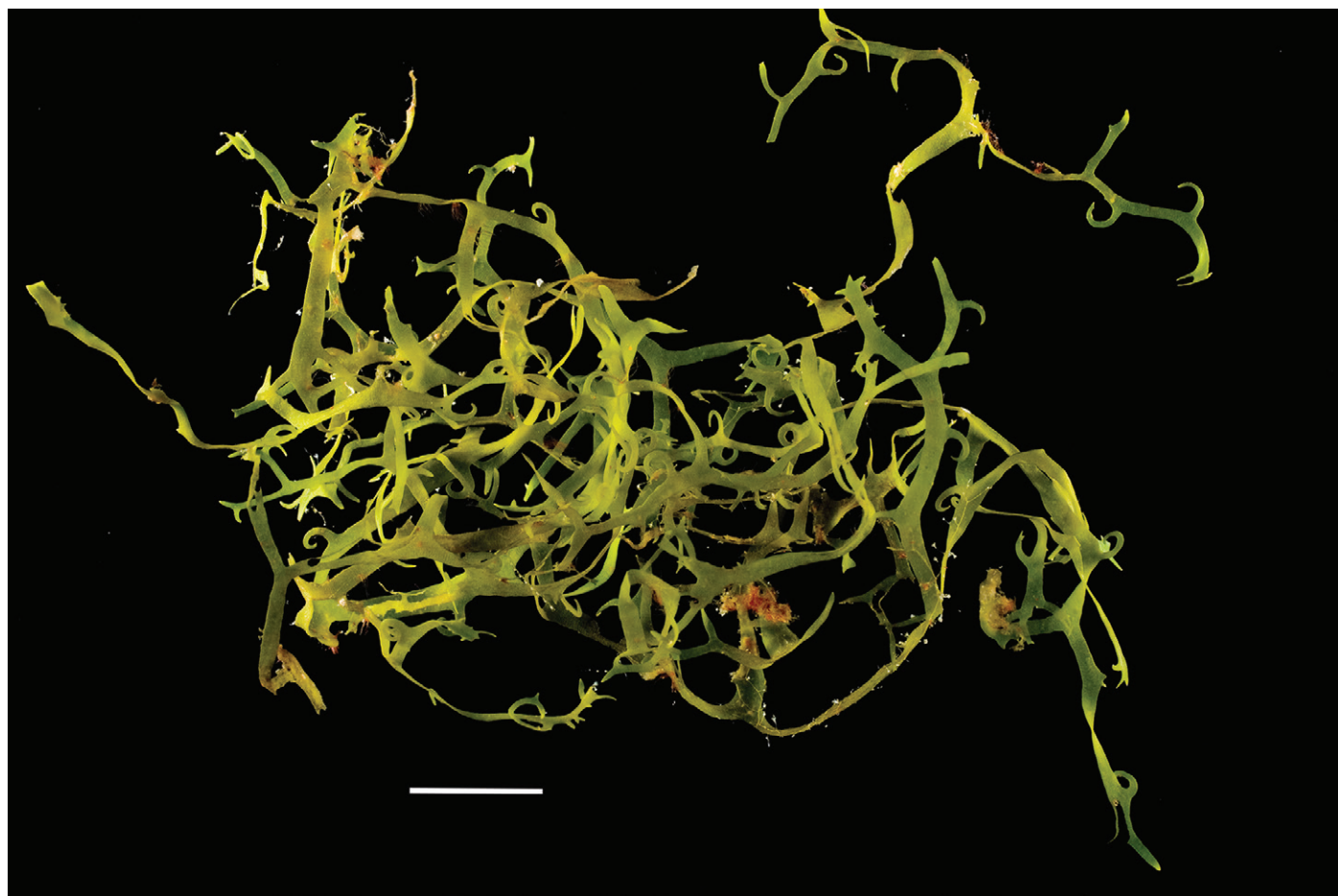


FIGURE 28. *Dictyota hamifera*. DLB6930, herbarium specimen: Mona Island (NE), 8.0 m (leg. Brandi Todd, ii.2000). Scale bar = 1.0 cm.

and margins possess regular short, curved lateral branchlets of limited growth. The medulla possesses a single layer of cells, 80–270 μm high.

Habitat and comments: *Dictyota hamifera* was collected growing epiphytically in Puerto Rico and is known locally only from Mona Island at 7.5 m and Bajo de Sico at 50 m. [Additional illustration: Wysor and De Clerck 2003: fig. 16.]

***Dictyota humifusa* Hörnig,
Schnetter et Coppejans**

FIGURE 29

Dictyota humifusa Hörnig, Schnetter et Coppejans in Hörnig et al. 1992: 57, fig. 6.

Puerto Rican Records: Ruiz and Ballantine 2009; Ballantine et al. 2016.

Western Atlantic Distribution: North America, Bermuda, Belize, Cuba, Martinique, Puerto Rico, Colombia.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Punta Chengue, Santa Marta, Departamento del Magdalena, Colombia, Caribbean Sea.

Thalli are prostrate, creeping, and delicate, 2.0–3.0(–4.0) cm in length. Branching is dichotomous or irregular. Blades possess broadly rounded sinuses, 70°–90°, and are (1.0–)2.0–4.0(–5.0) mm broad and 75–125 μm thick. Branches have smooth margins and obtuse apices. The medulla consists of a single layer, with medullary cells 50–80 μm high.

Habitat and comments: In southwestern Puerto Rico, *Dictyota humifusa* is very abundant at insular, shelf break, reef communities at approximately 18 m depths. The species has also been collected in deeper waters down to depths of 82 m (Ballantine et al. 2016). In the field *D. humifusa* is easily recognized by its frequently striking blue and greenish iridescence and its



FIGURE 29. *Dictyota humifusa*. In situ photograph, edge of insular shelf, offshore from La Parguera, 18 m. Field width = approximately 5.0 cm.

prostrate spreading habit. Although Bula-Meyer (1994) considered *D. humifusa* to be conspecific with *D. pfaffii* Schnetter (now considered to be a synonym of *D. friabilis*), others recognized the two as separate species (e.g., Littler and Littler 2000; Wysor and De Clerck 2003; Ruiz and Ballantine 2009; Ballantine et al. 2016). De Clerck (2003) indicated that *D. humifusa* typically lives in the shallow subtidal in the Indian Ocean.

***Dictyota implexa* (Desf.) J. V. Lamour.**

FIGURE 30

Dictyota implexa (Desf.) J. V. Lamour. 1809b: 43.

Basionym: *Fucus implexus* Desf. 1799: 423.

Heterotypic Synonym: *Dictyota linearis* C. Agardh Grev. 1930: xliii.

Puerto Rican Records: As *Dictyota linearis*: Taylor 1960; Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Belize, Cayman Islands, Cuba, Grenadines, Hispaniola, Jamaica, Netherland Antilles, Puerto Rico, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: “Habitat in mare mediterraneo” (Desfontaines 1799: 423); Mediterranean Sea.

Thalli are erect, 5–12 cm tall, and abundantly dichotomously branched. Branches measure 0.5–1.0 mm broad and are sometimes twisted with generally narrow sinuses. Branch tips are acute.



FIGURE 30. *Dictyota implexa*. Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 1.0 cm.

The medulla is 1 cell thick, with medullary cells measuring 126–141 μm high. Tetrasporangia, 95–100 μm diam, are solitary.

Habitat and comments: *Dictyota implexa* is relatively common in Puerto Rico and can be found in both shallow and deeper water, down to 20 m depths.

***Dictyota jamaicensis* W. R. Taylor 1960**

FIGURE 31

Dictyota jamaicensis W. R. Taylor 1960: 630, pl. 32, figs. 4, 5.

Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, Barbados, Belize, Cuba, Grenada, Jamaica, Martinique, Puerto Rico, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Oaxaca, Mexico.

Thalli are up to 12 cm tall and dichotomously branched. Twisted branches with erose-dentate margins are up to 7.0 mm broad in lower portions, narrowing to 1.0–4.0 mm distally.

Branching sinuses are broad below, becoming narrow above. Tetrasporangia measure up to about 80 μm diam and occur in small groups on blade surfaces. Oogonia occur in sori, about 500 μm long and 250 μm wide.

Habitat and comments: The distinction between *D. jamaicensis* and *D. crenulata* J. Agardh was questioned by Dawson (1962), Nizamuddin and Gerloff (1979), Hörnig et al. (1992), and De Clerck (2003), who all suggested the latter species be treated as a synonym. However, on the bases of molecular data, Tronholm et al. (2013) concluded that *D. crenulata* was restricted to Pacific Central America, and reinstated *D. jamaicensis*. [Additional illustrations: Wysor and De Clerck 2003: figs. 12–15.]

***Dictyota menstrualis* (Hoyt) Schnetter, Hörning et Weber-Peukert**

FIGURE 32

Dictyota menstrualis (Hoyt) Schnetter, Hörning et Weber-Peukert 1987: 195, figs. 5, 6.

Basionym: *Dictyota dichotoma* var. *menstrualis* Hoyt 1927: 616.

Puerto Rican Records: As *Dictyota menstrualis*: Ballantine 1977; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

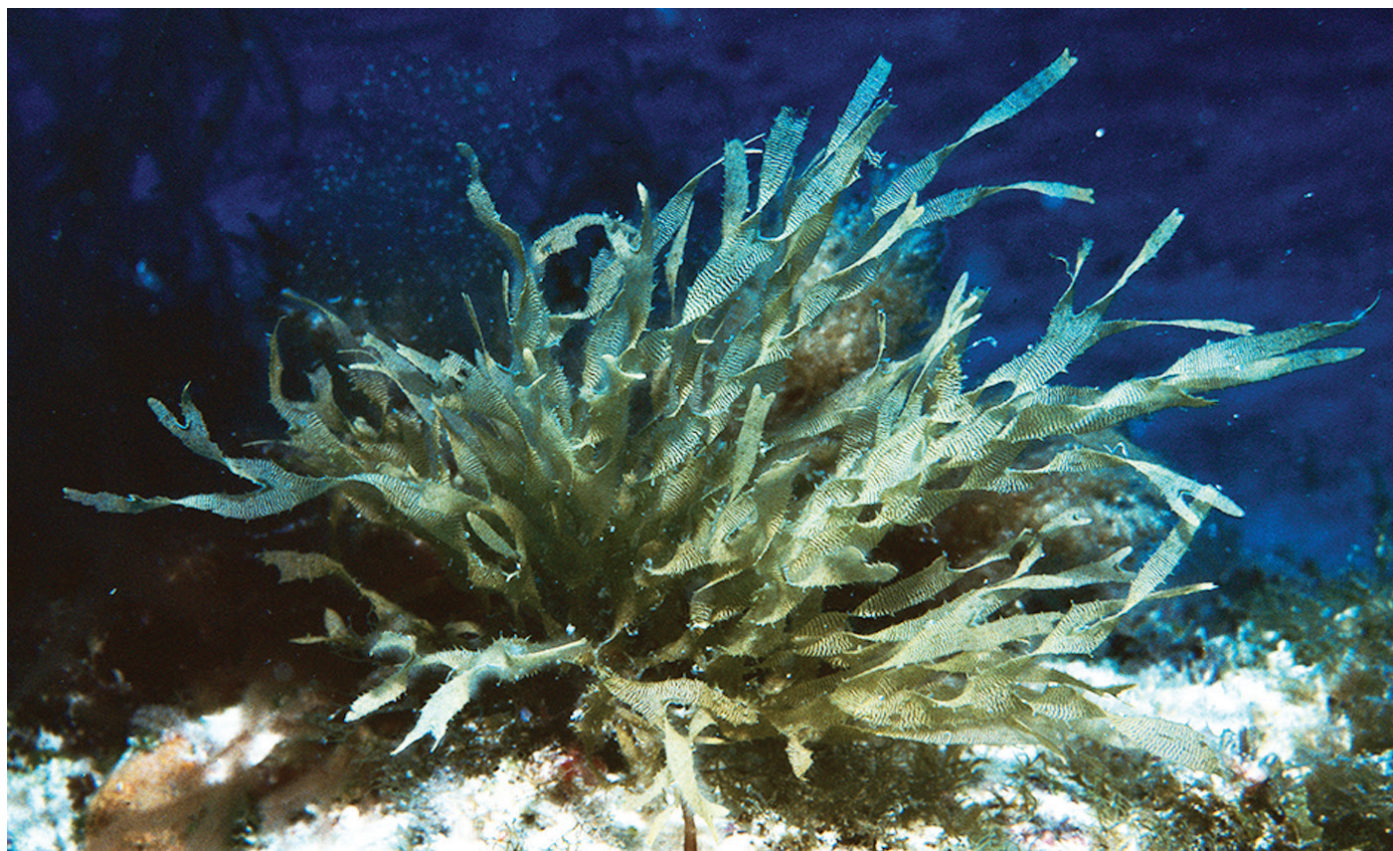


FIGURE 31. *Dictyota jamaicensis*. In situ photograph, 1.5 km seaward Media Luna Reef. Field width = approximately 20 cm.



FIGURE 32. *Dictyota menstrualis*. In situ photograph, 1.5 km seaward Media Luna Reef. Field width = approximately 10 cm.

As *Dictyota dichotoma* var. *menstrualis*: Hoyt 1927; Taylor 1960.

Western Atlantic Distribution: Mexico, North America, Bermuda, Belize, Cuba, Grenadines, Martinique, Puerto Rico, St. Eustatius, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Fort Macon Breakwater, Beaufort, North Carolina, USA. *Neotype*: U.S. Algal Collection 33622.

Thalli reach 15–25(–35) cm tall and are regularly dichotomously branched with 15°–45° sinus angles. Branches are 2.0–15 mm broad and 150–250 µm thick. Blade margins are smooth, and branches terminate in slightly tapered blunt tips. Medullary cells are mostly of 1 layer, 120–180 µm tall, but becoming more than 1 layer in older parts. Algae are yellow brown to dark brown in color.

Habitat and comments: Although usually found in shallow water, *Dictyota menstrualis* has been reportedly dredged at 55 m depth. Although Wynne (2017) followed Tronholm et al. (2013) in treating *D. menstrualis* as a synonym of *D. ciliolata*,

others continue to recognize them as separate species (e.g., Loos et al. 2017; Guiry and Guiry 2021). Tronholm et al. (2013) noted that although *D. menstrualis* and *D. plectens* (Allender et Kraft) Kraft (2009) were possibly conspecific, they may prove to be distinct lineages warranting species status. If so, it is likely that *D. ciliolata* will be subdivided into other cryptic and pseudocryptic species (see also W. Guiry in Guiry and Guiry 2021).

***Dictyota mertensii* (Mart.) Kütz.**

FIGURE 33

Dictyota mertensii (Mart.) Kütz. 1859: 15, pl. 36: fig. 1.

Basionym: *Ulva mertensii* Mart. 1828: 5, pl. I.

Heterotypic Synonym: *Dictyota dentata* J. V. Lamour. 1809b: 42.

Puerto Rican Records: As *Dictyota mertensii*: Ballantine et al. 1987; Ballantine and Aponte 1997, 2002. As *Dictyota dentata*: Hauck 1888; Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar and Ballantine 1983.

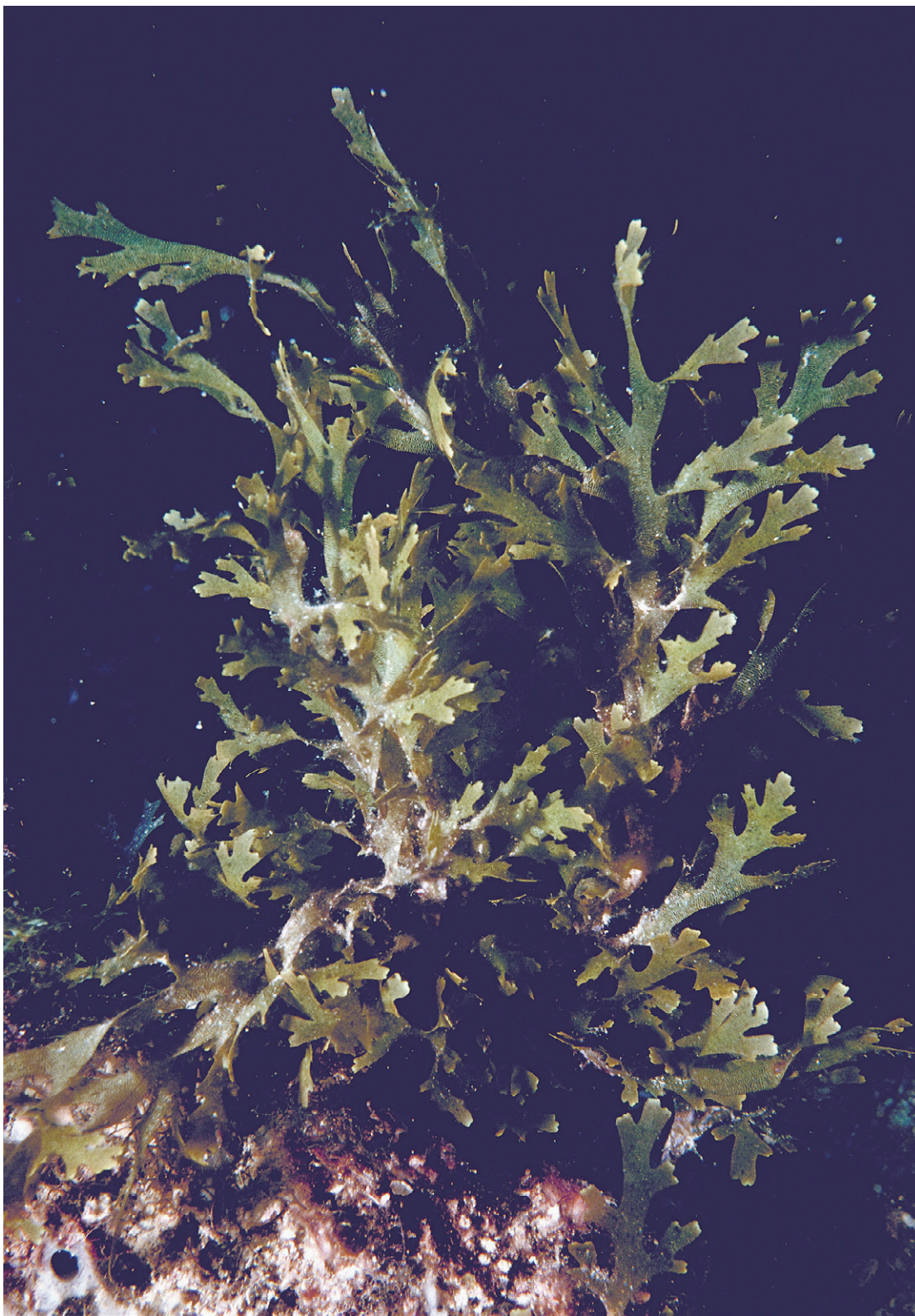


FIGURE 33. *Dictyota mertensii*. In situ photograph, algal plain, seaward Punta Brea, 17 m. Field width = approximately 8.0 cm.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Dominica, Grenadines, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Salvador, Brazil.

Thalli reach 10–20 cm tall with a well-defined main axis; laterals repeatedly alternately branched. Blades are up to 6.0 mm broad proximally, narrowing to 1.0–2.0 mm broad distally, and are 80–120 μm thick. Branch tips are aculeate. The medulla is a single cell thick, up to 100 μm tall. Oogonia are solitary or in groups of 2 or 3 on blades; 80–100 μm diam. Algae are brown in color.

Habitat and comments: *Dictyota mertensii* is relatively common in shallow, moderately exposed habitats. [Additional illustrations: Vickers 1908: pl. 15; Braune and Guiry 2011: fig. 35.9.]

***Dictyota pinnatifida* Kütz.**

FIGURE 34

Dictyota pinnatifida Kütz. 1859: 16, pl. 39: fig. 1.

Heterotypic Synonyms: *Dilophus alternans* J. Agardh 1882: 108; *Dictyota alternans* (J. Agardh) Hörnig, Schnetter et Prud'homme 1993: 169.

Puerto Rican Records: As *Dilophus alternans*: Ballantine and Norris 1989; Ballantine and Aponte 1997, 2002.



FIGURE 34. *Dictyota pinnatifida*. MAH4369, herbarium specimen: Culebra Island, leg. M. Howe, iii.1906. Scale bar = 2.0 cm.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Cuba, Dominica, Hispaniola, Jamaica, Martinique, Panama, Puerto Rico, St. Eustatius, St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Antigua, Leeward Islands (northern islands of Lesser Antilles), Caribbean Sea.

Densely bushy thalli reach 10–15 cm tall with primary branching alternate or irregular. Blades are (0.5–)2.0–4.0(–5.0) mm broad with 15°–45° branching sinuses. Lateral divisions are subdichotomously to dichotomously branched. Tips of branches are blunt or indented. The medulla has 2–5 layers at the edges and 1 layer in the center. Medulla cells are rectangular, 10–20 μ m high. Algae are dark yellow brown in color.

Habitat and comments: *Dictyota pinnatifida* occurs in shallow, moderately exposed habitats down to 26 m depths.

Hörnig et al. (1992) argued that the multilayered medulla of *Dilophus* was inadequate as a generic character to separate it from *Dictyota*. [Additional illustrations, as *Dilophus alternans*, Vickers 1908: pl. 10: figs. 1–4; Norris and Bucher 1982: fig. 95; Schnetter 1976: pl. 8: figs. G, H.]

***Dictyota pulchella* Hörnig et Schnetter**

FIGURE 35

Dictyota pulchella Hörnig et Schnetter 1988: 287, figs. 7–9.

Misapplied Name: *Dictyota divaricata* J. V. Lamour. 1809a: 531, sensu Taylor 1960.

Puerto Rican Records: As *Dictyota divaricata*: Almodóvar and Blomquist 1959; Almodóvar and Biebl 1962; Almodóvar 1964b, 1964c; Almodóvar and Pagán 1971; Almodóvar and Rehm 1971; Ballantine 1977; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine et al.

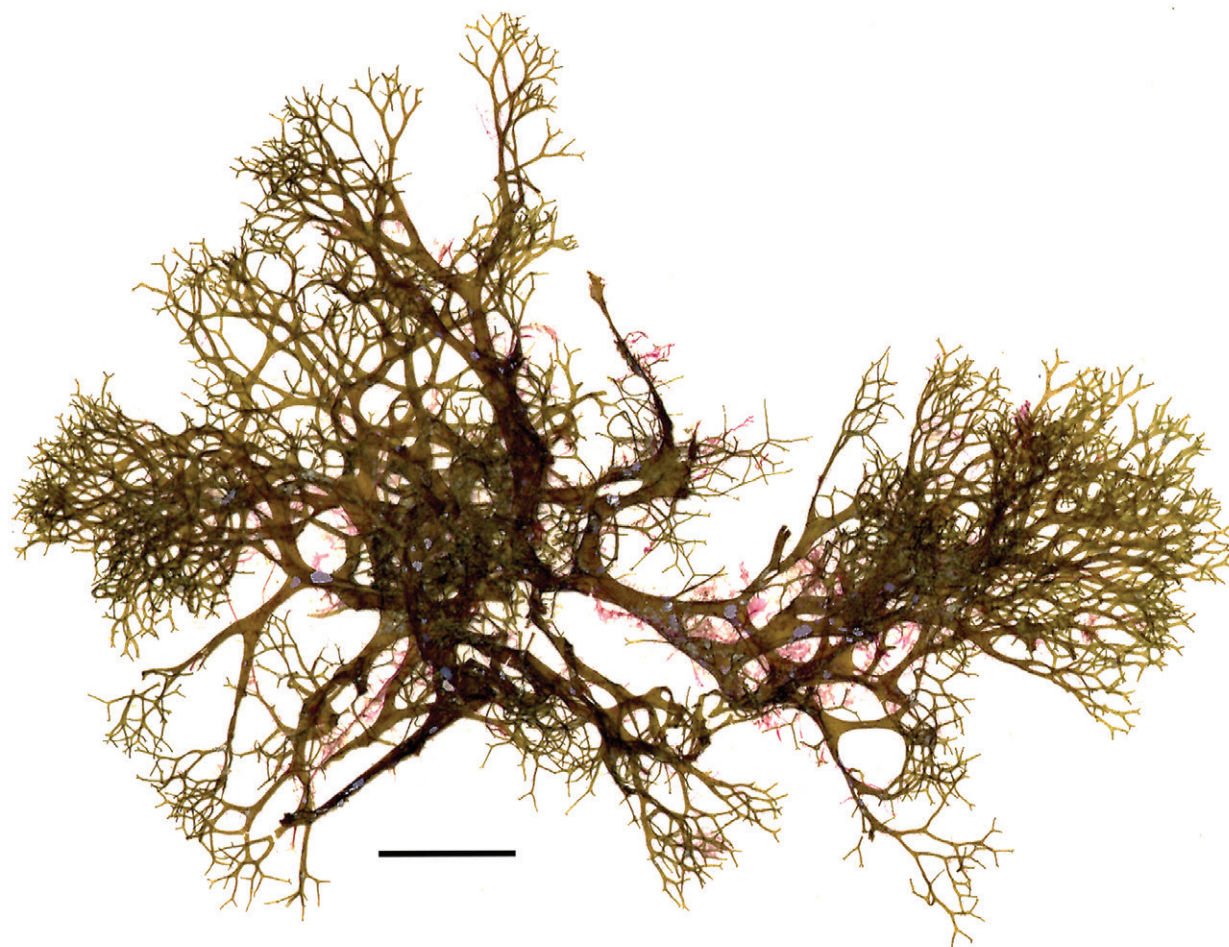


FIGURE 35. *Dictyota pulchella*. DLB7698, herbarium specimen: Punta Brea, 17 m. Scale bar = 1.0 cm.

1987. As *Dictyota pulchella*: Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Belize, Cuba, Martinique, Panama, Puerto Rico, St. Eustatius, Brazil, Colombia.

World Distribution: See Gallardo et al. 2016.

Type Locality: Punta La Loma, Santa Marta, Departamento del Magdalena, Colombia, Caribbean Sea.

Thalli reach 3.0–12 cm high and are regularly dichotomously branched. Branches have broad sinuses, (60°–)90°–120°. Branches are up to 3.0 mm broad in lower portions, becoming abruptly narrower, 0.1–0.2 mm near apices. The branches are 180–240(–300) μm thick. Rectangular medullary cells occur in a single layer and are 120–200 μm tall. Algae are brown in color.

Habitat and comments: *Dictyota pulchella* is common on rocks in shallow waters and dredged to 55 m. Almodóvar and Rehm (1971) reported *D. pulchella* (as *D. divaricata*) forming algal balls at Collado Reef, La Parguera.

***Dictyota stolonifera* E. Y. Dawson**

FIGURE 36

Dictyota stolonifera E. Y. Dawson 1962: 392, pl. 5: fig. A.

Puerto Rican Records: Ballantine et al. 2011, 2016.

Western Atlantic Distribution: Panama, Puerto Rico.

World Distribution: See De Clerck 2003; Guiry and Guiry 2021.

Type Locality: Intertidal, volcanic lava reef; Masachapa, Departamento de Managua, Nicaragua.

Thalli reach 4.0–6.0 cm tall with 1 to several, irregularly subdichotomously branched, strap-like blades, 3.0–4.0 mm wide. Branch margins are entire, and branch tips are obtuse. The medulla is typically a single cell layer, occasionally 2 or more layers. A single-layered cortex bounds the medulla. Algae are attached by simple to divided, stoloniferous growths (up to 500 μm diam) issued from a short compressed stipe on the lowermost branches.

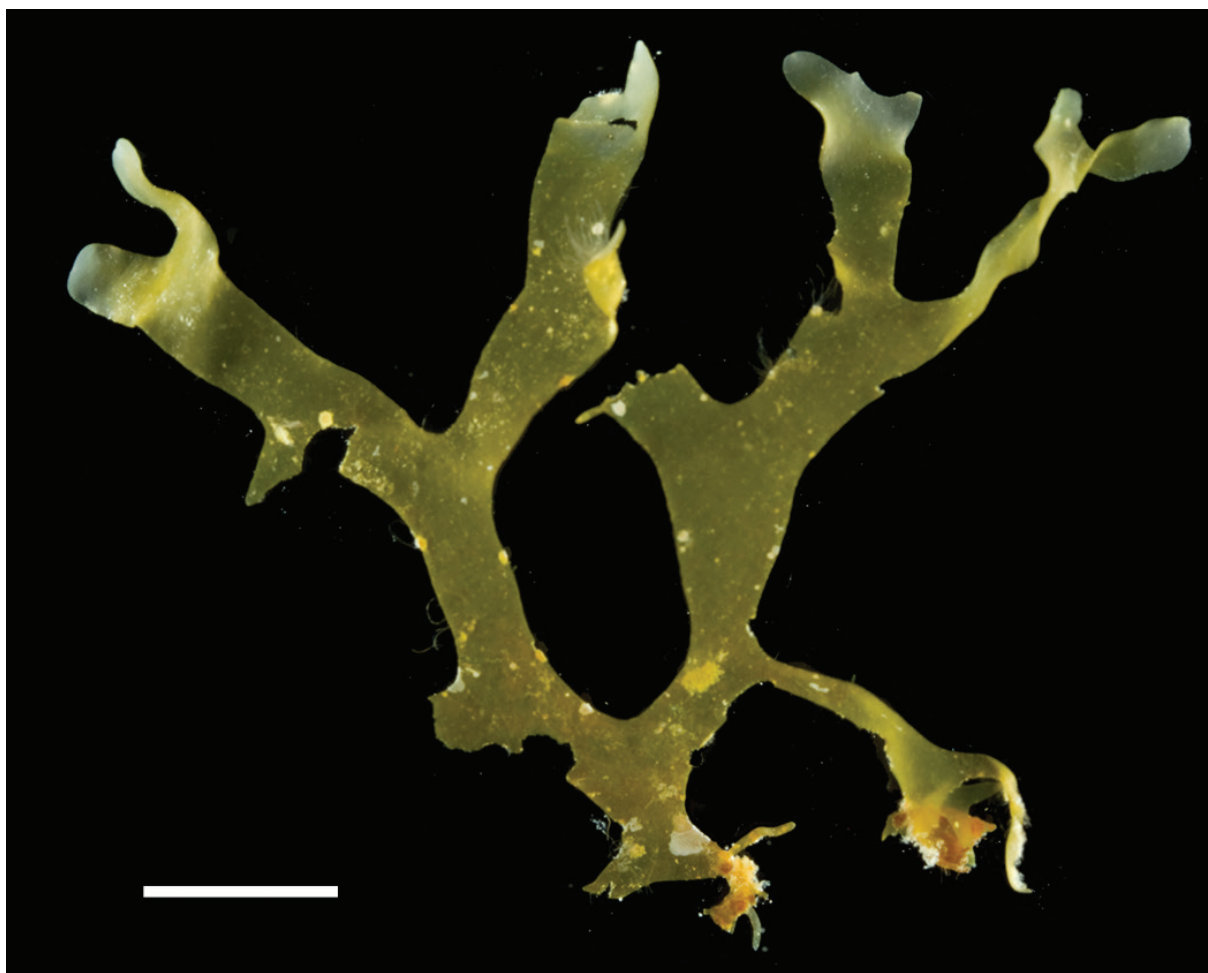


FIGURE 36. *Dictyota stolonifera*. DLB7989: South Mona Island, 62 m. Scale bar = 2.0 cm.

Habitat and comments: De Clerck (2003) indicated *Dictyota stolonifera* ranged from shallow to intermediate depths (to 20 m) throughout its distribution. In Puerto Rico, *D. stolonifera* has been collected in much deeper waters, down to 70 m depths (Ballantine et al. 2016).

***Lobophora* J. Agardh**

Lobophora J. Agardh 1894: 21.

Thalli are solitary or often clustered because of overgrowth. Blades are flattened and either strongly adhering to the substratum, partially adherent with unattached margins, or free and erect with fan-shaped blades (see Figure 37). The blades are simple at first, becoming lobed. Algae are attached by rhizoidal filaments, some forming a dense rhizoidal mat. Thalli grow from the lateral margins by a row of apical cells. Blades consist of a of 1 or 2 cell-layered medulla, a single layer cortex on each surface and a subcortex of 1 or more layers. Reproductive organs are in

scattered sori on both blade surfaces. Sporangia produce 4 or 8 aplanospores in sori lacking paraphyses.

Historically, in the Caribbean, a single species of *Lobophora* has been recognized, *L. variegata*. On the basis of genetic analyses combined with an anatomical reevaluation of the genus, Schultz et al. (2015) recognized five distinct western Atlantic species, all of which have been previously referred to *L. variegata*. More recently, Camacho et al. (2019) have added another five species, and Vieira et al. (2019) added still another species from the tropical western Atlantic.

Specimens referred to *Lobophora* in Puerto Rico are from a variety of habitats, ranging from intertidal to deep water. All require reevaluation and morphological and phylogenetic study to verify their taxonomic identification and relationships. Some deeper-water *Lobophora* specimens were reexamined by Ballantine et al. (2016, 2019), resulting in recognition of five species currently known to Puerto Rico. Below we add a sixth species to the algal flora. Genetic evidence suggests there may be more than 100 species of unknown, overlooked or cryptic new species of



FIGURE 37. *Lobophora* sp. In situ photograph, algal plain, Seaward Media Luna Reef, 17 m. Field width = approximately 20 cm.

Lobophora worldwide (Camacho et al. 2019; Viera et al. 2020). Presently, there are 18 *Lobophora* species recognized in the

western Atlantic (Camacho et al. 2019; Viera et al. 2020); 6 of these are now known from Puerto Rico.

KEY TO THE *LOBOPHORA* SPECIES OF PUERTO RICO

1. Thalli growing completely decumbent on substratum, with rhizoids present over the entire ventral surface *L. littlerorum*
Thalli not entirely decumbent 2
2. Thalli of 6–10 cell layers 3
Thalli typically with 5 cell layers 4
3. Thalli with 9 or more cell layers *L. brooksii*
Thalli with 7 cell layers *L. variegata*
4. Thalli greater than 150 μm thick *L. schneideri*
Thalli less than 100 μm thick 5
5. Thalli viewed in longitudinal section with 1 or 2 medullary layers; the dorsal cortex has 2 cells covering the width of each medullary cell *L. guadeloupensis*
Thalli viewed in longitudinal section with 1 medullary layer; the dorsal cortex usually of 4 cells covering the width of each medullary cell *L. canariensis*

***Lobophora brooksii* D. L. Ballant. et J. N. Norris sp. nov.**

FIGURE 38

Lobophora brooksii D. L. Ballant. et J. N. Norris sp. nov.

Holotype: LRA6185, Pozuelo, Guayama (southern coast of Puerto Rico), lee of nearshore reef, shallow water, east of Phillips breakwater, collectors L. R. Almodóvar and V. M. Rosado, 10.iii.1970. U.S. Algal Collection, 48313.

Paratypes: LRA6892, Yabucoa, on rocks. Collector A. E. Rehm. VII.1973. U.S. Algal Collection, 55377. PBA778a, as *Gymnosorus variegatus* (J. V. Lamour.) J. Ag. (= *L. variegata*), washed ashore, Florida, collector Mrs. G. A. Hall, 1890. LRA6892, Yabucoa, on rocks, collector A. E. Rehm, VII.1973. U.S. Algal Collection, 48313.55377.

Etymology: The species epithet recognizes Barrett Brooks, museum specialist in the Department of Botany, Smithsonian Institution, who has worked with the U.S. Algal Collection for more than 35 years. We acknowledge Barrett's substantial contributions in support of phycological studies at the U.S. National Museum of Natural History.

Erect solitary thalli, measuring to 5.2 cm tall, are briefly stipitate and expand to 1 or more fan-shaped blades. Blades range from 2.6 to 3.7 cm broad. Blades may lobe and become divided. Lower thallus portions possess a thick mound of rhizoids. Thalli measure to 175 μm thick and comprise 10 (less commonly 9) cell layers, including a single medullary layer. The medullary cells in transection measure from (35–)40 to 50(–60) μm tall and 17–30 μm wide. Medullary cells are covered dorsally by 5 (rarely 4) tiers of quadrate to rectangular cells that equal the width of the medullary cells. Ventrally, the medullary cells are covered by 4 tiers of cells (also quadrate to rectangular). The outer cortical

cells on both surfaces occur in pairs over the subtending cortical layer and are quadratic, measuring 9.0 μm long and 9.0 μm high or are somewhat elongate, to 18 μm long. In longitudinal section, medullary cells and inner cortical layers are elongate, measuring 56–72 μm long. Dorsally, each medullary cell is covered by 2 to 3 cortical cells. The third cortical layer from the medullary cell is covered by 1 or 2 cells, and the subcortical cells are covered by 2 or 4 epidermal cells. Sporangia lack paraphyses and are produced abundantly on the dorsal surface. The sporangia are pyriform or clavate and measure to 115 μm long and to 50 μm diam. Algae dry to a dark-brown color and are not strongly adherent to herbarium paper.

Habitat and comments: The new species occurs in shallow water on rocks. *Lobophora brooksii* differs from all western Atlantic congeners by nature of its thick thallus, to 175 μm , and large number of cell layers, to 10. *Lobophora schneideri* is the only other Caribbean species as thick as the new species; however, the former generally possesses only 5 cell layers. *Lobophora littlerorum* reaches 95–140 μm in thickness but is repent and possesses 6 cell layers. A number of Pacific and Red Sea *Lobophora* species have thickness and cell row numbers that equal or exceed those of the new species; however, most of these are repent. *Lobophora sonderi* C. W. Vieira, De Clerck et Payri, with 8–12 cell layers, is substantially thicker, reaching 168–252 μm thick, and also possesses taller medullary cells (Vieira et al. 2016). *Lobophora nigrescens* J. Agardh, the generitype originally collected in Hawaii, is differentiated from the new species by possessing 11 cell rows and a thickness of 160–210 μm . *Lobophora nigrescens* also differs in possessing ovate or spherical sporangia.

An examination of *Lobophora variegata* specimens in the U.S. Algal Collection (01558) revealed a single specimen attributable to the new species, *Phycotheca Boreali-Americana* (PBA; Collins et al. 1908) 778a. The specimen from Florida possesses 9 cell row layers. A second specimen, PBA 778b, on the same sheet is a different *Lobophora* species. Given that two

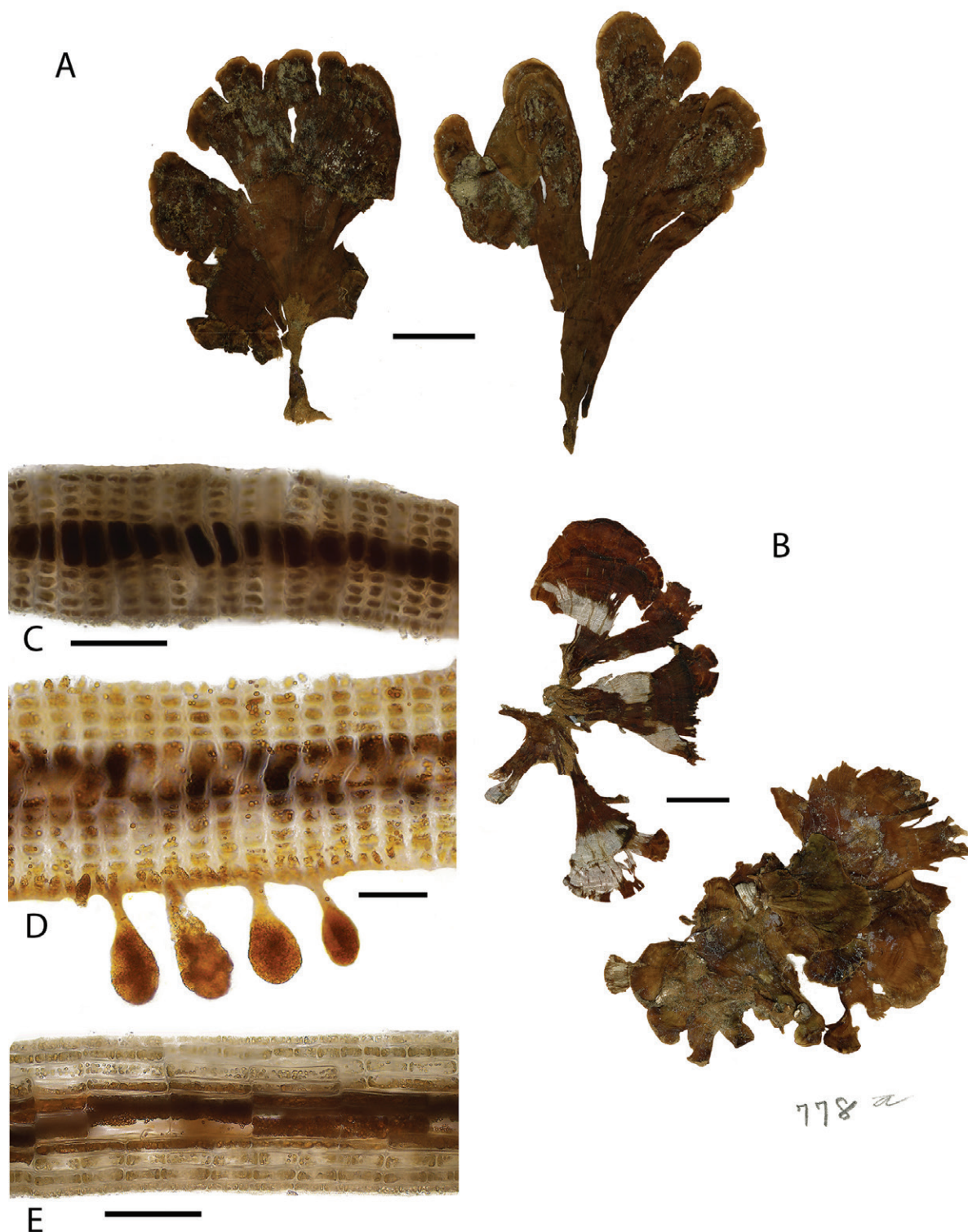


FIGURE 38. *Lobophora brooksii*. (A) LRA6185, herbarium specimen of holotype (on left): Pozuelo on rocks east of Phillips breakwater. Scale bar = 1.0 cm. (B) *Phycotheca Boreali-Americana* (PBA; Collins et al. 1908) exsiccatæ 778a, beach cast, Atlantic Florida. Collected by Mrs. C. E. Pease and Miss E. Bulter. Scale bar = 1.0 cm. (C) LRA6185, transverse section. Scale bar = 100 µm. (D). LRA6185, transverse section, showing clavate sporangia. Scale bar = 50 µm. (E). LRA6185, longitudinal section, PBA 778a. Scale bar = 100 µm.

Lobophora species are included in PBA 778, other corresponding PBA specimens require reexamination.

***Lobophora canariensis* (Sauv.)
C. W. Vieira, De Clerck et Payri**

FIGURE 39

Lobophora canariensis (Sauv.) C. W. Vieira, De Clerck et Payri in Vieira et al. 2016: 699.

Basionym: *Aglaozonia canariensis* Sauv. 1905: 79 in Sauvageau (1905).

Heterotypic Synonym: *Lobophora payriae* N. E. Schultz, C. W. Schneid. et F. Rousseau in Schultz et al. 2015: 497, figs. 20–22.

Puerto Rican Record: As *Lobophora canariensis*: Ballantine et al. 2016.

Western Atlantic Distribution: Bermuda, Guadeloupe, Martinique, Puerto Rico.

World Distribution: Guiry and Guiry 2021.

Neotype Locality: Punta del Hidalgo, Tenerife, Canary Islands, Spain (Vieira et al. 2016: 699).

Thalli erect, up to 4.0 cm high, or decumbent. Blades are reniform, measuring 2.0–3.8 cm long, 1.3–4.0(–5.0) cm broad, and 50–100 μ m thick. In section, the medulla is single celled and surrounded by 2 cortical layers on each surface. In longitudinal section, the subcortical layer of 1 or 2 cells covers a medullary



FIGURE 39. *Lobophora canariensis*. MDPsn, herbarium specimen: Fajardo, 12 m. Scale bar = 1.0.

cell. The dorsal outer cortical layer consists of 4 cells above the medullary cell. The ventral outer cortical layers consists of 2 cells covering the medullary cell. Sporangia are 65–80 μm in diameter. Algae are light brown in color.

Habitat and comments: *Lobophora payriae* N. E. Schultz, C. W. Schneid. et F. Rousseau (Schultz et al. 2015; west of High Point, Bermuda Island) was described on the basis of specimens from 35 to 36 m depths and others from Guadeloupe previously referred to *L. variegata*. Subsequently, Vieira et al. (2016) regarded *L. payriae* as a synonym of *Cutleria canariensis* (Sauv.) I. A. Abbott et Huisman (2003) and transferred the species as *L. canariensis*. Deepwater Puerto Rican *Lobophora canariensis* specimens from a depth of 82 m (Ballantine et al. 2016) were mostly extremely small, with flabella 0.9 mm high and 10 mm across. Larger deepwater specimens were up to 4.0 cm high and 5.0 cm broad. They were incorrectly reported (Ballantine et al. 2016) to have 3 cell layers and a thickness of 33–40 μm . It is likely that further collections and examination of herbarium specimens will reveal that *L. canariensis* is not restricted

to mesophotic depths in Puerto Rico. [Additional illustrations: Schultz et al. 2015, as *L. payriae*, figs. 20–22.]

Lobophora guadeloupensis
N. E. Schultz, F. Rousseau et L. Le Gall

FIGURE 40

Lobophora guadeloupensis N. E. Schultz, F. Rousseau et L. Le Gall in Schultz et al. 2015: 494–495, figs. 12–16.

Puerto Rican Record: Ballantine et al. 2016.

Western Atlantic Distribution: Guadeloupe, Martinique, Puerto Rico.

Type Locality: Îlet Gosier (or Îlet du Gosier), Guadeloupe, French West Indies.

Thalli are somewhat fan shaped, 2.0–4.0 cm long, 1.5–4.0 cm wide, and 65–95 μm thick. The medulla in longitudinal section is

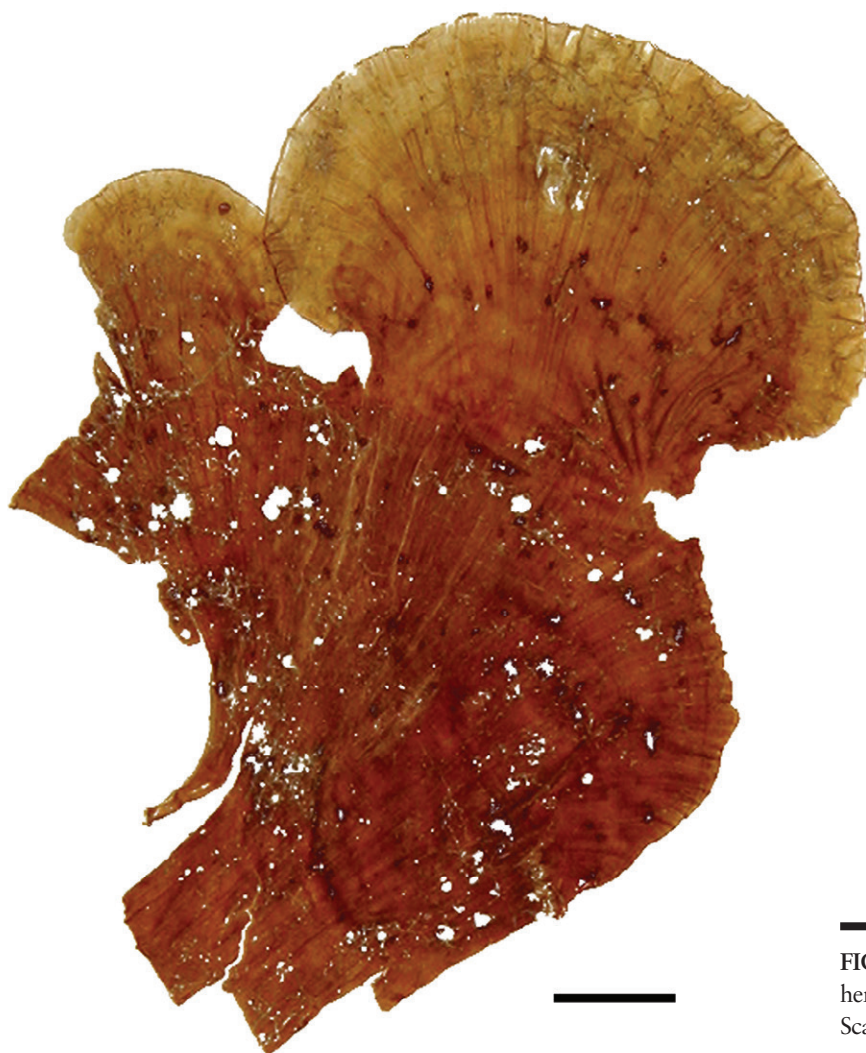


FIGURE 40. *Lobophora guadeloupensis*. DLBsn, herbarium specimen: Islote, 17 m (collected by RJZ). Scale bar = 1.0 cm.

1 or 2 cells thick, with 2 cortical layers across each (dorsal and ventral) surface. The subcortical layer, in longitudinal section, is of a single cell covering a medullary cell and an outer cortical layer of 2 or 3 cells covering each medullary cell. Sporangia are ovate, 90–105 μm in diameter and 125–150 μm long.

Habitat and comments: Puerto Rican specimens of *Lobophora guadeloupensis* have a flabellum up to 5.5 cm high and to 8.0 cm across. Once herbarium specimens attributable to deepwater “*L. variegata*” are studied and identifications confirmed, it is highly probable that broader distribution of both *L. guadeloupensis* and *L. canariensis* will be found. [Additional illustrations: Schultz et al. 2015, figs. 12–16.]

***Lobophora littlerorum* C. W. Schneid.,
N. E. Schultz et L. Le Gall**

FIGURE 41

Lobophora littlerorum C. W. Schneid., N. E. Schultz et L. Le Gall in Schultz et al. 2015: 495, figs. 17–19.

Misapplied Name: *Aglaozonia canariensis* Sauv. 1905: 79 [non *Aglaozonia canariensis* = *Lobophora canariensis* (Vieira et al. 2016: 699)].

Puerto Rican Records: As *Lobophora littlerorum*: Ballantine et al. 2019. As *Aglaozonia canariensis*: Almodóvar and Blomquist 1961.

Western Atlantic Distribution: Guadeloupe, Puerto Rico.

Type Locality: Petit-Havre, Le Gosier, Guadeloupe, French West Indies.

Thalli are crustose, lobed, 2.0–3.5 cm long, 3.0–5.0 cm wide, and 95–140 μm thick. The medulla, when viewed in longitudinal section. Is a single cell in thickness with 3 cortical layers dorsally and 2 cortical layers ventrally. When viewed in longitudinal section, the inner dorsal subcortical layer has 2 cells covering the medullary cell, and the outer cortical layer is of 2 rows each having 4 cells covering the medullary cell. The ventral inner cortical layer has a single cell covering the medullary cell, and the outer cortical layer has 2 cells covering the medullary cell. Rhizoids are abundant on the ventral surface. Algae are greenish to brown in color.

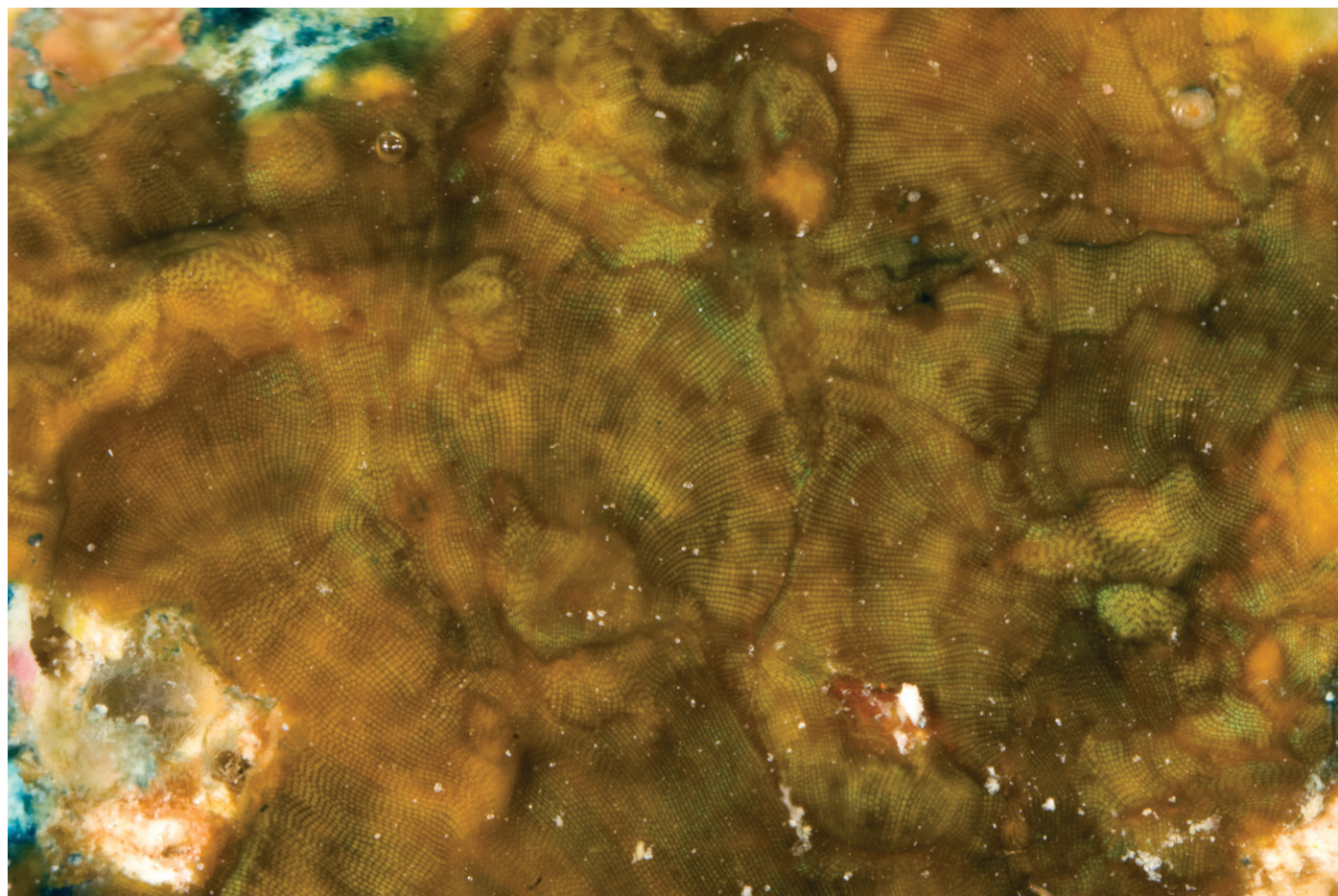


FIGURE 41. *Lobophora littlerorum*. In situ photograph, edge of insular shelf off La Parguera, 20 m. Field width = approximately 8.0 cm.

Habitat and comments: Until recently, the nature of its crustose habit easily separated *Lobophora littlerorum* from the other Caribbean species of *Lobophora*. Having observed and photographed *L. littlerorum* on a number of dives from the intertidal to shelf edge (about 20 m) habitats, the species is more common in Puerto Rico than might be inferred from the few documented collections. Godínez-Ortega et al. (2018) reported both *L. declerckii* and *L. littlerorum* from the neighboring U.S. Virgin Islands, which raises the strong possibility that the former species may be present in Puerto Rico as well.

The prostrate *Aglaozonia parvula* (Grev.) Zanardini, the generitype, has long been recognized as the sporophytic life history phase or *Aglaozonia* stage of *Cutleria* spp. (Guiry and Guiry 2021). Another taxon, the crustose *Aglaozonia canariensis* Sauv., has been considered conspecific (i.e., by Setchell and Gardner 1930; Price et al. 1978) with repent *Pocockiella variegata* (J. V. Lamour.) Papenf. (= *L. variegata*). Shultz et al. (2015), however, noted *A. canariensis* sensu Børgesen (1926) aligned well with the anatomical characters defining *L. littlerorum*, and examination of the Canary Island type specimen and genetic material might prove these two conspecific. Vieira et al. (2016) studied *A. canariensis* and proposed *Lobophora canariensis* as a distinct species and found sequences of *L. payrae* to be conspecific with *L. canariensis*. [Additional illustrations: Shultz et al. 2015, figs. 17–19.]

***Lobophora schneideri* C. W. Vieira**

FIGURE 42

Lobophora schneideri C. W. Vieira in Vieira et al. 2019: 164.

Puerto Rican Records: Newly reported herein for Puerto Rico: D&ML17310, 1.5 km seaward Media Luna Reef, La Parguera, 17 m, 11.v.1989; U.S. Algal Collection, 161828.

Western Atlantic Distribution: Bermuda, Guadeloupe, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Vieira et al. 2019.

Type Locality: Captain Williams' Bay, Bermuda Island, Bermuda.

Erect thalli possess reniform blades and bear proximal mounds of rhizoids. The algae are attached by basal rhizoids. Blades are 5(–7) cell layers and 156–180 µm thick. In both transverse and longitudinal sections, a single subcortical cell covers the medullary cell. The cortical layers possess 2 cells that cover each subcortical layer. Algae are greenish when living, becoming brown on drying.

Habitat and comments: In Puerto Rico the species has been collected from shallow habitats and a moderate-depth algal plain. Further examination of Puerto Rican *Lobophora*



FIGURE 42. *Lobophora schneideri*. M&DL17310, herbarium specimen: Algal plain, seaward Media Luna Reef, La Parguera, 17 m. Scale bar = 1.0 cm.

specimens will undoubtedly result in recognition of a broader habitat range. Schultz et al. (2015) assigned Bermudan *Lobophora* specimen sp39 to *L. variegata*, and on the basis of molecular evidence, Vieira et al. (2019) established the new species *L. schneideri*.

***Lobophora variegata* (J. V. Lamour.)
Womersley ex E. C. Oliveira**

FIGURE 43

Lobophora variegata (J. V. Lamour.) Womersley ex E. C. Oliveira 1977: 217.

Basionym: *Dictyota variegata* J. V. Lamour. 1809b: 40.

Heterotypic Synonym: *Pocockiella variegata* (J. V. Lamour.) Papenf. 1943: 467, figs. 1–15.

Previously Published Puerto Rican Records: As *Lobophora variegata*: Ballantine 1977, 1979; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002; Ruiz and Ballantine 2009; Ballantine et al. 2016. As *Pocockiella variegata*: Díaz-Piferrer 1963; Almodóvar 1964a, 1964c.

Confirmed Puerto Rican Specimens: MAH7084, dredged east of the mouth of Guánica Harbor, 40–50 m, 23.VII.1915. MAH7578, dredged west of Ratones Island, Ponce, 18 m. LRA5584, dredged off Margarita Reef, 18–30 m, 10.IV.1967. DLBsn, Punta Arenas, Vieques Island, 6.XII.1976.

Western Atlantic Distribution: The following western Atlantic locations have been cited as locations at which specimens have been identified as “*L. variegata*”; however, as mentioned above, all herbarium specimens require reexamination: Mexico, North America, Bermuda, Bahamas, Antigua,



FIGURE 43. *Lobophora variegata*. MAH7084, herbarium specimen: Dredged east of the mouth of Guánica Harbor, 40–50 m. Scale bar = 1.0 cm.

Barbados, Belize, Cayman Islands, Cuba, Grenadines, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, St. Kitts, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

Type Locality: “Habitat in Antillis” (Lamouroux 1809b: 40); Antilles, West Indies.

Thalli are erect and stipitate with frequently ruffled fan-shaped blades. The blades are simple or lobed, to 6.0 cm long and to 8.0 cm wide. Blades are 100–197 μm thick and possess a single medullary cell layer and 2 or 3 cortical layers on each (dorsal and ventral) surface, resulting in 5–7 cell layers; however, most specimens possess 7 cell layers. In longitudinal section, 2 subcortical layers each have a single cell covering the medullary cell. Algae are yellowish brown in color.

Habitat and comments: *Lobophora variegata* has been historically considered to have a broad, worldwide tropical distribution; however, Vieira et al. (2016) considered the species to be restricted to the Caribbean. In Puerto Rico, *Lobophora variegata* has been thought to be a very common element from shallow, nearshore environments and extending across the insular shelf into deeper water. In light of recent studies (e.g., Schultz et al. 2015; Vieira et al. 2016; Camacho et al. 2019), all specimens

referred to “*L. variegata*” require reevaluation, and thus, its range of habitats is not currently known with certainty. Currently, only several Puerto Rican specimens have been reevaluated as *Lobophora variegata*; however, Vieira et al. (2016: S5 Electronic Supplement) cautioned that “that morphological features may not be sufficient for a confident taxonomic identification of this species.” [Additional illustrations: Vieira et al. 2016: figs. 3A,B, 4A,B; Godínez-Ortega et al. 2018: fig. 2.]

***Padina* Adans.**

Padina Adans. 1763: 13, 586.

Thalli are generally fan-shaped blades borne on stipes that are often invested by rhizoids and attached by a felted rhizoidal holdfast. Blades generally are whitened by a thin layer of calcification on one or both blade faces. Blades may become split into narrow segments. Growth is from a marginal row of apical cells, and the margin is inrolled. Blades are 2 to 8 cells thick, often conspicuously zonate; the zones are marked by concentric rows of hairs. Tetrasterangia and gametangia occur in sori between the hair bands. Fifty-four species of *Padina* are currently recognized, 3 of which occur in Puerto Rico.

KEY TO THE *PADINA* SPECIES OF PUERTO RICO

1. Blades 6–8 cells thick in basal regions; slightly calcified at most *P. gymnospora*
Blades 2–4 cells thick; calcification substantial, if only on 1 surface 2
2. Blades 2 cells thick; calcification substantial on upper concave surface *P. sanctae-crucis*
Blades 3 cells thick in center *P. boergesenii*

***Padina boergesenii* Allender et Kraft**

Padina boergesenii Allender et Kraft 1983: 87, figs. 6H,I, 7C,D.

Heterotypic Synonym: *Padina gymnospora* sensu Vickers 1905; Børgesen 1914a; Taylor 1960 [non *P. gymnospora* (Kütz.) Sond. 1871: 47].

Puerto Rican Records: As *Padina gymnospora*: Ballantine et al. 1987. As *Padina boergesenii*: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Antigua, Barbados, Bequia, Cayman Islands, Costa Rica, Cuba, Dominica, Panama, Puerto Rico, St. Eustatius, St. Lucia, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: U.S. Virgin Islands.

Thalli, 5.0–20 cm tall, are fan shaped and rounded and may be split. The lower portions are stalklike. The blades are moderately calcified on upper surfaces, less so proximally. Blade margins are 2 cells and 50–70 μm thick distally, 3 cells and 75–125 μm thick at the blade center, and 4 cells and 110–130 μm thick at the blade base. Sporangia, 90–125 μm diam, occur in 1.0–1.5 mm wide discontinuous bands, without indusia. Algae are brown to tan in color.

Habitat and comments: *Padina boergesenii* is a shallow-water species, found in both protected and moderately exposed habitats. Allender and Kraft (1983) showed the tristrromatic *P. gymnospora* sensu Taylor (1960) non *P. gymnospora* (Kütz.) Sond. was a different species, *P. boergesenii*. *Padina boergesenii* has a wide distribution and has been found to be an introduced species in the Red Sea and Mediterranean (Verlaque et al. 2015). [Additional illustrations: Kraft 2009, fig. 70A–H; Diaz-Martinez et al. 2016, figs. 5, 19.]

***Padina gymnospora* (Kütz.) Sond.**

FIGURE 44

Padina gymnospora (Kütz.) Sond. 1871: 47.

Basionym: *Zonaria gymnospora* Kütz. 1859: 29, pl. 71: fig. II.

Heterotypic Synonym: *Padina vickersiae* Hoyt in Howe 1920: 595.

Puerto Rican Records: As *Padina gymnospora*: Almodóvar and Blomquist 1959; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002. As *Padina vickersiae*: Almodóvar and Blomquist 1961; Almodóvar 1964c; Almodóvar and Ballantine 1983.



FIGURE 44. *Padina gymnospora*. In situ photograph, algal plain, seaward Media Luna Reef, 17 m. Field width = approximately 15 cm.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Costa Rica, Dominica, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Kitts, St. Lucia, St. Vincent, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: St. Thomas, U.S. Virgin Islands.

Thalli are (4.0–)10–15(–22) cm tall with blades 5.0–15(–37) cm broad, becoming cleft and proliferous, split to narrow. Algae are stalklike below and invested with rhizoids. Blades are zonate without calcification or are very lightly calcified on the upper concave surface. The blades are 2 cells and 50–60 μm thick distally but 4 cells thick throughout most of blade and 6–9 cells and 150–220 μm thick proximally. Indusiate sporangial bands are about 0.5 mm broad. Sporangia measure 100–120 μm diam.

Habitat and comments: *Padina gymnospora* grows on roots of *Rhizophora* (mangroves) and in sheltered to moderately exposed habitats, as well as subtidally to 17 m depths. Allender

and Kraft (1983) concluded that Caribbean *P. vickersiae* with 4–8 cell layers was conspecific with *P. gymnospora*. [Additional illustrations: Littler and Littler 2000: 139; Braune and Guiry 2011, fig. 40.1; Diaz-Martinez et al. 2016, figs. 6, 20.]

***Padina sanctae-crucis* Børgesen**

FIGURE 45

Padina sanctae-crucis Børgesen 1914a: 45, figs. 27, 28.

Heterotypic Synonym: *Dictyerpa jamaicensis* Collins 1901: 251; *Padina jamaicensis* (Collins) Papenf. 1977: 272.

Puerto Rican Records: As *Padina sanctae-crucis*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Cuba, Dominica, Jamaica, Martinique, Nevis, Panama, Puerto



FIGURE 45. *Padina sanctae-crucis*. In situ photograph, algal plain, seaward Media Luna Reef, 17 m. Field width = approximately 10 cm.

Rico, St. Eustatius, St. Vincent, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.
World Distribution: See Guiry and Guiry 2021.
Type Locality: St. Croix, U.S. Virgin Islands.

Thalli are 5.0–15 cm tall with lower stalklike portions invested by rhizoids. The blades measure 5.0–7.0(–25) cm broad, are concentrically zonate, and are often split into narrower segments. Calcification is substantial on the upper concave side and is lacking or very light on the lower surface. Blades are bistratose throughout, up to 130 μm thick. Reproductive sori occur in bands, close to and above each second hair line on the blade.

Sporangia, to 120 μm in diameter, occur in irregular bands with an interrupted membranous cover. Oogonia are spherical, 30–50 μm diam.

Habitat and comments: Once considered a shallow-water species (e.g., Taylor 1960), *Padina sanctae-crucis* has since been reported in deeper waters, 73 m in Florida (Dawes and Van Breedveld 1969) and 37 m in Puerto Rico (Ballantine et al. 2016). Although the basionym, *Dictyerpa jamaicensis*, is considered to be a life history stage of *Padina*, it has not been assigned with certainty to any species (e.g., Dawes and Mathieson 2008; W. Guiry in Guiry and Guiry 2021). [Additional illustrations: Diaz-Martinez et al. 2016, figs. 7, 8, 21, 22.]

Excluded taxon

Padina commersoni Bory 1828: 144.

Padina commersoni was reported from Puerto Rico by Hauck (1888). The species whose type locality is in Mauritius is now considered to be a synonym of *Padina boryana* Thivy. The species has a mostly Pacific distribution; however, although it has been reported from Brazil (Taylor 1930), it has not been reported since in the western Atlantic.

***Spatoglossum* Kütz.**

Spatoglossum Kütz. 1843: 339.

Thalli are foliaceous, with flat, nonzonate, generally ecostate blades that are stalked below. The blades are irregularly subpalmately to pinnately lobed, possessing a marginal row of apical cells. Blades are several cells thick, and the medullary layers are surrounded by

a single cortical layer on each surface. Tetrasporangia are scattered over both surfaces. *Spatoglossum* is a genus of 20 currently recognized species, with a single species known from Puerto Rico.

***Spatoglossum schroederi* (C. Agardh) Kütz.**

FIGURE 46

Spatoglossum schroederi (C. Agardh) Kütz. 1859: 21, pl. 51: fig. 1.

Basionym: *Zonaria schroederi* C. Agardh 1824: 265.

Heterotypic Synonym: *Spatoglossum areschougii* J. Agardh 1894: 39.

Puerto Rican Records: As *Spatoglossum schroederi*: Almodóvar and Blomquist 1961; Almodóvar 1964b; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Bermuda, Barbados, Grenadines, Nevis, Puerto Rico, Brazil.

Type Locality: Brazil.



FIGURE 46. *Spatoglossum schroederi*. DLB2238, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 2.0 cm.

Thalli are bladelike and 10–30 cm tall, with narrowed stalk-like bases. Blades are repeatedly alternately, subdichotomously or palmately lobed with undulate and irregularly dentate margins. The lobed divisions measure 0.5–4.0 cm broad and 0.5–7.0 cm long. Blades are up to 180 μm thick, with a 4-celled medulla. The medullary cells measure to 50 μm diam, and pigmented cortical cells are to 30 μm diam. Algae are dark green to brown in color, sometimes iridescent.

Habitat and comments: Typically, *Spatoglossum schroederi* grows in sheltered, shady habitats and has been commonly collected at Ballena Bay, Guánica, and at the Media Luna algal plain. In deep water, *S. schroederi* is known from a single collection at 50 m depth at Bajo de Sico (Ballantine et al. 2016). [Additional illustration: as *Spatoglossum areschougii* J. Agardh, Vickers 1908: pl. 11: figs. 1–4.]

***Stypopodium* Kütz.**

Stypopodium Kütz. 1843: 341.

Erect thalli arising from a rhizoidal holdfast, reach to greater than 30 cm tall, with a membranous blade. Growth is from a marginal row of apical cells. The thallus is 2–4 cells thick distally and 6–10 cells thick proximally, constructed of an outermost layer of small cortical cells overlying larger medullary cells. The medullary cells are not strictly arranged in tiers. Concentric hair lines occur on both thallus surfaces. Sporangia are densely scattered or occur in irregularly shaped sori on both thallus surfaces. Six species of *Stypopodium* are recognized, one of which one occurs in Puerto Rico.

***Stypopodium zonale* (J. V. Lamour.) Papenf.**

FIGURE 47

Stypopodium zonale (J. V. Lamour.) Papenf. 1940: 205.

Basionym: *Fucus zonalis* J. V. Lamour. 1805: 38, pl. XXV: fig. 1.

Homotypic Synonym: *Zonaria zonalis* (J. V. Lamour.) M. Howe 1918: 507.

Heterotypic Synonym: *Zonaria lobata* C. Agardh 1824: 265.

Puerto Rican Records: As *Stypopodium zonale*: Taylor 1960; Almodóvar 1964b; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016. As *Zonaria zonalis*: Almodóvar and Blomquist 1961. As *Zonaria lobata*: Hauck 1888.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Belize, Cayman Islands, Cuba, Dominica, Grenadines, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil Colombia, Venezuela.

Type Locality: Dominican Republic, Hispaniola.

Thalli, measuring from 3.5 to 17 cm tall, are attached below by large rhizoidal holdfasts. Blades, to 15 cm broad, are initially

broadly fan shaped and distinctly transversely zonate. Blades become cleft into cuneate or strap-shaped segments, 1.0–5.0 cm broad and 120–240 μm thick. The medulla is 2 cell layers thick distally and 4 layers proximally. Unilocular sporangia are 100–140 μm in diameter. Algae are light brown in color, occasionally highly blue iridescent.

Habitat and comments: *Stypopodium zonale* occurs in moderately exposed habitats from shallow water down to 55 m depths. These algae can be truly spectacular when displaying iridescence (Figure 47B).

***Taonia* J. Agardh**

Taonia J. Agardh 1848: 101.

Thalli are erect, fan-shaped blades that are attached below by matted, branched rhizoids. Blades are complanate, flabellate or lacerate, often deeply divided. Growth is from a marginal row of apical cells. Thalli are 2 cells thick distally, increasing to 5–7 cells thick proximally; cells not arranged in rows when viewed in transverse section. Hairs occur in concentric lines across the blade surfaces. Sporangia are solitary, in irregularly scattered groups or in short concentric zones adjacent to the hair lines, partially embedded in or completely external to the frond. The sporangia either lack a stalk cell or have 1–3 stalk cells. Currently, six species of *Taonia* are known worldwide, with one occurring in Puerto Rico.

***Taonia abbottiana* D.S. Littler et Littler**

FIGURE 48

Taonia abbottiana D. S. Littler et Littler 2004: 420, figs. 1–7.

Puerto Rican Record: Littler and Littler 2004.

Western Atlantic Distribution: Bahamas, Puerto Rico.

Type Locality: Near Discovery Bay, Jamaica, Caribbean Sea.

Thalli consist of erect clusters of fan-shaped blades, up to 40 cm tall, to 15 cm wide, and 180–210 μm thick. With age, blades may split and become strap shaped. Initially, margins are smooth but often become irregular because of uneven growth or splitting. Lines of surface hairs are 1.0–3.0 mm apart distally and 6.0–8.0 mm apart proximally. The medulla comprises 2 cell layers distally and 4 cell layers proximally. The medullary cells, arranged in irregular rows, measure 50–125 μm long and 30–60 μm wide. Surface hairs occur in transverse narrow bands, most commonly on the dorsal side of the blade. Spherical to oval sporangia, 80–100 μm diam, develop on short, 2-celled stalks, 30 μm diam. Algae are iridescent yellow brown in color.

Habitat and comments: *Taonia abbottiana* occurs from intermediate depths down to 40 m. It was collected only once at the latter depth off Monito Island, Puerto Rico (collector Littler et al., U.S. Algal Collection 161869; Littler and Littler 2004).

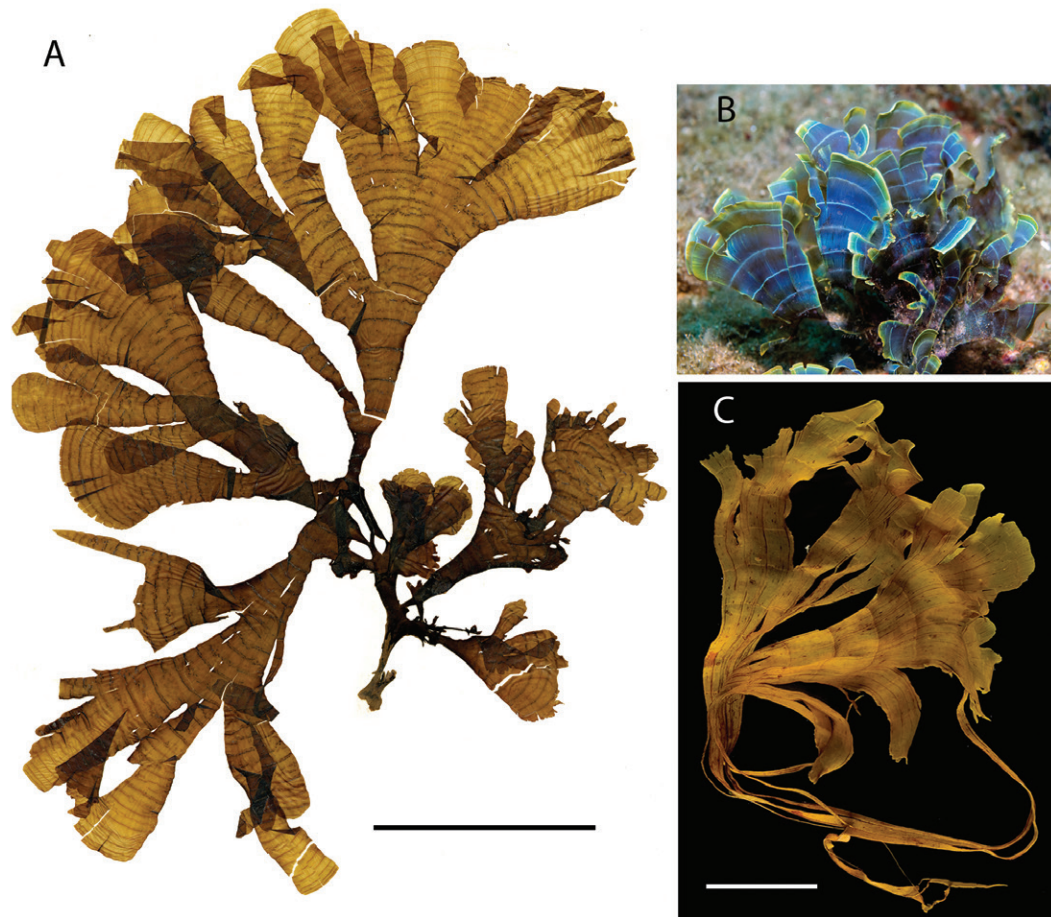


FIGURE 47. *Stypopodium zonale*. (A) DLB2244, herbarium specimen: Algal plain, seaward Media Luna Reef, 17 m. Scale bar = 5.0 cm. (B) In situ photograph, Rincón, 23 m. Field = approximately 15 cm. (C) Small plant. Scale bar = 5.0 cm.



FIGURE 48. *Taonia abbottiana*. M&DL1989, herbarium specimen: Monito Island. Scale bar = 2.0 cm.

Superficially, *Taonia abbottiana* bears a close resemblance to *Styopodium zonale*.

***Zonaria* C. Agardh**

Zonaria C. Agardh 1817: XX.

Thalli are simple or clefted erect blades above a stalklike stipe growing from substantial felted rhizoidal holdfasts. Stipes continue into the blades as midribs. The blades possess a distal margin of apical cells and are transversely banded by rows of hairs. The medulla is up to 6 cells thick, covered on both surfaces by 2 cortical cell layers. Sporangia occur in sori, lacking

paraphyses. Eleven species of *Zonaria* are recognized, one of which occurs in Puerto Rico.

***Zonaria tournefortii* (J. V. Lamour.) Mont.**

FIGURE 49

Zonaria tournefortii (J. V. Lamour.) Mont. 1846: 32.

Basionym: *Fucus tournefortii* J. V. Lamour. 1805: 44, pl. XXVI: fig. 1.

Puerto Rican Record: As *Zonaria tournefortii*: Ballantine et al. 2015.



FIGURE 49. *Zonaria tournefortii*. DLB8944: Between Punta Fraile and Punta Cerro Gorda, 18–27 m. Scale bar = 1.0 cm.

Western Atlantic Distribution: North America, Cuba, Martinique, Puerto Rico, Trinidad and Tobago, Brazil.

World Distribution: See Guiry and Guiry 2021.

Syntype Localities: Corsica, southern France, and Italy.

Thalli consist of erect, fan-shaped to strap-shaped blades, 3.5–17 cm tall. Densely tomentose stipes extend into the blades. Blades are flattened and cuneate with growth from a distal margin of initials. Medullary cells divide periclinally to give rise to up to 6 layers, the larger cells 80 μ m long and 110 μ m tall. The single layer of surface cortical cells are 10–15 μ m wide by 20 μ m high. Sporangia occur in scattered sori. Algae are yellowish brown when young and dark brown at maturity.

Habitat and comments: Known only from deepwater habitats off the north coast of Puerto Rico, *Zonaria tournefortii* was dredged from 18 to 27 m depths. Puerto Rican specimens have flabella to 3.0 cm long, 2.0 cm broad.

SPHACELARIALES MIG.

SPHACELARIACEAE DECNE.

Sphacelaria Lyngb.

Sphacelaria Lyngb. In Hornem. 1818: 8, pl. MDC.

Thalli are erect, filamentous, and branched. The erect filaments are attached below by entangled prostrate filaments. The lower portions are either ecorticate or corticated by rhizoids. Species generally possess large apical cells that divide transversely and subapical cells that divide longitudinally, giving rise to multiseriate axes. Species are largely discriminated on the basis of their asexual rinite morphology. Three of the currently known 37 species of *Sphacelaria* occur in Puerto Rico.

KEY TO THE *SPHACELARIA* SPECIES OF PUERTO RICO

1. Propagulae slender, biradiate *S. rigidula*
 Propagulae stout, arms little, if at all, extended 2
2. Propagulae arms little extended, terminal arm cells undivided; segments 1.0–1.5 diam long *S. tribuloides*
 Propagulae arms not extended, terminal arm cells transversely divided; segments 0.5–1.0 diam long
 *S. novae-hollandiae*

Sphacelaria novae-hollandiae Sond.

FIGURE 50

Sphacelaria novae-hollandiae Sond. 1845: 50.

Puerto Rican Records: Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Barbados, Cuba, Jamaica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: “Probably near Fremantle, Western Australia,” Australia (Silva et al. 1996: 576).

Thalli possess erect filamentous axes, up to 2.0 cm tall, that form dense tufts with somewhat corymbose branching. Algae are stoloniferous below. Axes measure 45–80 μ m diam, and 3–5 cell axial segments are seen in lateral view. Propagulae are triangular in shape, 80–150 μ m broad and 100–200 μ m long. Apical cells



FIGURE 50. *Sphacelaria novae-hollandiae*. DLB7122: Ballena Bay, Guánica, intertidal. Scale bar = 100 μ m.

of the propagulae arms are divided at right angles to the lateral margin.

Habitat and comments: *Sphacelaria novae-hollandiae* grows on rocks, generally in shallow-water habitats. [Additional illustrations: Mendoza-González et al. 2000: figs. 28–33; Littler and Littler 2008: 143; Huisman 2015: fig. 37D,E.]

***Sphacelaria rigidula* Kütz.**

FIGURE 51

Sphacelaria rigidula Kütz. 1843: 292.

Heterotypic Synonym: *Sphacelaria furcigera* Kütz. 1855: 27, pl. 90: fig. II.

Puerto Rican Records: As *Sphacelaria rigidula*: Ballantine 1977; Hinds and Ballantine 1987; Ballantine and Aponte 1997, 2002. As *Sphacelaria furcigera*: Díaz-Piñer 1963; Almodóvar and Ballantine 1983.



FIGURE 51. *Sphacelaria rigidula*. DLB2317: Arraial do Cabo, Rio de Janeiro, Brazil, intertidal. Scale bar = 25 μ m.

Western Atlantic Distribution: Mexico, North America, Bermuda, Barbados, Costa Rica, Cuba, Dominica, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Epiphytic on *Hormophysa triquetra* (C. Agardh) Kütz. [= *H. cuneiformis* (J. F. Gmel.) P. C. Silva]; Nuweiba, Sinai, Gulf of Aqaba, Red Sea, Egypt.

Thalli with sparsely branched filamentous axes are up to 2.0 cm tall and 16–45 μ m diam. Algae originate from a stoloniferous base or are endo-epiphytic below. Axial and branch segments are as long as or somewhat longer than broad, sparingly longitudinally divided. Propagulae are slender, bi- or triradiate, distally with 2 cylindrical arms having a span of 450 μ m. The propagulae are up to 24 μ m diam and 150–250 μ m in length.

Habitat and comments: *Sphacelaria rigidula* is epiphytic on *Sargassum* and *Turbinaria* and occasional on other algae or growing on rocks. [Additional illustrations: Vickers 1908: pl. 25: figs. 1–6 (as *S. furcigera*); Prud'Homme van Reine 1982: figs. 508–553; Mendoza-González et al. 2000: figs. 34–37; Huisman 2015: fig. 37F,G.]

***Sphacelaria tribuloides* Menegh.**

Sphacelaria tribuloides Menegh. 1840: [2].

Puerto Rican Records: Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Hinds and Ballantine 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cuba, Dominica, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: On submerged rocks; La Spezia, Gulf of Spezia, Ligurian Sea, northern Italy.

Thalli form tufts 0.5–3.0 cm tall, attached below by short stolons. Axes measure 25–60 μ m diam. Axial and branch segments are sparingly longitudinally divided, showing 2 or 3 cells in lateral view, with segments as long as they are broad or a little longer. Propagulae are pedicellate, bi- or triradiate, and broadly triangular. The propagule arms are thick, little projecting, with a span of 140–164 μ m and 200 μ m in length.

Habitat and comments: *Sphacelaria tribuloides* grows on rocks and coralline algae or may be epiphytic on other algae in shallow water or sometimes in wave-exposed habitats. [Additional illustrations: Vickers 1908: pl. 26: figs. 1–9; Prud'Homme van Reine 1982: figs. 441–453; Mendoza-González et al. 2000: figs. 38–41.]

DESMARESTIALES SETCH. ET N. L. GARDNER**DESMARESTIACEAE (THUR.) KJELLM.*****Desmarestia* J. V. Lamour.****Excluded taxa***Desmarestia aculeata* (L.) J. V. Lamour. 1813: 25.*Desmarestia lingulata* (Stackh.) J. V. Lamour. 1813: 25.

Although appearing in floristic lists of Puerto Rican marine algae (e.g., Ballantine and Aponte 1997, 2002), the two species of *Desmarestia* listed above were considered to be doubtful records by Ballantine and Aponte (2002). The only report of these species in Puerto Rico was by Díaz-Piferrer (1969). Since then, neither has been collected again or observed in the field, and no voucher specimens of these two species from Puerto Rico are to be found in the herbaria of MSM or the U.S. Algal Collection.

ECTOCARPALES SETCH. ET N. L. GARDNER**ACINETOSPORACEAE HAMEL*****Acinetospora* Bornet***Acinetospora* Bornet 1892: 370.

Thalli comprise 1 to several uniseriate filaments with intercalary growth zones above a filamentous or discoid base. Branching is irregular and sparse, with most branches short and at right angles to the axes. Cells possess numerous discoid or slightly elongated chromatophores. Currently, there are 4 recognized species of *Acinetospora*, 1 of which is known in Puerto Rico.

***Acinetospora crinita* (Carmich.) Sauv.**

FIGURE 52

Acinetospora crinita (Carmich.) Sauv. 1899: 118 in Sauvageau (1899).*Basionym:* *Ectocarpus crinitus* Carmich. in Harvey 1833: 326.*Heterotypic Synonym:* *Acinetospora pusilla* (A. W. Griffiths ex Harv.) De Toni 1895: 566

Puerto Rican Records: As *Acinetospora crinita*: Ballantine and Aponte 1997, 2002. As *Acinetospora pusilla*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: North America, Bermuda, Barbados, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Appin, Scotland.



FIGURE 52. *Acinetospora crinita*. LRA3924, herbarium specimen: Guánica, growing on *Rhizophora* prop roots. Scale bar = 1.0 cm.

Thalli are tufted, 4.0–8.0 cm tall, with filaments forming an entangled mat below. Erect axes are flexuous, with paired, oppositely placed, sometimes curved lateral branches. Cells are 15–56 μm diam and 1–6 μm diam long. Monosporangia are subspherical to oval, 31–42 μm diam and 45–53 μm long. They are sessile, on 1-celled pedicels or occurring in groups of 2 or 3 together at bases of branches. Plurilocular gametangia are ovoid-lanceolate to fusiform, measuring 24–42 μm diam and 75–130 μm in length.

Habitat and comments: *Acinetospora crinita* is usually epiphytic and encountered in shallow-water habitats. [Additional illustration: Littler and Littler et al. 2008: 145.]

KEY TO THE FELDMANNIA SPECIES OF PUERTO RICO

1. Axial filaments 20–34 μm in diameter; sporangia/gametangia 112–250 μm long *F. duchassaingiana*
 Axial filaments 35–50 μm in diameter; sporangia/gametangia 50–150 μm long *F. mitchelliae*

***Feldmannia duchassaingiana* (Grunov Aisha et Shameel)**

Feldmannia duchassaingiana (Grunov) Aisha et Shameel 2011: 131, fig. 1a–g.

Basionym: *Ectocarpus duchassaingianus* Grunov 1868: 45, footnote, pl. 4: fig. 1.

Homotypic Synonym: *Giffordia duchassaingiana* (Grunov) W. R. Taylor 1960: 207, pl. 29: fig. 10.

Heterotypic Synonym: *Feldmannia indica* (Sond.) Womersley et A. Bailey 1970: 288.

Puerto Rican Records: As *Ectocarpus duchassaingianus*: Hauck 1888. As *Giffordia duchassaingiana*: Taylor 1960; Almodóvar and Blomquist 1965. As *Feldmannia indica*: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Antigua, Bermuda, Barbados, Dominica, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Guadeloupe, French West Indies.

Filamentous thalli form tufts, up to 2.0 cm tall, that are attached by entangled, rhizoid-like filaments below. Axes are irregularly branched filaments, 20–34 μm diam, that terminate in hairlike tips. Proximal cells are half the length of their diameter, 10–17 μm long, and distal cells are 1.5 times longer than their diameter, 30–51 μm long. Sporangia are sessile, obovate or oval, up to 70 μm diam and 110 μm long. Gametangia, 19–50 μm diam and 112–250 μm long, are sessile or with a single stalk cell. They are cylindrical to clavate or fusiform and bluntly rounded at the apex.

Habitat and comments: *Feldmannia duchassaingiana* grows epiphytically or on rocks. The species occurs in shallow

***Feldmannia* Hamel**

Feldmannia Hamel 1939a: xli.

Thalli consist of uniseriate filaments, usually in tufts that are attached basally by rhizoids. Branching originates mostly proximally. Axes and branches terminate in vegetative hairs and exhibit intercalary growth. Cells have numerous discoid chromatophores. There are 2 species of *Feldmannia* in Puerto Rico of the 25 species recognized in the genus.

protected habitats and has been dredged to 20 m depths. Although *Ectocarpus duchassaingianus* Grunow was considered conspecific with *Feldmannia indica* (Sond.) Womersley et A. Bailey (1970) by Wynne (2017), the two were more recently treated as distinct species by Aisha and Shameel (2011). Both of these species have also been considered conspecific with *Hincksia mitchelliae* (Harv.) P. C. Silva in Silva et al. 1987 by Schneider and Searles (1991). However, the latter, as *F. mitchelliae* (Harv.) H.-S. Kim (2010), is now recognized as being distinct by Wynne (2017). [Additional illustrations: Vickers 1908: pl. 27: figs. 1–8 (as *Ectocarpus duchassaingianus*); Aisha and Shameel 2011, fig. 1a–g.]

***Feldmannia mitchelliae* (Harv.) H.-S. Kim**

Feldmannia mitchelliae (Harv.) H.-S. Kim 2010: 51, figs. 21, 22.

Basionym: *Ectocarpus mitchelliae* Harv. 1851: 142, pl. 12G.

Homotypic Synonyms: *Hincksia mitchelliae* (Harv.) P. C. Silva in Silva et al. 1987: 73, 130; *Giffordia mitchelliae* (Harv.) Hamel 1939a: 66.

Puerto Rican Records: As *Giffordia mitchelliae*: Díaz-Piferrer 1963; Miller and Ballantine 1974; Ballantine 1977; Almodóvar and Ballantine 1983. As *Hincksia mitchelliae*: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Barbados, Dominica, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Nantucket, Massachusetts.

Thalli are filamentous, 2.0–3.0(–12) cm or taller, from a base of creeping filaments. Abundant branching is alternate or secund. Main axial cells measure 5.0–50 μm diam and 70–200 μm long, decreasing in diameter distally. Lateral branch cells are 15–20 μm diam. Gametangia, 20–30 μm diam and 50–150(–220) μm long,

are linear-cylindrical with obtuse apices and are borne adaxially on branches. Algae are brownish green in color.

Habitat and comments: *Feldmannia mitchelliae* is epiphytic on seagrasses and algae and also grows on rocks in shallow water. [Additional illustrations: Schnetter and Bula-Meyer 1982: pl. 7: figs. C, D (as *Giffordia mitchellae*); Littler et al. 2008: 149 (as *Hincksia mitchelliae*).]

***Herponema* J. Agardh**

Herponema J. Agardh 1882: 55.

Thalli are minute epiphytes with short, erect, uniseriate, and unbranched filaments forming a feltlike cover on their host. Algae possess creeping or endophytic branched filaments of shorter cells below. Growth in free filaments is intercalary to diffuse. The filaments are often attenuate, with the apical cell often narrowing to become hairlike. Cells possess a pyrenoid and several parietal, disk-shaped chromatophores. Both unilocular and plurilocular sporangia occur terminally on short filaments. One of the 11 currently recognized species of *Herponema* is known from Puerto Rico.

***Herponema tortuguense* (W. R. Taylor) W. R. Taylor**

Herponema tortuguense (W. R. Taylor) W. R. Taylor 1960: 204.

Basionym: *Ectocarpus tortugensis* W. R. Taylor 1928: 108, pl. 14: fig. 1.

Puerto Rican Records: As *Herponema tortuguense*: Díaz-Piferrer 1963; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Cuba, Netherlands Antilles, Puerto Rico, Brazil.

Type Locality: Bush Key, Dry Tortugas, Florida.

Minute thalli are epiphytic with simple or little-branched filaments, about 10 cells, and 0.2 mm in height. Algae arise from a mat of decumbent short, branched filaments. Cells of basal filaments are irregularly cylindrical, 7.5–12.5 µm diam and 12–27 µm long. Sporangia, 7.5–15 µm diam and 25–50 µm long (=gametangia sensu Taylor 1960), are oval to cylindrical and occur 1–3 per bearing filament.

Habitat and comments: Algae are epiphytic on *Zonaria* and probably other algae in shallow water. [Additional illustrations: Mateo-Cid et al. 2002: 216, figs. 18, 19.]

***Hincksia* J. E. Gray**

Hincksia J. E. Gray 1864: 12.

Thalli consist of erect tufts of uniseriate filaments attached below by rhizoids. Branching is variable: unilateral or secund, irregular, alternate or opposite. Growth is diffuse by intercalary

cell divisions. Meristems are scattered throughout axes and near the base of most lateral branches, with additional meristems distally. Cells are more or less isodiametric to barrel shaped, with numerous discoid chloroplasts and a single pyrenoid. There are 26 species of *Hincksia* recognized worldwide, with a single representative from Puerto Rico.

***Hincksia conifera* (Børgesen) I. A. Abbott**

Hincksia conifera (Børgesen) I. A. Abbott 1989: 226, 231 (footnote).

Basionym: *Ectocarpus conifer* Børgesen 1914a: 8, figs. 5, 6.

Homotypic Synonym: *Giffordia conifera* (Børgesen) W. R. Taylor 1960: 207.

Heterotypic Synonyms: *Giffordia rallsiae* (Vickers) W. R. Taylor 1960: 208; **basionym:** *Ectocarpus rallsiae* Vickers 1905: 59.

Misapplied Name: *Feldmania irregularis* (Kütz.) Hamel 1939a.

Puerto Rican Records: As *Giffordia conifera*: Díaz-Piferrer 1963. As *Giffordia rallsiae*: Ballantine 1977; Hinds and Ballantine 1987. As *Feldmania irregularis*: Ballantine and Aponte 2002.

Western Atlantic Distribution: North America, Bermuda, Antigua, Barbados, Martinique, Puerto Rico, U.S. Virgin Islands, Colombia.

World Distribution: See Guiry and Guiry 2021.

Type Locality: St. John, U.S. Virgin Islands.

Thalli measure 5.0–7.0 cm tall and are attached below by rhizoids. Branching is secund to alternate and at right angles to axes. Branches are of unequal lengths, terminating in long hairs. Cells of main axes measure 25–40 µm diam and 12.5–160 µm long. Gametangia, limited to basal areas of axes, are elongate conical, 20–40 µm diam and 40–200 µm long.

Habitat and comments: *Hincksia conifera* has been collected as an epiphyte or growing on stones in shallow water in either exposed or sheltered habitats. The taxonomic status of *H. conifera* is somewhat unsettled; Amsler (1985) regarded *H. conifera* to be conspecific with *G. rallsiae* (Vickers) W. R. Taylor (1960), whereas Wynne (2017) and Guiry and Guiry (2021) treat the two species as independent taxa. [Additional illustration: Aisha and Shameel 2011: fig. 5.]

CHORDARIACEAE GREV.

***Cladosiphon* Kütz.**

Cladosiphon Kütz. 1843: 329.

Macrosporophyte thalli are erect, and the narrow branched cylindrical axes are gelatinous and spongy. Branches are sometimes hollow, with the filamentous medulla united into a pseudoparenchyma. The subcortex consists of 1–3 layers of small cells that bear sharply differentiated, simple or proximally branched assimilatory filaments. Plurilocular sporangia are terminal in

assimilator fascicles. One of the 15 currently known species of *Cladosiphon* is reported in Puerto Rico.

***Cladosiphon occidentalis* Kylin**

FIGURE 53

Cladosiphon occidentalis Kylin 1940: 27, fig. 15f, pl. 3: fig. 8.

Puerto Rican Records: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Belize, Cuba, Panama, Puerto Rico, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Dry Tortugas, Florida.

Thalli consist of narrow, cylindrical axes and branches, 15–20(–30) cm tall, that are abundantly and paniculately branched. Axes, 0.75–3.0 mm diam, are covered with fine, colorless hairs and are mostly hollow or proximally solid with strands of coherent filaments, 50–112 μ m diam and 200–400 μ m long.

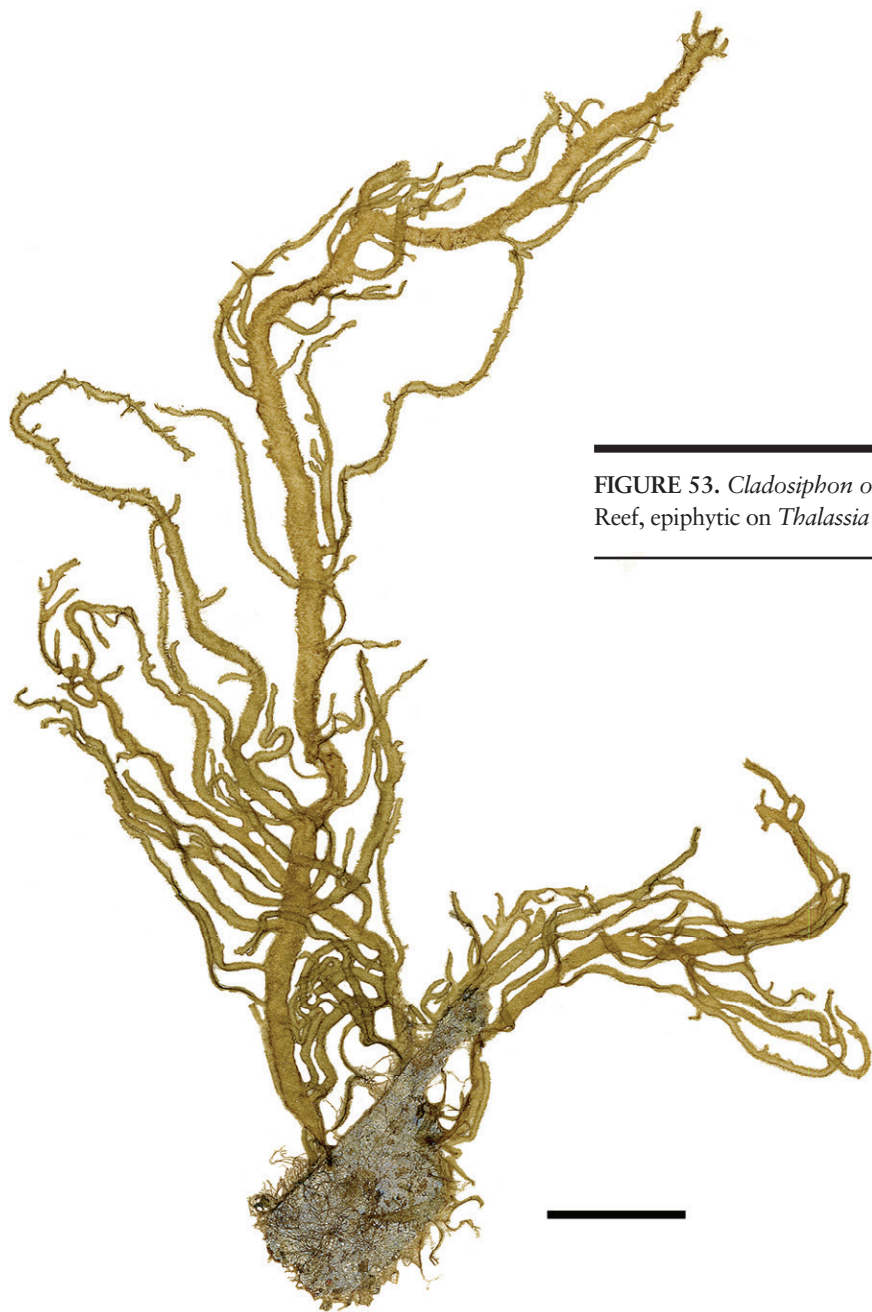


FIGURE 53. *Cladosiphon occidentalis*. DLBsn, herbarium specimen: Margarita Reef, epiphytic on *Thalassia testudinum* König. Scale bar = 1.0 cm.

Axial strands give rise to a lateral assimilatory cortex, 100–300 µm thick, of cells 5.6–7.5(–9.0) µm diam and 19–28 µm long. Plurilocular sporangia, 15–35 µm long and 5–20 µm diam, are terminal in assimilatory fascicles. Sessile unilocular sporangia, 30–45 µm long and 25–40 µm diam, are borne proximally on cortical filaments. Algae are dull brown to yellow brown in color.

Habitat and comments: *Cladosiphon occidentalis* is usually epiphytic on the seagrass *Thalassia* in shallow water and down to 11 m depths. The species has only rarely been collected in Puerto Rico.

***Hecatonema* Sauv.**

Hecatonema Sauv. 1898: 248.

Excluded taxon

Hecatonema terminale (Kütz.) Kylin 1937: 8, fig. 2.

Basionym: *Ectocarpus terminalis* Kütz. 1845: 236.

The species was reported for Puerto Rico by Hauck (1888) and has not been reported since. The presence of *Hecatonema terminale* in the Caribbean is further questionable as the taxon appears to be largely restricted to subboreal to temperate waters. The taxonomic status of the species is also problematic (e.g., Guiry and Guiry 2021). Fletcher (1987) suggested it may be a synonym of *H. maculans* (Collins) Sauv. (1898), and Wynne (1998) noted that the species may be the microthallus of various taxa, including *Punctaria* (Clayton 1974), *Myriotrichia* (Loiseaux 1969), and *Asperococcus* (Pedersen 1984).

***Kuetzingiella* Kornmann**

Kuetzingiella Kornmann 1956: 293, 314.

Thalli consist of erect unbranched, sparsely branched, or branched filaments that issue from monostromatic disks. Filament cells are isodiametric and irregular, containing several disk-shaped chloroplasts. Plurilocular sporangia are sessile or short stalked, and their development prior to the formation of erect filaments is a characteristic feature of the genus. Subsequently, plurilocular sporangia are borne laterally on the erect filaments. Unilocular sporangia are sessile or borne on a single-celled stalk, sometimes occurring with sessile plurilocular sporangia. The mostly epiphytic genus has a “wooly” appearance on its hosts. Four species of *Kuetzingiella* are known, one of which occurs in Puerto Rico.

***Kuetzingiella elachistaeformis* (Heydr.) M. S. Balakr. et Kinkar**

Kuetzingiella elachistaeformis (Heydr.) M. S. Balakr. et Kinkar 1981: 25, figs. 20, 98–100.

Basionym: *Ectocarpus elachistaeformis* Heydr. 1892: 470, pl. 25: fig. 14.

Homotypic Synonym: *Feldmannia elachistaeformis* (Heydr.) Pham-Hoàng 1969: 299, fig. 3.3.

Puerto Rican Records: As *Ectocarpus elachistaeformis*: Almodóvar and Blomquist 1965; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Belize, Cuba, Netherlands Antilles, Puerto Rico, Sargasso Sea, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Epiphytic on *Sargassum cristaeifolium* var. *upolense* Grunov; Mandang, near Bogia (Hatzfeldthaven), Papua New Guinea.

Thalli consist of short, erect, and sparsely branched filaments. Algae reach 1.0–1.5 mm in height and are attached below by decumbent, sometimes penetrating filaments. The filaments become hair tipped; cells of erect filaments measure 10–18 µm diam and 10–54 µm long. Gametangia, 15–25 µm diam and 63–200 µm long, are fusiform to narrowly conical and are borne near the bases of erect filaments. Algae are brownish green in color.

Habitat and comments: *Kuetzingiella elachistaeformis* is epiphytic on various macroalgae in shallow-water habitats. [Additional illustrations: Taylor 1960: pl. 29: fig. 9 (as *Ectocarpus elachistaeformis*); Littler et al. 2008: 153.]

***Myriotrichia* Harv.**

Myriotrichia Harv. 1834: 299.

Thalli are initially uniseriate and sometimes arise from a creeping base of decumbent, uniseriate filaments. Filaments possess terminal hairs. With development, thalli become terete and parenchymatous, with few-celled determinate lateral branchlets developing in apical portions that may transform into plurilocular sporangia. Unilocular sporangia are separately developed from cortical cells of thalli and may be found among plurilocular sporangia. Growth is intercalary. Of the six known species of *Myriotrichia*, one is recorded in Puerto Rico.

***Myriotrichia occidentalis* Børgesen**

Myriotrichia occidentalis Børgesen 1920: 437, figs. 413, 414.

Puerto Rican Records: Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Puerto Rico, U.S. Virgin Islands.

Type Locality: Epiphytic on *Dictyota indica* Sonder ex Kütz. (= *D. cervicornis* Kütz.), dredged at 10 m depth; off Frederiksted, St. Croix, U.S. Virgin Islands.

Thalli short, consisting of erect uniseriate filaments, up to 1.0 mm tall, arising from irregularly branched basal filaments that are attached by very short rhizoids. Some main axial filaments,

rarely with short branchlets, bear lateral or terminal hairs. Cells of the erect filaments measure 12–24 μm diam and 150 μm long. The basal filaments measure 10 μm diam and are 20 μm long. Plurilocular sporangia, 12–30 μm diam and 50–100 μm long, are sessile or pedicellate (1 to few celled) and fusiform to subconical.

Habitat and comments: *Myriotrichia occidentalis* is a small epiphyte on seagrasses and algae in shallow water.

***Stictyosiphon* Kütz.**

Stictyosiphon Kütz. 1843: 301.

Thalli are simple and tubular or membranous fronds that arise from a basal disk. The medulla consists of large, cylindrical

inner cells and a cortex of small, rounded and angular cells. Plurilocular sporangia, associated with paraphyses, form broad or localized patches and are developed from cortical cells. A single species of *Stictyosiphon* is known from Puerto Rico of the 10 recognized species worldwide.

***Stictyosiphon lutarius* W. R. Taylor**

FIGURE 54

Stictyosiphon lutarius W. R. Taylor 1974: 60, 67, figs. 6–13.

Puerto Rican Records: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Jamaica, Puerto Rico.

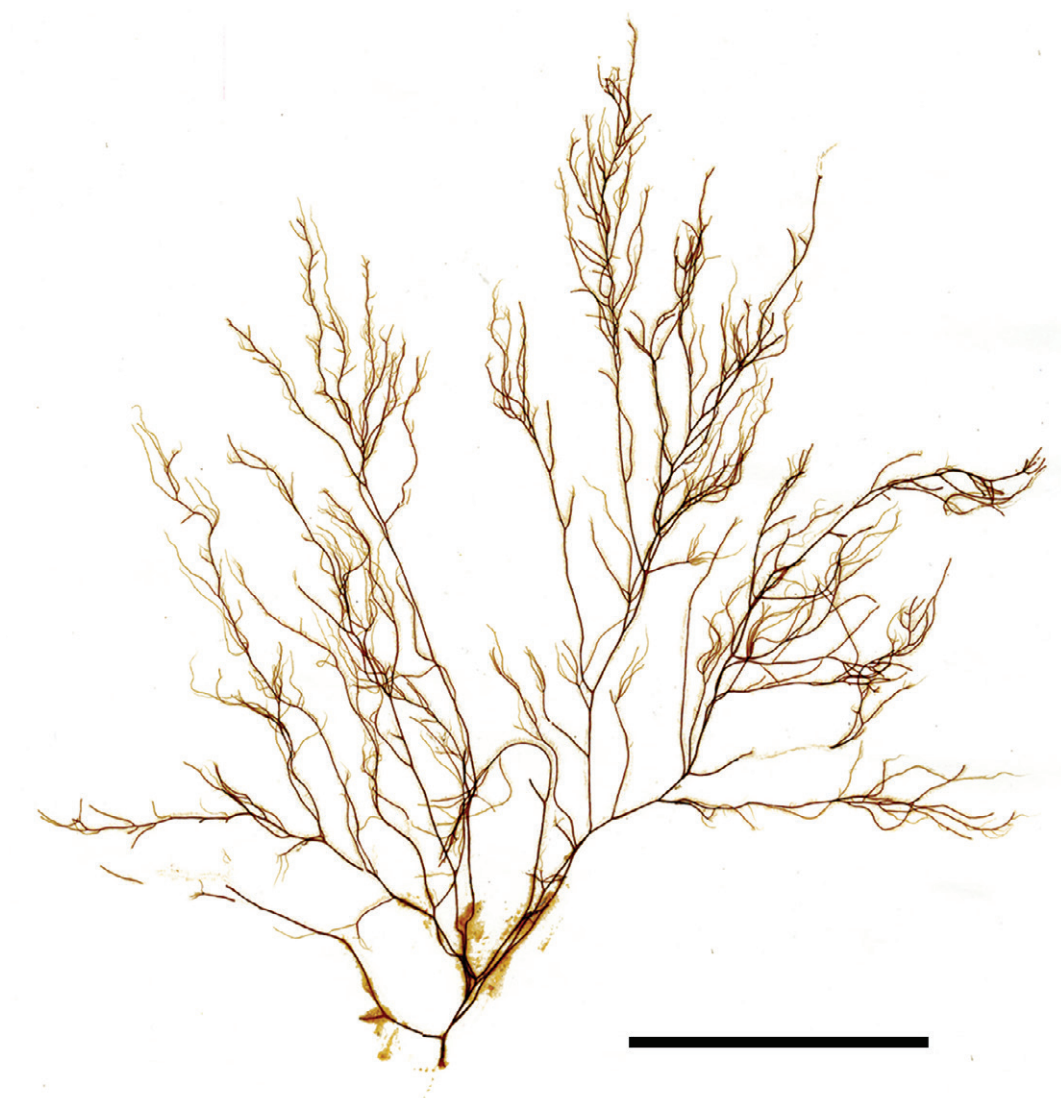


FIGURE 54. *Stictyosiphon lutarius*. MDP3311: Combate, Cabo Rojo. Scale bar = 5.0 cm.

Type Locality: On muddy slope, about 4.5 m depth; Cow Bay, St. Thomas Parish, Jamaica.

Extremely flaccid thalli consist of long, narrow, cylindrical, irregularly branched main axes, up to 36 cm in length. Algae form clumps and may be entangled in substantial masses. Long, slender branches are produced laterally and radially. The medulla consists of 4 major rows of large cells that, at maturity, measure 45–65 μm diam and 265–530 μm long. The cortex is a single layer of small cells, 10–18 μm diam. Algae (when dried) are pale yellowish brown in color.

Habitat and comments: *Stictyosiphon lutarius* occurs in muddy bottom habitats down to 30 m depths. The species is known in Puerto Rico only from the collection of multiple specimens (U.S. Algal Collection 081555–081559) from Punta Arenas, Mayaguez, by Díaz-Piferrer (3.vii.1965).

ECTOCARPACEAE C. AGARDH

Ectocarpus Lyngb.

Ectocarpus Lyngb. 1819: 130.

Thalli consist of erect, uniseriate, branched filaments above a decumbent or rhizoidal base. Cells possess parietal band-shaped or ribbon-shaped chromatophores. Pseudohairs are present, and growth is intercalary. Unilocular sporangia are terminal on short laterals. Plurilocular gametangia are terminal or may also develop from vegetative cells below pseudohairs. Life histories are isomorphic to slightly heteromorphic (Pedersen in Guiry and Guiry 2021). Of the more than 100 species of *Ectocarpus* recorded worldwide, only 2 of these species are currently known from Puerto Rico.

KEY TO THE ECTOCARPUS SPECIES OF PUERTO RICO

1. Thalli up to 2.0 mm high; filaments 9–12 μm in diameter; plurilocular gametangia 20–30 μm in diameter, 45–75 μm long *E. variabilis*
- Thalli up to 5 mm high; filaments 27–40 μm in diameter; plurilocular gametangia 27–49 μm in diameter, 80–120 μm long *E. rallsiae*

Ectocarpus rallsiae Vickers

Ectocarpus rallsiae Vickers 1905: 59.

Homotypic Synonyms: *Giffordia rallsiae* (Vickers) W. R. Taylor 1960: 208; *Hincksia rallsiae* (Vickers) P. C. Silva in Silva et al. 1987: 73, 130 [see *Hincksia conifera*].

Puerto Rican Records: As *Ectocarpus rallsiae*: Ballantine and Aponte 2002. As *Hincksia rallsiae*: Ballantine and Aponte 1997. As *Giffordia rallsiae*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Barbados. Epiphytic on *Galaxaura cylindrica* (J. Ellis et Sol.) J. V. Lamour. [= *Tricleocarpa cylindrica* (J. Ellis et Sol.) Huisman et Borow.].

Thalli consist of erect branched filaments, up to 5.0 mm tall, above creeping, basal filaments. Branching is sparse, irregular, and flexuous. Filaments may be hair tipped. Cells are variable in diameter, 27–40 μm , and are 135–200 μm long. Oval or ovate unilocular sporangia measure 45 μm diam and 70 μm long. Sessile or stalked plurilocular sporangia appear conical or fusiform and are scattered on filaments or on bases of longer branches. They measure 27–40 μm diam and are 80–120 μm long. The sporangial apices are acute or attenuate.

Habitat and comments: *Ectocarpus rallsiae* is an epiphyte on larger algae in shallow water. [Additional illustrations: Vickers 1908: 44, pl. 32: figs. 1–8; Schnetter and Bula-Meyer 1982: pl. VII: figs. F, G (as *Giffordia rallsiae*).]

Ectocarpus variabilis Vickers

Ectocarpus variabilis Vickers 1905: 59.

Puerto Rican Records: Díaz-Piferrer 1963; Almodóvar and Blomquist 1965; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Barbados, Cuba, Jamaica, Puerto Rico, U.S. Virgin Islands, Brazil.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Epiphytic on *Gelidium spathulatum* (Kütz.) Bornet [referred to *G. crinale* (Hare ex Turner) Gaillon (Taylor 1960)], *Galaxaura cylindrica* (J. Ellis et Sol.) J. V. Lamour. [= *Tricleocarpa cylindrica* (J. Ellis et Sol.) Huisman et Borow.], and *Gracilaria* sp.; Bathsheba, Barbados.

Thalli consist of erect filaments from basal creeping filaments, reaching up to 2.0 mm tall. Algae are sparsely branched; filaments have rounded apices and cells that measure 9.0–12 μm diam and to 3 μm long. Chromatophores are band shaped. Sessile or stalked plurilocular sporangia, borne proximally on branches, are lanceolate-oblong and obtuse, measuring 20–30 μm diam and 45–75 μm long.

Habitat and comments: *Ectocarpus variabilis* is epiphytic, growing in shallow water on other larger algae. [Additional illustrations: Vickers 1908: 43, pl. 31: figs. 1–9.]

CHNOOSPORACEAE SETCH. ET N. L. GARDNER

Comment: Although Chnoosporaceae is recognized by some (e.g., Abbott and Huisman 2003; Pedroche et al. 2008; Norris 2010; Norris et al. 2017; Wynne 2017), it has also been treated as synonymous with Scytosiphonaceae Farl. (e.g., Silberfeld et al. 2014).

Chnoospora J. Agardh

Chnoospora J. Agardh 1847: 7.

Thalli are erect to partly decumbent tufts or mats. The axes are usually subdichotomously branched, tapering toward the acute or blunt tips. Branches are subterete or distinctly compressed. The medulla is solid, composed of colorless elongated,

pseudoparenchymatous cells beneath the cortex of 1 or 2 small cells. The cortical layer in surface view consists of irregularly arranged small cells with numerous pits containing tufts of hairs (cryptoblasts). Unilocular sporangia are unknown. Plurilocular gametangia may or may not be associated with cryptoblasts.

Of the 4 currently accepted species of *Chnoospora*, 1 is reported from Puerto Rico.

Chnoospora minima (K. Hering) Papenf.

FIGURE 55

Chnoospora minima (K. Hering) Papenf. 1956: 69.

Basionym: *Fucus minimus* K. Hering 1841: 92.

Puerto Rican Records: As *Chnoospora minima*: Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Cuba, Grenadines, Guadeloupe, Martinique, Netherlands Antilles,



FIGURE 55. *Chnoospora minima*. DLB3596: Vega Baja, intertidal, ii.1990. Scale bar = 2.0 cm.

Panama, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Port Natal, Durban, South Africa.

Thalli are erect and up to 15 cm in height. Axes are subterete to compressed and are repeatedly subdichotomously branched. Branch segments measure 2.0 mm broad and up to 1.0 mm thick. The medulla comprises many, up to 40 μ m diam and 7.0–40 mm long, rounded cells. The cortical cells are smaller, up to 10 μ m diam. Algae are dull greenish brown in color.

Habitat and comments: *Chnoospora minima* grows on rocks in exposed intertidal habitats.

SCYTOSIPHONACEAE FARL.

Colpomenia (Endl.) Derbès et Solier

Colpomenia (Endl.) Derbès et Solier in Castagne 1851: 95.

Gametophytic macrothalli are spherical or globose and hollow. They may become compressed to flattened, sometimes

expanded or sheetlike. In section, the walls are 2 layered, with a cortical layer of small, pigmented cells that bear hairs in scattered tufts and an inner medulla of large, rounded pseudoparenchymatous cells that surround the hollow cavity. Plurilocular sporangia occur in small superficial sori, associated with paraphyses. One of the 10 currently recognized species of *Colpomenia* species occurs in Puerto Rico.

Colpomenia sinuosa (Mert. ex Roth) Derbès et Solier

FIGURE 56

Colpomenia sinuosa (Mert. ex Roth) Derbès et Solier in Castagne 1851: 95.

Basionym: *Ulva sinuosa* Mert. ex Roth 1806: 327, pl. XII.

Homotypic Synonym: *Hydroclathrus sinuosus* (Mert. ex Roth) Zanardini 1843: 39.

Puerto Rican Records: As *Hydroclathrus sinuosus*: Hauck 1888.

As *Colpomenia sinuosa*: Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

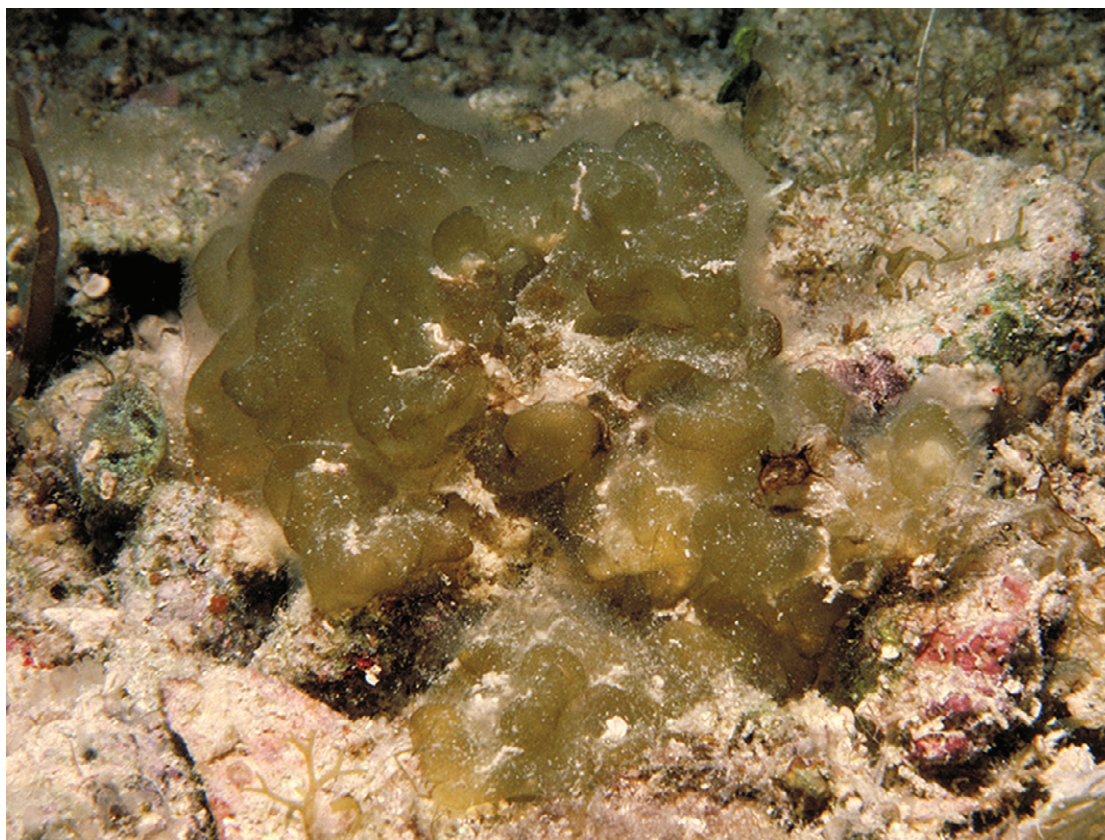


FIGURE 56. *Colpomenia sinuosa*. In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field width = approximately 15 cm.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cuba, Dominica, Jamaica, Martinique, Netherlands Antilles, Nevis, Panama, Puerto Rico, St. Kitts, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Argentina, Brazil, Colombia, Uruguay, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: “Inter Algas e mari Atlantico prope Gades” (Roth 1806: 327); near Cádiz, Bahía de Cádiz, Andalusia region, SW Spain.

Colpomenia sinuosa is the generitype species. Macroscopic gametophytic thalli, 3.0–12(–15) cm in extent, are attached by rhizoids on their lower surface. Algae are globose, sessile, solitary, or clustered and can become compressed, irregularly convoluted, and expanded. The wall is 0.3–0.5 mm thick. The cortex consists of 1 or 2 layers of small, cuboidal cells, 3.7–7.5 μm diam. The medulla consists of 4–6 layers of large, colorless cells, up to 180(–240) μm diam, that surround the hollow interior. Plurilocular sporangia/gametangia are cylindrical, 3.7–7.5 μm diam and 19–30 μm long. They occur in sori covered with a cuticle and are often grouped around an invaginated tuft of hairs. The paraphyses are usually longer than the plurilocular sporangia, up to 55 μm long. Microscopic sporophyte thalli are prostrate with an *Ectocarpus*-like morphology. Algae are light yellowish brown in color.

Habitat and comments: *Colpomenia sinuosa* is reported to occur on intertidal rocks, mostly in exposed habitats. In Puerto Rico it is most frequently collected at the Media Luna algal plain in 17 m. Sporophytic thalli have not been collected in Puerto Rico.

***Hydroclathrus* Bory**

Hydroclathrus Bory 1825: 419.

Gametophytic macrothalli are initially spherical and hollow, later becoming open or torn and then flattened and expanded. The algae are irregularly convoluted or clathrate, often “net-like.” The algal wall consists of 5 or 6 cell layers with a cortex of small, pigmented cells and a medulla of larger colorless cells. Plurilocular structures form scattered sori over the surface. The filamentous microthallus life history phase produces both plurilocular and unilocular structures (that are known only in culture studies). One of the 6 currently recognized species of *Hydroclathrus* is present in Puerto Rico.

***Hydroclathrus clathratus* (C. Agardh) M. Howe**

FIGURE 57

Hydroclathrus clathratus (C. Agardh) M. Howe 1920: 590.

Basionym: *Encoelium clathratum* C. Agardh 1823: 412.

Puerto Rican Records: As *Hydroclathrus clathratus*: Almodóvar and Blomquist 1965; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Barbados, Belize, Cayman Islands, Cuba, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

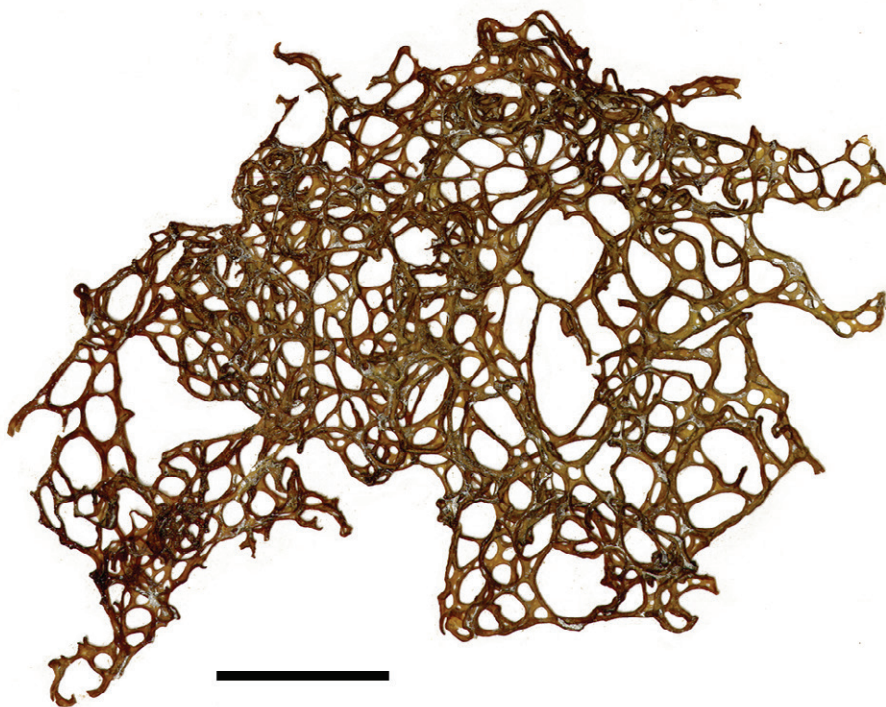


FIGURE 57. *Hydroclathrus clathrata*. DLBsn, herbarium specimen: Cueva Island, La Parguera. Scale bar = 2.0 cm.

Type Locality: “Uncertain” (Silva et al. 1996: 631; Guiry and Guiry 2021). *Lectotype Locality*: Belle-île, Brittany, France (Howe 1920), but Hamel (1937) noted that mollusk shells included with the lectotype collection of *H. clathratus* were not known from this locality. (For syntype localities see C. Agardh 1823; Guiry and Guiry 2021.).

Macrothalli are initially saccate, becoming irregularly shaped and convoluted with perforations of various sizes or forming netlike sheets. Algae are 5.0–10(–100) cm in extent and 100–200 µm thick, with abundant small to large holes that measure 0.1–3.0 cm diam, separated from each other by 1.0–3.0 mm. Pigmented cortical cells are small, 5.5–9.0 µm diam. The medulla consists of 3–6 layers of large colorless cells, mostly 50–150 µm diam, usually surrounding a hollow center. Hairs occur in shallow depressions scattered over the thallus surface. Algae are attached or seemingly loose on the bottom or may be attached at many points. Plurilocular sporangia, 9.0–17 µm diam and 13–23 µm long, occur on macrothalli.

Habitat and comments: *Hydroclathrus clathratus* is collected in exposed, intertidal habitats and shallow waters down to

17 m depths; usually unattached or adrift. [Additional illustrations: as *Hydroclathrus cancellatus* Bory, Vickers 1908: pl. 23: figs. 1–5.]

***Rosenvingea* Børgesen**

Rosenvingea Børgesen 1914a: 22.

Gametophytic macrothalli are erect, bushy, and mostly lax. Terete to compressed axes are alternately, oppositely, subdichotomously, or irregularly branched. The branches are tubular and hollow, except near their base, where the cavity is filled with rhizoid-like filaments. Axial and branch walls consist of 3 or 4 cell layers; a cortex of small, pigmented outer cortical cells and, inwardly, a medulla of large colorless pseudoparenchymatous cells. Hairs occur over the thallus surface. Growth is both apical and intercalary. Plurilocular sporangia, scattered over thallus surfaces, are formed from surface cells in sori with groups of hairs. Two of the 8 known species of *Rosenvingea* occur in Puerto Rico.

KEY TO THE ROSENVINGEA SPECIES OF PUERTO RICO

1. Thalli entangled and subrepent; branching mostly distal; branch apices tapered *R. endiviifolia*
- Thalli erect, branching evenly distributed; branch apices not tapered *R. sanctae-crucis*

***Rosenvingea endiviifolia* (Martius) M. J. Wynne**

FIGURE 58

Rosenvingea endiviifolia (Martius) M. J. Wynne in Wynne and Nunes 2021: 2.

Basionym: *Ulva endiviifolia* Martius 1833: 21.

Heterotypic Synonym: *Rosenvingea intricata* (J. Agardh) Børgesen 1914a: 26.

Puerto Rican Records: As *Rosenvingea intricata*: Almodóvar 1964c; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Cuba, Jamaica, Netherlands Antilles, Panama, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: São Salvador da Bahia de Todos os Santos, Bahia, Brazil.

Thalli are low-growing clumps, sometimes densely matted and tangled, 30–40 cm in extent. Algae are usually abundantly, subdichotomously to irregularly branched; branches may anastomose. Branches are more or less cylindrical to compressed,

hollow and contorted, (1.0–)3–10 mm diam. Branches display a marked decrease in diameter distally; apices mostly rounded. The algal wall consists of (1–)3–4 cell layers, 70–150 µm thick. Cortical cells measure 9.0–19 µm diam; medullary layer cells are 28–37 µm broad and 56–131 µm long. Hairs are scattered over the algal surface. Plurilocular sporangia are biserial, occurring in small discrete sori scattered over the thallus surface. Algae are green to olive brown in color.

Habitat and comments: *Rosenvingea endiviifolia* grows on rocks in exposed, shallow-water habitats and has been dredged to 35 m depths. Reproductive plants have not been observed in Puerto Rican collections. Wynne and Nunes (2021) pointed out that *Ulva endiviifolia* Martius 1833 was a taxonomic synonym of *Rosenvingea intricata*, thus the Martius epithet possesses taxonomic priority. [Additional illustrations: Taylor 1928: pl. 15: figs. 15–17.]

***Rosenvingea sanctae-crucis* Børgesen**

Rosenvingea sanctae-crucis Børgesen 1914a: 22, figs. 14–17.

Puerto Rican Records: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Barbados, Belize, Cuba, Dominica, Jamaica, Puerto Rico, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: St. Croix, U.S. Virgin Islands.

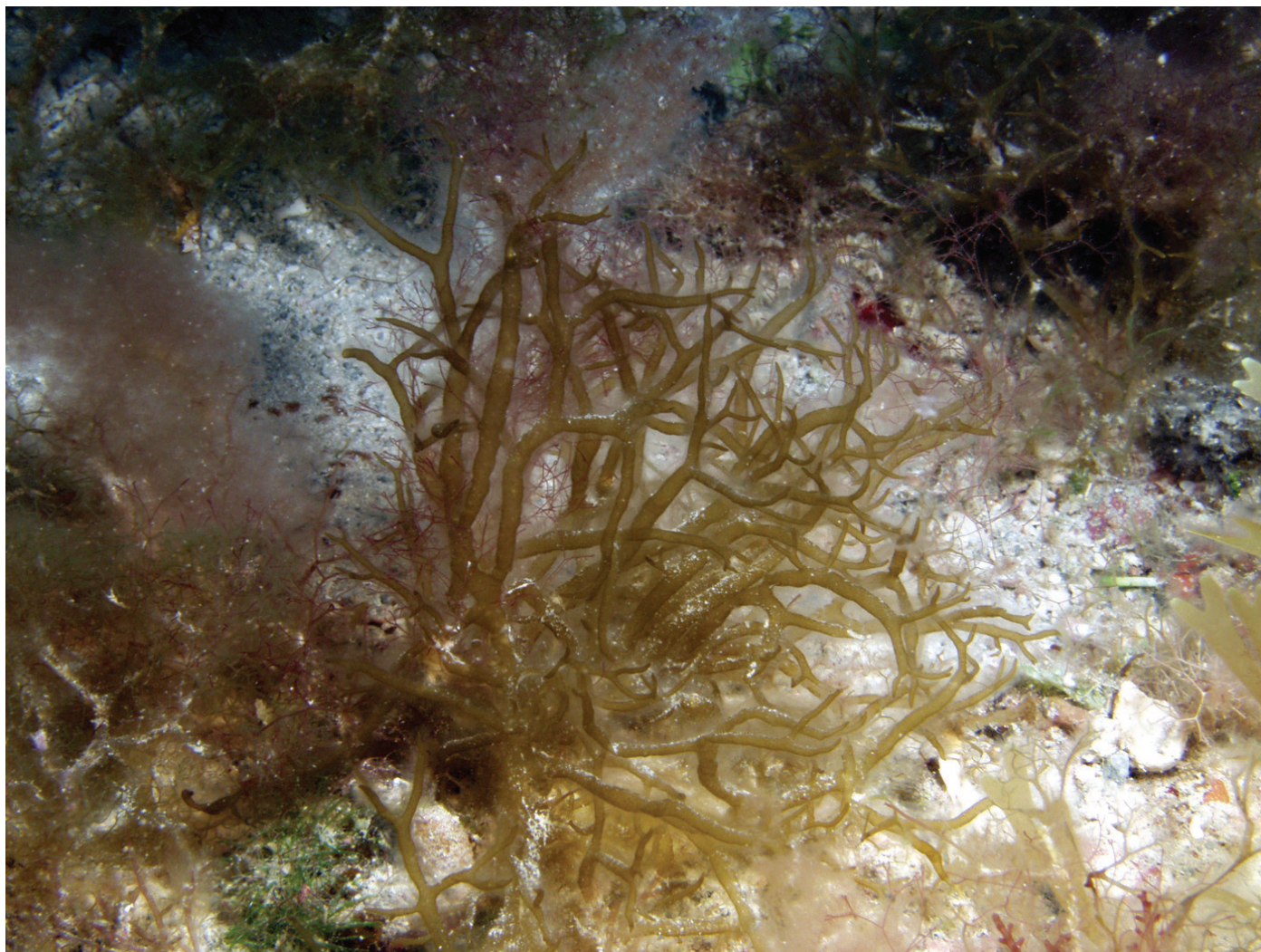


FIGURE 58. *Rosenvingea endiviifolia*. In situ photograph, 1.5 km seaward Media Luna Reef, 17 m. Field width = approximately 25 cm.

Rosenvingea sanctae-crucis is the generitype species. Thalli, up to 20 cm tall, are briefly stipitate and consist of terete branches that form clumps or mats, often becoming entangled. The sparse branches are terete or somewhat compressed with obtuse apices. Branching is irregularly alternate or subdichotomous. Axes are hollow, to 2.0 mm diam with walls 3 or 4 cell layers thick. Inner medullary cells measure 80–200 μm diam and 100–300 μm long. Cortical cells are 10–20 μm diam. Gametangia are cylindrical to clavate, 5–12 μm diam and 20–40 μm long, in irregular sori. Algae are golden to dark brown in color.

Habitat and comments: *Rosenvingea sanctae-crucis* occurs in sheltered habitats in shallow waters. [Additional illustrations: Littler et al. 2008: 162.]

FUCALES BORY

SARGASSACEAE KÜTZ.

Sargassum C. Agardh

Sargassum C. Agardh 1820: 1.

Sargassum represents “one of the most anatomically complex genera in the Phaeophyta” (Kilar et al. 1992: 96). Thalli comprise terete to compressed axes and branches that bear leaflike blades, vesicles, and reproductive branchlets. Algae either arise from a stipe, attached below by discrete holdfasts or a stoloniferous base, or are pelagic and lack polarity. Ultimate

branchlets are leaflike blades that are simple or divided, broad to filiform, and with or without a midrib or cryptostomata. The leaflike blades possess entire, dentate, or serrate margins. Buoyant vesicles, borne on lateral stalks, are usually present, with or without terminal extensions. Reproductive receptacles, occurring in axils of lateral branches, are terete or compressed, with monoecious or dioecious conceptacles. *Sargassum* is a large genus with approximately 351 currently accepted species. Fifteen species occur in Puerto Rico, although 1 of these, *S. lendigerum*, is considered doubtful and is not included in the key.

Comments: As detailed by Kilar et al. (1992), the genus is notoriously difficult taxonomically because of high phenotypic plasticity, ontogenetic forms, and polymorphism in addition to other complicating factors. For these reasons Kraft (2009) declined to apply subdivisions to *Sargassum* species in his treatment of Lord

Howe Island, Australia, brown algae. A morphological grouping of the Gulf of California species into taxonomic sections was proposed by Norris (2010, based on Dawson 1944), and Mattio and Payri (2010, 2011) utilized molecular approaches to resolve subgeneric relationships among Pacific *Sargassum*. In a study of *Sargassum* collected from the coasts of the western Gulf of Mexico and Caribbean Mexico, Gonzalez-Nieto et al. (2020: 262) considered one large group of 10 species to be a single taxon and referred to the species complex, “*Sargassum* cf. *cymosum*.” Their study included morphological and molecular analyses of only specimens collected and identified from southeast mainland Mexico and one from Brazil. However, their proposal that 10 species represent a single species needs further morphological and molecular analyses, including study of the type and type locality specimens of each of these species to test and verify their taxonomic status.

KEY TO THE SARGASSUM SPECIES OF PUERTO RICO

1. Thalli free-floating, without basal attachment structures and lacking polarity; cryptostomata absent 2
Thalli with holdfast, at least originally basally attached; cryptostomata generally present 4
2. Thalli very small (less than 5.0 mm in length) *S. pusillum*
Thalli substantially larger, reaching to 0.5 m or greater in length 3
3. Vesicles with spine or extension; blades dentate, with slender teeth *S. natans*
Vesicles without a spine; blades with broad teeth *S. fluitans*
4. Blades sometimes forked 5
Blades not forked 6
5. Thalli up to 25 cm tall; axes mostly smooth; blades 3.0–5.0 cm long *S. ramifolium*
Thalli up to 50 cm tall; axes spinose; blades 1–3 cm long *S. furcatum*
6. Blades with prominent raised midrib *S. pteropleuron*
Blades without a prominent raised midrib 7
7. Blades mostly lanceolate linear, 7–50 times longer than broad 8
Blades narrowly oblong or lanceolate to oval 10
8. Axes muriculate; blades serrate or nonserrate *S. acinarium*
Axes smooth; blades entire or serrate 9
9. Blades entire, 2.0–4.0 cm long *S. cymosum*
Blades serrate, 3.0–8.0 cm long *S. filipendula*
10. Cryptostomata large, 0.6–0.9 mm diam *S. platycarpum*
Cryptostomata absent, minute, or smaller 11
11. Cryptostomata minute or lacking; blades large, ovate *S. buxifolium*
Cryptostomata obvious 12
12. Blade base symmetrical, axes smooth *S. vulgare*
Blade base asymmetrical, axes smooth to slightly spiny 13
13. Axes smooth *S. hystrix*
Axes muriculate *S. polyceratium*

***Sargassum acinarium* (L.) Setch.**

FIGURE 59

Sargassum acinarium (L.) Setch. 1933: 208.

Basionym: *Fucus acinarius* L. 1753: 1160.

Puerto Rican Records: As *Sargassum acinarium*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Cuba, Martinique, Puerto Rico, St. Lucia, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Syntype Localities: “Habitat in Italia & Oceano australiori” (Linnaeus 1753: 1160).

Lectotype Locality: Mediterranean Sea (Setchell 1933).

Thalli reach up to 30 cm in height and are basally attached. Main axes are short and stout, dividing into several muriculate



FIGURE 59. *Sargassum acinarium*. DLB5230: Adrift, Lee Stocking Island, Exuma Chain, Bahamas. Scale bar = 2.0 cm.

axes. Leaflike branches are thin and lanceolate to linear with acute apices. They measure 3.0–7.0 mm long and 1.5–3.0 mm wide, possessing evident midribs and serrate margins. The leaflike branches are borne on short stalks, to 1.0 mm long. Cryptostomata are moderately sized, 100–150 μm diam, and occur in irregular rows on either side of the midrib. Vesicles are

spherical, borne on flattened stalks, 1.0–1.5 times the vesicle diameter.

Habitat and comments: *Sargassum acinarium* occurs in shallow-water habitats in Puerto Rico. Silva (in Silva et al. 1996: 931) reviewed the complex and confusing nomenclature history of this species. [Additional illustration: Littler et al. 2008: 63.]

***Sargassum buxifolium* (Chauv.) M. J. Wynne**

FIGURE 60

Sargassum buxifolium (Chauv.) M. J. Wynne 2011: 58, 110.

Basionym: *Sargassum hystrix* var. *buxifolium* Chauv. in J. Agardh 1848: 322.

Puerto Rican Record: As *Sargassum hystrix* var. *buxifolium*; Almodóvar and Blomquist 1961.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Barbados, Belize, Cuba, Puerto Rico, St. Lucia, Trinidad and Tobago, Brazil, Venezuela.

Type Locality: Unknown.



FIGURE 60. *Sargassum buxifolium*. LRA 3684, herbarium specimen: Cabo Rojo, dredged 25–30 m. Scale bar = 2.0 cm.

Thalli reach to 50 cm tall, with few smooth main axes and numerous short lateral branches bearing large crowded leaflike blades. The blades are oval or obtuse-oblong, up to 6.0 cm in length and 1.5 cm broad. Leaflike blade margins are entire or minutely dentate; midribs are obscure, and blades possess few scattered cryptostomata. Spherical vesicles have scattered spines.

Habitat and comments: *Sargassum buxifolium* differs from *S. hystrix* primarily in possessing larger leaflike blades, to 6.0 cm long, that are mostly entire. Moreira and Cabrera (2007) found in support of their earlier recognition of “*S. buxifolium*” (Moreira and Cabrera 2005) that this taxon differed significantly from *S. hystrix* var. *hystrix* and placed each in different sections of the genus. Wynne (2011) noted their species transfer was invalid and made the correct combination. González-Nieto et al. (2020) referred their Mexican specimens identified as *S. buxifolium* to a large species complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustration: Taylor 1960: pl. 38: fig. 2.]

***Sargassum cymosum* C. Agardh**

FIGURE 61

Sargassum cymosum C. Agardh 1820: 20.

Synonym: *Sargassum rigidulum* Kütz. 1849: 615.

Puerto Rican Records: As *Sargassum cymosum*: Ballantine and Aponte 2002. As *Sargassum rigidulum*: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Barbados, Dominica, Hispaniola, Puerto Rico, Trinidad and Tobago, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Brazil.

Basally attached thalli reach 10–30(–100) cm tall with few to several slender main axes. The axes are smooth and measure 1.7–2.6 mm diam. The upper leaflike blades are elliptical, oblong-lanceolate, or linear, measuring 2.0–4.0 cm long and 2.0–3.5 mm wide. The leaflike blades possess entire margins and evident midribs. Cryptostomata are small, 33–100 µm diam, and scattered. Elliptical or spherical vesicles are few, measuring 1.7–5.7 mm long and 1.5–4.5 mm diam. They are borne on often mucronate stalks that are about equal in length to the vesicle diameter. Algae are dark brown in color.

Habitat and comments: *Sargassum cymosum* occurs in shallow-water habitats, including the rocky subtidal. Both Schnetter (1976) and Camacho et al. (2015) reported the species to be highly polymorphic. González-Nieto et al. (2020), on the basis of Mexican specimens, referred a number of Caribbean *Sargassum* species to *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustrations: Taylor 1960: pl. 38: fig. 4; Littler et al. 2008: 65; Camacho et al. 2015: figs. 9–11.]



FIGURE 61. *Sargassum cymosum*. MDP1481, herbarium specimen: Playa Bajura (NW, Puerto Rico), intertidal. Scale bar = 2.0 cm.

***Sargassum filipendula* C. Agardh**

FIGURE 62

Sargassum filipendula C. Agardh 1824: 300.
Heterotypic Synonym: *Sargassum affine* J. Agardh.

Puerto Rican Records: As *Sargassum affine*: Hauck 1888. As *Sargassum filipendula*: Taylor 1960; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Belize, Hispaniola, Jamaica, Martinique, Puerto Rico, St. Eustatius, St. Kitts, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: West Indies.

Thalli are 30–100(–200) cm tall and basally attached by a discoid holdfast. Primary axes are smooth, 1.0–1.5(–3.0) mm diam and sparingly branched. The leaflike blades are stalked,



FIGURE 62. *Sargassum filipendula*. DLB4032, herbarium specimen: Pta. Caracoles, Arecibo. Scale bar = 2.0 cm.

thin, and linear-lanceolate, measuring 3.0–10 cm long and 3.0–8.0 mm broad. They are mostly simple; however, occasionally, on lower thallus portions, they may be forked. The blades, possessing either a symmetrical or asymmetrical base, possess a clearly defined midrib and have serrate margins and numerous scattered cryptostomata, 50–100 μm diam. The vesicles, borne on stalks up to 5.0 mm long, are spherical, 3.0–5.0 mm diam. The vesicles possess cryptostomata and sometimes bear a small terminal spine. Algae are brown in color.

Habitat and comments: Although not particularly common in Puerto Rico, *Sargassum filipendula* occurs from shallow to deep waters and has been collected to 55 m depths (Schneider and Searles 1991; Ballantine et al. 2016). González-Nieto et al. (2020) referred their Mexican specimens identified as *S. filipendula* to a large species complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustrations: Littler et al. 2008: 166; Braune and Guiry 2011: fig. 101.6; Camacho et al. 2015: figs. 9–11.]

***Sargassum fluitans* (Børgesen) Børgesen**

FIGURE 63

Sargassum fluitans (Børgesen) Børgesen 1914a: 66.

Basionym: *Sargassum hystrix* var. *fluitans* Børgesen 1914b: 11, fig. 8.

Puerto Rican Records: As *Sargassum fluitans*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Costa Rica, Cuba, Dominica, Florida, Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, U.S. Virgin Islands, Colombia.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Sargasso Sea, oceanic region (70°W to 40°W by 20°N to 35°N) of the North Atlantic.

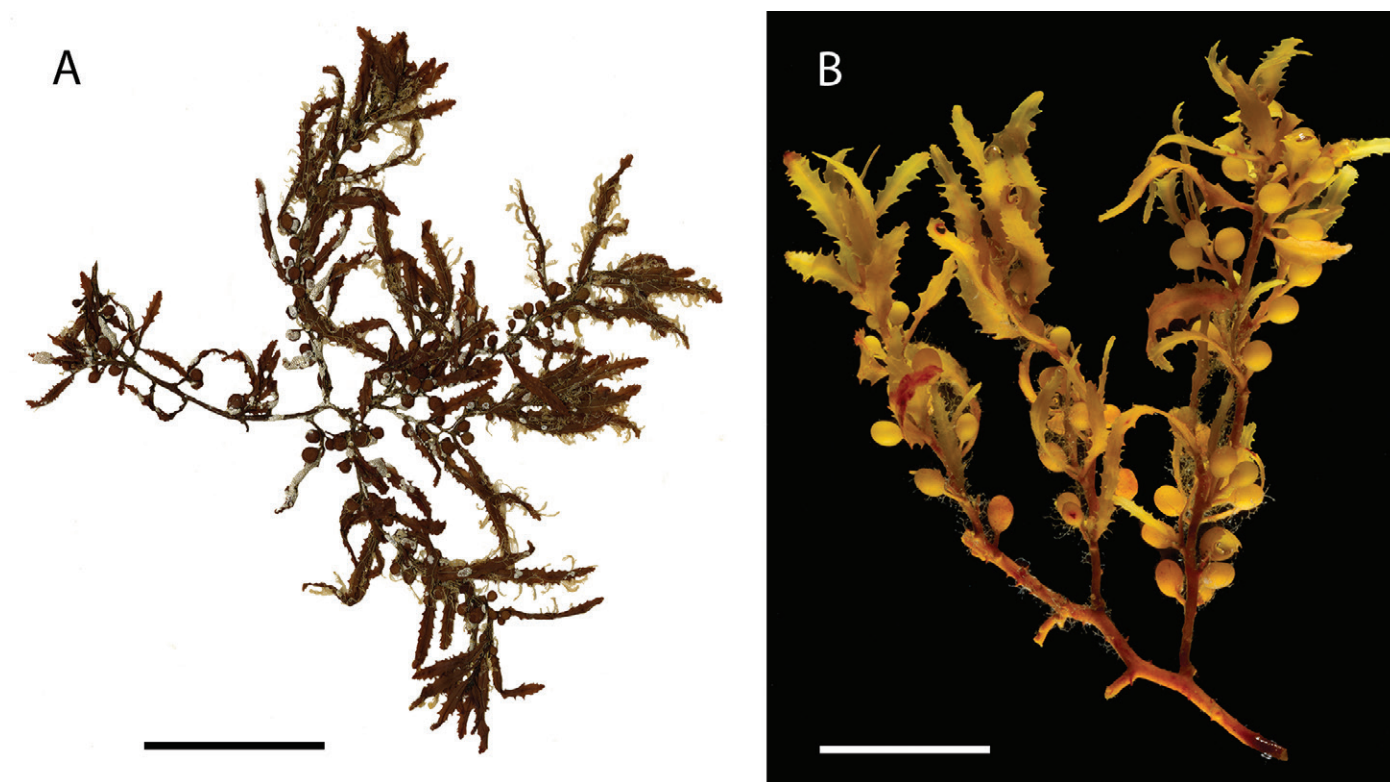


FIGURE 63. *Sargassum fluitans*. (A) MDP2934, herbarium specimen: Punta Yabucoa, in drift among mangrove roots. Scale bar = 2.0 cm. (B) Close-up of apices. Scale bar = 1.0 cm.

A pelagic species (free-floating and lacking a holdfast), the species typically lacks a dominant axis. Thalli form mats to 1.0 m or substantially more in extent. Axes and branches are smooth or sparingly spinulose. Leaflike blades are numerous; they are short stalked and narrow to lanceolate with asymmetric bases. Blades are 2.0–6.0 cm long and 3.0–8.0 mm broad, with serrate margins and acute apices. Cryptostomata are absent. Vesicles are oval to subspherical, (3.0–)4.0–5.0(–6.0) mm diam; borne on occasionally winged stalks, 2.0–3.0 mm long. Algae are golden brown in color.

Habitat and comments: *Sargassum fluitans* is known exclusively as a pelagic species, always found adrift and free-floating. Along with *S. natans*, *S. fluitans* is 1 of the 2 predominant pelagic *Sargassum* species in Puerto Rico. González-Nieto et al. (2020) referred their Mexican specimens identified as *S. fluitans* to a large species complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustrations: Littler and Littler 2008: 167; Braune and Guiry 2011: fig. 101.7; Camacho et al. 2015: figs. 16–17.]

***Sargassum furcatum* Kütz.**

FIGURE 64

Sargassum furcatum Kütz. 1843: 362.

Misapplied Name: *Sargassum bermudense* Grunov 1916: 147.

Puerto Rican Records: As *Sargassum furcatum*: Ballantine 1977; Ballantine and Aponte 1997, 2002. As *Sargassum bermudense*: Almodóvar and Ballantine 1983.

Western Atlantic Distribution: Mexico, North America, Bermuda, Cuba, Dominica, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: St. Thomas, U.S. Virgin Islands.

Thalli reach up to 50 cm tall, possess muriculate axes, and are basally attached. The leaflike blades measure 1.5–5.0 cm long and 1.0–5.0 mm wide and are frequently forked, with cryptostomata scattered or in irregular rows on either side of the midrib. The blades are borne on short stalks, and the margins are irregularly toothed. Blade bases are symmetrical, and apices are acute. Vesicles are 3.0–6.0 mm diam, borne on stalks, to 9.0 mm long. Algae are olive brown to dark brown in color.

Habitat and comments: *Sargassum furcatum* is usually collected in shallow waters, down to 5.0 m depths; however, the species occurs to 17 m depths in Puerto Rico. González-Nieto et al. (2020) referred their Mexican specimens identified as *S. fluitans* to a large species complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustration: Suárez et al. 2015: fig. 120.]



FIGURE 64. *Sargassum furcatum*. RJZsn, herbarium specimen: Monito Island. Scale bar = 1.0 cm.

***Sargassum hystrix* J. Agardh**

FIGURE 65

Sargassum hystrix J. Agardh 1847: 7.

Puerto Rican Records: Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Belize, Costa Rica, Cuba, Dominica, Jamaica, Puerto Rico, St. Kitts, St. Lucia, U.S. Virgin Islands.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Campeche Bank, Gulf of Mexico, Mexico.

Thalli reach up to 40 cm tall, are often bushy and basally attached by a discoid holdfast. The main axes are smooth, to 2.0 mm diam, and branching is radial or irregular. Leaflike blades

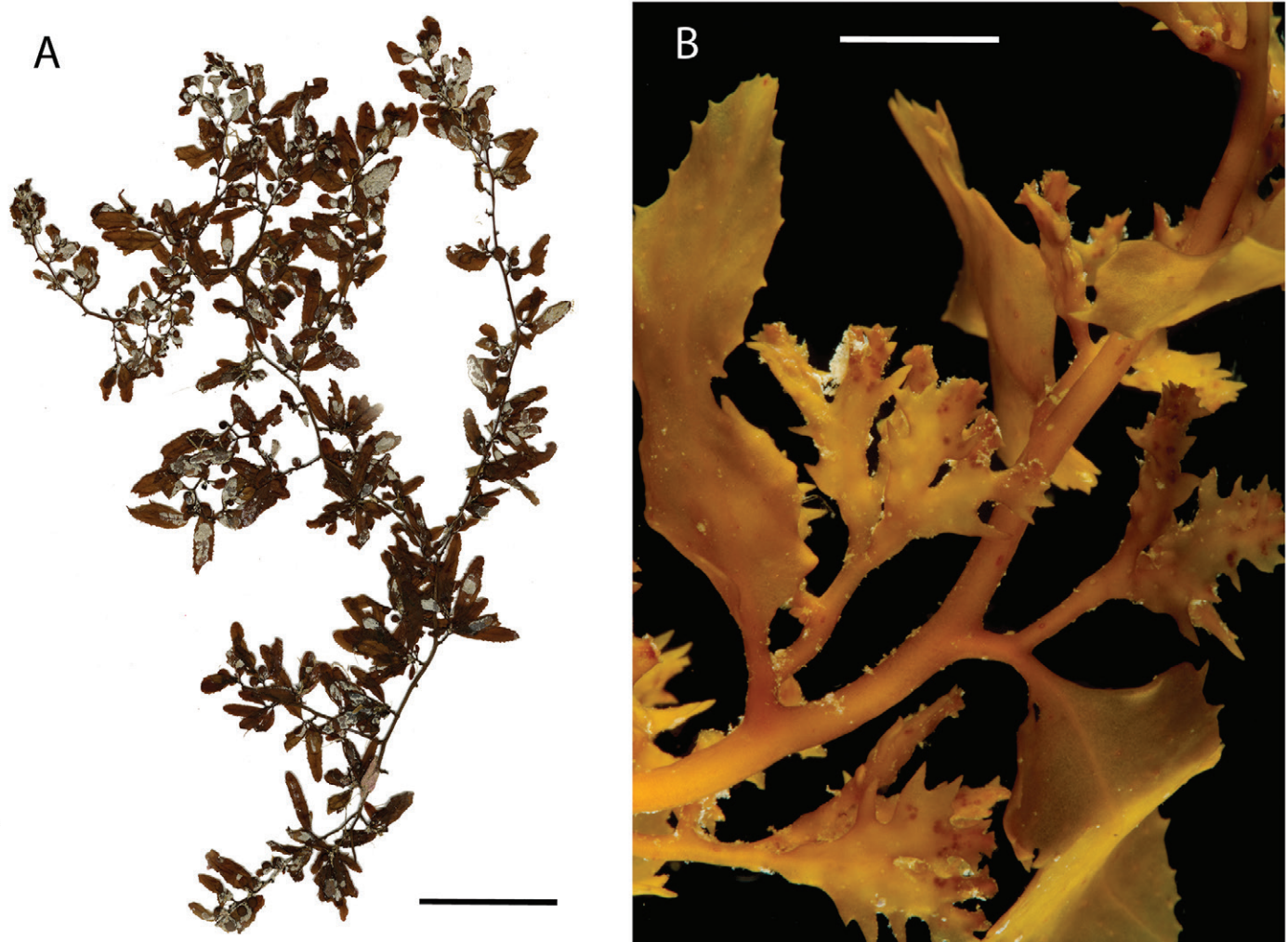


FIGURE 65. *Sargassum hystrix*. (A) DLBsn, herbarium specimen: Drifting, Guayacan Island, La Parguera. Scale bar 5.0 cm. (B) Detail near apex showing receptacles. Scale bar = 1.0 cm.

are oblong-elliptical, 1.0–4.0 cm long and up to 1.0 cm broad, with serrate margins and small, scattered cryptostomata, up to 160 μm diam. Blade bases are strongly asymmetrical, and mid-ribs are costate. Blade margins are serrate, and apices are acute. Vesicles are spherical, mucronate, 3.0–4.0 mm diam on short, terete, sometimes compressed stalks. Reproductive branchlets are densely crowded, with branching becoming palmate with slightly compressed lobes and conceptacle pores.

Habitat and comments: *Sargassum hystrix* occurs mostly in deeper waters and was collected growing attached at 70 m in Puerto Rico (Ballantine et al. 2016). Previously, it was reported dredged in 57 m (Taylor 1960) and to 137 m depths (Littler and Littler 2000). González-Nieto et al. (2020) referred their Mexican specimens identified as *S. hystrix* to a large complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional

illustrations: Taylor 1960: pl. 37: fig. 1, pl. 38: fig. 2, pl. 40: fig. 6; Camacho et al. 2015: figs. 18, 19.]

***Sargassum lendigerum* (L.) C. Agardh**

FIGURE 66

Sargassum lendigerum (L.) C. Agardh 1820: 9.

Basionym: *Fucus lendigerus* L. 1753: 1160.

Puerto Rican Records: As *Sargassum lendigerum*: Almodóvar and Blomquist 1961; Almodóvar 1964b, 1964c.

Western Atlantic Records: Cuba, Puerto Rico, Brazil.

World Distribution: See Guiry and Guiry 2021.



FIGURE 66. *Sargassum lendigerum*. HLBsn, herbarium specimen: Palmas Altas, Barceloneta. Scale bar = 2.0 cm.

Type Locality: “Ad insulam Adensionis” (Linnaeus 1753: 1160); Ascension Island, South Atlantic. *Lectotype:* Spencer et al. (2009: 249).

Thalli possess serrate, linear-elliptic leaflike blades that measure 3.0 cm long and 4.0–5.0 mm wide. These are either sessile or borne on short stalks. Leaflike blades possess scattered cryptostomata, sometimes arranged in series along both sides of the midrib. Vesicles are infrequent or are not present.

Habitat and comments: *Sargassum lendigerum*, although currently recognized as taxonomically valid (Guiry and Guiry 2021), is very poorly known, and its published characters (e.g., Børgesen 1914b) are insufficient to allow discrimination from some other species of *Sargassum*. Without comment on its taxonomic status, Taylor (1960) treated varieties of *S. lendigerum* from Bermuda and Brazil to be uncertain records. Puerto Rican specimens of *S. lendigerum* (in MSM and U.S. Algal Collection) are from rocks near the low-water mark, as well as on

wave-exposed rocks, and reach 15 cm tall. These specimens appear to represent several entities; thus, its presence in Puerto Rico is considered doubtful, and specimens require further verification. Børgesen (1914b: 4) remarked that the “species appears to be closely related to *S. vulgare*,” and *S. lendigerum* may represent a variety of that species. Price et al. (1978) later treated eastern Atlantic specimens referred to *S. lendigerum* as *S. vulgare*.

***Sargassum natans* (L.) Gaillon**

FIGURE 67

Sargassum natans (L.) Gaillon 1828: 355.

Basionym: *Fucus natans* L. 1753: 1160.

Puerto Rican Records: As *Sargassum natans*: Díaz-Piferrer 1963; Almodóvar 1964b; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba,

Hispaniola, Jamaica, Nevis, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, Turks and Caicos, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2021.

Lectotype Locality: “Indica” (Linnaeus 1753); “probably Jamaica” (Silva et al. 1996: 687).

Thalli are pelagic and free-floating and lack a holdfast. Algae are up to 50 cm in extent, without a dominant axis and frequently with entangled branches. Axes and branches are smooth. Leaflike blades are linear, acute, 2.5–7.0(–10) cm long and 2.0–3.5 mm wide. Midribs are not prominent on serrate leaflike blades, and cryptostomata are absent. Vesicles, 3.0–5.0 mm diam, are borne on stalks equal in length to the vesicle diameter. The vesicles are tipped with a reduced leaflike extension or elongate spine.

Habitat and comments: A pelagic species, *Sargassum natans* is collected only unattached and floating or cast ashore. As noted under the discussion of pelagic communities, *S. natans* is also a component of large *Sargassum* blooms in the Caribbean that have been observed in recent years. González-Nieto et al. (2020) referred their Mexican specimens identified as *S. natans* to a large complex, *S. cf. cymosum* (see also Comments

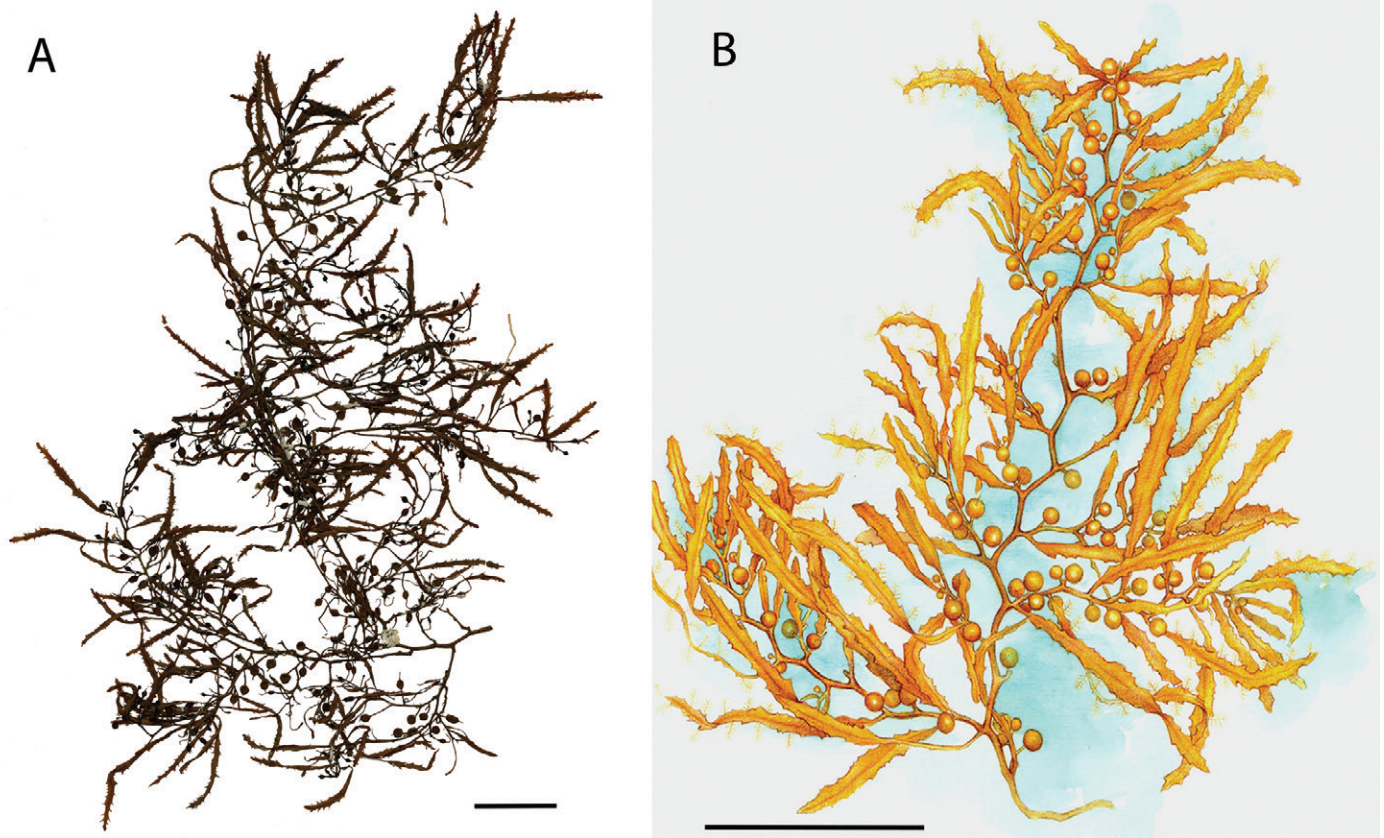


FIGURE 67. *Sargassum natans*. (A) MDP2035, herbarium specimen: Humacao. Scale bar = 2.0 cm. (B) Water color rendition of live specimen. Scale bar = 2.0 cm.

herein under *Sargassum*). [Additional illustrations: Camacho et al. 2015: figs. 20, 21.]

***Sargassum platycarpum* Mont.**

FIGURE 68

Sargassum platycarpum Mont. 1842: 248.

Puerto Rican Records: Hauck 1888; Taylor 1960; Almodóvar 1964c; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Bermuda, Bahamas, Antigua, Barbados, Cayman Islands, Cuba, Dominica, Grenadines,

Hispaniola, Jamaica, Martinique, Nevis, Panama, Puerto Rico, St. Eustatius, St. Kitts, St. Lucia, Trinidad and Tobago, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Martinique.

Thalli reach up to 40 cm tall and are basally attached. Main axes are short, stout, and sparingly branched; axes and branches are smooth. Leaflike blades are 2.0–3.0(–7.5) cm long and 2.0–6.0(–9.0) mm broad. Blades are lanceolate with midribs and possess acute apices; the margins are acutely serrate. Cryptostomata are very large, 0.6–0.9 mm diam, situated in single rows on either side of the midrib. Vesicles are on short, usually muriculate, compressed stalks.



FIGURE 68. *Sargassum platycarpum*. DLBsn: 1.5 km seaward Media Luna Reef. Scale bar = 5.0 cm.

Habitat and comments: *Sargassum platycarpum* is common in shallow water, near shore habitats. [Additional illustrations: Vickers 1908: pl. 1; Braune and Guiry 2011: fig. 101.13.]

***Sargassum polyceratium* Mont.**

FIGURE 69

Sargassum polyceratium Mont. 1837: 356.

Puerto Rican Records: Almodóvar and Blomquist 1959; Taylor 1960; Almodóvar 1964b, 1964c; Ballantine 1977;

Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002; Camacho et al. 2015.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Antigua, Barbados, Belize, Cayman Islands, Cuba, Guadeloupe, Hispaniola, Martinique, Netherlands Antilles, Panama, Puerto Rico, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Havana, Cuba.

Thalli reach up to 90 cm tall and are basally attached by irregularly shaped holdfasts. The main axes, 1.7–5.0 mm diam,



FIGURE 69. *Sargassum polyceratium*. DLB4707: 1.5 km seaward Media Luna Reef. Scale bar =5.0 cm.

often possess numerous lateral branches and short, spur-like branchlets. The branches are usually muriculate, less often smooth or smooth only in older portions. The leaflike blades are sessile and asymmetrical proximally. They are lanceolate or, more typically, broadly ovate, 1.5–3.5 cm long and 5.0–10 mm broad. Leaflike branch apices are obtuse to acute, and margins are deeply dentate-serrate. Cryptostomata are small and scattered. Spherical vesicles are numerous, 3.0–6.0 mm diam, usually sessile, less commonly on 2.0–6.0 mm long pedicels.

Habitat and comments: *Sargassum polyceratum* grows on hard substratum in shallow to moderate depths, to about 15 m. González-Nieto et al. (2020) referred their Mexican specimens identified as *S. polyceratum* to a large species complex, *S. cf. cymosum* (see also Comments herein under *Sargassum*). [Additional illustrations: Braune and Guiry 2011: fig. 101.14; Camacho et al. 2015: figs. 22–24.]

***Sargassum pteropleuron* Grunov**

FIGURE 70

Sargassum pteropleuron Grunov 1868: 55, pl. 5: fig. 1.

Puerto Rican Records: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Cuba, Dominica, Martinique, Puerto Rico, St. Eustatius, Turks and Caicos, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Nassau, New Providence Island, Bahamas.

Thalli reach 0.6–0.9(–4.0) m tall and are basally attached by discoid holdfasts. The axes are abundantly muriculate, up to 8.0 mm diam proximally, narrowing to 2.0 mm distally. The



FIGURE 70. *Sargassum pteropleuron*. MDP7782: Punta Arenas, Mayagüez. Scale bar = 5.0 cm.

leaflike blades have a symmetrical base and are generally narrowly lanceolate, sometimes broadly lanceolate, 2.5–9.5 cm long and 2.5–4.0(–7.5) mm broad. The blades are strongly and mostly irregularly serrate-dentate, with a distinct midrib that varies from a raised rib to a serrate wing. Cryptostomata are small, 75–150 μm diam, few and scattered, sometimes along the midrib. Spherical vesicles, 3.0–8.0 mm diam, are numerous and subsessile or on short, 2.0–3.0 mm long stalks.

Habitat and comments: *Sargassum pteropleuron* grows below the low tide level in shallow waters and extends down to about 20 m depths. [Additional illustrations: Camacho et al. 2015: figs. 6–8.]

***Sargassum pusillum* W. R. Taylor**

Sargassum pusillum W. R. Taylor 1975: 73, figs. 1, 2.

Puerto Rican Records: Taylor 1975; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Bermuda, Antigua, Cuba, Puerto Rico.

Type Locality: Floating “off the Atlantic side of the Antilles between Antigua and Puerto Rico” (Taylor 1975: 74) [note that the linear distance between these islands is about 525 km].

Thalli are pelagic and free-floating, lack a holdfast, and lack a leading axis. Algae are densely bushy, 3.0–4.0 cm in extent. Axes and branches are muriculate, frequently with forked spines, 0.2–2.0 mm long. The abundant vesicles are spherical, nonsessile, 1.5–3.0 mm diam, occasionally with an acute tip. Leaflike blades are not abundant; they are asymmetrical proximally, compressed linear to lanceolate, with obtuse to attenuate tips and irregularly dentate margins. Midribs are obscure except near the short leaf stalk. Cryptostomata are generally absent, but if present, they are inconspicuous, measuring 100–130 μm diam.

Habitat and comments: The precise Puerto Rican location of *Sargassum pusillum* is not certain, as the type collection was designated as floating between the islands of Antigua and Puerto Rico. Since the date of its publication (Taylor 1975), *S. pusillum* (Taylor 1975) has not been collected in Puerto Rico. [Additional illustrations: Suarez et al. 2015: fig. 130a–d.]

***Sargassum ramifolium* Kütz.**

FIGURE 71

Sargassum ramifolium Kütz. 1843: 362.

Puerto Rican Records: Ballantine 1977; Almodóvar et al. 1979; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: North America, Cuba, Hispaniola, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Brazil.

Thalli reach to 30 cm tall and are basally attached. Several leading axes arise from the short primary axes; they are completely smooth and sparingly laterally branched. Leaflike blades are simple, sparingly pinnate or forked, measuring 3.0–5.0 cm long and 1.0–2.0(–3.0) mm wide. Blade margins are entire, with an occasional minute tooth. The blade midribs are distinct. Cryptostomata are small, 80–100 μm diam, located in a single series along blade margins. Vesicles, 3.0–8.0 mm diam, are usually few, sometimes absent; they are borne on terete stalks, 2.5–3.5 mm long.

Habitat and comments: Although *Sargassum ramifolium* is generally considered a shallow-water species (e.g., Littler and Littler 2000), in Puerto Rico it is known from offshore algal plains (in 17 m depth) and in deeper waters, down to 36 m depths (Ballantine et al. 2016).

***Sargassum vulgare* C. Agardh, nom. illeg.**

FIGURE 72

Sargassum vulgare C. Agardh 1820: 3, nom. illeg. [see Silva et al. 1996: 707].

Puerto Rican Records: Hauck 1888; Taylor 1960; Ballantine 1977; Almodóvar and Ballantine 1983; Ballantine et al. 1987; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Belize, Costa Rica, Mexico, North America, Bermuda, Bahamas, Anguilla, Antigua, Barbados, Bequia, Cuba, Dominica, Grenadines, Guadeloupe, Jamaica, Martinique, Netherlands Antilles, Nevis, Puerto Rico, St. Barthélemy, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Syntype Localities: “Ad litora Oceani Atlantici; ex India Occidentali” (Agardh 1820: 5).

Thalli reach to 40 cm tall and are basally attached. Axes and branches are smooth or sometimes muriculate in younger portions; spines, when present, are 0.3–0.7 mm long. Leaflike blades are narrowly lanceolate above a generally asymmetrical base, 1.5–3.0 cm long and 2.0–4.0 mm broad. The margins are sharply serrate or subentire below. A midrib is evident, and cryptostomata are small and scattered. Spherical vesicles, 2.5–8.0 mm diam, are numerous and borne on 0.5–2.0 mm long pedicels.

Habitat and comments: The species “*Sargassum vulgare*” occurs in shallow waters from the intertidal to 6.0 m depths. Silva et al. (1996) discussed the complex nomenclature history of this species and noted it was an illegitimate name. Athanasiadis (2021) has referred *S. vulgare* to *S. atlanticum* Bory; however, this apparently applies only to eastern Atlantic entities. For now, the species from the western Atlantic is still referred to “*Sargassum vulgare*” and lacks a valid name. [Additional illustration: Børgesen (1914b): fig. 1.]

FIGURE 71. *Sargassum ramifolium*. Watercolor rendition of live specimen. Scale bar = 2.0 cm.



FIGURE 72. *Sargassum vulgare*. MDP2259, herbarium specimen; Manati, 2.0–3.0 m depth. Scale bar = 2.0 cm.

Excluded taxa

Sargassum polyphyllum J. Agardh 1848: 308.

The Hauck (1888) record from Yabucoa is apparently the only report of the species from the western Atlantic, outside the Pacific Ocean. The species type locality is Hawaii.

Sargassum pteropus Kütz. 1849: 608.

Reported from Manatí by Hauck (1888). The origin of the specific epithet is unknown; the species is not included in Guiry and Guiry (2021).

***Turbinaria* J. V. Lamour.**

Turbinaria J. V. Lamour. 1825: 71.

Thalli are erect, with crowded subsimple or freely branched axes above a sometimes-extensive rhizomatous base. Axes are smooth, except for scars of old branchlets and branches. Axes bear numerous peltate, obconic or obpyramidal, turbinate branches that bear numerous cryptostomata. The branches possess dentate tips and longitudinally serrate ridges. Of the 23 currently accepted species of *Turbinaria*, 2 occur from Puerto Rico.

KEY TO SPECIES OF *TURBINARIA*

- | | |
|--|-----------------------|
| 1. Turbinate branches with a vesicle | <i>T. turbinata</i> |
| Turbinate branches lacking a vesicle | <i>T. tricostrata</i> |

***Turbinaria tricostrata* E. S. Barton**

FIGURE 73

Turbinaria tricostrata E. S. Barton 1891: 218, pl. 54: figs. 3, 4.

Puerto Rican Records: Taylor 1960; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Belize, Cayman Islands, Guadeloupe, Jamaica, Netherlands Antilles, Puerto Rico, St. Eustatius, Turks and Caicos, U.S. Virgin Islands, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Guadeloupe, French West Indies.

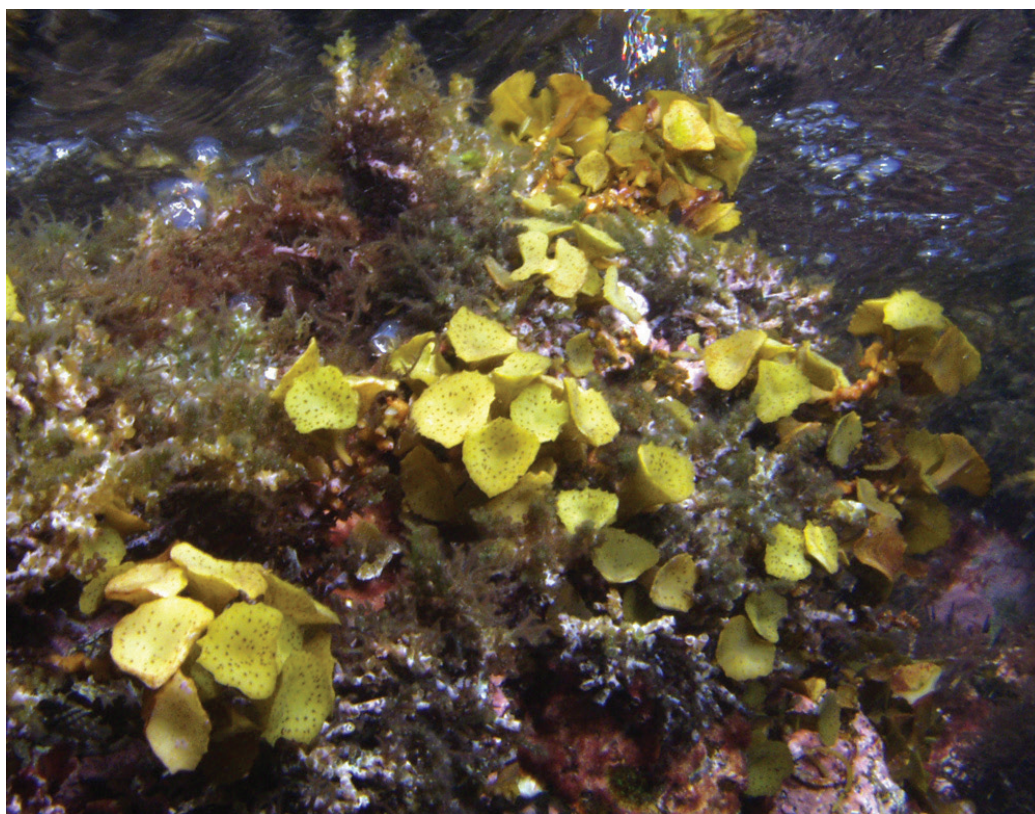


FIGURE 73. *Turbinaria tricostrata*. In situ photograph, on rock outcropping, Cabo Rojo. Field width = approximately 10 cm.

Thalli are erect, reaching up to 15 cm tall. The axes are sparingly branched, with short branches. Turbinate branches are obpyramidal, rounded-triangular on the truncate distal ends without vesicles. The 3-angled petiolar sides of the turbinate branches are about twice as long as the distal diameter, usually with serrate ridges.

Habitat and comments: *Turbinaria tricostrata* grows on intertidal rocks and tidal platforms into the very shallow subtidal slightly below the low-tide line. The species can develop considerable-sized colonies on wave-exposed rocks.

***Turbinaria turbinata* (L.) Kuntze**

FIGURE 74

Turbinaria turbinata (L.) Kuntze 1898: 434.

Basionym: *Fucus turbinatus* L. 1753: 1160.

Heterotypic Synonym: *Turbinaria trialata* (J. Agardh) Kütz. 1860: 24, pl. 67.

Puerto Rican Records: As *Turbinaria trialata*: Hauck 1888.

As *Turbinaria turbinata*: Taylor 1960; Almodóvar and Blomquist 1961; Almodóvar 1964a; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bahamas, Anguilla, Antigua, Belize, Cayman Islands, Cuba, Dominica, Guadeloupe, Hispaniola, Jamaica, Martinique, Netherlands Antilles, Nevis, Panama, Puerto Rico, St. Barthélemy, St. Kitts, Turks and Caicos, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: “In Americae rupibus marinis” (Linnaeus 1753: 1160); Jamaica (Howe 1920; Silva et al. 1996).

Turbinaria turbinata is the generitype. Thalli are erect, reaching up to 17(–40) cm tall above a branching holdfast. The axes are leathery, with long branches and short spur-like branches bearing turbinate branches. Turbinate branches are



FIGURE 74. *Turbinaria turbinata*. Water color rendition of live specimen. Scale bar = 2.0 cm.

obpyramidal, up to 1.0 cm (or more) in length and width. The petiolar part possesses 3 nearly smooth margin ridges. The upper center portion generally has an embedded air bladder (vesicle). The flattened top of the turbinate branch is broad and rounded-triangular to nearly circular. The margins are commonly aculeate-dentate or occasionally may be entire. Cryptostomata are numerous and scattered.

Habitat and comments: *Turbinaria turbinata* generally grows on intertidal rocks and coral reefs and in tide pools or shallow waters slightly below the low-tide line. [Additional illustrations: Braune and Guiry 2011: fig. 102.2; Littler and Littler 2008: 170.]

RALFSIALES Y. NAKAM. EX P.-E. LIM ET H. KAWAI

NEORALFSIACEAE P.-E. LIM ET H. KAWAI

***Neoralfsia* P.-E. Lim et H. Kawai**

Neoralfsia P.-E. Lim et H. Kawai in P.-E. Lim et al. 2007: 464.

Thalli consist of an expanded crust, 1.0 to several cm diam, attached to the substratum by many rhizoids and later tending to be free. The algae are pseudoparenchymatous, comprising 2 distinct layers, consisting of a medulla with 1 or 2 layers of radiating filaments and a cortical layer of parallel ascending, tightly adjoined filaments, with hair pits. Unilocular zoidangia/sporangia possess pedicels and paraphyses. Plurilocular zoidangia/gam-etangia are intercalary, with a single terminal cell. *Neoralfsia* is a genus of 2 currently accepted species, with 1 species recognized from Puerto Rico.

***Neoralfsia expansa* (J. Agardh) P.-E. Lim et H. Kawai ex Cormaci et G. Furnari**

Neoralfsia expansa (J. Agardh) P.-E. Lim et H. Kawai ex Cormaci et G. Furnari in Cormaci et al. 2012: 510.

Basionym: *Myrionema? expansum* J. Agardh 1847: 7.

Homotypic Synonyms: *Ralfsia expansa* (J. Agardh) J. Agardh 1848: 63;
Neoralfsia expansa (J. Agardh) P.-E. Lim et H. Kawai in Lim et al. 2007: 464, *comb. inval.*

Puerto Rican Records: As *Ralfsia expansa*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Antigua, Cuba, Hispaniola, Martinique, Netherlands Antilles, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Veracruz (estado), Gulf of Mexico, Mexico.

Neoralfsia expansa is the genotype. Thalli form smooth, rounded crusts that are weakly attached to the substratum by rhizoids ventrally. The crusts become irregular and wrinkled and

conrescent, expanding up to 3.0 cm or more in extent and are 300–350 µm thick. Internally, there is a basal layer of radiating filaments that curve upward to form an upper cortical layer of erect, parallel filaments. Cells of the erect cortical filaments are compact, laterally united, with chloroplasts denser near the dorsal crust surface. Clavate paraphyses of 5–14 cells, up to 12 µm diam and 100–170 µm long, are produced. Upper paraphysal cells are shorter than broad, and lower cells are up to 4–7 times longer than wide (48–84 µm in length). Unilocular zoidangia are pedicellate, oval-pyriform, measuring 30 µm diam and 75–120 µm long. Plurilocular zoidangia are cylindrical, 15–20 cells long and 5.0–6.0 µm diam. Algae are dark brown in color.

Habitat and comments: *Neoralfsia expansa* grows on rocks or stones in shallow water. [Additional illustrations: as *Ralfsia expansa*, Huisman et al. 2007: 212; Kraft 2009: fig. 31A–K.]

SCYTOTHAMNALES A. F. PETERS ET M. N. CLAYTONE

ASTERONEMATACEAE SILBERFELD, RACAULT, R. L. FLETCHER, F. ROUSSEAU ET REVIERIS

***Asteronema* Delépine et Asensi**

Asteronema Delépine et Asensi 1975: 296.

Thalli are filamentous, with a heterotrichous organization. Erect, uniseriate filaments arise from coalescent bases of rhizoidal filaments. Branching is sparse and sometimes unilateral. Longitudinal growth is by apical and intercalary divisions. Cells possess stellate chloroplasts that are parietally located within cells and pyrenoids that are axial in position. Unilocular and plurilocular sporangia are both terminal on 1- to 2-celled laterals. Monosporangia have been reported for 1 species. A single species of the 3 recognized species of *Asteronema* is reported from Puerto Rico.

***Asteronema breviarticulatum* (J. Agardh) Ouriques et Bouzon**

Asteronema breviarticulatum (J. Agardh) Ouriques et Bouzon 2000: 271.

Basionym: *Ectocarpus breviarticulatus* J. Agardh 1847: 7.

Homotypic Synonym: *Hincksia breviarticulata* (J. Agardh) P. C. Silva in Silva et al. 1987: 73.

Puerto Rican Records: As *Asteronema breviarticulatum*: Ballantine and Aponte 2002. As *Ectocarpus breviarticulatus*: Almodóvar and Blomquist 1959; Almodóvar 1964c; Almodóvar and Ballantine 1983. As *Hincksia breviarticulata*: Ballantine and Aponte 1997.

Western Atlantic Distribution: Mexico, North America, Antigua, Barbados, Cayman Islands, Costa Rica, Cuba, Dominica, Jamaica, Martinique, Netherlands Antilles, Puerto Rico, St. Lucia, Trinidad and Tobago, U.S. Virgin Islands, Brazil, Colombia, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: San Agustín, Oaxaca, Pacific coast of Mexico.

Thalli are filamentous, 2.0–4.0 cm tall. Filaments are repent below, and erect axes are spongy, comprising twisted filaments. Branching is irregular, with filaments developing numerous short hooked branchlets. Filament cells, with numerous discoid chromatophores, measure 27–54 μm diam and 27–108 μm long. Sporangia/gametangia are borne on a stalk cell and are ovoid to spherical, 57 μm diam and 62 μm long.

Habitat and comments: *Asteronema breviarticulatum* grows on rocks in exposed habitats. [Additional illustrations: as *Ectocarpus hamatus* P. Crouan et H. Crouan, Vickers 1908: pl. 29; figs. 1–7.]

**BACHELOTIACEAE SILBERFELD, RACAULT, R. L. FLETCHER,
A. F. PETERS, F. ROUSSEAU ET REVIERS**

***Bachelotia* (Bornet) Kuck. ex Hamel**

Bachelotia (Bornet) Kuck. ex Hamel 1939b: 66.

Thalli are mat-like from a filamentous entangled base that gives rise to erect sparingly branched, uniseriate filaments.

Growth is diffuse. Chromophores are rod shaped. Unilocular sporangia are intercalary, seriate. *Bachelotia* as presently circumscribed is monotypic.

***Bachelotia antillarum* (Grunov) Gerloff**

FIGURE 75

Bachelotia antillarum (Grunov) Gerloff 1959: 38.

Basionym: *Ectocarpus antillarum* Grunov 1868: 46, pl. IV: fig. 2.

Homotypic Synonym: *Pylaiella antillarum* (Grunov) De Toni 1895: 535–536.

Misapplied Name: *Bachelotia fulvescens* sensu Taylor 1960.

Puerto Rican Records: As *Bachelotia antillarum*: Ballantine and Aponte 1997, 2002. As *Pylaiella antillarum*: Blomquist 1958. As *Bachelotia fulvescens*: Taylor 1960; Almodóvar and Blomquist 1965.

Western Atlantic Distribution: Mexico, North America, Bermuda, Bahamas, Barbados, Cuba, Guadeloupe, Puerto Rico, Trinidad and Tobago, U.S. Virgin Islands, Argentina, Brazil, Colombia, Guyana, Venezuela.



FIGURE 75. *Bachelotia fulvescens*. MDP1851, herbarium specimen: Tamarindo, Guánica, epiphytic on *Rhizophora*. Scale bar = 2.0 cm.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Guadeloupe (Leeward Islands of the Lesser Antilles), French West Indies, Caribbean Sea.

Thalli consist of erect filaments above a prostrate filamentous base. Prostrate filaments, 20–35 μm diam, are widely spreading and irregularly branched. The erect filaments reach 1.5–3.0 cm tall, with cells 30–47 μm diam and 23–108 μm long. Growth is intercalary. Sporangia occur in long intercalary series or, less frequently, oppositely in pairs, 57–65 μm diam and 26–31 μm long.

Habitat and comments: Algae are frequently intertidal; *Bachelotia antillarum* occurs on rocks, sometimes partially covered with sand. [Additional illustrations: Blomquist 1958: figs. 1–3; Littler et al. 2008: 157.]

SPOROCHNALES SAUV.

SPOROCHNACEAE GREV.

Nereia Zanardini

Nereia Zanardini 1846: 899.

Thalli are erect to repent, consisting of long terete to compressed flexuous axes and branches. Branches bear numerous papillae that may elongate into short spur branchlets that terminate in conspicuous hairlike tufts of brown filaments. Unilocular sporangia are sessile on short papillae proximal to the hair tufts. Four species of *Nereia* are recognized, one of which occurs in Puerto Rico.

Nereia tropica (W. R. Taylor) W. R. Taylor

FIGURE 76

Nereia tropica (W. R. Taylor) W. R. Taylor 1955: 74, pl. 5.

Basionym: *Stilophora tropica* W. R. Taylor 1928: 115, pl. 3: fig. 9, pl. 14: figs. 5, 6, pl. 19: fig. 2.

Puerto Rican Records: As *Nereia tropica*: Almodóvar et al. 1979; Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: North America, Bermuda, Bahamas, Cuba, Puerto Rico.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Dredged 9.2–14.6 m depths; Southwest Channel, Dry Tortugas (Dry Tortugas National Park), Monroe County, Florida, USA.

Thalli are erect, reaching up to 35 cm in height. Axes, 1.0–2.0 mm diam, are usually indistinct and sparsely branched, 2 or 3 times irregularly alternate. Axes and branches bear tufts of hairlike filaments that are either sessile on axes or terminal on spur branchlets and branch tips, 17–26 μm diam and 3.0–6.0 mm long. Older portions may be without hair tufts. Sori of unilocular sporangia are crowded in sori around hair tuft bases; sporangia are subcylindrical to obovoid, 11–19 μm diam and 26–42 μm long. Cortical uniseriate filaments (paraphyses) are narrow, clavate or obpyriform, measuring 17–28 μm diam and 32–51 μm long, with inflated terminal cells.

Habitat and comments: *Nereia tropica* grows at moderate depths to deeper water. The only Puerto Rican collections are from 17 m depth at the Media Luna algal plain. Prud'homme van Reine et al. (1994) regarded use of hairs and paraphyses as characters to discriminate between the species *N. tropica* and *N. filiformis* (J. Agardh) Zanardini as not suitable and considered them conspecific, an opinion later followed by Dawes and Mathieson (2008). However, Yee (2007) argued that differences in branching and axial structure distinguished the 2 species as separate entities (see also Kraft 2009; Wynne 2011, 2017). [Additional illustrations: Taylor 1960: pl. 35: fig. 1; Earle 1968: figs. 68, 88.]

Sporochnus C. Agardh

Sporochnus C. Agardh 1817: xii.

Sporophyte thalli are erect, above a compact, conspicuous fibrous holdfast. Although usually up to 35 cm long, at least 1 species may reach to 1.0 m in length. Thalli possess 1 to several cylindrical and distinct wiry primary axes. These bear few to numerous lateral branches, with radial branching, up to several orders. Axes and branches are slender, bearing numerous determinate branchlets. The branchlets are usually stalked (a few species are without stalks), distally with a swollen sporangial receptacle and terminal brown, hairlike tufts. Indeterminate axes and ultimate branches bear terminal trichothallic filaments. Unilocular sporangia encircle the fertile portions of determinate distal branchlet receptacles or, in some, are separated by short, sterile sections. The unilocular sporangia are borne laterally on unbranched or branched paraphyses with swollen spherical to subspherical terminal cells. Monoecious or dioecious gametangia are borne on microscopic branched filaments; sexual reproduction is oogamous. Fourteen species are currently recognized, making it the largest genus of the Sporochneales. Two of the species occur in Puerto Rico.

KEY TO THE SPECIES OF *SPOROCHNUS*

1. Swollen distal ultimate branchlets cylindrical, up to 10 mm long, terminating in tufts *S. bolleanus*
- Swollen distal ultimate branchlets short, ovoid to short spindle shaped, up to 2 mm long, terminating in tufts
..... *S. pedunculatus*

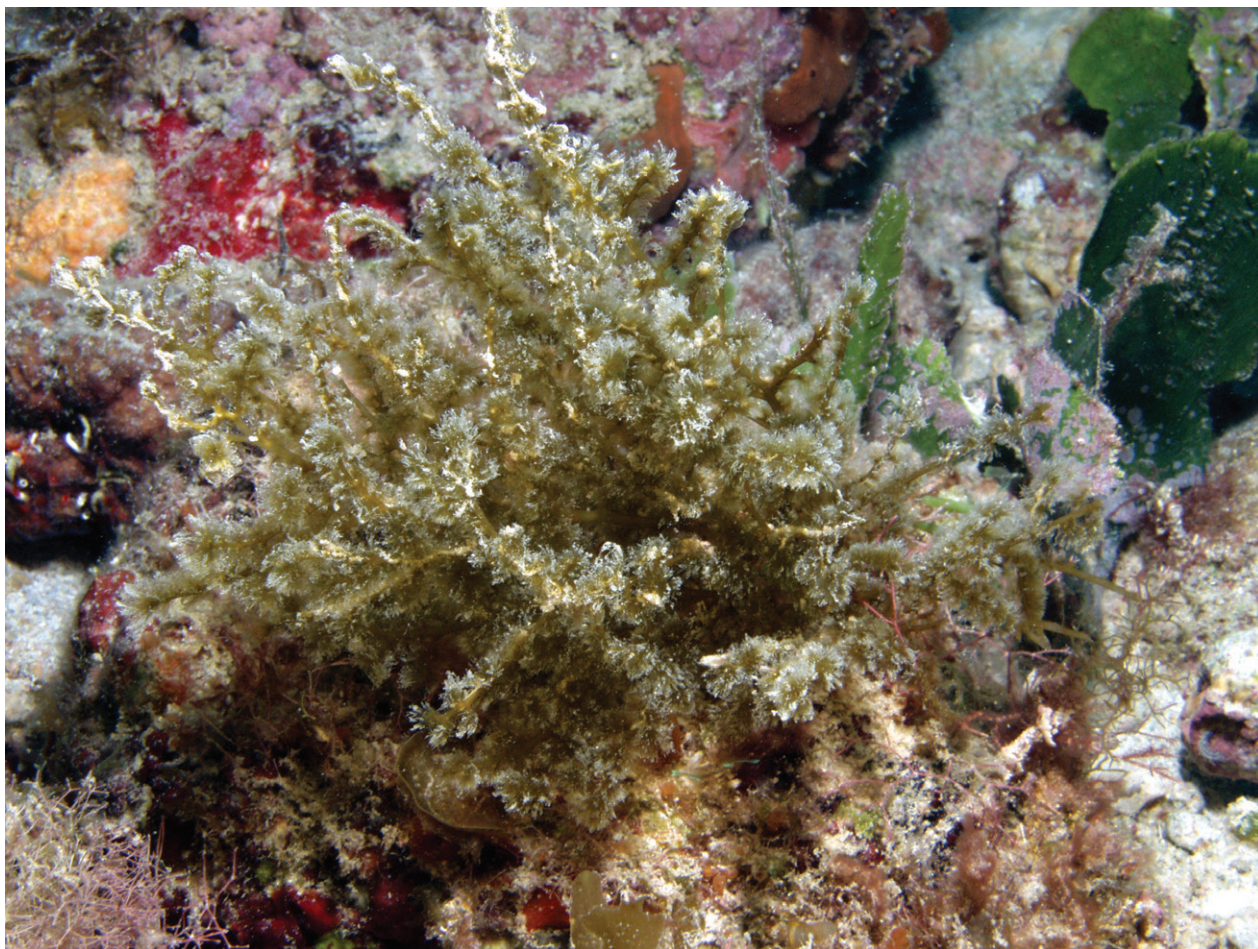


FIGURE 76. *Nereia tropica*. In situ photograph, algal plain, seaward Media Luna reef, 17 m. Field width = approximately 20 cm.

***Sporochnus bolleanus* Mont.**

FIGURE 77

Sporochnus bolleanus Mont. 1856: 393.

Puerto Rican Records: Hauck 1888; Taylor 1960; Ballantine and Aponte 1997, 2002; Ballantine et al. 2016.

Western Atlantic Distribution: North America, Bermuda, Cuba, Puerto Rico, Brazil, Venezuela.

World Distribution: See Guiry and Guiry 2021.

Type Locality: Isleta de Lobos (off NE end of island of Fuerteventura), Canary Islands, Spain (Montagne 1856; Afonso-Carrillo and Sansón 1999).

Thalli reach up to 1.0 m tall above discoid holdfasts. Axes possess numerous alternate to irregular branches. Axes and branches are beset with short, stalked pedicels, 3.0–10 mm long. The ultimate cylindrical branchlets, measuring up to 0.5 mm

diam and 3.6 mm long, bear terminal tufts of brown hairlike filaments, 8.0–10(–15) mm in length. The leading axes are also tipped with tufts of brown hairs, 12–15 mm long.

Habitat and comments: *Sporochnus bolleanus* occurs in drift and grows on rocks or limestone from shallow waters, just below low-water level, down to 90 m (Taylor 1960). [Additional illustrations: Taylor (1960: pl. 35: figs. 4, 5); Earle (1968: figs. 84, 85, 90–92).]

***Sporochnus pedunculatus* (Huds.) C. Agardh**

FIGURE 78

Sporochnus pedunculatus (Huds.) C. Agardh 1817: xii.

Basionym: *Fucus pedunculatus* Huds. 1778: 587.

Puerto Rican Records: As *Sporochnus pedunculatus*: Díaz-Piferrer 1963; Almodóvar and Ballantine 1983; Ballantine and Aponte 1997, 2002.



FIGURE 77. *Sporobolus bolleanus*. LRA6843, herbarium specimen: Arecibo. Scale bar = 1.0 cm.

FIGURE 78. *Sporochnus pedunculatus*. DLB2971, herbarium specimen: South Charlotte Amalie, U.S. Virgin Islands, dredged 36 m, VIII.1987. Scale bar = 2.0 cm.



Western Atlantic Distribution: North America, Bermuda, Cuba, Puerto Rico, Brazil

World Distribution: See Guiry and Guiry 2021.

Type Locality: Isle of Portland, Dorsetshire, southern England.

Sporochnus pedunculatus is the generitype. Thalli usually reach up to 30 cm tall above a small, discoid holdfast. The terete axes are irregularly alternately branched, and the branches are beset with short branchlets, 0.5 mm diam and 0.75–1.25(–2.0) mm long, that are borne on pedicels, 1.0–2.0 mm long. Branchlets are tipped with tufts of brown filaments, 3.0–4.0 mm long. Long branches are also tipped with tufts of filaments, to 5.0 mm long.

Habitat and comments: The species grows on rocks and limestone at 55(–110) m depths. [Additional illustrations: Taylor 1960: pl. 35: figs. 2, 3; Earle 1968: figs. 87, 89; Braune and Guiry 2011, fig. 60.1.]

XANTHOPHYCEAE V. ALLORGE EX F. E. FRITSCH

VAUCHERIALES (NÄGELI) BOHLIN

VAUCHERIACEAE DUMORT.

Vaucheria DC

Vaucheria DC. 1801: 20.

Thalli are of unbranched to sparsely branched coenocytic filaments. The filaments are tufted and loosely entangled or form “feltlike” mats. Cells possess numerous discoid plastids, with or without pyrenoids. Asexual reproduction is by zoospores or aplanospores. Sexual reproduction is oogamous, and species are either monoecious or dioecious. Cylindrical antheridia are sessile

or stalked. Sessile or stalked oogonia are single or grouped. *Vaucheria* is a large genus of 99 currently accepted species, of which 1 occurs in Puerto Rico.

Vaucheria dichotoma (L.) Mart.

Vaucheria dichotoma (L.) Mart. 1817: 304.

Basionym: *Conferva dichotoma* L. 1753: 1165.

Misapplied Name: *Vaucheria submarina*: Ballantine and Aponte 1997, 2002 [non *V. submarina* (Lyngb.) Berk. 1832: 24; *basionym:* *V. dichotoma* var. *submarina* Lyngb. 1819: 76, pl. 20A].

Puerto Rican Records: As *Vaucheria submarina*: Ballantine and Aponte 1997, 2002.

Western Atlantic Distribution: Jamaica, Puerto Rico, U.S. Virgin Islands, Argentina, Venezuela.

Type Locality: “Habitat in Angliae fossis pratorum” [and also cited] “Dillenius (1742: fig. 9)” (Linnaeus 1753: 1165); in ditches and streets, England. *Lectotype:* Christensen (1987) designated illustration of Dillenius (1742: fig. 9); herbarium voucher selected by Spencer et al. (2009).

Thalli are filamentous, forming expanding mats or free-floating. The filaments are dichotomously branched, measuring (80–)100–135(–225) μm diam. Subspherical to obovoid oogonia, 260–360 μm diam and 280–380 μm long, are solitary or occur in small groups. They are unilateral and sessile. Algae are dark green to occasionally brownish in color.

Habitat and comments: *Vaucheria dichotoma* is considered to be both a marine and terrestrial species. In Puerto Rico, it occurs in the muddy shallow waters of mangrove habitats. *Vaucheria* species may easily be mistaken for a green alga. [Illustration: Christensen 1987: fig. 3G.]

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Glossary

aculeate With a sharp point
acute With a sharp point
adaxial Toward the bearing axis
alternate With reference to branching, at different levels along an axis
anastomose Secondary fusion of cells or branches
antheridia Structure bearing male gametes
apiculate With a sharp point
aplanospore A nonmotile spore
assimilatory Refers to pigmented cells
attenuate Gradually narrowing
axil Location that is immediately between an axis and a branch
bistratose With two cell layers
cervicorn With reference to branching, in a manner similar to antlers of a deer
chromatophore Chloroplast
clathrate With holes
clavate Club shaped
cleft Partially divided
coenocyte A single cell with multiple nuclei
complanate In a single plane
conceptacle Sunken structures found in Phaeophyceae in which reproductive bodies are located
concrecent Growing together
conical Having the shape of a cone geometrically; in three dimensions, usually from a flat circular base tapering to an apex
cortex Outer layer of cells that have chloroplasts, normally cells to the exterior of the medulla
corticate Possessing a cortex
corymbose With the shape of a corymb; result of having branches arising at different points but terminating at the same level, giving the cluster a flat-topped appearance
costa Rib
costate Ribbed
crenulate Minutely scalloped
crustose Possessing a thallus (sometimes thin) that adheres closely to the substrata
cryptoblast A sterile conceptacle

cryptostomata As in Fucales; sterile cavities that once may have had a reproductive function

cuticle A protective filmlike covering, such as sometimes occurs over sporangia in *Padina*

decumbent Growing in a prostrate manner, directly on the substratum

dentate Toothed

denuded Without branches

determinate Of limited growth potential

dichotomous As in branching, with two equal branches

dichotomy A forking, such as a branch dichotomy

distal Toward the apex of a thallus or structure, opposite of proximal

distromatic With two cell layers

dorsal The top surface

ecorticate Without a corticating layer

endophyte A plant that grows within the tissue of a host plant

entire A margin that is undivided and continuous, not broken up by teeth or serrations

epiphyte A plant attached to and growing directly on top of another plant

erose Having an irregularly notched or jagged margin

filiform Very slender, filament-like

flabellate Fan shaped

flabellum Fan-shaped blade (pl. flabella)

flaccid Lacking rigidity

flexuous Bending, lacking rigidity

fusiform Spindle shaped; narrowing from the middle toward each end

gametangia Structures in which gametes are formed

gametophyte Haploid phase in species with an alternation of generations; typically, the generation that produces male or female gametes

generitype The type species of a genus

globose Having a rounded form, but not strictly defined

heteromorphic With respect to a life history, having generations that differ morphologically

heterotrichous Having a thallus comprising both a prostrate and erect system

holotype A single specimen on which the description of a species is based

imbricate Overlapping layers

indusium Membrane covering sporangia (pl. indusia)

intercalary Located between the base and apex of a branch or filament

interdichotomy Between two branching points

involutrum With respect to Phaeophyceae, sterile filaments that surround reproductive organs

isodiametric Cells or structures whose length and diameter are the same

lacerate Ragged, as the margin of a blade

lanceolate Elongate, tapering distally

linear Narrow with respect to length

longitudinal Perpendicular to the long axis, as in a section

macrothallus With respect to life histories with an alternation of heteromorphic, a stage that typically is the larger of the generations

medulla Internal tissue

meristem Dividing cells that are responsible for growth

microthallus With respect to life histories with an alternation of heteromorphic alternation of generations, a stage that is highly reduced in size

midrib A visible linear structure that runs the length of a blade or leaflike structure

monosporangia A sporangia that gives rise to a single spore

monostromatic Single cell thick

monotypic A taxonomic group that contains only one subordinate taxon (such as *Chrysocystis*)

mucronate Terminating in a short, sharp point

multiseriate Comprising multiple filaments

muriculate See mucronate

obconic Inversely conical

oblanceolate See lanceolate; however, broadest in the upper third

oblong Having a length several times greater than the width and with rounded ends

obovate Egg shaped, attached at narrower end

obpyriform Pear shaped; attached at narrower end

obtuse Having a blunt or rounded end

ontogenetic Referring to morphogenesis in the course of development

oogamous With reference to reproduction in which the female gamete is large and immobile

oogonium A cell that divides to form eggs

ovate Egg shaped; attached at broader end

ovoid Egg shaped

palmate Branching that radiates from a common point, as in fingers radiating from the palm of a hand

paniculate A branched cluster

papillae Small, elongated protuberances

paraphyses Normally uniseriate, sterile filaments lying between reproductive structures

paratype A specimen from the type collection, specifically stated to be the same species as the holotype

parenchyma Three-dimensional tissue formed by closely abutting cells

parietal Internal and positioned against the periphery

pedicel A stalk, normally one or a few cells

pedicellate Possessing a pedicel

pelagic Living free in the water column or ocean surface; in the sense of *Sargassum*, it implies never having been attached

peltate Shield shaped, borne by a more or less centrally placed stalk

periclinal As a cell division that is parallel to the surface

petiole The stalk of a leaflike structure

phenotypic plasticity The capability of a genotype to produce more than one morphological form under different environmental conditions

- pinnate** Branches arranged on opposite sides of a common axis
- plurilocular** Reproductive structure that is divided into multiple cells
- pluriseriate** Having multiple lengthwise axial filaments
- polymorphism** Having multiple morphologies
- propagulum** A portion of an alga that can break off, leading to asexual reproduction; the propagulum may have a defined morphology
- proximal** Toward the base of a thallus or structure, opposite of distal
- psammophytic** With respect to marine plants, those capable of establishment in unconsolidated sediment
- pseudohair** Hair type found in Ectocarpaceae, with a long basal cell beneath a meristem of several cells distal to it
- pseudoparenchyma** Tissue resembling a parenchyma, but originating from the close association of axial filaments
- pyrenoid** Structure within some chloroplasts; site of starch synthesis
- pyriform** Pear shaped
- radial** With structures radiating from a central point
- receptacle** Swollen areas in Phaeophyceae in which conceptacles are located
- reniform** Kidney shaped
- repent** Lying or creeping along the substrata
- rhizoid** Attachment, absorptive or corticating filament
- secund** Bearing branches produced from the same side of an axis
- seriate** Arranged in rows
- serrate** Marginally toothed
- sessile** Immobile; attached without a stalk
- simple** Unbranched
- sinus** A recess between two structures; also used in reference to branching angle
- sorus** A cluster of reproductive bodies in a specific patch on thallus surface; sometimes elevated (pl. sori)
- sporangia** Structures in which spores are formed
- sporophyte** Diploid phase in species with an alternation of generations
- stipe** Stalk
- stipitate** Bearing a stalk
- stolon** A prostrate axis; see also rhizome
- sub** A prefix, indicating (1) nearly or almost or (2) beneath
- terete** Cylindrical
- tetrasporangia** Sporangia divided into four spores (tetraspores)
- thallus** The body of an alga (pl. thalli)
- tomentose** Covered with hairs
- transverse** Perpendicular to the direction of the axis
- trichothallic** Terminal filaments resulting from growth of an intercalary meristem
- truncate** Possessing an abrupt transverse end
- turbinate** Inversely conically shaped
- type locality** The geographical location where the specimen that serves as the holotype was collected
- type species** See holotype
- unilateral** With branches produced from only one side of a bearing axis
- unilocular** Referring to a reproductive organ bearing a single chamber
- uniseriate** Having a single lengthwise axial filament
- ventral** Pertaining to the lower surface; opposite of dorsal
- vesicle** Spherical or bladder-like shape
- zonate** Demonstrating banding
- zooidangia** A sporangia that gives rise to reproductive cells with one or more flagella
- zoospore** A motile reproductive cell

Index of Scientific Names

Names of Ochrophyta taxa recognized in Puerto Rico are shown in **bold** type. Taxa that are synonyms or have a distribution outside of Puerto Rico are in nonbold type. Page numbers in ***bold italic*** type refer to illustrations. Page numbers in plain, nonbold type refer to taxa mentioned in the text.

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