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Marine Algae of the Northern Gulf of California: Chlorophyta and Phaeophyceae

James N. Norris

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ABSTRACT

Norris, James N. Marine Algae of the Northern Gulf of California: Chlorophyta and Phaeophyceae. *Smithsonian Contributions to Botany*, number 94, x + 276 pages, 109 figures, 2010. — The present treatment constitutes a taxonomic study of the green and brown benthic marine algae currently known in the northern Gulf of California. In all, 133 species were found: 4 classes, 7 orders, 13 families, 20 genera, and 63 species of Chlorophyta and 9 orders, 15 families, 26 genera, and 70 species of Phaeophyceae. The systematic account is a guide to the identification of marine algae from the northern Gulf of California, with the accepted name, keys, and descriptions of the orders, families, genera, and species. The date, place, and author(s) of valid publication of each taxon are cited. The current name for each species is given along with its basionym, type locality, synonyms, relevant taxonomic studies, habitat, and distribution in the Gulf of California and in the Pacific Ocean. Illustrations are provided for most species. A remarks section includes additional information on taxonomy, nomenclature, ecology, and/or other problems or facts of interest. In addition to reviewing the taxonomic phycological literature pertinent to the Gulf of California and Pacific México, new records and distribution extensions are given. Four new sections of *Sargassum* subgen. *Sargassum* are proposed: *S. sect. herporhizum* E. Y. Dawson ex J. N. Norris, *S. sect. johnstonii* E. Y. Dawson ex J. N. Norris, *S. sect. lapazeanum* E. Y. Dawson ex J. N. Norris, and *S. sect. sinicola* E. Y. Dawson ex J. N. Norris; five new combinations are made: *Desmareestia munda* subsp. *mexicana* (E. Y. Dawson) J. N. Norris, *Epicladia condensata* (Setchell et N. L. Gardner) J. N. Norris, *Epicladia mexicana* (Setchell et N. L. Gardner) J. N. Norris, *Hinckesia bryantii* (Setchell et N. L. Gardner) J. N. Norris, and *Sargassum sinicola* subsp. *camouii* J. N. Norris et Jensen. One new species, *Sporochmus neushulii* J. N. Norris, is described.

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* Contributed by Daniel León Álvarez and James N. Norris.

** Contributed by Luis E. Aguilar-Rosas, Raúl Aguilar-Rosas, and James N. Norris.

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Marine Algae of the Northern Gulf of California: Chlorophyta and Phaeophyceae

INTRODUCTION

Spanish explorer Hernán Cortés described an island, “Baja California,” in a letter to the King of Spain (1524). Cortés’ account was based on reports of his ships’ captains who were exploring the Pacific Ocean (León-Portillo, 1972). It was still considered an island 10 years later when Cortés himself sailed into the southern region and established a colony at Santa Cruz in 1535 (later renamed La Paz by Sebastián Viscaíno in 1596) (Lindsay, 1983). In 1539 Cortés sent Francisco de Ulloa with three ships from Acapulco to explore northward along the west coast of Mexico (León-Portillo, 1995). During the expedition Francisco de Ulloa became the first nonnative to circumnavigate what he called the “Mar de Cortés” (Sea of Cortez) (Lindsay, 1983), revealing Baja California to be a peninsula and not an island. The Gulf of California has also been called “Mar Bermejo” (Vermilion Sea) for the reddish color given by the muddy Río Colorado waters flowing into the upper Gulf; it was not named, as generally assumed, for the reddish color of the plankton blooms (van Andel and Shor, 1964).

A structurally complex trough reaching nearly oceanic depths, the Gulf of California is a large evaporation basin (Roden, 1964) lying between the arid, mountainous Baja California peninsula on the west and the dry Sonoran and Sinaloan coasts of the Mexican mainland on the east (Figure 1) (Álvarez-Borrego, 1983, 2002). The Gulf of California is approximately 1400 km in length and narrow in width, varying from 150 to 200 km (average width is less than 166 km), and has a surface area of 258,593 km² (=99,843 mi²) (Brusca et al., 2005).

The Gulf is composed of five physiographic zones (Lavín and Marinone, 2003:figs. 1, 2): (Zone1) The entrance at the Gulf’s southern end, where the outer mouth extends from Cabo San Lucas (Baja California Sur) to Cabo Corrientes (Jalisco), is about 204 km wide, more than 3000 m deep, and in open communication with the eastern tropical Pacific Ocean. (2) The southern Gulf of California begins at the inner mouth from Cabo San Lucas to El Dorado (Sinaloa) and extends northward to the southern end of the Midriff Islands (Las Islas de la Cintura), and it has more oceanic conditions than zones 3 to 5 to the north. (3) The Midriff Islands have narrow channels and sill depths of 300–600 m (note that Ballenas Channel (Canal de Ballenas) is extraordinarily deep, with



FIGURE 1. Northern Gulf of California. *Gemini V* photograph taken by astronauts Gordon Cooper and Charles Conrad, 21 August 1965 (courtesy of NASA).

depths to 1600 m, and the Guaymas Basin, a geologically active spreading center with depths of 2000 m and hydrothermal vents, may be considered oceanographic provinces themselves). (4) The northern Gulf of California has continental shelf sea characteristics. (5) The upper Gulf of California, north of 31°N to the Río Colorado Delta, is very shallow, with depths less than 30 m.

For the purpose of this study, the Gulf of California was divided into halves near latitude 28°N (Figure 2), separated south of the Islas de la Cintura (Midriff Islands), which includes the Gulf's two largest islands, Isla Ángel de la Guarda and Isla Tiburón. The northern Gulf (Figures 1, 2), surveyed in this study, extends eastward from Bahía San Francisquito (Baja California) across the Gulf to Guaymas (Sonora) and northward to the Río Colorado. The area studied herein approximates the "Northern Gulf of California Faunal Region" of Brusca et al. (2005:fig. 9.1) and covers more than 60,000 km² (=24,000 mi²). The southern Gulf, as referred to herein, extends from Bahía San Francisquito across the Gulf to Guaymas and southward to Cabo San Lucas (tip of Baja California Sur) and southeast to Cabo Corrientes (Jalisco).

The semi-enclosed Gulf is divided into a series of basins and trenches separated from one another by transverse ridges (Shepard, 1950; Rusnak et al., 1964; Álvarez-Borrego, 1983). Allison (1964) reviewed the geology of the areas bordering the Gulf of California, and Lavín and Marinone (2003) provided an overview of its unique physical oceanographic features. Brusca (1980) summarized the tectonic origin of the Gulf, and more recent studies on the tectonic evolution of northwestern Mexico are in Johnson et al. (2003). Although earlier estimates of the age of the Gulf were up to 10 million years ago (Ma), the origin of the Gulf ("proto-Gulf") began in the late Miocene about 8 Ma, and by the early Pliocene, about 4 Ma, the Gulf was open to the Pacific Ocean (Carreño and Helenes, 2002).

The temperature-moderating effect of the Pacific Ocean upon the climate of the Gulf is greatly reduced by the series of mountain ranges that run the length of the Baja California peninsula (i.e., the Peninsular Ranges: Sierra Juárez, Sierra San Pedro Mártir, Tres Virgenes, Sierra de la Giganta, and Sierra de la Laguna). The mountains of Baja California, together with the Sierra Madre Occidental mountains of the mainland of western Mexico, isolate the Gulf's atmosphere topographically, thus creating a semi-enclosed Gulf in a meteorological as well as an oceanic sense (Badan-Dangon et al., 1991; Álvarez-Borrego, 2002). As a result of these barriers, the climate along the Gulf coasts of Baja California and Sonora is more continental than oceanic (Roden, 1964), with greater

extremes in temperature, hotter summers, and colder winters than on the Pacific (western) coast of the Baja California peninsula.

The effects of the surrounding deserts and their seasons influence ocean conditions in the northern Gulf and have a clear impact on its marine flora. For example, the harsh physical extremes in the upper Gulf are a naturally occurring seasonal disturbance that can induce algal mortality when conditions are beyond the physiological tolerance of a species. In the upper Gulf the benthic algal community is maintained in a subclimax condition by the strongly fluctuating environmental conditions (Littler and Littler, 1981).

GENERAL OCEANOGRAPHIC FEATURES OF THE GULF OF CALIFORNIA

The oceanography of the Gulf of California has been described by Roden (1964), van Andel and Shor (1964), Maluf (1983), Álvarez-Borrego (1983, 2002), Badan-Dangon (1998), and Lavín and Marinone (2003). Several oceanographic features make the Gulf unique among the semi-enclosed seas of similar latitude and size, most notably the strong tidal mixing, some of which is close to deep stratification (Lavín and Marinone, 2003). The climate of the Gulf of California can be depicted as two seasons: a midlatitude winter and a subtropical summer (Mosiño and García, 1974). A summary of the general meteorological, hydrographic, and oceanographic features of this unique body of water is given herein.

Air Temperature: The mean annual air temperature range increases from about 6°C at Cabo Corrientes to 18°C at the Río Colorado Delta. During winter the air temperatures are higher near the southern entrance and decrease to their lowest at the Gulf's northern end, while during summer the air temperatures shift to being lowest near the Gulf's southern entrance and highest at the northern end. The differences in air temperature between the east (Gulf) and west (Pacific) coasts of the Baja California peninsula in summer are large, sometimes over 10°C, while in winter the differences are small, about 2°C. Within the Gulf, air temperatures on its bordering coasts are usually the same at the same latitude. The water temperatures, are also generally equal to each other on both sides of the Gulf at the same latitude.

Precipitation: Generally, there is more rain on the east coast of the Gulf of California (Sonora and Sinaloa) than on its west coast (Baja California). With an annual rainfall of less than 10 cm, the northern Gulf is drier and more influenced by the surrounding desert than the

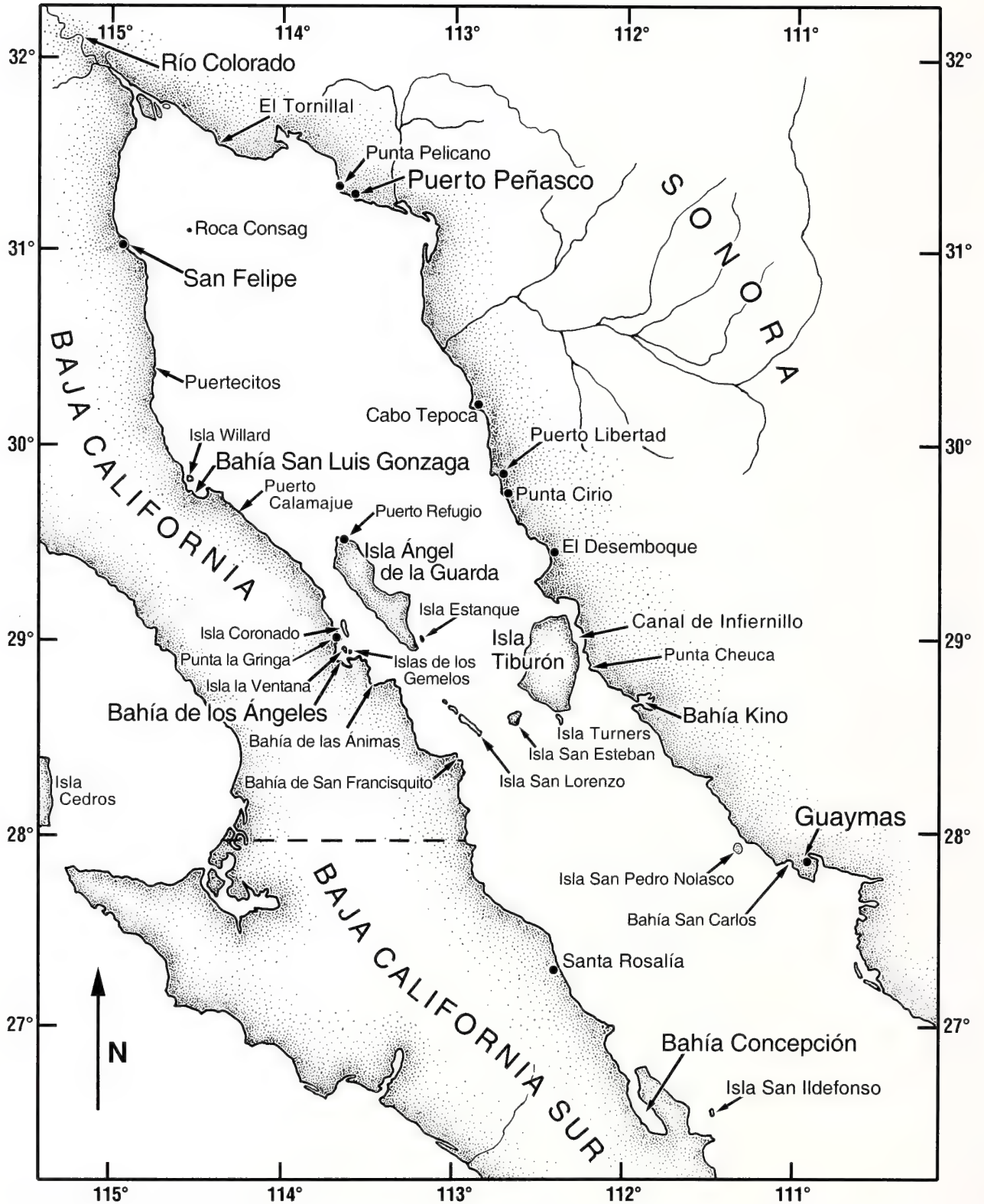


FIGURE 2. Map of the northern Gulf of California, Mexico (drawn by Alice R. Tangerini, National Museum of Natural History, Smithsonian Institution).

southeastern part of the Gulf, where the annual rainfall can be greater than 100 cm. From Isla Ángel de la Guarda and Isla Tiburón northward, rains occur mostly during winter, while south of the Midriff Islands the most rain usually occurs from June to October. The amount of rain on land increases with altitude, the mountains of the Baja California peninsula having an average rainfall of 25–75 cm/y. In contrast, the rainfall on the coasts is less than 10 cm/y. However, month-to-month variations can be large, and year-to-year variations can change by as much as a factor of seven. The number of rainy days decreases from an average of 60 days/y at Cabo Corrientes (Jalisco) to only 5 days/y along the Baja California and Sonora coasts of the central Gulf.

Sediments: The chief source of waterborne sediments to the Gulf was the Río Colorado until the construction of Hoover Dam was completed in 1936. When the Río Colorado ran free, this river alone contributed 50% of the total sediment brought to the Gulf annually, or about 600 m³/s (mean annual). After the construction of Hoover Dam, sediment from the Río Colorado dramatically decreased to only an average of about 120 m³/s (ranging from about 11 m³/s in October to 260 m³/s in January). Today, the combined diversion of waters by the Hoover Dam, Glenn Canyon Dam (completed in 1963), and other smaller dams in the United States and Mexico (e.g., Morelos Dam) has resulted in virtually no surface freshwater from the Río Colorado reaching the Gulf, except during winters with abundant rainfall or snowmelt or when water is released from the dams. Other rivers that contribute sediment and nutrients to the Gulf occur along its eastern coast: Río Concepción, Río Yaqui, and Río Mayo (Sonora); Río Fuerte, Río Sinaloa, Río Piaxtla, Río Presidio, and Río Baluarte (Sinaloa); and Río Grande de Santiago (Nayarit).

The sediment composition of these rivers is similar, being high in sulfate, sodium, and calcium ions, followed by bicarbonate, chlorides, and magnesium. Along with the waters of the Río Colorado, water from these ecologically important rivers has been increasingly put to use to support agriculture, ranching, and urban use by growing human populations, so that now little river water bearing sediments reaches the Gulf (Gilmartin and Revelante, 1978; Álvarez-Borrego, 1983). Dispersion of sediments in the northern Gulf is now mostly cross-basinal rather than long-basinal, suggesting dispersion is mainly controlled by oceanic forcing rather than fluvial processes (Carriquiry et al., 2001).

The loss of both sediments and freshwater to the upper Gulf has resulted in the loss or degradation of wetland, lagoon, and estuarine environments. These are

critical habitats for aquatic plants, birds, invertebrates, and spawning and nursery grounds for commercially important shrimp and fish, such as *Totoaba macdonaldi* Gilbert (Thomson et al., 2000). Habitat loss of their spawning and nursery grounds, along with overfishing and fishnet capture of juveniles (Guevara-Escamilla, 1973), and natural factors have had disastrous effects on totoaba populations, a Gulf-endemic species that once supported a commercially important fishery (Lercari and Chávez, 2007). While it is assumed or suspected that the loss of river water with its sediments and nutrients has also had an effect on the benthic marine flora, there have been no quantitative ecological temporal and spatial studies on the impact to the marine intertidal and subtidal benthic communities of the upper or northern Gulf.

Evaporation: In the coastal areas of the Gulf the mean annual rate of evaporation is 200–250 cm/y, with a minimum in winter and a maximum during summer. Evaporation is less in the open waters; e.g., it has been estimated to be 128 cm/y in the southern Gulf. As water evaporates, residual salts are concentrated in the remaining seawater, and as freshwater input and precipitation are both extremely low in the northern Gulf, the salinity of northern Gulf waters increases.

Salinities: In general, salinities within the Gulf of California are 1.0–2.0‰ greater than at comparable latitudes outside the Gulf (Bray, 1988a, 1988b). In the northern Gulf, where evaporation exceeds precipitation, salinities range from 35.3‰ to 37.2‰ (Lavín et al., 1998). These increases are related to the Gulf's geographical isolation from the Pacific Ocean and enhanced evaporation and higher water temperatures in the upper Gulf. Salinities greater than 36‰ are encountered locally (e.g., the Río Colorado Delta is now usually hypersaline, with salinities up to 39.0‰ in summer) and in semienclosed and shallow esteros (coastal lagoons) and bays of the northern Gulf (e.g., Bahía Cholla, Bahía de Adair, Bahía las Ánimas, and Bahía San Jorge) and in Bahía Concepción of the southern Gulf. In the upper Gulf, with no freshwater release from the Río Colorado, the salinities typically increase northwestward, ranging from 35.28‰ in October to over 38.50‰ in July (Álvarez-Borrego et al., 1973; Lavín et al., 1998; Álvarez-Borrego, 2002). In the southern third of the Gulf the offshore salinity, usually 34.6–35.8‰, is closer to that of oceanic waters. However, in the coastal areas of the southern Gulf it may be less than 34.6‰ during the rainy season, June to October.

Winds: The marked seasonal changes in the prevailing winds in the Gulf result from changes of atmospheric pressure in the vicinity of the Gulf and the channeling effect

of the mountain chains on both sides of the Gulf. Winds are northwesterly from November to May, typically with speeds of 8–12 m/s (meters per second). During the winter months, strong winds blow out of the north, sometimes for several days at a time, with wind speeds that gust 10–15 m/s (Bray and Robles, 1991). Southeasterly winds predominate from June to October, with mean speed of about 5 m/s (Badan-Dangon, 1998; Lavín and Marinone, 2003). During summer, the hot desert winds strongly influence the coastal marine systems of the upper Gulf.

In the northern Gulf, winds can be extremely variable and, as any fisherman or sailor of these waters knows, often unpredictable. Near the coast the land and sea breeze system prevails, with diurnal wind changes larger than annual ones. Sea breezes reach a maximum velocity in early afternoons and usually calm down after sunset. Land breezes are generally weaker, but mountain and valley winds predominate in the northern mountainous coasts.

Storms: Northwest gales occur in the northern Gulf from December to February and are particularly strong in the Ballenas Channel, between the mountainous Isla Ángel de la Guarda and the Gulf coast of Baja California. The southern Gulf has violent, short-duration storms, called chubascos, during the rainy season of June through October. Some of these may occasionally move northward.

Large tropical storms and hurricanes are generated in the eastern North Pacific off the southern coast of mainland Mexico, from June to November (mainly in September and October). These can either continue west or, although not often (Serra, 1971), turn north to northeast and enter the Gulf (Álvarez-Borrego, 1983), where they usually dissipate along the Sinaloa and Sonora coasts before reaching Isla Tiburón and Isla Ángel de la Guarda. However, those that do proceed up the Gulf, occasionally as far north as Arizona, can cause much damage and can be devastating to humans, but no short-term or long-term studies have been done on their ecological effects on the Gulf's marine communities (Álvarez-Borrego, 1983).

Wave Action: The seasonal winds in the Gulf of California drive ocean swells that influence the wave intensity. Wave action is characteristically stronger on the north sides of the islands and on coastal peninsulas. In general, wave action is much reduced on the Gulf of California coasts when compared to outer coasts of Pacific Mexico, except during large storms, such as chubascos, tropical storms, and hurricanes, when waves can be high and damaging, especially when in combination with high tides.

Water Circulation: Beier (1997) developed a model that showed a seasonal reversing gyre that forms in the

northern Gulf (Lavín et al., 1997). Typically, in the northern Gulf there is an anticyclonic (clockwise) circulation during winter and a cyclonic (counterclockwise) circulation during summer (Lepley et al., 1975; see Álvarez-Borrego, 2002:fig. 3.5), with two transitional periods (Carrillo and Palacios-Hernández, 2002). However, there are continuous changes throughout the year, and it is not always clearly one or the other (Álvarez-Borrego, 2002). The water masses of the Gulf of California have been reviewed by Bray and Robles (1991) and Badan-Dangon (1998).

Tides: Tides are a mixture of semidiurnal (twice a day) and diurnal (once a day) components. In the regions of the Gulf's entrance and in the upper Gulf and, to a lesser extent, in the southern Gulf and the northern Gulf, the semidiurnal tidal components are dominant, larger than the diurnal components. In the central Gulf, around Santa Rosalía, the diurnal tidal components dominate over the semi-diurnal components (Marinone and Lavín, 1997). The tidal range increases gradually from the Gulf entrance to Isla Tiburón and Isla Ángel de la Guarda, and then increases rapidly northward to the Río Colorado.

The lowest tides of the year are from February to April, and the highest are from July to September. The time of the daily high and low tides gets later as one proceeds north from the Gulf's entrance to the upper Gulf. The time difference is approximately 5.5 hours for high water and 6.0 hours for low water, resulting in high water at one end of the Gulf while it is low at the other (Roden, 1964). These tidal changes contribute to high water velocities in the central Gulf area, with the strongest tidal currents in the narrow channels between the large Midriff Islands and the adjacent coasts (e.g., Canal de Ballenas and Canal de Infiernillo; Figure 2). The speed of the currents is variable, dependent on the stage of the moon and prevailing winds. Current speeds increase from 3 cm/s at the Gulf's mouth to 60 cm/s at the head of the Gulf (Álvarez-Borrego, 2002:fig. 3.4). Tidal currents are strong in the narrow passages to shallow bays and estuaries and are especially notable in the narrow channels between the Midriff Islands and Gulf coasts, with speeds reported up to 3 m/s (=6 knots) in the Ballenas Channel (Álvarez-Sánchez et al., 1984).

The semidiurnal tidal amplitude in the region of the Gulf entrance is moderate, about 30 cm. In contrast, the tidal amplitude increases dramatically northward. During spring tides, vertical amplitude is greater than 4 m in the Midriff Islands, up to 7 m in the northern Gulf, and even more pronounced in the upper Gulf, greater than 9 m (Álvarez-Borrego, 2002). The difference between the semidiurnal tide and diurnal tide is also striking (Álvarez-Borrego, 2002). The amplitude of the diurnal tide slowly

increases northward to the upper Gulf to about twice that of the mouth of the Gulf.

The northern Gulf has some of the greatest tides in the world (Brusca et al., 2005). The large vertical amplitude covers and exposes vast areas and is especially pronounced at low tides in the shallow, low-angle sloping, mudflats, sandy beaches, and rocky reefs, tide pools, terraces, and platforms.

Currents: At the Gulf entrance (Cabo San Lucas to Cabo Corrientes) the surface current is variable. In winter, north of Cabo Corrientes, the wind-driven southward currents characterize surface circulation. During summer a northward current flowing along the mainland coast of western Mexico enters the Gulf at the central to eastern regions of the mouth (entrance) and continues north, while a southward current flows along the Gulf coast of Baja California (Roden, 1958; Granados-Gallegos and Schwartzlose, 1974). Tidal currents predominate north of Isla Tiburón. In the narrows between the Midriff Islands and adjacent coasts, they are often accompanied by rips and eddies, where currents of 1–3 m/s have been measured. The largest interannual variations in current patterns in the Gulf of California are due to the ENSO (El Niño–Southern Oscillation) phenomenon (Bray and Robles, 1991; Lavín and Marinone, 2003).

Net outflow of surface currents at the Gulf entrance is –10 cm/s in February, and net inflow is +21 cm/s in August. However, compensation must take place or sea level changes would take place. How that compensation occurs is not fully understood, but there are three hypotheses: (1) opposite flow at different levels (depths), (2) opposite flow along shores, or (3) a combination of both processes.

Sea Temperature: From April to September, the Gulf seawater is warmer than that of Pacific Baja California at 10 m depths, while from October to March their sea temperatures at 10 m are about the same.

Within the Gulf, diurnal fluctuations are greater at the surface and become more pronounced in the northern portions of the Gulf. The annual range of seawater temperatures is about 15°C at Río Colorado, in comparison to about 9°C at the Gulf's southern entrance. In the northern Gulf there are marked seasonal changes in coastal seawater temperatures. They are lowest in winter, 8°C–12°C, whereas in summer they are significantly higher, 30°C or more. The coldest sea surface temperatures occur where mixing is strongest, e.g., Canal de Ballenas–Canal de Salsipuedes (Martínez-Díaz de León et al., 2006; Marinone, 2007).

Vertical Distribution of Water Properties: The northern Gulf is relatively shallow; it has large seasonal and year-to-year variations of temperature and salinity in

the upper 150 m. The strong tidal components contributing to the vertical mixing, some of it close to deep stratification, make the Gulf unique from other semi-enclosed seas (Lavín and Marinone, 2003).

The thermocline in winter is almost isothermal, whereas in late summer, it is strongest, with the water temperature difference between the surface and 150 m depth approximately 14°C. During spring, salinities are higher along the Gulf's Baja California peninsula side than off the coast of Sonora, while in summer the highest salinities are in the central Gulf. Oxygen at the surface is 5.5 ml/L in April but decreases to 4.5 ml/L in August because of the increase in water temperature. At 150 m there is a slight salinity increase from spring to summer, despite the temperature increase and strong thermocline (Roden 1964). There may be a convective overturn in the upper Gulf (i.e., surface density exceeds the density of subsurface layers). This is possible because the density increases with decreasing temperature and increasing salinity, and because the lowest temperatures and highest salinities occur near the coastal regions of the upper Gulf.

Upwelling and Downwelling: Upwelling in the Gulf of California occurs along the Mexican mainland coast (e.g., Lluch-Cota, 2000) at the same time downwelling is occurring along the Baja California Gulf coast and vice versa. The dominant effects of atmospheric pressure, wind directions, and temperature cause this phenomenon.

The prevailing winds in the Gulf produce upwelling in some areas. In summer, southeasterly winds lead to upwelling and cooler temperatures along the Gulf side of the Baja California peninsula. The low temperatures along the lee side (east coast) of Isla Tiburón in winter are related to upwelling, caused by the prevailing northwesterly winds.

GENERAL FEATURES OF THE MARINE FLORA OF THE NORTHERN GULF OF CALIFORNIA

The most conspicuous feature of the marine flora of the northern Gulf, especially to those familiar with the marine flora of the Pacific coast of North America, is the relatively smaller size of the algae present. This general impression is due mostly to the absence of large brown kelps (Laminariales) and Fucales other than *Sargassum*. Although the marine flora of the northern Gulf is rich in species (over 430 species recorded), the brown algal species of *Sargassum* (Fucales) and those of *Padina* (Dictyotales) compose the greatest portion of the biomass of fleshy macroalgae.

Largely influenced by its desert surroundings, the uniqueness of the northern Gulf is due, in part, to its



FIGURE 3. Summer marine flora. Intertidal platform with characteristic yellow-brown hue of summer flora, Playa Estación, Puerto Peñasco, Sonora, Mexico (July 1973).



FIGURE 4. Winter marine flora. Intertidal platform with the dark brown color of winter flora, Playa Estación, Puerto Peñasco, Sonora, Mexico (February 1973).

continental rather than oceanic climate, with wide air temperature variation between summer, 31.2°C–32.8°C (88°F–91°F), and winter, 10.0°C–11.1°C (50°F–52°F). The intertidal regions of the northern Gulf are subject to extreme tidal exposure during the low tide series: up to 4 m vertical amplitude in the Midriff Islands, as much as 7 m in Puerto Peñasco, and up to 10 m at the Río Colorado Delta. This tidal exposure subjects the intertidal algae and sea grasses to severe desiccation, high light intensity (solar burn), temperature extremes, and low surf action. The northern Gulf has a distinctive and diverse flora because of these unique variations of temperatures, tides, and water circulation, along with seasonally alternating desert conditions of winter cold and summer heat, which operate on a great diversity of protected and exposed shore environments, from estuaries, esteros (lagoons), shallow bays, intertidal mudflats, sand/rock, coquina limestone, caliche shell-hash, and rocky tidal platforms (Figures 3, 4), sandy and rocky shores (Figures 5B, 6), and subtidal reefs and sand plains.

While the benthic marine flora of the northern Gulf of California is largely subtropical/warm temperate, there are also some tropical and temperate elements. A high percentage, 19% of the 133 species of northern Gulf Chlorophyta and Phaeophyceae, are endemic species (see Appendix 2) (about 11% of the greens, 7 of the 63 species, and about 27% of the browns, 19 of the 70 species).

Dawson (1941, 1960c) observed that some of the prominent benthic algae of the northern Gulf of California are species also known in Japan. For example, the Japanese brown algae *Dictyopteria undulata* and *Dictyota coriacea* were possibly introduced as viable fragments in ballast water of Japanese fishing boats operating in the northern Gulf of California in the early 1900s (Dawson, 1960c, as "*Pachydictyon coriaceum*"). Ballast waters from Japan would have been dumped into Gulf waters, most likely as the catch of shrimp or fish was unloaded. Other species of marine algae, such as *Gracilaria textorii* and *Lomentaria bakodatensis*, with a similar Gulf of California–Japan distribution may have also been unintentionally transported by Japanese fishing boats as viable fragments, spores or zygotes, and subsequently introduced into the Gulf. It is also conceivable that these same boats may have inadvertently transported some Gulf algal species back to Japan along with their catch. Without any significant collections of the Gulf's benthic macroalgae prior to 1921 (Setchell and Gardner, 1924a; Dawson, 1960c; Norris, 1976b), it is difficult to discern if this was the case. However, with current molecular analyses and systematic, phylogenetic, and phylogeographic studies (e.g., Gavio and Fredericq,

2002; Gurgel et al., 2004; De Clerck et al., 2006), it is now possible to test this hypothesis.

In the upper Gulf there is a strong seasonal turnover in species and their relative abundance, resulting in a pronounced alternation of a summer flora with a winter flora. At low tide, these seasonal changes are obvious to a novice observer who returns to the same locality at different seasons. An example of the marked contrast between the seasons is seen on the tidal platform at Playa Estación, Puerto Peñasco, Sonora (Figure 2). The marine flora of this region in summer (July) has a yellow-brown appearance (Figure 3). This color hue is caused by the turf-forming community of the mid intertidal zone, due mostly to *Chondrophycus paniculatus* (= *Laurencia paniculata*), which grows in association with *Porolithon sonorense* (a crustose coralline that may be responsible as a cementing agent for the rock/shell hash material which comprises the tidal platform). In contrast, during winter (February), the tidal platform takes on its characteristic dark-brown color (Figure 4) because of the conspicuous ephemeral and annual brown algal species that grow, mostly epiphytically on and among the *Chondrophycus*. These are predominately the large, coarse, and wart-like *Colpomenia tuberculata*, the more delicate and smooth, but often convoluted, *C. sinuosa* (Figure 5A), the brown finger-like hollow sacs of *C. phaodactyla*; and the fan-shaped *Cutleria hancockii*.

Although usually not growing on the top of the Playa Estación platform, other perennials, such as species of *Sargassum* and *Padina*, also contribute to the dark-brown winter coloration. Occurring in the numerous tide pools (such as the large Cupleaños Tide Pool, Playa Estación), tidal runoff areas, and crevices throughout the platform, these brown algae can obtain their largest sizes in winter to spring in these habitats. Some of the intertidal macroalgae can persist through the summer in these less-exposed habitats off the platform top.

Midriff Island Environments: There are more than 900 islands and islets in the Gulf of California (Carreño and Helenes, 2002; Brusca et al., 2005). The largest are the Midriff Islands (Islas de la Cintura) of the central Gulf (Figure 2), where large bathymetric gradients in combination with currents and tidal forces cause great volumes of water to accelerate in the narrow passages between the islands and the nearby coasts. Around the Midriff Islands, strong mixing and turbulence occur year round, advecting deep cool water with high nutrient concentrations to upper water layers, boosting biological productivity (Douglas et al., 2007). Isla Tiburón, the largest of the Gulf's islands, is separated from mainland Sonora (Bahía Sargento to Bahía Kino) by the Infiernillo Channel (Canal de Infiernillo), and

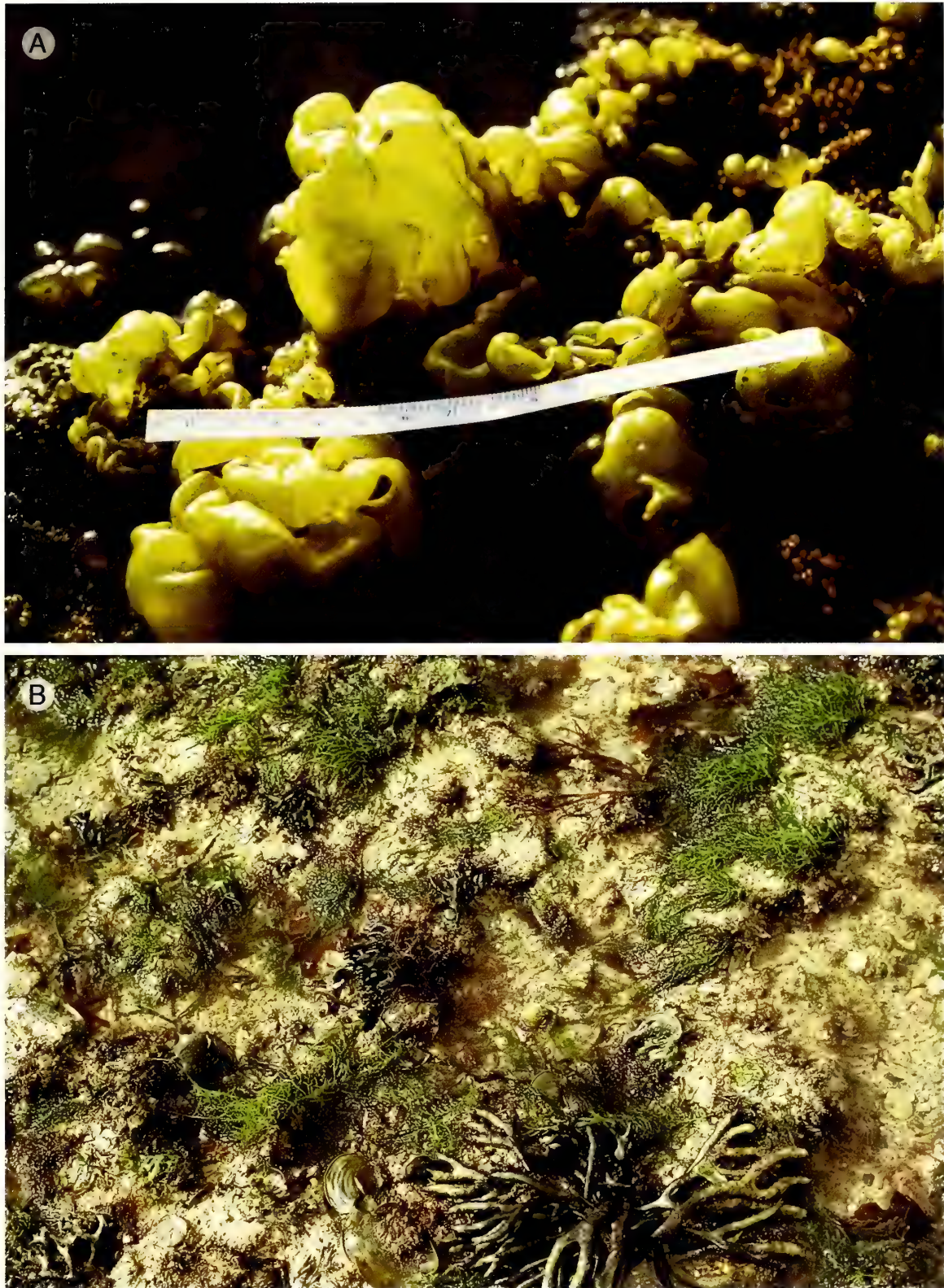


FIGURE 5. A. *Colpomenia sinuosa*, low intertidal platform, Playa Estación, Puerto Peñasco, Sonora (February 1974). B. *Codium simulans*, intertidal rock-sand flat at low tide, El Desemboque, Sonora, Mexico (April 1973).



FIGURE 6. Intertidal zonation, low tide at Puerto Refugio, Isla Ángel de la Guarda, Mexico. High intertidal zone dominated by green algae, particularly *Ulva* species; mid to low intertidal zone dominated by large, dark brown *Sargassum johnstonii*, with scattered individuals of golden-brown species of *Colpomenia* (R/V *Dolphin* cruise, April 1974).

the second largest, Isla Ángel de la Guarda is separated from the Gulf coast of Baja California (Punta Bluff to Bahía de Los Ángeles), by the Ballenas Channel (Figure 2). The Ballenas Channel is characterized by strong deep-water currents near deep basins (800–1000 m depths) that create conditions resembling persistent upwelling (López et al., 2006) and provide sustained nutrient enrichment to the shallow upper water layers.

At Puerto Refugio, a protected bay on the north end of Isla Ángel de la Guarda (Figure 2), these conditions support abundant seaweed populations that along with other primary producers sustain an associated wealth of animal populations (e.g., invertebrates, fish, and marine mammals and bird and sea lion rookeries). The algal communities at Puerto Refugio are diverse and luxuriant (Figure 6), with some of the Gulf's macroalgal species reaching their largest size on the Midriff Islands. While most of the northern Gulf's marine flora is generally considered to be warm temperate to subtropical, the cooler, more stable subtidal water temperatures associated with the Ballenas Channel (López et al., 2006) influence the species composition of the marine flora of the Midriff Islands. For example, subtidal brown algal species of *Desmarestia* and *Sporochnus*, both with cool-temperate to cold-temperate affinities, have been found in the Gulf of California only in the Midriff Islands (Dawson, 1941, 1944; Norris and Bucher, 1976). Deep subtidal populations of *Desmarestia* and *Sporochnus*, although different species than those of the northern Gulf, have also been reported in the tropical northwest Pacific, off Necker Island (Northwest Hawaiian Islands [NWHI], Papahānaumokuākea Marine National Monument) by Abbott and Huisman (2003b, 2004).

Graham et al. (2007) presented a predictive model for kelp refugia in the tropics by identifying habitats where kelp (Phaeophyceae) could survive. While there is no evidence of kelps (i.e., Laminariales) in the northern Gulf, certain subtidal habitats of the Midriff Islands host populations of cold-water large brown algae, such as *Desmarestia*, that are often associated with kelps. Whether these are relic or pioneering populations, their island subtidal habitats are unique within the Gulf due to their stable cool, nutrient-rich waters and may serve as refugia (sensu Graham et al., 2007) for these ecologically and geographically isolated brown algae.

HISTORICAL REVIEW OF MARINE BOTANICAL EXPLORATION

January 1870 marked the collection of the first known scientific specimen of a marine alga from the Gulf of California when *Wurdemannia miniata* (Rhodophyta) was

obtained by Edward Palmer (McVaugh, 1956; Beaty, 1964; Lindsay, 1983), a professional plant collector and an early ethnobotanist, on the shore of Isla Carmen, off Loreto (Baja California Sur) (Dawson, 1944; Norris, 1976b). The next known algal collections, consisting mostly of specimens of *Sargassum*, came from the third expedition of the California Academy of Sciences (San Francisco) to the Gulf in 1890 (Dawson, 1944; Lindsay and Engstrand, 2002) and were collected by Townshend S. Brandege (Setchell, 1928) and Walter E. Bryant (Fisher, 1905; Godínez-Ortega, 2008). M. Paul Hariot (1895) published the earliest account of some Gulf of California algae on the basis of a small collection of marine (mostly corallines) and freshwater algae obtained by Léon Diguët, a French chemical engineer who became interested in the natural history and ethnology of Baja California while employed at the Boleo mines in Santa Rosalía between 1888 and 1892 (Lindsay, 1955, 1983). His collections were of such interest to the Museum d'Histoire Naturelle (Paris) that he returned to Baja California as a field investigator and collector for the Paris museum from 1893 to 1913 (Godínez-Ortega, 2008). During his exploration, Diguët spent some time in La Paz and on Isla Espiritu Santo investigating the pearl fisheries then under French concession and used their facilities at La Paz to study the marine fauna.

The first marine algal collections from the northern Gulf were made in 1904 by Daniel T. MacDougal (Humphrey, 1961), while he collected for the New York Botanical Garden on a boat trip from Yuma, Arizona, to San Felipe, Baja California. Shortly thereafter, drift material was gathered in the southern Gulf at La Paz by Gastón L. Vives in 1911, which together with the San Felipe collections of MacDougal, were the basis for the first detailed study of several Gulf algae by Marshall A. Howe (1911; Setchell, 1938). Both of these collectors had species named for them by Howe (1911), i.e., *Cladophora macdougalii* and *Dictyota vivesii* and *Gracilaria vivesii*.

The expedition of the California Academy of Sciences to the Gulf of California in 1921 yielded extensive collections during the over 2914.5 km (= 1811 miles) covered by the schooner *Silver Gate* (Slevin, 1923). The marine algal specimens were collected by the botanist aboard, Ivan M. Johnston (Thomas, 1969), who was then a student of W. A. Setchell. These specimens comprised the largest part of the monograph of Gulf of California algae (1924a) by William A. Setchell (Drouet, 1943; Campbell, 1945; Papenfuss, 1976) and Nathaniel L. Gardner (Setchell, 1937c; Papenfuss, 1976). For Johnston's efforts, Setchell and Gardner (1924a) named nine species for him, including *Sargassum johnstonii*. Their study also incorporated

the 1917 collection of Dr. and Mrs. Daisy R. Marchant (Godínez-Ortega, 2008), and the earlier materials of T. S. Brandegee and W. E. Bryant, with several new species named after those collectors, e.g., *Pringsheimia marchantiae*, *Gonodia marchantiae*, *Codium brandegeei*, *Sargassum brandegeei*, and *Ectocarpus bryantii*. In all, 144 species and varieties of red, brown, and green algae were reported, 111 of which were described as new taxa (Setchell and Gardner, 1924a). In a separate publication, Setchell and Gardner (1924b) described another new brown alga from the Gulf, *Nemacystus brandegeei*.

Collections of D. T. MacDougal in 1923 from Puerto Libertad, Sonora, resulted in two new species being described by Gardner (1927), and later two more, *Codium macdougalii* and *Sargassum macdougalii*, were described by E. Yale Dawson (1944). The 1932 Templeton Crocker Expedition of the California Academy of Sciences on the yacht *Zaca* from Isla Guadalupe to the Galápagos yielded several specimens from the southern end of the Gulf. The algae, collected mostly by John Thomas Howell (Daniel et al., 1994), were included in the studies of Setchell (1937b) and Dawson (1944). Waldo L. Schmitt (National Museum of Natural History, Smithsonian Institution (Chace, 1978) obtained algae from Baja California during the Allan Hancock Pacific Expedition of 1933 and, from his dredging of the cape region of southern Baja California during the Presidential Cruise of 1938. Both collections were later treated by William R. Taylor (1939, 1945, respectively; Wynne, 1991). The Field Museum (Chicago) Expedition to Sonora, made by Francis Drouet (Forest, 1983) and Donald Richards in the winter of 1939, yielded numerous algal collections, including many blue-greens, from the Sonoran coast. Other upper Gulf specimens were obtained in the spring of 1941 by John Poindexter at Puerto Peñasco, Sonora. Edward F. Ricketts (Astro, 1976, 2001; Rodger, 2006) made some algal and sea grass collections from Puerto Refugio, Isla Ángel de la Guarda, in April 1940 (for an excellent account of this Sea of Cortez trip and natural history, particularly of the marine fauna, see Steinbeck and Ricketts, 1941; Steinbeck, 2001). During the fall of 1940, J. Wyatt Durham brought in some algae while aboard the schooner *E. W. Scripps* on a research expedition of the Geological Society of America and Scripps Institution of Oceanography (Anderson et al., 1950).

E. Yale Dawson studied the Gulf of California marine algae for his doctoral dissertation (University of California, Berkeley, 1942; published 1944) under the joint direction of Lee Bonar (UC Berkeley) and Gilbert M. Smith (Stanford University; Silva, 1960; Wiggins, 1962).

All of the previous Gulf of California collections mentioned above, except the earliest of Diguët (Hariot, 1895) and those of Schmitt (Taylor, 1939, 1945), were studied by Dawson. While a student at UC Berkeley, his phyco-logical interests were encouraged early on and mentored by William “Uncle Bill” Setchell. As a boy of 14, Dawson was first introduced to plants of the desert and coast during a trip to Baja California with his father in 1933, and his interest in cacti (e.g., Setchell and Dawson, 1941) and seaweeds persisted throughout his life (Hawkes, 2005). Dawson’s first sea voyage to the Gulf was aboard the *M/Y Velero III* expedition of the Allan Hancock Foundation (University of Southern California) in 1940 (Garth, 1967), allowing him to be the first marine botanist to visit and collect marine algae of the Gulf of California (Dawson, 1941). After serving in the U.S. Army Air Corps during World War II (1943–1945), Dawson, as a fellow of the John Simon Guggenheim Foundation in 1946–1947, made several overland collecting trips in Baja California and along the Mexican mainland from Punta Peñasco (Sonora) to Tapachula (Chiapas) and obtained additional collections from the Midriff Islands while aboard the boat *Guanero* of Guaneros y Fertilizantes de México. Beginning in 1948 and continuing to 1954, Dawson participated in five other expeditions aboard the *M/Y Velero IV* of the Allan Hancock Foundation. While Research Director and Vice President of the Beaudette Foundation (Santa Ynez, California) and, later, as Curator of Botany (Los Angeles County Museum), Dawson made other cruises (1957–1964) on the *M/Y Stella Polaris* (Figure 7) that resulted in further knowledge of the marine algae of the southern Gulf (Dawson, 1959a). Having learned to scuba dive, he became the first marine botanist to dive and explore the subtidal waters of the Gulf of California and Central America (Figure 8A, B). Several friends and biologists, including Carl L. Hubbs, Bibiano F. Osorio-Tafall, J. Laurens Barnard, Michael Neushul Jr., Robert D. Wildman, Wheeler J. North, and Robert W. Hoshaw, made or shared collections with him. Among the scuba divers he dove with in Mexico were pioneering underwater photographer Don Ollis (Beaudette Foundation, Santa Barbara) and Michael Neushul, Robert D. Wildman, Richard H. Rosenblatt, James R. Stewart (Scripps Institution of Oceanography), and John Bleck (Santa Barbara). Acknowledging their interest and appreciating their help, Dawson named species for them, e.g., *Myriogramme osorioi*, *Botryocladia neushulii*, *Kallymenia bleckii*, *Fauchea hoshawii*, *Lejolisia hoshawii*, and *Antithamnion hubbsii*.



FIGURE 7. E. Yale Dawson (left) with Palmer T. Beaudette (right) during an expedition to Pacific Mexico and Central America in 1959; note the M/V *Stella Polaris* anchored in the background.

In all, E. Yale Dawson made more than 20 expeditions into the Gulf of California from 1940 until his untimely death in 1966, with over 50,000 specimens collected from 130 different stations during those years (Dawson's field notebooks are deposited in the Phycology Library of the Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, where he was curator from 1965 to 1966). Dawson's published accounts of marine algae are numerous, with taxonomic, floristic, and distributional studies on the algae from the Gulf of California and the Pacific Coast of Mexico (see Abbott, 1966; Zaneveld, 1966; Garth, 1967; Silva, 1967; Norris, 1976b). Among his major contributions to Mexican phycology, resulting from more than 25 years of research, are "Marine Algae of the Gulf of California" (Dawson, 1944) and eight monographs: "Marine Red Algae of Pacific Mexico" (Dawson, 1953a, 1954c, 1960b, 1961a, 1962a, 1963a, 1963b). Of the studies published after his death, two concerned Gulf marine algae: an annotated list of marine algae of Puerto Peñasco,

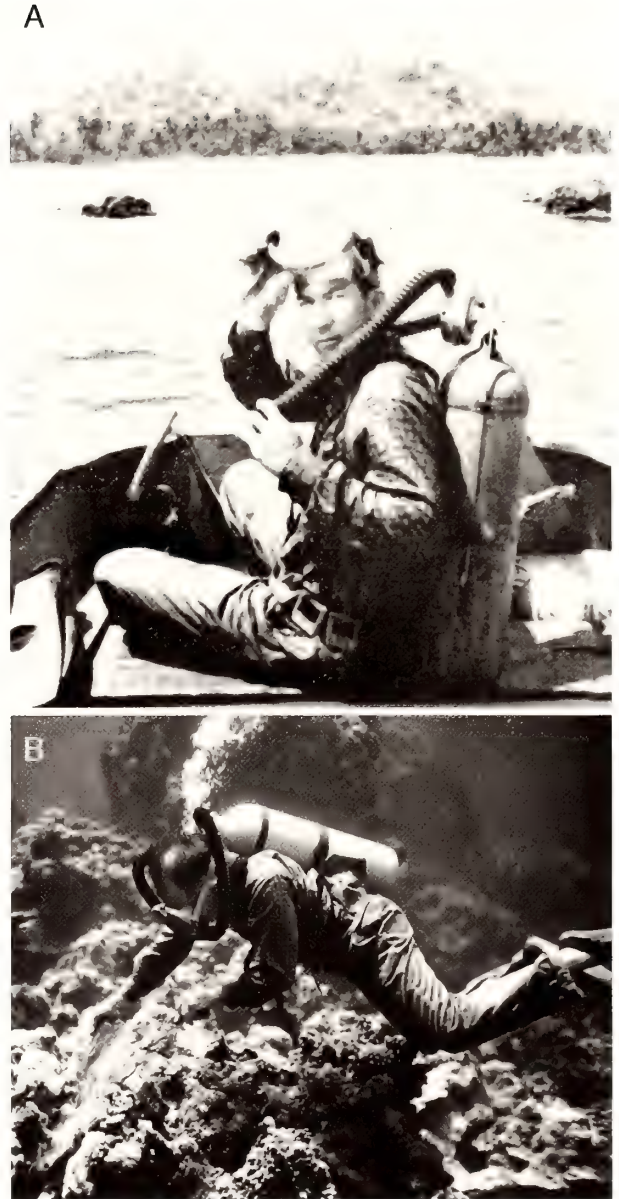


FIGURE 8. E. Yale Dawson (A) preparing for algal collecting dives using scuba during the 1958 cruise of the M/V *Stella Polaris* and (B) diving and collecting subtidal algae in 1959 in Costa Rica. (Photos by Don Ollis, formerly of Beaudette Foundation for Biological Research [now defunct]; photos now part of Dawson papers collection at NMNH Department of Botany).

Sonora (Dawson, 1966a), and new species and distribution records (Dawson, 1966b).

Contributions to our knowledge of the marine algae of the Gulf of California from 1965 to 1986 were furthered

by the collections of Robert W. Hoshaw (University Arizona, Tucson) and his students, particularly, Arthur E. Dennis, Nichols P. Yensen, and Richard M. McCourt. Marine flowering plants (sea grasses) were recorded from the Sonoran coast by Steinbeck and Ricketts (1941), Dawson (1960c), and Norris (1985c). The ecological and natural history knowledge of the Seri Indians (Comcaac) has contributed to our understanding the plants and animals of coastal Sonora; e.g., their use of the eel grass seed has added to our knowledge of distribution and ecology of *Zostera marina* in the Gulf (Felger and Moser, 1973), sea turtle temporal distribution (Felger et al., 1976), and Seri ethnobotany (Felger and Moser, 1985; Norris, 1985).

Professor Laura Huerta-Múzquiz (Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional; Calderón de Rzedowski and Rzedowski-Rotter, 2000) began studying Gulf and Baja California algae in the late 1950s (e.g., Huerta-Múzquiz, 1960), and her students, more recently Catalina Mendoza-Gonzalez and Luz Elena Mateo-Cid, are among those who have continued to make contributions to our knowledge of Gulf of California and Pacific Mexico algae. In the 1980s, Professor Marta M. Ortega (Universidad Nacional Autónoma de México) and her students also worked on algae of Sonora and Sinaloa, although focusing primarily on marine algae of the Gulf of Mexico and the Caribbean Sea (e.g., Ortega et al., 2001).

The 1980s also marked the beginning of phycological research centered at Universidad Autónoma de Baja California, Ensenada, with Luis E. Aguilar-Rosas and Raúl Aguilar-Rosas and marine botanists Marcos A. Aguilar-Rosas, Isai Pacheco-Ruiz, and José A. Zertuche-González, along with their students, all making numerous contributions based on their collections and studies of the marine algae of Baja California and the Gulf of California (see References).

Jorge González-González (Universidad Nacional Autónoma de México) and his students, including Daniel León-Alvarez, Hilda León-Tejera, and Elisa Servièrre-Zaragoza, have been adding to our knowledge of Gulf of California and Pacific Mexico marine algae with their studies, including their useful catalogue of benthic marine algae of Mexico (González-González et al., 1996). More recently, Jose Espinoza-Ávalos and Rafael Riosema-Rodriguez (Universidad Autónoma de Baja California Sur), Francisco F. Pedroche (Universidad Autónoma Metropolitana, Unidad Iztapalapa), and others studying the Gulf marine algae have continued to further our knowledge of the floristics, taxonomy, and ecology of Gulf algae. Today, the marine botanists of Mexico represent an active and productive era in Gulf of California phycology (see,

for example, their numerous publications on Gulf greens and browns among the References).

CURRENT STUDY

Although my visits to Baja California and the Gulf of California via vehicle began in 1963, my first trip as a student of marine biology was by sea in 1969 on the cruise of the *M/Y Makrele* (Moss Landing Marine Laboratories of the California State Universities) to the northern Gulf of California (Norris, 1973). During 1972–1975, while a graduate student at the University of California, Santa Barbara, it was my pleasure to be in residence as Station Director of Laboratorio de Biología Marina of the University of Arizona and Universidad de Sonora in Puerto Peñasco, supported and encouraged by Robert W. Hoshaw, Donald A. Thomson, and John R. Hendrickson (University of Arizona). Field explorations on the Sonora and Baja California coasts were made possible through support from National Science Foundation grants (BMS-73-07000-A01 and BMS-75-13960) and USDC NOAA-04-5-158-20. The Islas de la Cintura were surveyed during the 1974 cruise of the *R/V Dolphin* (Scripps Institution of Oceanography) to the northern Gulf of California (Norris and Bucher, 1976, 1977). From 1972 to 1979, selected localities on the Baja California and Sonora coasts (Figure 2) of the northern Gulf were sampled several times to assess seasonal changes of the marine algae. The algal collections from these field trips form the basis for the present taxonomic study and were supplemented by the appreciable collections of E. Y. Dawson (US Alg. Coll.; AHFH, now UC [see below for list of definitions for abbreviations used in this paper]) and those of Ivan Johnston and others that were included in the studies of W. A. Setchell and N. L. Gardner (CAS, now UC; US Alg. Coll.).

Specimens were obtained by intertidal collecting and subtidally with use of scuba by me and Katina E. Bucher; collection numbers designated by the prefix *JN-* refer to our field notebooks (Algal Collection, National Museum of Natural History, Smithsonian Institution). Methods for field handling of algal collections and their subsequent preservation, mounting as herbarium specimens, and preparation for light microscope study are as given by Tsuda and Abbott (1985). Photomicrographs were made using an Olympus Q-5 digital camera mounted on a Zeiss Universal microscope; all images used herein were prepared using Adobe Photoshop PS-3 on a Macintosh G-5 computer.

Specimens studied or examined for this work are deposited in collections at the institutions listed below, which are abbreviated for subsequent mention in the text. Herbarium

abbreviations herein follow the Index Herbariorum (Holmgren et al., 1990; Holmgren and Holmgren, 1998, continuously updated, <http://sweetgum.nybg.org/ih/>).

AHFH	Herbarium of the Allan Hancock Foundation, University of Southern California, Los Angeles; Algae Collection to LAM now UC
CAS	Herbarium of the California Academy of Sciences, San Francisco; now UC
CMMEX	Algae Herbarium of the Universidad Autónoma de Baja California, Ensenada, Mexico
LAM	Herbarium Los Angeles County Museum, Los Angeles; Algae Collection now UC
LD	Botanical Museum, Lund, Sweden
MICH	Herbarium of the University of Michigan, Ann Arbor
PC	Muséum National d'Histoire Naturelle, Laboratoire de Cryptogamie, Paris
UC	Herbarium of the University of California, Berkeley
US Alg. Coll.	Algal Collection of the U.S. National Herbarium, National Museum of Natural History, Smithsonian Institution, Washington, D.C.

Several botanical and phycological references were invaluable throughout this study, notably the second edition of *Taxonomic Literature* (referred to as TL-2) by

Stafleu and Cowan (1976–1988) and its supplement volumes (Stafleu and Mennega, 1992–2000; Dorr and Nicolson, 2008), Stafleu (1972) on dates of publication of the extensive volumes of Engler and Prantl, Stearn's (2004) *Botanical Latin*, and the thorough *AlgaeBase* (<http://www.algaebase.org>) developed, updated, and maintained by Michael and Wendy Guiry (Guiry and Guiry, 2008). The citation of the authors of taxa names follows Brummitt and Powell (1992).

Place and locality names of the land-based collection sites and ship-based cruise stations that are used herein are from the U.S. National Oceanic and Atmospheric Administration (NOAA) charts 21008, 21120, 21124, 21141, 21161, 21181, 21182, and 21014, Carta de Fondeo e Hidrografía de México F.H. 600, and the boating and cruising sea guides to Baja California and the Gulf of California by Lewis (1971), Williams (1996), Cunningham (2004, 2006a, 2006b), and Rains (2006).

It is hoped this publication will encourage algal taxonomic and phylogenetic research as it makes available a taxonomic baseline for further biodiversity and marine botanical and ecological investigations in the northern Gulf of California. Accurate identification of the marine algae is essential for conservation studies and ecosystem management of this unique region. The biological uniqueness of the northern Gulf of California is today internationally recognized, and conservation of its ecosystems biodiversity is hopefully provided by the several marine biosphere reserves, marine protected areas (for natural resources or flora and fauna), marine sanctuaries, and national marine parks in the Gulf of California (e.g., Case et al., 2002; Cartron et al., 2005a, 2005b; Danemann and Ezcurra, 2008).

PART I: GREEN ALGAE

CHLOROPHYTA

Chlorophyta Pascher, 1914:158

The Chlorophyta (green algae) are an extremely large, diverse group with wide variation in vegetative morphologies, ranging from unicellular to structurally complex species. Members of this group are found in freshwater (including snow and ice), estuarine, marine, terrestrial, and subaerial (e.g., on trees, walls, sloth fur, and polar bear hairs, etc.) habitats. In marine environments, they range from microscopic phytoplankton to the benthic microalgae and minute to large macroalgae of intertidal and subtidal habitats, down to 210 m depths (Littler et al., 1985, 1986; Norris and Olsen, 1991).

The color of these algae varies greatly, from dark green to pale or yellow green, because of the dominance of the green photosynthetic pigments, chlorophylls *a* and *b*, over the various accessory pigments, such as the carotenes (alpha, beta, and gamma) and xanthophylls (lutein, antheraxanthin, neoxanthin, violaxanthin, and zeaxanthin). While most are noncalcified, some marine genera are calcified. Cells are either uninucleate or multinucleate, with cellulose found in the cell walls in all but a few unicellular species. Chloroplasts vary in size, shape, and number per cell but always have two encircling membranes without a periplastid endoplasmic reticulum and often contain one or more pyrenoids (storage reserves of starch). Thylakoids (structures inside chloroplasts where light-dependent reactions of photosynthesis occur) are singular or stacked. Cell division occurs with a phragmoplast (cytoskeletal structure instrumental in deposition of new cell wall material).

Vegetative reproduction occurs by cell division and fragmentation. Reproduction can be by non-motile aplanospores and sometimes resting spores (akinetes). Swimming cells have two flagella or multiples of two, with a stellate structure linking nine pairs of microtubules at the basal transition region. Zoospores are usually biflagellate or quadriflagellate, with acronematic (whiplash) type of flagella. Parthenogenesis is also reported in a few species. Sexual reproduction may be isogamous or anisogamous, usually with biflagellate gametes, or oogamous.

REMARKS. The most recent classification system considers the Chlorophyta to be within the Chloroplastida Adl et al. (2005; Lewis and McCourt,

2004, as “Chlorobionta C. Jeffery 1982”) as members of the Archaeplastida; the latter is one of the seven clusters that represent the basic groups (or traditional kingdoms) of the eukaryotes (Adl et al., 2005).

The benthic green macroalgae found in the Gulf of California are in four classes: Ulvophyceae, Cladophorophyceae, Bryopsidophyceae, and Dasycladophyceae.

KEY TO THE CLASSES OF CHLOROPHYTA IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae unicellular or multicellular; cells uninucleate or multinucleate; chloroplasts with pyrenoids; no cytoplasmic streaming within cells 2
- 1b. Algae coenocytic; a single large multinucleate cell or simple to branched tubes or siphons; chloroplasts with or without pyrenoids; with cytoplasmic streaming (observable in living specimens) 3
- 2a. Cells uninucleate, containing only a single parietal chloroplast with 1 to several pyrenoids **Ulvophyceae**
- 2b. Cells multinucleate, with numerous chloroplasts; in many (but not all) there is a single pyrenoid per chloroplast **Cladophorophyceae**
- 3a. Algae siphonous and radially symmetrical, with a central axis that bears lateral branches in whorls; chloroplasts without pyrenoids **Dasycladophyceae**
- 3b. Algae of various filamentous or vesiculate forms (not radially symmetrical); numerous chloroplasts with or without pyrenoids **Bryopsidophyceae**

ULVOPHYCEAE

Ulvophyceae Mattox et K. D. Stewart, 1984:41, 66, *nom. invalid.* [see McNeill et al., 2006:Art. 36.2; Pröschold and Leliaert, 2007:129]; O’Kelly and Floyd, 1984:123.

Species range from individual to colonial unicellular forms to the macrothalli of variable morphologies that include (1) multicellular filamentous forms, (2) multicellular monostromatic or distromatic sheets, or (3) multicellular or siphonous forms, mostly of cushion-like clumps of entangled or compacted filament-like tubes. Members are predominately marine or estuarine and may be simple and unbranched or branched. Each cell has a single cup-shaped or band-shaped chloroplast that contains one to

several pyrenoids. Cell division occurs by the furrowing of the persistent, closed, centric mitotic spindle.

Life histories, where known, involve an isomorphic or heteromorphic alternation of generations. Mobile reproductive cells, occurring in most members, have one or two pairs of flagella without mastigonemes (flagellar “hairs”). Each flagellum has basal bodies with four microtubular roots arranged in a cruciate pattern and smaller rootlets of two sizes that alternate between two or more microtubules.

One of the orders, the Ulotrichales Borzi (1895) is present in the southern Gulf, based on the report of *Ulothrix* Kützing (1843) by Rocha-Ramírez and Siqueiros-Beltrones (1991).

Three of the orders, the Ctenocladales, Phaeophilales, and Ulvales, are represented in the northern Gulf of California.

KEY TO THE ORDERS OF THE ULVOPHYCEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae macroscopic, and either biserial filaments; or tubular (1 cell layer); or membranaceous and partially tubular and partially bladelike (1–2 cell layers); or membranaceous blades throughout (1–4 cells layers) **Ulvales**
- 1b. Algae microscopic or minute, uniseriate branched filaments that may be erect or prostrate or prostrate with erect axes; uniseriate filaments either remain free and not adjoined throughout or, in some, are partially or entirely consolidated into pseudoparenchyma (1 cell thick at margins and 1–4 cells thick centrally) 2
- 2a. Algae microscopic to macroscopic, but minute; mostly endophytic or epiphytic on cells of other algae; uniseriate filaments free or partially or completely consolidated into pseudoparenchyma, 1–4 cells thick **Ctenocladales**
- 2b. Algae microscopic, uniseriate filaments; mostly endolithic in dead shells, coral rubble, or crustose corallines; 1 cell thick throughout, and further separated by zoosporangia formation, and zoospore ultrastructure **Phaeophilales**

Ctenocladales

“Ctenocladales” Silva, 1982:147.

Ctenocladales P. C. Silva in Silva, Meñez et Moe, 1987:131.

Algae are uniseriate, branched filaments, which may be (1) entirely erect, (2) entirely prostrate, or (3) a combination of both with an attached prostrate portion from which erect branching filaments develop. Prostrate filaments may form a pseudoparenchyma. Cells are uninucleate, with a single chloroplast and usually one or more pyrenoids. Unicellular colorless hairs or multicellular setae (hair-like) branches are present in some species.

Asexual reproduction is by fragmentation or by akinetes. Sporangia are formed within vegetative cells and produce aplanospores, or biflagellate, tririflagellate, or quadriflagellate zoospores. Sexual reproduction has not been confirmed for most species. Where reported, sexual reproduction, may be isogamous or anisogamous, with biflagellate gametes formed within enlarged vegetative cells (gametangia). Sporangia and gametangia may form a pore, papilla, or neck.

REMARKS. The taxonomy of the members of the Ctenocladales and Chaetophorales group has been largely based on culture and ultrastructural studies, and the ordinal and family placement of their members has been variously interpreted. The reliability of certain taxonomic characters has been questioned, and taxonomic placement of some genera is still in a state of flux (e.g., Silva et al., 1996b). For example, the Ulvellaceae is placed in the Ctenocladales herein (following, e.g., Silva et al., 1996b; Abbott and Huisman, 2004; Pedroche et al., 2005), but others consider the family in the Ulvales (e.g., Schneider and Searles, 1991; Kraft, 2007). At present,

their taxonomy and phylogenetic relationships are somewhat problematic and in need of further elucidation.

There is one family in the northern Gulf of California.

Ulvellaceae

Ulvellaceae Schmidle, 1899:57, *emend.* O’Kelly and G. L. Floyd, 1983:162.

Algae are usually microscopic, prostrate, and composed of filaments that are freely branched or laterally coherent or coalesced to form a pseudoparenchyma, and may be, endophytic or epiphytic on other algae or marine plants, or grow on other marine organisms. Cells have a lateral, band-shaped or platelike chloroplast and are with or without pyrenoids. Colorless setae or hair-like projections from the cell wall are present in some genera and absent in others.

Sporangia and gametangia are developed in vegetative cells and become larger than vegetative cells. Asexual reproduction is usually by biflagellate or quadriflagellate zoospores or aplanospores. Sexual reproduction where known, is usually by biflagellate isogametes or anisogametes but is in need of investigation for many species.

REMARKS. Members are found in brackish and marine environments. Species are based on the growth form of the filaments (i.e., if the filaments are consolidated into pseudoparenchyma versus not consolidated and free), differences in cell size and number of pyrenoids, and habitat and host (Nielsen, 1984; Ricker, 1987; Kraft, 2000). O’Kelly and Yarish (1981b) suggested detailed features of sporangial development may be more reliable taxonomic characters.

Four genera are known in the northern Gulf of California.

KEY TO THE GENERA OF ULVELLACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Microscopic, prostrate filaments spreading, remaining free of each other throughout (not coalescing into a pseudoparenchyma) *Entocladia* (in part)
- 1b. Microscopic, disc-shaped to spreading; prostrate filaments either entirely coalesced into a pseudoparenchyma, or partially coalescing in varying degrees with some filaments free 2
- 2a. Crusts initially a single cell layer, developing to 2 to 4 cell layers (polystromatic) centrally and a single cell layer (monostromatic) outward *Ulvella*
- 2b. Crust or sheet-like, a single cell layer thick (monostromatic) throughout 3
- 3a. Filaments originating from a central point; forming a more or less circular disc, with or without filaments extending from margin 4
- 3b. Filaments not originating from a central point, not circular, but forming a crust with irregular outer margins 5
- 4a. Filaments with setae (hair-like structures without nuclei; not always present in field-collected material) *Entocladia* (in part)
- 4b. Filaments without “hairs” or setae *Epicladia*

- 5a. Filaments forming pseudoparenchymatous, sheet-like thallus, with outer noncoalesced to loosely coalesced filaments; percurrent axes sometimes visible as primary and lateral branches develop; cells with 1(–3) pyrenoids *Stromatella*
- 5b. Filaments loosely to tightly coalescing in some portions, with outer short to long filaments remaining free of each other; cells with 1–3 (–7) pyrenoids *Entocladia* (in part)

***Entocladia* Reinke**

Entocladia Reinke, 1879:476.

Algae are microscopic prostrate filaments, usually epiphytic on or endophytic within the cell walls of various larger algae, sea grasses, or other aquatic vascular plants. Filaments are either unconsolidated and irregularly branched and free; or may be compacted in varying degrees into a pseudoparenchyma. Cells are quadrate to elongated, with a single nucleus and chloroplast that contains one to several pyrenoids. Hairs or setae-like structures are present (observable in culture, but not always seen in field collections).

Life histories, where known, are with isomorphic sporophytes and gametophytes. Asexual reproduction is by

quadriflagellate zoospores, formed by sequential division in cells near the center of the thallus. Sexual reproduction is by biflagellate isogametes formed in the same manner as zoospores.

REMARKS. *Entocladia* and *Epicladia* are recognized herein; the two usually separated by growth form and if the cells of the filaments have hairs or setae (*Entocladia*) or lack them (*Epicladia*) (see Nielsen, 1980, 1984). This generic separation is problematic; e.g., Kraft (2000) noted that hairs were rarely (if at all) found in field collections, but they have been shown to occur under culture conditions for some species.

Four species of *Entocladia* and two of *Epicladia* are known in the northern Gulf of California.

KEY TO THE SPECIES OF *ENTOCLADIA* AND *EPICLADIA* (ULVELLACEAE) IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Prostrate filamentous thallus disc-shaped (more or less circular) in surface view 4
- 1b. Prostrate filamentous thallus not disc-shaped in surface view 2
- 2a. Filaments free of each other (not consolidated into pseudoparenchyma); cells mostly elongated, some irregular in shape, 3–5 µm wide, 10–40 µm long *Entocladia polysiphoniae*
- 2b. Filaments mostly free, sometimes with portions consolidated to varying degrees to form a pseudoparenchyma 3
- 3a. Filaments mostly free, with portions aggregated (i.e., not closely consolidated); cells variable in shape, squarish to rectangular, most 6–8 µm wide, 6–20 (–35) µm long; 1–3 pyrenoids per cell *Entocladia viridis*
- 3b. Filaments extensively consolidated, spreading and covering host cells; margins with extending filaments; 3–7 pyrenoids per cell *Entocladia* sp. A
- 4a. Disc somewhat circular; inner cells isodiametric, with few to several central cells empty; outer cells narrower, much longer; margin border more or less even *Entocladia marchantiae*
- 4b. Disc irregular in outline, with filaments extending from the margins 5
- 5a. Disc-shaped with only a few, short marginal filaments; central cells 12–16 µm wide; marginal cells 5–9 µm in diameter *Epicladia condensata*
- 5b. Discoid, with fringelike margin of numerous longer filaments; central cells 15–18 µm in diameter; marginal cells 5–7 µm in diameter *Epicladia mexicana*

***Entocladia marchantiae* (Setchell et N. L. Gardner) Cribb**

FIGURE 9A

Pringsheimia marchantiae Setchell et N. L. Gardner, 1924a:720 [as "*P. marchantiae*"], pl. 12: fig. 8; Dawson, 1944:205; González-González et al., 1996:138.

Entocladia marchantiae (Setchell et N. L. Gardner) Cribb, 1995:23, pl. 1: fig. 5; Pedroche et al., 2005:18.

Acrochaete marchantiae (Setchell et N. L. Gardner) Nielsen et McLachan, 1986b:516, figs. 3–14.

Pringsheimiella marchantiae (Setchell et N. L. Gardner) Schmidt et Petrak in Schmidt, 1935:29 [as "*P. marchantiae*"]; Dawson, 1961b:372; Nielsen and McLachan, 1985:511; González-González et al., 1996:138.

Algae microscopic, more or less discoid, 100–120 (–170) μm in diameter; monostromatic pseudoparenchyma with few to several empty central cells (released spores?); outer marginal filaments of 1–7 cells, unbranched or sparsely, alternately branched; some outer filaments free. Cells with a parietal chloroplast and 1(–2) pyrenoids. Central cells isodiametric, (8–)10–20 μm wide. Outer marginal cells narrower and longer (more or less rectangular), (2–)3–5 μm wide and (4–)5–10 μm long. Hairs not observed; reported in culture studies (Nielsen and McLachan, 1986b).

HABITAT. Epiphytic on species of *Laurencia* and *Gracilaria textorii*; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Coronado (Isla Smith), off Bahía de Los Ángeles; La Paz.

TYPE LOCALITY. Epiphytic on *Laurencia*, La Paz, Baja California Sur, Gulf of California.

REMARKS. *Entocladia marchantiae* from Isla Coronado, represents a new record for the northern Gulf (JN-4411; US Alg. Coll. slide 4257). Regarding the species epithet, Nielsen and McLachan (1986b) thought it was named only for Mrs. Marchant and corrected the spelling to “*marchantiae*.” However, Setchell and Gardner (1924a) are rather vague in their species dedication, citing only the collection number (“*Marchant no. 68x*”), then in their introduction “a collection made by Dr. and Mrs. Marchant in 1917” (p. 696), and later acknowledging “our indebtedness to Dr. and Mrs. Marchant...for collections of marine algae” (p. 697). If it can be shown that it was their intention to name the species for both Dr. and Mrs. Marchant, then the species name would be correctable to “*marchantiorum*” (McNeill et al., 2006:Art. 60C.1).

***Entocladia polysiphoniae*
Setchell et N. L. Gardner**

FIGURE 9B

Entocladia polysiphoniae Setchell et N. L. Gardner, 1924a:718, pl. 13: fig. 18; Dawson, 1944:204; Dawson, 1961b:371; Noda, 1968:56, fig. 4; Nielsen, 1972:265; Konno and Noda, 1980:27, fig. 2; Espinoza-Ávalos, 1993:333; González-González et al., 1996:137; Yoshida, 1998:18; Kraft, 2000:518, fig. 3F–H; Pedroche et al., 2005:18; Kraft, 2007:31, fig. 11A–E.

Entocladia viridis sensu Mendoza-González and Mateo-Cid, 1999:45, figs. 37, 38 [non *Entocladia viridis* Reinke, 1879:476].

Algae endophytic, microscopic; composed of irregularly branched filaments, mostly 3–5 μm in width, that

remain free of each other (not consolidated into a pseudoparenchyma) within cells of the host, and covering an area up to 1 mm in diameter. Cells irregularly variable in shape, mostly elongated, 10–40 μm in length and 3–5(–9) μm in width; parietal chloroplast with a single pyrenoid.

Sporangia (?) intercalary in filaments, up to 24 μm in diameter, numerous, formed at irregular intervals.

HABITAT. Endophytic in *Polysiphonia*.

DISTRIBUTION. Gulf of California: El Desemboque to Guaymas; La Paz. Pacific coast: Oaxaca; Japan.

TYPE LOCALITY. Endophytic in cell walls of *Polysiphonia marchantiae* (now *P. johnstonii*), Guaymas, Sonora, Gulf of California.

REMARKS. In the Gulf, *Entocladia polysiphoniae* is only known from the type specimen and a few other collections. It is distinguished by filaments that remain free of each other (never consolidated) and branches that can develop, often at right angles, from the middle or toward the ends of intercalary cells. *Entocladia polysiphoniae* has also been reported from Japan (Noda, 1968, 1975; Konno and Noda, 1980; Yoshida, 1998) and from Lord Howe Island, Australia (Kraft, 2000, 2007). Further collections of Gulf *E. polysiphoniae* will be helpful in accessing its life history, taxonomic, and phylogenetic status.

***Entocladia* sp. A**

FIGURE 9C

Algae microscopic, cells of filaments coalescing forming a spreading, monostromatic pseudoparenchyma; up to 2 mm across; sometimes completely surrounding cell of host *Cladophora*; cells of outer marginal filaments mostly coherent or occasionally with some outermost filaments extending distally up the host cell and remaining free. Cells with a parietal chloroplast and (2–)3–7 pyrenoids; cells mostly irregularly squarish or polygonal, (8–)10–16 μm in diameter; cells of outer filaments more or less rectangular, elongated, rectilinear, 15–30 μm long and 8–12 μm wide. Hairs not observed in Gulf specimen.

HABITAT. Endophytic within lower cells of *Cladophora*; shallow subtidal.

DISTRIBUTION. Gulf of California: Islas de Los Gemelos (west island), vicinity of Bahía de Los Ángeles.

REMARKS. The northern Gulf specimen of *Entocladia* sp. A (JN-4492; US Alg. Coll. slide 4154) is apparently an unknown species. It is somewhat similar to *Entocladia robustum* Cribb (1995; = *Endoderma viride* f. *major* Børgesen, 1920) in cell shape and size and the number of pyrenoids per cell. It is also remotely similar to

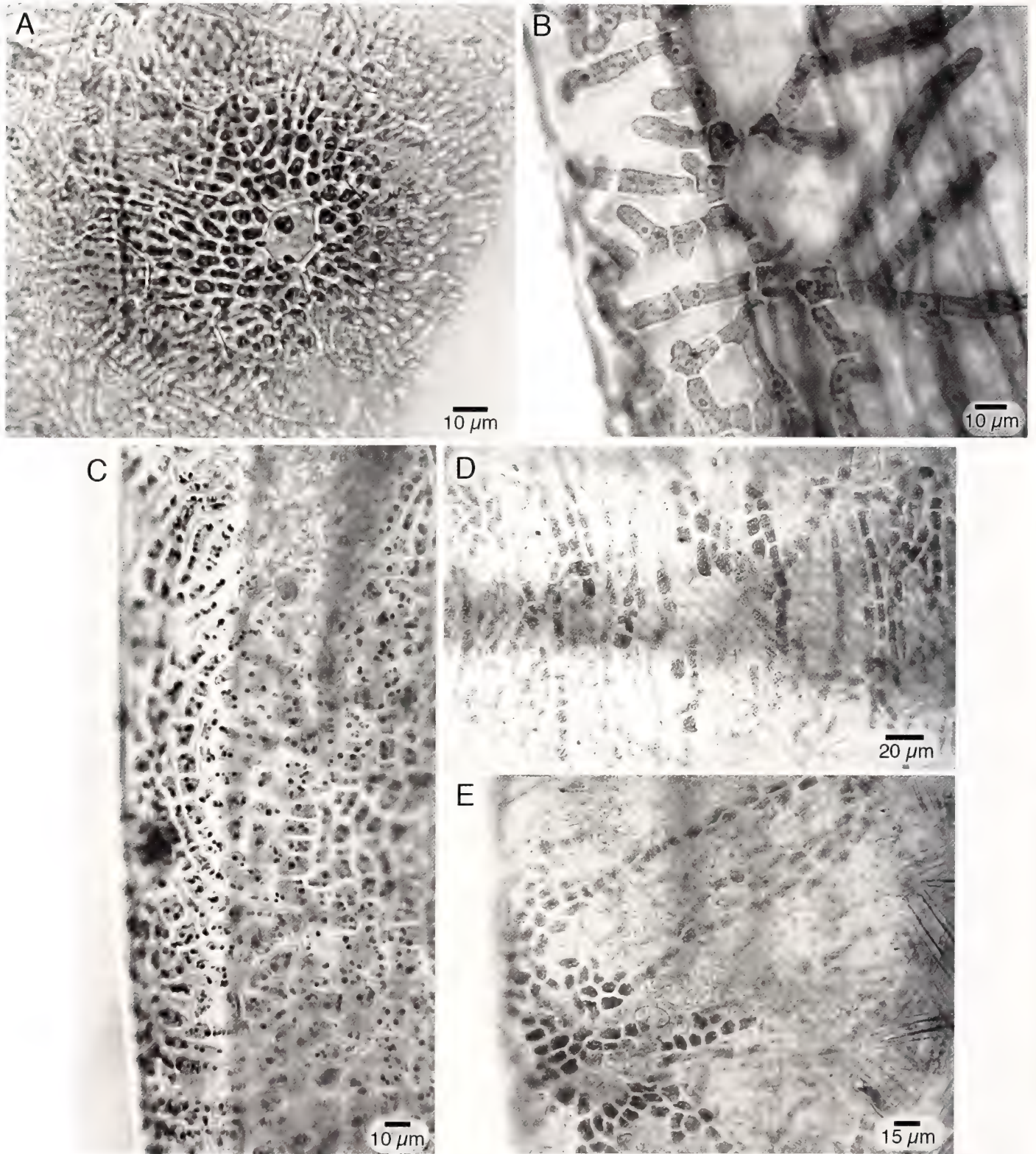


FIGURE 9. Species of *Entocladia*. A. *Entocladia marchantiae*: Surface view, disc of consolidated cells, isodiametric in interior (some central cells empty), and narrower, elongated cells toward margin; epiphytic on *Gracilaria textorii* (JN-4411b). B. *Entocladia polysiphoniae*: Free filaments, branching mostly from midregions of intercalary cells; epiphytic on *Polysiphonia* (JN-5190). C. *Entocladia* sp. A: Filaments aggregated into loose pseudoparenchyma; several pyrenoids per cell; covering cell wall of host *Cladophora* (JN-4492b). D, E. *Entocladia viridis*: Free filaments extending from aggregated cells; growing horizontally across a basal cell of *Chaetomorpha aerea* (JN-5180b).

Entocladia velutina Cribb (1995) in cell shape and number of pyrenoids per cell, but the cell sizes are smaller in the Gulf *Entocladia* sp. A, and the hair cells described in the Australian type (Heron Island, Queensland) were not observed.

***Entocladia viridis* Reinke**

FIGURE 9D,E

Entocladia viridis Reinke, 1879:476, pl. VI: figs. 6–9; Setchell and Gardner, 1920b:289; Smith, 1944:35; Dawson, 1957a:2; Dawson, 1961b:372; Dawson and Neushul, 1966:174; Abbott and Hollenberg, 1976:64, fig. 18; O’Kelly and Yarish, 1981a:549, figs. 1–4; O’Kelly and Yarish, 1981b:33, figs. 1–12; O’Kelly and Floyd, 1983:153, figs. 1–29; Huerta-Múzquiz -Múzquiz and Mendoza-González, 1985:42; Ortega et al., 1987:77, pl. 13: fig. 52; Santelices and Abbott, 1987:5; Cribb, 1995:25, pl. 5: figs. 1–3; González-González et al., 1996:286; León-Tejera and González-González, 2000:327 [as “*E. aff. viridis*”]; Kraft, 2000:517, fig. 3D,E; Abbott and Huisman, 2003a:283, fig. 13; Abbott and Huisman, 2004:43, fig. 4A; Pedroche et al., 2005:18; Mateo-Cid et al., 2006:58; Kraft, 2007:30, fig. 10A–D.

Endoderma viride (Reinke) Lagerheim, 1883:74; Collins, 1909b:279; Børgesen, 1920:416, figs. 397–399.

Endoderma viride (Reinke) De Toni, 1889:209.

Acrochaete viridis (Reinke) R. Nielsen, 1979:442, fig. 2A–L; Nielsen and McLachan, 1986a:809; Mendoza-González et al., 1994:111.

Phaeophila viridis (Reinke) Burrows in Parke and Dixon, 1976:568.

Algae minute epiphytes, of irregularly branched filaments, mostly 5–8(–10) μm in width, usually remaining free (not coalesced; or slightly coalescing to varying degrees) on cell walls of host. Cells variable in shape, inner cells squarish to rectilinear, and outer cells elongate, 5–8(–10) μm in diameter and (5–)10–20(–30) μm long. Cells contain a parietal chloroplast with up to 3 pyrenoids.

HABITAT. Growing on outer cell walls of *Acartabularia*, *Chaetomorpha*, and probably other algae; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Estero de Bacorehuis (Laguna Agiabampo) to Bahía Balandra (north of La Paz); Playa Los Cerritos (vicinity of Mazatlán), Sinaloa. Pacific coast: British Columbia to southern California; Oaxaca; Hawaiian Islands; Rapa Nui (Easter Island); Galápagos Islands.

TYPE LOCALITY. Napoli (Naples), Italy.

REMARKS. *Entocladia viridis* may be a species complex of more than one taxon (Kylin, 1938; Kraft, 2000). O’Kelly and Yarish (1981b) also noted *Entocladia viridis* is a polyphyletic assemblage and that specimens from California reported by Setchell and Gardner (1920b) as “*E. viridis*” are possibly another species. Reports of *Entocladia viridis* in the Gulf of California (Huerta-Múzquiz and Mendoza-González, 1985; Ortega et al., 1987; Mateo-Cid et al., 2006) are probably this species in the sense of Smith (1944) and Abbott and Hollenberg (1976).

***Epicladia* Reinke**

Epicladia Reinke, 1889b:31.

Algae are microscopic, uniseriate branched filaments, usually growing as endophytes or epiphytes on various algae and sea grasses or epizoid on invertebrates; also on shells. Most species are prostrate and composed of either irregularly branched filaments from the center portion or of cells compacted into pseudoparenchyma, usually with short to long filaments extending from the margin. Hairs and setae are not present. Vegetative cells are uninucleate with a single parietal, platelike or band-shaped chloroplast and one or more pyrenoids.

Sporangia are formed by sequential division in vegetative cells near the center of the thallus; pyriform-shaped, biflagellate or quadriflagellate zoospores exit through a papilla or short tube. Sexual reproduction is by biflagellate isogametes formed in a similar manner as the zoospores.

REMARKS. Although *Epicladia* has been considered a synonym of *Entocladia* by O’Kelly and Yarish (1981a, 1981b), Nielsen (1980, 1984) concluded the genera were distinct, with species referred to *Epicladia* differing primarily from those of *Entocladia* by the absence of hairs or seta in both nature and in culture.

There are two species of *Epicladia* known from the Gulf of California (see “Key to the species of *Entocladia* and *Epicladia*”).

***Epicladia condensata* (Setchell et N. L. Gardner) J. N. Norris, comb. nov.**

FIGURE 10A,B

Entocladia condensata Setchell et N. L. Gardner, 1924a:718, pl. 12: figs. 4, 5; Dawson, 1944:204; Dawson, 1961b:371; Espinoza-Ávalos, 1993:333; González-

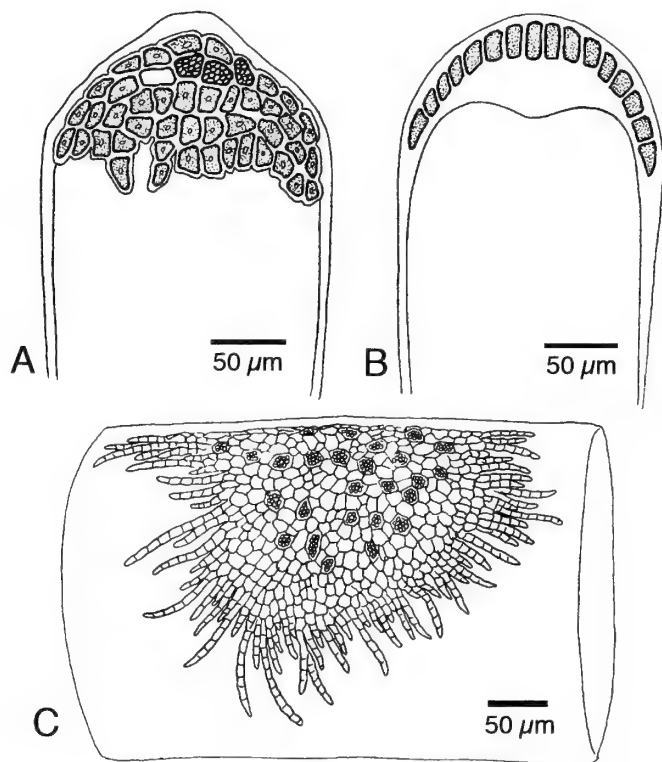


FIGURE 10. Species of *Epicladia*. A, B. *Epicladia condensata*: A. Surface view, endophytic on upper portion of a *Codium* utricle (after Setchell and Gardner, 1924a: pl. 12, fig. 4). B. Longitudinal section of a *Codium* utricle showing *E. condensata* within the utricle cell wall (after Setchell and Gardner, 1924a: pl. 12, fig. 5). C. *Epicladia mexicana*: Surface view, pseudoparenchymatous center with scattered sporangia, and free filaments extending from around the margin (after Setchell and Gardner, 1924a: pl. 19, fig. 57).

González et al., 1996:137; Pedroche et al., 2005:17; Pacheco-Ruíz et al., 2008:201.

Algae disc-shaped, with compacted cells in the center and a few short filaments extending outward from the margin. Hairs or setae absent. Vegetative cells in center, angular, 12–16 µm in diameter in surface view; cells of short marginal filaments, 7–9 µm in diameter.

Sporangia (?) slightly larger than central vegetative cells.

HABITAT. Endophytic within the cell wall of utricles of various species of *Codium*; intertidal.

DISTRIBUTION. Gulf of California: Puerto Libertad; Bahía San Francisquito; Isla San Esteban.

TYPE LOCALITY. In utricles of *Codium*; Bahía San Francisquito, Baja California, Gulf of California.

REMARKS. Apparently a Gulf endemic, *Epicladia condensata* is found in the utricles of *Codium*.

Similarly, *Acrochaete codicola* (Setchell et N. L. Gardner) O'Kelly (in Gabrielson et al., 2006; basionym: *Entocladia codicola* Setchell et N. L. Gardner, 1920a, 1920b) from the Pacific coast is found in the utricles of *Codium fragile* (Suringar) Hariot (1889). *Epicladia condensata* is disc-shaped, with an irregular margin, and composed of a much larger central pseudoparenchyma of cells (12–16 µm in diameter) that is more compacted throughout and has only a few short marginal filaments of 1–2 angular cells (7–9 µm in diameter) (Setchell and Gardner, 1924a), thus differing from *A. codicola*, which has a smaller central pseudoparenchyma and numerous, free (not adjoined), much longer, branched filaments that are up to at least six, long, cylindrical cells (3–4 µm in diameter, 7.5–21 µm in length) (see Smith, 1944; Abbott and Hollenberg, 1976; both as "*Entocladia codicola*").

***Epicladia mexicana* (Setchell et N. L. Gardner)
J. N. Norris, comb. nov.**

FIGURE 10C

Entocladia mexicana Setchell et N. L. Gardner, 1924a:719, pl. 19: fig. 57; Dawson, 1944:205; Dawson, 1961b:371; Espinoza-Ávalos, 1993:333; González-González et al., 1996:137; Pedroche et al., 2005:18; Pacheco-Ruíz et al., 2008:201.

Algae endophytic, disc-shaped, 350–450 µm in diameter; pseudoparenchymatous in center, and with numerous free filaments around the margin. Cells of pseudoparenchymatous center of thallus 15–18 µm in diameter; cells of marginal filaments, 7.5–17.5 µm long and 5–7 µm in diameter.

Sporangia (?) numerous, scattered, up to 20 µm in diameter.

HABITAT. Endophytic within *Chaetomorpha antennina* and *Valoniopsis hancockii*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; La Paz.

TYPE LOCALITY. Endophytic in cell wall of *Chaetomorpha*; La Paz, Baja California Sur, Gulf of California.

REMARKS. Although not well known, *Epicladia mexicana* is apparently an endemic species in the Gulf of California.

***Stromatella* Kornmann et Sahling**

Stromatella Kornmann et Sahling, 1985:223.

Stromatella Kornmann et Sahling, 1983:10, *nom. inval.*

[note that lacking their selection of a species as the gene-

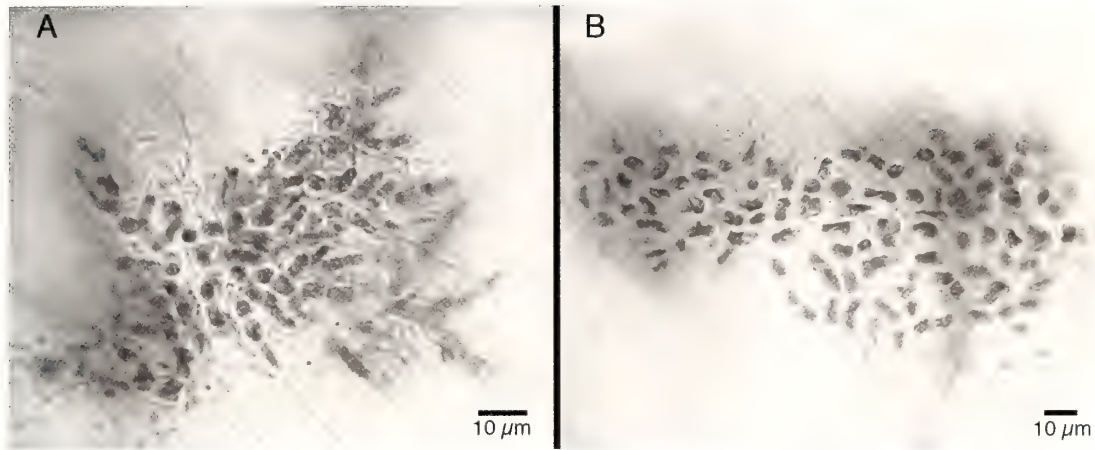


FIGURE 11. *Stromatella monostromatica*, epiphytic on *Polysiphonia* (JN-4442b): A. Aggregation of cells forming monostromatic pseudoparenchyma; margins irregular with branching peripherally extending filaments. B. Filaments consolidate forming a single-layer pseudoparenchyma spreading over host; percurrent axes barely discernible.

riotype, the first use of the generic name was invalid (see McNeill et al., 2006:Art. 37.1); *Stromatella* was later validly published by Kornmann and Sahling (1985)].

Algae are microscopic filaments, forming monostromatic crusts that grow as prostrate epiphytes on various algae. Cells of the filaments coalesce to form a single-layer pseudoparenchyma with laterally branched, marginal filaments that are loosely aggregated (not coalescing). Cells have a single chloroplast with one pyrenoid.

Reproduction is by the conversion of vegetative cells into sporangia and the subsequent division into eight zoospores. Sporangia develop progressively from the interior of the pseudoparenchyma outward toward the margin.

REMARKS. Although superficially similar to *Ulvella*, *Stromatella* differs in vegetative anatomy (monostromatic throughout) and reproductive characters (Kornmann and Sahling, 1983). Cells of *Stromatella* have a chloroplast with one pyrenoid, whereas in *Ulvella* there are 0–3 pyrenoids per cell. The taxonomic status of *Stromatella* was subsequently corroborated by studies of Nielsen (1988b).

There is one species in the northern Gulf of California.

***Stromatella monostromatica* (P. J. L. Dangeard)
Kornmann et Sahling**

FIGURE 11A,B

Ulvella monostromatica P. J. L. Dangeard, 1965:45, pl. I: figs. 8–13, pl. III: fig. 1.

Stromatella monostromatica (P. J. L. Dangeard) Kornmann et Sahling, 1985:223 [footnote]; Nielsen, 1988a:255, fig. 22a–h; Nielsen, 1988b:427, figs. 1–17; Kraft, 2000:516, fig. 3B,C; Abbott and Huisman, 2003a:283, fig. 12; Abbott and Huisman, 2004:43, fig. 4B; Kraft, 2007:23, fig. 7A–C.

Stromatella monostromatica (P. J. L. Dangeard) Kornmann et Sahling *comb. inval.*, 1983:10, fig. 4.

Algae epiphytic, monostromatic crusts. Interior of compact angular cells, 8–12 µm long and 6–8 µm in width, forming a pseudoparenchyma; with filaments at margins loose and unconsolidated, laterally branched, of narrow, elongated cells, 6–15 µm long and 4–5 µm in width. Cells with a single pyrenoid.

HABITAT. Epiphytic on *Polysiphonia*, *Bryopsis*, and probably other algae; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Coronado (Isla Smith) and Isla la Ventana, Bahía de Los Ángeles. Pacific coast: Washington; Hawaiian Islands.

TYPE LOCALITY. Collioure, Pyrénées-Orientales, southern France.

REMARKS. Apparently a highly variable species (Nielsen, 1988a, 1988b), *Stromatella monostromatica* has been reported on many different hosts and from a wide range of habitats and geographical localities. The collections from Isla la Ventana (JN-4442b; US Alg. Coll. slide 4160) and Isla Coronado (JN-4401; US Alg. Coll. slide 4142), off Bahía de Los Ángeles, are the first records for

the Gulf of California and are similar to thalli reported from Hawaii (Abbott and Huisman, 2003a, 2004) and Australia (Kraft, 2000, 2007).

***Ulvella* P. Crouan et H. Crouan**

Ulvella P. Crouan et H. Crouan, 1859:288.

Algae are microscopic to minute, prostrate, more or less circular discs, usually less than 2 mm in diameter, and attached directly (without rhizoids) to algae, sea grasses, or other substratum. Initially, a monostromatic disc of rounded to angular cells in the center with outward radiating, bifurcate filaments. As development continues, the central portion of the disc becomes 2–4 cell layers thick, while the outer portion remains monostromatic. Cells are uninucleate and have a parietal chloroplast with (0–)1–3 pyrenoids. Hairs are usually not present in field collections but may develop under certain culture conditions (Nielsen, 1977; Notoya, 1983).

KEY TO THE SPECIES OF *ULVELLA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Central cells mostly rounded; marginal cells 6–10 μm wide, and <20 μm in length *U. lens*
 1b. Central cells mostly elongate; marginal cells thinner and longer, 3–5 μm wide, usually >20 μm in length . . . *U. setchellii*

***Ulvella lens* P. Crouan et H. Crouan**

FIGURE 12A

Ulvella lens P. Crouan et H. Crouan, 1859:288, pl. 22: fig. E; Nielsen, 1977:1, figs. 1–14; Kornmann and Sahling, 1983:16, Notoya, 1983:9, fig.1; Burrows, 1991:130; Hoffman and Santelices, 1997:42, fig. 2 (1–2); Yoshida, 1998:19; Kraft, 2000:514, figs. 2D–G; Abbott and Huisman, 2003a:283, fig. 9; Abbott and Huisman, 2004:44, fig. 4C; Kraft, 2007:25, fig. 8A–D.

Algae minute prostrate epiphytes, disc-shaped, usually less than 500 μm in diameter; initially monostromatic, then becoming polystromatic, up to 2–3 cell layers, in the central portion; outer portions of 1 cell layer. Cells of central portion, rounded to angular, (6–)10–12 μm in diameter; outer cells and margin cells, elongate and narrower, 10–18 μm in length, 6–10 μm in width; a few marginal cells bifid (more readily seen in smaller, developing specimens). Cells either lacking pyrenoids or with a single pyrenoid.

Sporangia not observed in Gulf specimens (sporangia, slightly larger than vegetative cells, develop from central

Reproduction by quadriflagellate zoospores has been reported (Nielsen, 1977).

REMARKS. The genera distinction of *Ulvella* and *Pseudulvella* Wille (1910) has long been considered problematic (e.g., Dangeard, 1931), with the nature of the zoospores (quadriflagellate in *Ulvella* and biflagellate in *Pseudulvella*) the only apparent character separating them (Papenfuss, 1962; Yarish, 1975). The two were merged into a single genus by Nielsen (1977), but later she noted that not all of the species of *Pseudulvella* belong in *Ulvella* (Nielsen in Silva et al., 1996a:725). Recent studies of the generitype, *Pseudulvella americana* (Snow) Wille (1910), have shown the two to be distinct genera, belonging not only to different families but in different classes of green algae (Sanchez-Puerta et al., 2006). The taxonomic status of the species of *Ulvella* in the Gulf of California, as well as those on the Pacific coast (Abbott and Hollenberg, 1976), needs to be critically studied.

Two species of *Ulvella* are now known in the northern Gulf of California.

cells; zoospores released through a hole in top of sporangium [Nielsen, 1977:1, fig. 12].

HABITAT. Epiphytic on *Cladophora* and probably on other algae as well and possibly epizoid on mollusk shells; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda. Pacific coast: Japan; Hawaiian Islands; Chile.

TYPE LOCALITY. Rade de Brest, Finistère, Atlantic coast of France (Burrows, 1991:130).

REMARKS. *Ulvella lens* is now reported for the Gulf of California (EYD-271; US Alg. Coll. slide 4165) but is probably more common in the Gulf than the current record indicates. Thalli of northern Gulf *U. lens* are relatively small in diameter but have been reported up to 2 mm in diameter elsewhere. Although similar to *U. setchellii*, *U. lens* differs in having rounded to angular central cells and shorter outer cells.

The Pacific coast *Ulvella applanata* (Setchell et N. L. Gardner) G. R. South et Tittley (1986; = *Pseudulvella applanata* Setchell et N. L. Gardner, 1920a; Abbott and Hollenberg, 1976) has been considered to be a synonym of *U. lens* (see Guiry and Guiry, 2008); however,

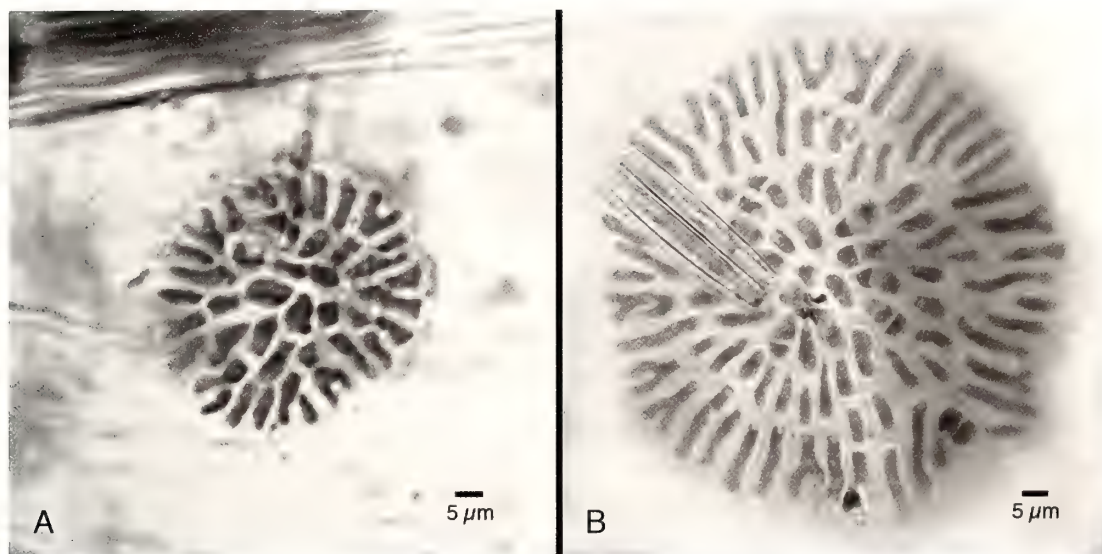


FIGURE 12. Species of *Ulvella*. A. *Ulvella lens*: Immature specimen, nearly circular with some bifurcate cells at disc margin; epiphytic on *Cladophora* (EYD-271). B. *Ulvella setchellii*: Disc with elongate cells outward from central region and long, narrow, commonly bifurcate marginal cells; epiphytic on *Cladophora microcladioides* (EYD-46-980).

the taxonomic relationship of these two taxa needs to be reinvestigated.

***Ulvella setchellii* P. J. L. Dangeard**

FIGURE 12B

Ulvella setchellii Dangeard, 1931:317, figs. 1D,1E, pl. 1; Feldmann, 1937:188, fig. 9C; Smith, 1944:38; Hollenberg, 1948:155; Dawson, 1961b:372; Abbott and Hollenberg, 1976:59, fig. 9; Nielsen, 1977:3, figs. 15–21; Stewart and Stewart, 1984:140; Stewart, 1991:25; González-González et al., 1996:140; Cribb, 1995:28, pl. 6: fig. 5, pl. 7: fig. 7; Kraft, 2000:514, fig. 3A; Abbott and Huisman, 2003a:283, fig. 10; Abbott and Huisman, 2004:45, fig. 4D; Pedroche et al., 2005:18; Kraft, 2007:27, fig. 9A–E.

Ulvella lens sensu Setchell and Gardner, 1920b:295, pl. 33; Setchell and Gardner, 1930:138; Dawson, 1946b:169; Mendoza-González et al., 1994:111 [non *Ulvella lens* P. Crouan et H. Crouan 1859:288].

Algae minute epiphytes, circular to irregularly disc-shaped, 30–300 µm in diameter; initially monostromatic, later becoming polystromatic of 2–4 cell layers in central portion; outer portions of 1 cell layer. Cells of central portion angular to slightly elongate, mostly 5–8 µm in

diameter. Marginal cells of Gulf specimens, long and narrow, 12–27 µm long and 3–5 µm wide, most terminating with divided tips (appearing Y-shaped, with one side usually longer than the other). Cells uninucleate, chloroplast with 2–3 pyrenoids.

Sporangia not observed in Gulf specimens (central cells become sporangia and develop conical protuberances that function as exit tubes for zoospores [Nielsen, 1977:4, fig. 16]).

HABITAT. Epiphytic on *Cladophora* and probably on other algae as well; intertidal.

DISTRIBUTION. Gulf of California: Bahía Agua Dulce (Bahía Tecomate), Isla Tiburón; Bahía Kino; Playa Los Cerritos (vicinity Mazatlán), Sinaloa. Pacific coast: British Columbia to Isla Guadalupe (Baja California).

SYNTYPE LOCALITIES. Roscoff, Finistère, France (on *Polysiphonia*); Croisic, Loire Inférieure, France (on *Phyllophora*); and Pacific Grove, Monterey County, California (on *Laurenica*).

REMARKS. Specimens of *Ulvella setchellii* from Bahía Agua Dulce, Isla Tiburón (US Alg. Coll. slide 892), epiphytic on *Cladophora* (EYD-46-980), and Bahía Kino (US Alg. Coll. slide 4166), also epiphytic on a *Cladophora* (EYD-2928), represent the first records for the northern Gulf of California. Although the cell diameters of Gulf *U. setchellii* and *U. setchellii* from California (e.g., Abbott and Hollenberg, 1976) are in general agreement, the outer

marginal cells differ in length; Gulf *U. setchellii* are not as long (only up to 27 µm) compared to those from California (up to 50 µm in length). This may be a reflection of a smaller, immature state of the Gulf specimens.

PHAEOPHILALES

Phaeophilales Chappell, O'Kelly, L. W. Wilcox, et G. L. Floyd, 1990:516.

Algae are microscopic, multicellular, and filamentous. Vegetative cells contain a single nucleus.

The order is defined on developmental and ultrastructural characters. Reproductive development: initially the zoosporangia become multinucleate, and then the zoospores are formed by simultaneous cleavage (O'Kelly and Yarish, 1981a). Zoospore ultrastructure: reproduction is by scaleless, quadriflagellate zoospores that are formed in the zoosporangia. The anterior-most pair of flagellar basal bodies in the zoospores has simple, convex terminal caps.

REMARKS. On the basis of the ontogeny of the zoosporangia and ultrastructural characters of the zoospores of the generitype *Phaeophila dendroides*, Chappell et al. (1990) removed the genus from the Ulvellaceae and established a new family and order. Although the Phaeophilales and Phaeophilaceae are recognized herein, their status is problematic. O'Kelly et al. (2004) noted that while their molecular phylogenetic reconstructions supported six lineages, including a *Phaeophila* lineage, it may be premature to interpret their higher level classification, including the proposed order and family of Chappell et al. (1990).

PHAEOPHILACEAE

Phaeophilaceae Chappell, O'Kelly, L. W. Wilcox, et G. L. Floyd, 1990:516.

Algae are branched uniseriate filaments, with the characteristics of the order.

REMARKS. The taxonomic status of the family is unresolved (O'Kelly et al., 2004; see also Remarks for Phaeophilales).

A monotypic family, its single genus is represented in the northern Gulf of California.

Phaeophila Hauck

Phaeophila Hauck, 1876:56.

Algae minute, endophytic or epiphytic, and composed of branching uniseriate filaments, with cells that bear hairs (without a septa separating them from the cell). Cells contain parietal chloroplasts with few to several pyrenoids.

Zoosporangia can be similar in size to the vegetative cells or slightly larger and are often terminal on the branches. The zoospores are quadriflagellate.

REMARKS. Although Nielsen (1972) recognized 11 species in *Phaeophila* (some of which have been subsequently transferred to other genera [Nielsen, 1983, 1988a; Nielsen et al., 1995]), most have considered it to be a monotypic genus (e.g., O'Kelly and Yarish, 1981a; Chappell et al., 1990; Kitayama and Yoshida, 1992). More recently, O'Kelly et al. (2004) noted it is unclear whether any species other than *P. dendroides* actually belong in *Phaeophila*. For example, results from culture studies by Moewus (1949) of *Ectochaete ramulosa* L. Moewus (1949; = *Phaeophila ramulosa* (L. Moewus) Nielsen) and by Yarish (1975) of *Endoderma vagans* Børgesen (1920; = *P. vagans* (Børgesen) Nielsen) suggest both are not *Phaeophila* but belong to *Acrochaete* sensu Nielsen (1979).

There is one species in the northern Gulf of California.

Phaeophila dendroides (P. Crouan et H. Crouan) Batters

Ochlochaete dendroides P. Crouan et H. Crouan, 1852:Vol. 3, No. 346; Crouan and Crouan, 1867:128, pl. 8.

Phaeophila dendroides (P. Crouan et H. Crouan) Batters, 1902:13; Taylor, 1945:47; van den Hoek, 1958:212, fig. 6d-f; Dawson, 1961b:371; Nielsen, 1972:255-257, 261, figs. 2, 3, pl. 3a-f; O'Kelly and Yarish, 1981a:549, figs. 1, 15-27; Garbary et al., 1985:43; Mendoza-González and Mateo-Cid, 1986:419; Nielsen, 1987:435, figs. 9C-E, 10A-P; Kitayama and Yoshida, 1992:47, figs. 1-12; Mendoza-González and Mateo-Cid, 1992:23; Servièrre-Zaragoza et al., 1993:482; Cribb, 1995:21, pl. 1: fig. 4; González-González et al., 1996:288, 372; Yoshida, 1998:21, fig. 1-1F; O'Kelly et al., 2004:789-798; Wysor, 2004:214; Pedroche et al., 2005:19; Mateo-Cid et al., 2006:58; Tribollet et al., 2006: 292-303; Servièrre-Zaragoza et al., 2007:7.

Phaeophila engleri Reinke, 1889a:86; Thivy, 1943:245, pls. 1, 2; Taylor, 1945:46; Dawson, 1961b:371; Earle, 1972:85; León-Tejera and González-González, 1993:498; González-González et al., 1996:372; Mendoza-González and Mateo-Cid, 1998:24.

Minute algae of uniseriate filaments, irregularly alternate or oppositely branched; endophytic or epiphytic, endoeplithic or penetrating shells or dead coral. Cells elongated, cylindrical, (5–)7–25 μm in diameter and 15–55 μm long; some may be swollen (subglobose) up to 25 μm in diameter; with parietal chloroplast with 1–13 pyrenoids; and wavy setae (hairs), up to 400 μm long and (1–)2–5 μm in diameter.

Sporangia 10–40 μm in diameter, with an emission tube, 3.5–7.7 μm in diameter and up to 4 times longer than diameter of sporangium.

HABITAT. In shells, coral rubble, and crustose corallines; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas. Pacific coast: British Columbia to Washington; Isla Clarión (Islas Revillagigedo); Isla María Magdalena (Islas Tres Marías), Nayarit to Oaxaca; Panamá; Hawaiian Islands; Galápagos Islands.

TYPE LOCALITY. Brest, Finistère, France.

REMARKS. *Phaeophila dendroides* is usually reported to be within mollusk or barnacle shells and crustose corallines. However in the northern Gulf it was reported as epiphytic on non-calcareous algae, i.e., on “*Laurencia*” (Mendoza-González and Mateo-Cid, 1986) and *Chaetomorpha* (Mateo-Cid et al., 2006).

ULVALES

Ulvales Blackman et Tansley, 1902:136.

Algae are multicellular and consist of biseriate filaments or monostromatic or distromatic thalli that are tubular or compressed or form partly to completely flattened blades. Growth is by intercalary cell division. Cells are uninucleate, with a single laminate or cup-shaped chloroplast and one or more pyrenoids.

Life histories are generally isomorphic with phases of morphologically similar asexual and sexual thalli, but a few species are known to be heteromorphic, with dissimilar gametophytes and sporophytes. Asexual reproduction is by bi- or quadriflagellate zoospores, which are formed within cells. Many can also reproduce vegetatively by fragmentation. Sexual reproduction may be isogamous, anisogamous, or oogamous.

One family is well represented in the northern Gulf of California.

ULVACEAE

Ulvaceae Lamouroux ex Dumortier, 1822:71.

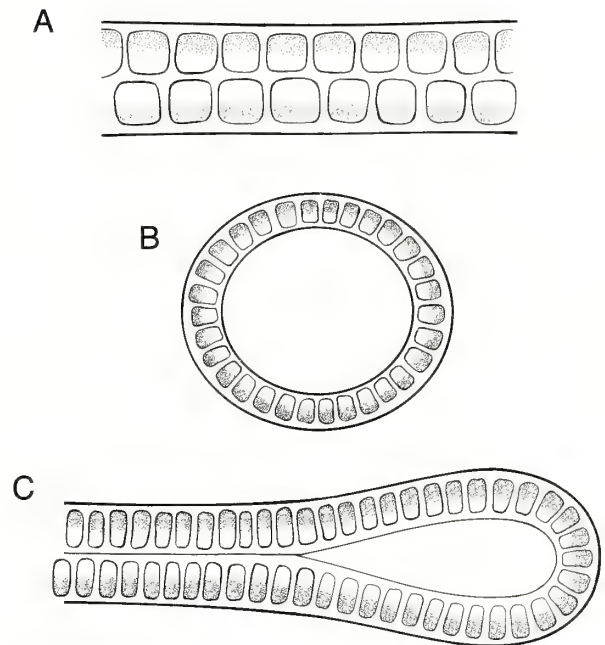


FIGURE 13. *Ulva* anatomy, diagrammatic transections: A. *Ulva* sect. *ulva*: Flat blade of two cell layers throughout. B, C. *Ulva* sect. *enteromorpha*: B. Cylindrical, hollow, and one cell layer throughout. C. Flattened blade of two cell layers, with hollow, one-cell-layer margins. (drawn by Alice R. Tangerini, NMNH)

Most members of the Ulvaceae are marine species that are membranous and exhibit high morphological variability within species, often overlapping between species. They may be (1) flat, distromatic (two cells thick throughout; Figure 13A), and entire, divided, or branched, with smooth, ruffled, or puckered surfaces; (2) tubular to compressed, monostromatic (one cell thick throughout; Figure 13B), and simple to extensively branched; or (3) with both a flattened portion (two cell layers) and tubular margins and/or a tubular basal portion (both one cell layer) (Figure 13C). Members are attached to the substratum by a basal disc or rhizoidal outgrowths from basal cells of blade margins.

Asexual reproduction is by biflagellate or quadriflagellate zoospores. For most, where the life history is known, there is an alternation of isomorphic gametophytes and sporophytes. Sometimes a single phase, either gametophytic or sporophytic, is repeated without alternating phases, and for a few the life history is entirely sporophytic. Gametophytes produce biflagellate isogametes or anisogametes.

REMARKS. *Ulva* is a cosmopolitan genus and widespread in distribution throughout the Gulf of

California. The reports of *Blidingia minima* (Nägeli ex Kützing) Kylin (1947b) from La Paz (Huerta-Múzquiz and Mendoza-González, 1985; Rodríguez-Morales and Siqueiros-Beltrones, 1999, both as "*E. micrococca*"), Pacific Baja California (Huerta-Múzquiz, 1978, as "*E. minima* and *E. micrococca*"), and Oaxaca (Huerta-Múzquiz and Tirado-Lizárraga, 1970, as "*E. micrococca*") and *B. marginata* (J. Agardh) P. J. L. Dangeard ex Bliding (1963) from Isla San Benedicto (Islas Revillagigedo), Oaxaca, and Chiapas (Huerta-Múzquiz and Garza-Barrientos, 1975, as "*E. marginata*") establish another genus, *Blidingia* Kylin (1947b), in the southern Gulf and Pacific Mexico.

One genus, *Ulva*, is known in the northern Gulf of California.

***Ulva* Linnaeus**

Ulva Linnaeus, 1753:1163.

Enteromorpha Link in Nees, 1820:5.

Chloropelta Tanner, 1980:129.

Although members are of two basic forms, they can exhibit widely variable morphologies. One group, *Ulva* sect. *ulva*, includes flattened blades of two layers (distromatic) of closely adherent cells with gelatinous walls of varying thickness (Figure 13A). These blades range from narrowly lanceolate to broadly expanded forms and may be entire, irregularly lobed, cuneate, or deeply divided, with most having a smooth surface (some may have perforations or holes), and smooth, ruffled, or dentate margins. The blades are attached to the substratum by a basal holdfast of compacted rhizoidal cells either directly (without stipe) or below a stipitate portion, and/or rhizoidal extensions of cells from the lower portions of the blade that may run between the two cell layers of the blade. Growth is diffuse by cell divisions, primarily along the margins. Vegetative cells are uninucleate, with a single laminate or cup-shaped chloroplast, and usually one pyrenoid. However, rhizoidal cells are often multinucleate.

Most members of the other group, *Ulva* sect. *enteromorpha*, are cylindrical to compressed, hollow, and one cell layer (monostromatic) throughout (Figure 13B), while a few others may be a flat, distromatic blade with margins and/or a basal portion that are hollow and monostromatic (Figure 13C). These may be unbranched or branched (often repeatedly), sometimes with uniseriate or pluriseriate proliferations or branchlets, and are basally attached by a system of rhizoidal nonseptate filaments that form a holdfast or by rhizoids growing from the lower basal cells. These rhizoidal extensions may fill the basal portion of the

thallus to form a solid stipe. Cells are uninucleate with a single (laminate or cup-shaped) chloroplast and one to several pyrenoids; rhizoidal cells are sometimes multinucleate.

Vegetative reproduction can be by fragmentation or by developing new upright thalli from basal cells or persistent holdfasts. Life histories are usually an isomorphic alternation of generations of a diploid sporophyte and haploid gametophytes. Some are capable of parthenogenetic development, and for other species a sexual generation is apparently lacking. All cells of the thallus, except some of basal and rhizoidal cells, are capable of becoming reproductive. Asexual reproduction is by quadriflagellate zoospores or aplanospores produced within the thallus cells. Sexual reproduction is by the formation of biflagellate isogametes or anisogametes. In some species the biflagellated swimmers develop parthenogenetically. Spores, parthenogenetic gametes, and fertilized gametes initially develop into a uniseriate filament that forms a tubular monostromatic germling. As the tube develops, it either (1) remains one cell layer throughout, or becomes partially flattened with or without a hollow basal portion and/or hollow margins (*Ulva* sect. *enteromorpha*) or (2) becomes compressed throughout with the cell walls adhering to form a distromatic blade (*Ulva* sect. *ulva*).

REMARKS. Species of *Ulva* are found worldwide in marine, estuarine, and freshwater habitats. While most are attached, some become unattached and can be free-floating or form mats on intertidal mud and sand flats. Other unattached species sink and grow in shallow to deep subtidal waters (e.g., one species formed extensive meadows at 650 m depths in the Hawaiian Islands; Sylvia A. Earle, NOAA [currently with Deep Ocean Exploration and Research], personal communication).

Species concepts of the "*Ulva-Enteromorpha* complex" are based on morphology and anatomy and are complicated by a high degree of plasticity. Characters primarily used to separate the species are (1) morphological, if cylindrical, compressed or flattened, entire or branched, and smooth or dentate margins; (2) anatomical, one or two layers thick; and (3) cytological, such as cell shape and arrangement (regularly or irregularly arranged), dimensions and thickness of cell walls (in transections and surface views), chloroplast shape, and number of pyrenoids. Many studies have shown these characters to be highly variable within species, varying with age, reproductive condition, and influenced by ecological factors such as wave exposure, tidal factors, currents, temperature, salinity, and light and biotic factors such as grazing or microorganisms in seawater (e.g., Provasoli and Pintner, 1964, 1980, 1981; L. Fries, 1975; Bonneau, 1977).

Studies of field-collected specimens, combined with morphological and reproductive details, cytological developmental patterns in culture, and the apparent inability of species to interbreed, have also been used to evaluate species concepts (Bliding, 1963, 1968; Koeman and van den Hoek, 1981, 1982a, 1982b, 1984; Hoeksema and van den Hoek, 1983; Tanner, 1986; Phillips, 1988). Originally considered a single genus by Linnaeus (1753), it was Link (in Nees, 1820) who divided *Ulva* and described the genus *Enteromorpha*. Since then, it has long been suggested that *Enteromorpha* and *Ulva* are closely related, perhaps the same genus. Recent molecular analyses support that they are a single genus (Tan et al., 1999; Shimada et al., 2003; Hayden et al., 2003; Hayden and Waaland, 2004).

Two Asian species, potentially invasive, have been recently reported in Pacific Mexico. *Ulva fasciata* Delile

(1813), apparently introduced (Mateo-Cid and Mendoza-González, 2003), is reported from Pacific Baja California and Sinaloa to Oaxaca (R. Aguilar-Rosas et al., 2005a). A Japanese species, *U. pertusa* Kjellman (1897), first reported in southern California (Hayden and Waaland, 2004), has now been identified in northwest Baja California (R. Aguilar-Rosas et al., 2008). Hopefully, continued monitoring and measures taken, if necessary, will prevent their introduction and spread into the Gulf of California.

A broadly expanding species, *U. expansa* (Setchell) Setchell et N. L. Gardner (1920a), has been reported in the southern Gulf, from Bahía de La Paz (Howe, 1911, as "*U. fasciata* f. *expansa*"; Huerta-Múzquiz and Mendoza-González, 1985; Rocha-Ramírez and Siqueiros-Beltrones, 1991; Cruz-Ayala et al., 2001; Pedroche et al., 2005).

Twelve species of *Ulva*, in two separate morphological sections, are present in the northern Gulf of California.

KEY TO THE SPECIES OF *ULVA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli flat, linear to rounded blades; 2 cell layers thick throughout [Figure 13A] *Ulva* sect. *ulva* 2
- 1b. Thalli either: tubular to compressed and hollow and 1 cell layer throughout; or with upper flat or blade-like portion of 2 cell layers with hollow margins of 1 cell layer, and a tubular hollow basal portion of 1 cell layer [Figure 13B,C]
 *Ulva* sect. *enteromorpha* 7
- 2a. Blades mostly less than 2 cm tall; in small clumps *U. californica* (in part)
- 2b. Blades mostly over 5 cm tall; usually not in clumps 3
- 3a. Cells in transection of middle portion of blade, quadrate to only slightly elongate *U. lactuca*
- 3b. Cells in transection of middle portion of blade, subquadrate to anticlinally elongate 4
- 4a. Blades digitate, with a lower basal or bicular portion and up to 6 lanceolate segments tapering upward *U. nematoidea*
- 4b. Blades not digitate, either orbicular to wider than tall or linear and much taller than wide, entire or divided, with basal portion narrowed toward base 5
- 5a. Blades linear, up to 6 times taller than wide, often spirally twisted with ruffled margins *U. californica* (in part)
- 5b. Blades not linear; obovate (broadest near upper end) or wider than tall 6
- 6a. Blades obovate and deeply lobed; margins smooth; transection, thicker in central portion, of cells up to 2 times taller than wide *U. lobata*
- 6b. Blades orbicular (circular and flattened) to wider than tall; margins usually dentate; in transection, more or less same thickness throughout, of elongated cells, up to 3 times taller than wide *U. rigida*
- 7a. Thalli bladelike; flattened upward (2 cells thick), with hollow (1 cell thick) margins and/or tubular basal portions
 *U. linza*
- 7b. Thalli tubular to compressed, simple to much branched; hollow and 1 cell layer throughout 8
- 8a. Thalli more or less tubular throughout; axes and branches usually densely covered with numerous short branchlets and spinelike projections *U. acanthophora*
- 8b. Thalli tubular to compressed, simple and unbranched to branched; axes and branches without spiny projections; short branchlets, if present, not dense 9
- 9a. Cells in surface view irregularly arranged throughout (not arranged in longitudinal rows in any part of thallus) 10
- 9b. Cells in surface view in distinct to more or less clearly arranged longitudinal rows (often more evident in younger or narrower portions of axes and branches) 11
- 10a. Thallus tubular throughout (or rarely only slightly compressed); usually not branched (or if branched, only one to few simple branches); in transection outer cell wall thin *U. intestinalis*
- 10b. Thallus compressed, usually widening upward and branched; in transection outer cell wall thick *U. compressa*

- 11a. Thalli cylindrical to slightly compressed; repeatedly and usually densely branched up to several orders; ultimate branchlets multiseriate or partly to entirely uniseriate *U. clathrata*
- 11b. Thalli either: simple and unbranched, or with branches only near base, or a main axis with lateral branches 12
- 12a. Thallus with lateral branches or proliferations (rarely unbranched); cells in surface view in longitudinal but not transverse rows *U. radiata*
- 12b. Thallus either: unbranched, or with branches only from or near base; cells in surface view in longitudinal and transverse rows (although sometimes may be obscure) *U. flexuosa*

Ulva* sect. *ulva

Members of this section include species of *Ulva* that are flat, bladelike, and distromatic throughout (Figure 13A). The two cell layers of the blade are developmentally independent but closely adherent.

Five of the known species of this section are in the northern Gulf of California.

***Ulva californica* Wille**

FIGURE 14A,B

Ulva californica Wille in Collins, Holden and Setchell, 1899:Exsiccata No. 611; Collins, 1909b:215; Setchell and Gardner, 1920b:264; Dawson, 1945c:23; Doty, 1947:11, pl. 2: figs. 6–10; Dawson, 1960a:31; Dawson, 1961b:374; Abbott and Hollenberg, 1976:78, fig. 35; Littler and Littler, 1981:149, 150; Pedroche and González-González, 1981:63; González-González, 1993:443; L. Aguilar-Rosas and Bertsch, 1983:114, 120; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mendoza-González and Mateo-Cid, 1986:419; Tanner, 1986:517, figs. 1–19; Sánchez-Rodríguez et al., 1989:39; L. Aguilar-Rosas and Pacheco-Ruíz, 1989:81; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Stewart, 1991:27; León-Tejera et al., 1993:199; Servièrre-Zaragoza et al., 1993:482; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517, 529; González-González et al., 1996:139; Núñez-López et al., 1998:39; Servièrre-Zaragoza et al., 1998:169, 177; Hayden and Waaland, 2004:378, tbl. 3; Pedroche et al., 2005:22; Kawai et al., 2007:223–226, figs. 3, 4.

Ulva angusta Setchell et N. L. Gardner, 1920a:283, pls. 27, 31: fig.1; Setchell and Gardner, 1920b:264, pls. 22, 26: fig.1; Setchell and Gardner, 1930:137; Dawson, 1944:201; Smith, 1944:45, pl. 4: figs. 1–3; Dawson, 1961b:374; Abbott and Hollenberg, 1976:78, fig. 34; Silva, 1979:341; L. Aguilar-Rosas and Bertsch,

1983:114; Stewart and Stewart, 1984:140; L. Aguilar-Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1986:419; González-González et al., 1996:139.

Enteromorpha angusta (Setchell et N. L. Gardner) Doty, 1947:20, pl. 1: figs. 1–6.

Ulva scagelii Chihara, 1968:87, figs. 3–8.

Ulva taeniata sensu Dawson, 1945b:59, 64 [non *Ulva taeniata* (Setchell) Setchell et N. L. Gardner, 1920a:286].

Algae variable in size and shape in the Gulf: blades usually small, up to 2 cm tall and 1.5 cm wide, cuneate or more or less triangular-shaped, with undulate margins; but blades can also be larger, lanceolate to oblanceolate (much taller than wide) up to 15 cm long and to 5 cm wide, usually with ruffled margins; attached below by a slender stipe and along base of the blade. Two cell layers, 30–40(–60) μm thick in transection; usually thicker near base. Cells in surface view polygonal with rounded corners, usually irregularly arranged, (5–)10–23 μm in diameter by (5–)10–15 μm long; chloroplast with 1–2(–4) pyrenoids. Cells in transection more or less quadrate to slightly elongate, 5–12 μm wide by 5–18 μm tall.

Quadriflagellate zoospores develop into gametophytes. Anisogamous gametes fuse to form a zygote; female gametes capable of developing parthenogenetically; male gametes can also develop without fertilization (Tanner, 1986).

HABITAT. On rocks or occasionally epiphytic; high to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to La Paz. Pacific coast: Alaska to Baja California Sur; Isla Guadalupe; Isla Magdalena; Nayarit to Michoacán; Japan.

TYPE LOCALITY. Pacific Beach, south of La Jolla, San Diego County, California.

REMARKS. In the northern Gulf, *Ulva californica* is usually found growing in its smaller, more or less triangular-shaped form (cf. Tanner, 1986:514, figs. 1, 4, 5). On the basis of similarities in morphology, cytology, and life histories, the absence of interfertility barriers, and preliminary electrophoretic data, two larger Pacific species, *U. angusta* and *U. scagelii*, were placed in synonymy with

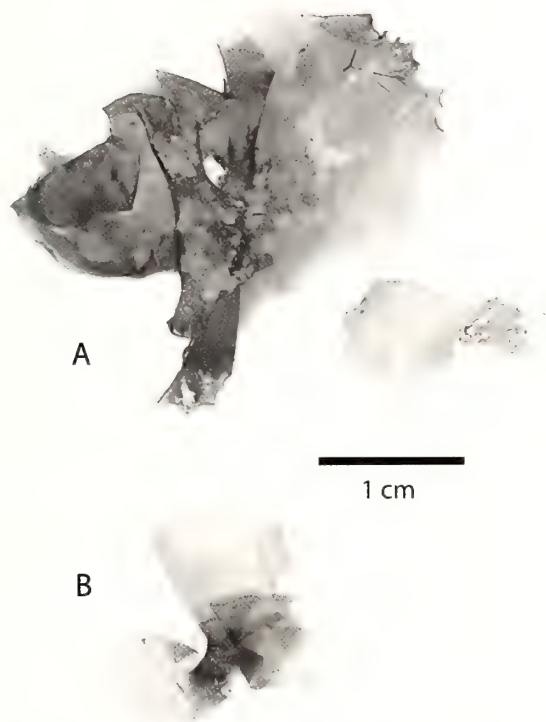


FIGURE 14. *Ulva californica*: Habits, small cuneate forms, typically found in the northern Gulf. A. EYD-27407. B. JN-5425.

U. californica (Tanner, 1986); this has been supported by the molecular analyses of Hayden and Waaland (2004). The larger thalli of *U. californica* are not common in the northern Gulf but have been reported from Guaymas as "*U. angusta*" (Dawson, 1961b; Mendoza-González and Mateo-Cid, 1986).

Ulva lactuca Linnaeus

FIGURE 15

Ulva lactuca Linnaeus, 1753:1163; Setchell and Gardner, 1920b:265; Collins, 1909b:214; Setchell and Gardner, 1924a:717; Setchell and Gardner, 1930:138; Dawson, 1944:202; Smith, 1944:45, pl. 3: figs. 6,7; Dawson, 1945b:64; Taylor, 1945:42; Dawson, 1959a:5, 8–11; Dawson, 1961b:374; Dawson, 1962b:228; Dawson, 1962c:278; Scagel, 1966:60, pl. 31: figs. I–K; Bliding, 1968:537, figs. 1–5; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Chávez B., 1972:268; Norris, 1973:3, 17; Abbott and Hollenberg, 1976:83, fig. 39; Huerta-Múzquiz, 1978:336, 337, 339; Pedroche and González-

González, 1981:63; R. Aguilar-Rosas, 1982:84; L. Aguilar-Rosas et al., 1982:52, fig. 8; L. Aguilar-Rosas and Bertsch, 1983:115, 120; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; Ibarra-Obando and R. Aguilar-Rosas, 1985:96; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Ortega et al., 1987:77, 90, pl. 13: figs. 56, 57; Sánchez-Vargas and Hendrickx, 1987:161; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:39; Santelices, 1989:243, pl. AA: fig. 4; Dreckmann et al., 1990:24, 37; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid and Mendoza-González, 1991:27; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Martínez-Lozano et al., 1991:23; Mateo-Cid and Mendoza-González, 1992:24; González-González, 1993:443; Mateo-Cid et al., 1993:51; Stout and Dreckmann, 1993:4; León-Tejera et al., 1993:199, 202; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:51, 60; Mateo-Cid and Mendoza-González, 1994b:34, 44; Mendoza-González et al., 1994:103, 112; González-González et al., 1996:289; Pacheco-Ruíz and Zertuche-González, 1996a:432; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Bucio-Pacheco and Dreckmann, 1998:42; Yoshida, 1998:40; Mendoza-González and Mateo-Cid, 1998:24, 27; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Mateo-Cid et al., 2000a:69; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Cruz-Ayala et al., 2001:190; Pacheco-Ruíz et al., 2002:200; Pacheco-Ruíz et al., 2003:447; Hayden and Waaland, 2004:373, tbl. 3; Riosmena-Rodríguez et al., 2005:101; Hernández-Herrera et al., 2005:146; R. Aguilar-Rosas et al., 2005b:36; Pedroche et al., 2005:28; Mateo-Cid et al., 2006:48; Servièrre-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:191, 201.

Algae cuneate, ovate to oblanceolate, up to 5 cm tall, light green, usually entire, occasionally lacinate, with undulate margins; attached by a small discoid holdfast. Thickness at margins 40–55 μm ; in midportions up to 85 μm ; and in basal region 80–100 μm thick. Cells irregularly arranged in surface view; quadrangular to polygonal, 12–20 μm by 10–25 μm in diameter, with a single parietal chloroplast and 1–2 pyrenoids. Cells in transection, more or less quadrate, 15–25(–30) μm tall by 10–25 μm wide.

HABITAT. On rocks; high intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo. Pacific coast: Alaska to central California; northern Baja California to Oaxaca; Costa Rica; Ecuador; Galápagos Islands; Peru; Chile; China; Japan.

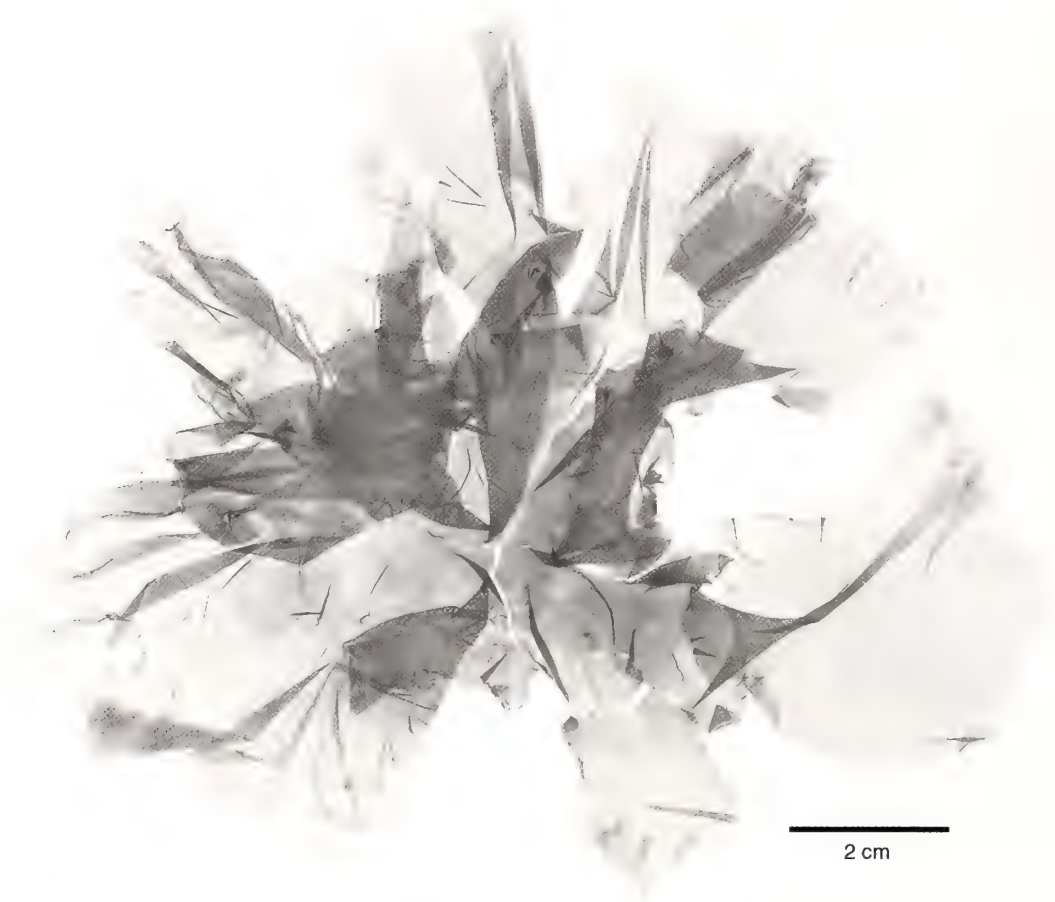


FIGURE 15. *Ulva lactuca*: Habit (US Alg. Coll.-36624).

TYPE LOCALITY. “*In Oceano*” (Linnaeus, 1753); probably west coast of Sweden (Womersley, 1984).

REMARKS. *Ulva lactuca*, the type species of the genus, has been reported worldwide. In the northwest Gulf of California, the effects of an El Niño year (1997–1998) on populations of *U. lactuca* were dramatic (Pacheco-Ruíz et al., 2003). Stands of *U. lactuca* along the Gulf coast of Baja California across from Canal de Ballenas were significantly reduced in aerial coverage by 70% and biomass by 80% during El Niño in comparison to the pre-El Niño years (May 1995, 1996) and the post-El Niño year (May 2000) recovery.

***Ulva lobata* (Kützling) Harvey**

FIGURE 16

Phycoseris lobata Kützling, 1847:54; Kützling, 1849:477; Kützling, 1856:10, pl. 27.

Ulva lobata (Kützling) Harvey, 1855:265; Silva et al., 1996a:748; Silva et al., 1996b:235; Pedroche et al., 2005:30.

Ulva lobata (Kützling) Setchell et N. L. Gardner, 1920a:284; Setchell and Gardner, 1920b:268; Smith, 1944:46, pl. 4: figs. 4, 5; Taylor, 1945:43; Doty, 1947:10; Dawson, 1957a:2, 4; Dawson, 1959a:4; Dawson, 1959c:4; Dawson, 1961b:374; Guzmán del Próo et al., 1972:260; Abbott and Hollenberg, 1976:85, fig. 40; Silva, 1979:341; Pedroche and González-González, 1981:64; Sánchez-Rodríguez et al., 1989:39; Santelices, 1989:242, pl. AA: fig. 6; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; León-Tejera et al., 1993:199; Servière-Zaragoza et al., 1993:482; González-González et al., 1996:140; Hoffmann and Santelices, 1997:65, fig. 10; León-Alvarez et al., 1997:397; Servière-Zaragoza et al., 1998:169; Paul-Chávez and Riosmena-Rodríguez, 2000:146; L. Aguilar-Rosas et al., 2000:133, 134; Hayden et al., 2003:279; Hayden and Waaland, 2004:377, tbl. 3.

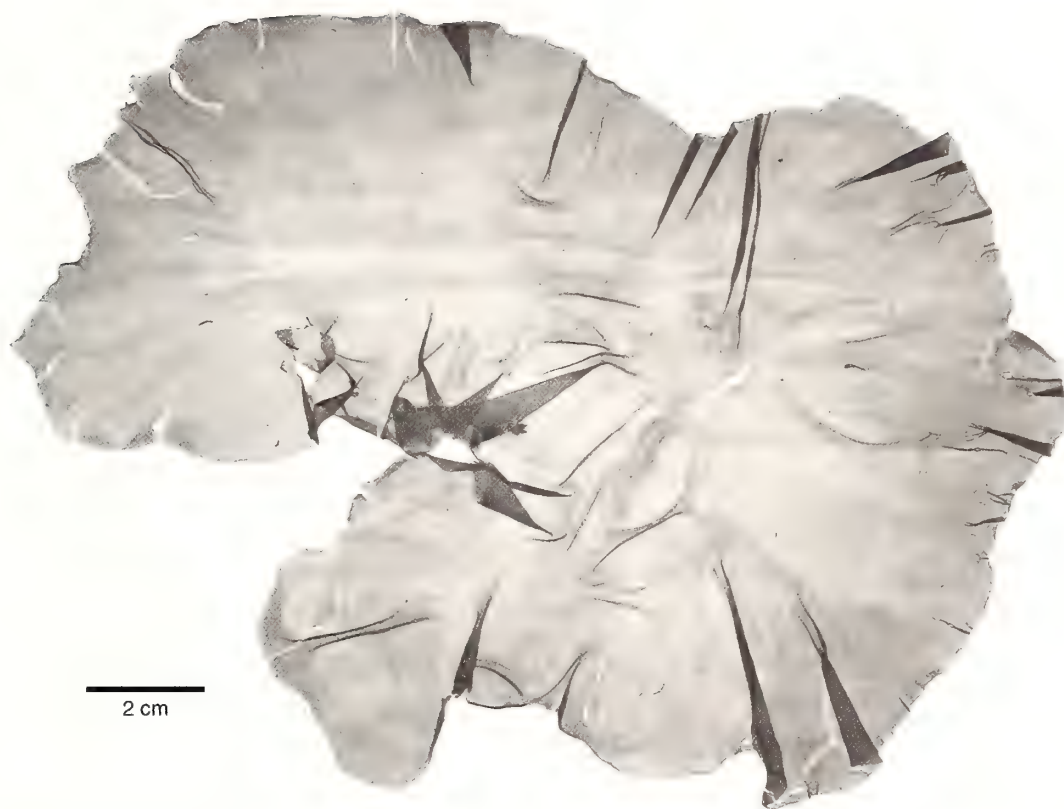


FIGURE 16. *Ulva lobata*: Habit (JN-6103a).

Ulva fasciata f. *lobata* Setchell in Collins, Holden and Setchell, 1901b:No. 863; Collins, 1909b:216.

Blades up to 15 cm tall, obovate, mostly deeply lobed or divided; margins smooth to ruffled; gradually narrowed in lowermost portion, sometimes more or less stipe-like at holdfast. Blades in transection 40–50 μm thick at margins and noticeably thicker in midportion, up to 90 μm . Cells viewed in transection appear vertically elongated, almost twice as tall as wide; with a cup-shaped chloroplast.

HABITAT. On rocks or mud and sand; mid to low intertidal.

DISTRIBUTION. Gulf of California: Santa Teresa; Bahía de La Paz. Pacific coast: Oregon to Baja California; Jalisco to Guerrero; Clipperton Island; Ecuador; Galápagos Islands; Chile; Juan Fernandez Island.

TYPE LOCALITY. Chile.

REMARKS. Although Levring (1941, as “*Phycoseris lobata*”; see also Wynne, 2002) listed *U. lobata* as a synonym of *U. nematoidea*, molecular analyses have not supported this (Hayden and Waaland, 2004), and these two are recognized as separate species.

***Ulva nematoidea* Bory de Saint-Vincent**

FIGURE 17A,B

Ulva nematoidea Bory de Saint-Vincent, 1828:190; Levring, 1941:605, figs. 1B–D, pl. 49: fig. 1; Levring, 1960:9; Wynne, 2002: figs. 1–3.

Ulva fasciata f. *costata* M. Howe, 1914:20, pl. 1, pl. 2: figs. 10–23; Taylor, 1947:60; Dawson et al., 1964:8, pl. 3; Acleto O., 1977a:16, fig. 13; Acleto O., 1977b:3, fig. 4.

Ulva costata (M. Howe) Hollenberg, 1971:283, fig. 1, *nom. illeg.* [since it is a later homonym of *Ulva costata* Wollny, 1881:30]; Abbott and Hollenberg, 1976:80, fig. 36; Santelices and Abbott, 1978:215; Acleto O. 1980:2, figs. 1–3; L. Aguilar-Rosas and Bertsch, 1983:114, 120; R. Aguilar-Rosas et al., 1984a:151; R. Aguilar-Rosas et al., 1984b:159; L. Aguilar-Rosas and Pacheco-Ruíz, 1985:71; L. Aguilar-Rosas et al., 1985:125; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Acleto O., 1986:38, fig. 4; Santelices, 1989:241, pl. AA: fig. 3; R. Aguilar-Rosas and Machado-Galindo, 1990:188; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517, 526;



FIGURE 17. *Ulva nematoidea*: A. Thallus narrowly linear and twisted (EYD-10421). B. Thallus with central planar region and ruffled margins (US Alg. Coll.-8799).

Mateo-Cid and Mendoza-González, 1994a:51; Mateo-Cid and Mendoza-González, 1994b:34, 44; Mendoza-González et al., 1994:112; González-González et al., 1996:139; Hoffman and Santelices, 1997:59, fig. 8; Mendoza-González et al., 1999:60; R. Aguilar-Rosas et al., 2005b:36.

Ulva dactylifera Setchell et N. L. Gardner, 1920a:285, pl. 26: fig. 1; Setchell and Gardner, 1920b:272, pl. 21: fig. 1; Setchell and Gardner, 1924a:717; Dawson, 1944:201; Dawson, 1959a:6, 11; Dawson, 1961b:374; Abbott and Hollenberg, 1976:80, fig. 37; Huerta-Múzquiz, 1978:339; Pedroche and González-González, 1981:63; L. Aguilar-Rosas and Bertsch, 1983:115, 120; González-González, 1993:443; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1986:419; Stewart, 1991:28; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mendoza-González and Mateo-Cid, 1992:23; Servièze-Zaragoza et al., 1993:482; González-González et al., 1996:140; Bucio-Pacheco and Dreckmann, 1998:42; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; L. Aguilar-Rosas et al., 2000:133, 134; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Pedroche et al., 2005:25; Hernández-Herrera et al., 2005:146.

Ulva fasciata f. *taeniata* Setchell in Collins, Holden and Setchell, 1901b: No. 862.

Ulva taeniata (Setchell) Setchell et N. L. Gardner, 1920a:286, pl. 28; Setchell and Gardner, 1920b:273, pl. 23; Smith, 1944:48, pl. 3: figs. 1–3; Dawson, 1945b:64; Doty, 1947:8, pl. 2: figs. 11, 12, pl. 4: figs. 3, 4; Dawson, 1961b:374; Abbott and Hollenberg, 1976:87, fig. 43; Santelices and Abbott, 1978:215; Huerta-Múzquiz, 1978:335; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Santelices, 1989:247, pl. AA: figs. 1, 2; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mateo-Cid and Mendoza-González, 1991:27; Mendoza-González and Mateo-Cid, 1992:24; Servièze-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:51; Mateo-Cid and Mendoza-González, 1994b:34, 44; Mendoza-González et al., 1994:103, 112; González-González et al., 1996:140; Hoffmann and Santelices, 1997:71, fig. 12; Cruz-Ayala et al., 2001:190; Hayden and Waaland, 2004:379, tbl. 3; Pedroche et al., 2005:33.

Algae up to 10 cm tall, with upper blade divided into 4–6 narrow, linear segments, each 5–15 mm wide; often twisted, sometimes with a central planar region (midrib), and usually with crisped, ruffled margins that may or may not be dentate; lower portion of blade orbicular and attached along the basal margin or attached by a short

stipe. Cells in surface view isodiametric, 15–20 µm in diameter; in transection (16–)20–40 µm tall by 16–20 µm wide. Middle of upper lanceolate segments, up to 190 µm thick; with cells in surface view, 12–16 µm in diameter, and in transection, elongated, 12–16 wide and 35–60(–80) µm tall. Cells of margins in transection, mostly slightly elongate, 12–16 µm wide and 12–16 µm tall.

HABITAT. On rocks; upper to mid intertidal.

DISTRIBUTION. Gulf of California: Santa Teresa to Bahía La Paz; Playa Los Cerritos (vicinity Matzalán), Sinaloa. Pacific coast: Oregon to Punta Eugenia, Baja California Sur; Sinaloa to Michoacán; Peru; Chile; Juan Fernandez Island. (Galápagos Islands and Ecuador [Taylor, 1945:43, with a query].)

TYPE LOCALITY. Concepción, Provincia Concepción, Chile.

REMARKS. Tanner (1979) and Stewart (1991) suggested that *U. costata*, *U. dactylifera*, and *U. taeniata* were conspecific; this has been recently supported by molecular evidence (Hayden and Waaland, 2004). Although Levring (1941, 1960) considered *U. costata* and *U. nematoidea* to be one species, this has been largely ignored. Recently, Wynne (2002) provided morphological evidence that these two were the same, with *U. nematoidea* having nomenclatural priority.

***Ulva rigida* C. Agardh**

FIGURE 18

Ulva rigida C. Agardh, 1823:410; Howe, 1914:18; Setchell and Gardner, 1920b:269; Setchell and Gardner, 1924a:717; Setchell and Gardner, 1930:137; Levring, 1941:606; Dawson, 1944:202; Smith, 1944:47; Dawson, 1949:239, 242; Taylor, 1947:60; Papenfuss, 1960:305, text-fig. 4, pl. 1: fig. 11; Dawson, 1961b:374; Dawson et al., 1964:8; Dawson, 1966a:5; Scagel, 1966:61, pl. 30: figs. A–C, pl. 31: figs. A–H; Bliding, 1968:546, figs. 6–10; Acleto O., 1973:9; Abbott and Hollenberg, 1976:87, fig. 41; Huerta-Múzquiz, 1978:338; Koeman and van den Hoek, 1981:37, figs. 78–107; Littler and Littler, 1981:151–153; Hoeksema and van den Hoek, 1983:74, figs. 20–24; Littler and Littler, 1984:15, 24; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Dungan, 1986:295; Phillips, 1988:445, figs. 24–26; Santelices, 1989:243, pl. AA: fig. 5; R. Aguilar-Rosas and Machado-Galindo, 1990:188; R. Aguilar-Rosas et al., 1990:123; Stewart, 1991:28; Mateo-Cid and Mendoza-González, 1991:27; Rocha-Ramírez and

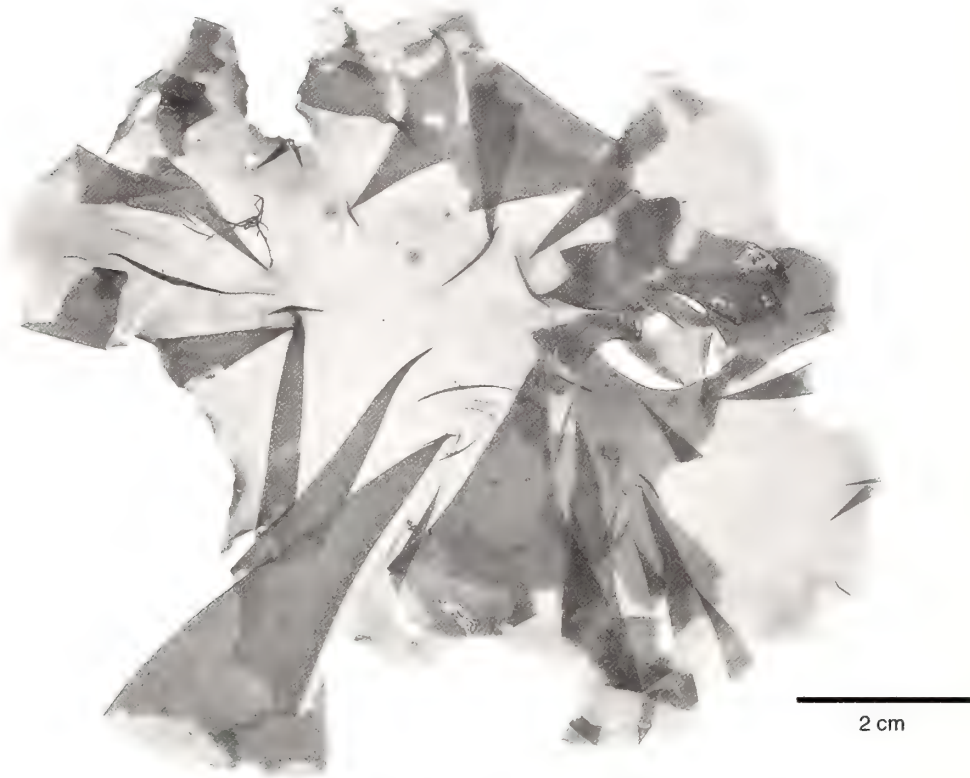


FIGURE 18. *Ulva rigida*: Habit, showing the wider than tall nature of the thallus (JN-5742).

Siqueiros-Beltrones, 1991:30; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517, 526; Mateo-Cid and Mendoza-González, 1994b:44; González-González et al., 1996:290; Hoffmann and Santelices, 1997:68, fig. 11; Mendoza-González and Mateo-Cid, 1998:25; Mendoza-González et al., 1999:60; L. Aguilar-Rosas et al., 2000:133; Kraft, 2000:532, fig. 11A–E; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:57, fig. 12A–D; Hayden and Waaland, 2004:379, tbl. 3; Pedroche et al., 2005:32; Mateo-Cid et al., 2006:48; Kraft, 2007:46, fig. 19A–E; Pacheco-Ruíz et al., 2008:191, 201.

Ulva lactuca var. *rigida* (C. Agardh) Le Jolis, 1863:38; Collins, 1903:8, pl. 41: fig.1; Collins, 1909b:215; Howe, 1911:490; Huerta-Múzquiz, 1978:335; Huerta-Múzquiz and Mendoza-González, 1985:42; Pacheco-Ruíz and Zertuche-González, 1996a:432.

Blades broader than tall, up to 5 cm tall and to 10 cm wide in the Gulf, dark green; sometimes deeply lobed, usually with dentate margins (spines 1–3 cells long); firm

and comparatively stiff, narrowed abruptly at base to a short solid stipe above a small discoid holdfast. Cells in surface view irregularly arranged, polygonal to rounded, 10–15 μm in diameter; with a single chloroplast and 1–3 pyrenoids. Transection of 2-cell-layer blade, up to 100 μm thick (thickest in lowermost portion), with a distinct thick hyaline, mucilage layer between cell layers. Cells in transection predominately elongated (most evident in mid to lower portions), occasionally squarish, 15–45 μm tall by 10–15 μm wide.

HABITAT. On rocks, usually exposed; high to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía La Paz. Pacific coast: Alaska to Colima; Peru; Chile; Juan Fernandez Island; Hawaiian Islands.

TYPE LOCALITY. Cádiz, southern Spain (Papenfuss, 1960).

REMARKS. *Ulva rigida* is distinguished from other species of the Gulf by blades that are generally wider than tall, darker green in color, and usually with microscopic teeth along the blade margins.

***Ulva* sect. *enteromorpha*
(Link in Nees) Endlicher**

Enteromorpha Link in Nees, 1820:5.

Ulva sect. *enteromorpha* (Link in Nees) Endlicher, 1843:19.

Unlike *Ulva* sect. *ulva*, thalli of the members of *U.* sect. *enteromorpha* are completely monostromatic throughout or not completely distromatic throughout. This section includes species that are either (1) tubular to slightly compressed and only one cell thick (monostromatic) throughout (Figure 13B) or (2) compressed to flattened upward to form two-cells-thick (distromatic) blades that have hollow, one-cell-thick (monostromatic) margins (Figure 13C) and/or a one-cell thick (monostromatic) tubular base (Figure 13B).

Seven species are known in the northern Gulf of California.

***Ulva acanthophora* (Kützting)
Hayden, Blomster, Maggs, P. C. Silva,
Stanhope et Waaland**

FIGURE 19A,B

Enteromorpha acanthophora Kützting, 1849:479; Kützting, 1856:pl.34: fig.1; Setchell and Gardner, 1920b:254; Setchell and Gardner, 1924a:715, pl. 16: fig. 43, pl. 38; Dawson, 1944:203; Dawson, 1949:234; Dawson et al., 1960b:9, 13; Dawson, 1961b:373; Dawson, 1962c:278; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Norris, 1973:3; Huerta-Múzquiz, 1978:337, 338; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; Norris, 1985:211; Mendoza-González and Mateo-Cid, 1986:419; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Martínez-Lozano et al., 1991:23; González-González et al., 1996:136; Pacheco-Ruíz and Zertuche-González, 1996a:432; Cruz-Ayala et al., 2001:190.

Ulva acanthophora (Kützting) Hayden, Blomster, Maggs, P. C. Silva, Stanhope et Waaland, 2003:288; Pedroche et al., 2005:21; Pacheco-Ruíz et al., 2008:201.

Enteromorpha ramulosa var. *acanthophora* (Kützting) Chapman, 1956:419, fig. 67; Paul-Chávez and Riosmena-Rodríguez, 2000:146 [Pedroche et al., 2005:21 noted this combination was invalid].

Enteromorpha ramulosa sensu Adams, 1994:29, 51, pl. 3 [non *Enteromorpha ramulosa* (J. E. Smith) Carmichael in W. J. Hooker, 1833:315; basionym: *Ulva ramulosa*

J. E. Smith, 1810: pl. 2137, which is a synonym of *Ulva clathrata* (Roth) C. Agardh, 1811:23].

Algae more or less tubular throughout, usually profusely branched, up to 30(–45) cm tall, 1–2 mm in diameter; branches tubular, constricted at base; axes and branches beset with numerous short and spinose ultimate branchlets. Cells in surface view, mostly 10–15 µm in diameter, and not arranged in longitudinal series in main axes and branches; but more or less in longitudinal series in ultimate branchlets and spinose projections.

HABITAT. On rocks and tidal platforms, often exposed, and in sand in shallow protected waters; mid intertidal to shallow subtidal; also dredged 22–36 m (Dawson, 1944).

DISTRIBUTION. Gulf of California: Bahía Tepoca to Bahía La Paz; Isla Espiritu Santo. Pacific coast: Bahía San Quintín, Baja California; Bahía Tortuga and Bahía Almejas (Isla Santa Margarita), Baja California Sur; Golfo de Tehuantepec, Oaxaca.

TYPE LOCALITY. Bay of Islands, northeast coast of North Island, New Zealand.

REMARKS. Within the Gulf of California, *Ulva acanthophora* has been collected in November but appears to be more common from February to June. It can be distinguished from other Gulf species by its large size and the characteristic, numerous, short branchlets and spine-like projections along its axes and branches. The presence of the New Zealand species in the Gulf and Pacific Mexico shows a very disjunct distribution. It would be interesting to comparatively test Gulf *U. acanthophora* with the New Zealand type and type locality specimens of *U. acanthophora* (Chapman, 1956; Adams, 1994) using morphological and molecular studies, such as those of Blomster et al. (1998, 1999), Hayden et al. (2003), and Hayden and Waaland (2004).

***Ulva clathrata* (Roth) C. Agardh**

FIGURE 20

Conferva clathrata Roth, 1806:175.

Ulva clathrata (Roth) C. Agardh, 1811:23; Blomster et al., 1999:579; Pedroche et al., 2005:23; Servière-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:191, 201.

Enteromorpha clathrata (Roth) Greville, 1830:lxvi, 181; Collins, 1909b:199; Setchell and Gardner, 1920b:260; Dawson, 1959a:7, 10; Dawson, 1961b:373; Dawson, 1962b:228; Bliding, 1963:107, figs. 64–69; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Norris,

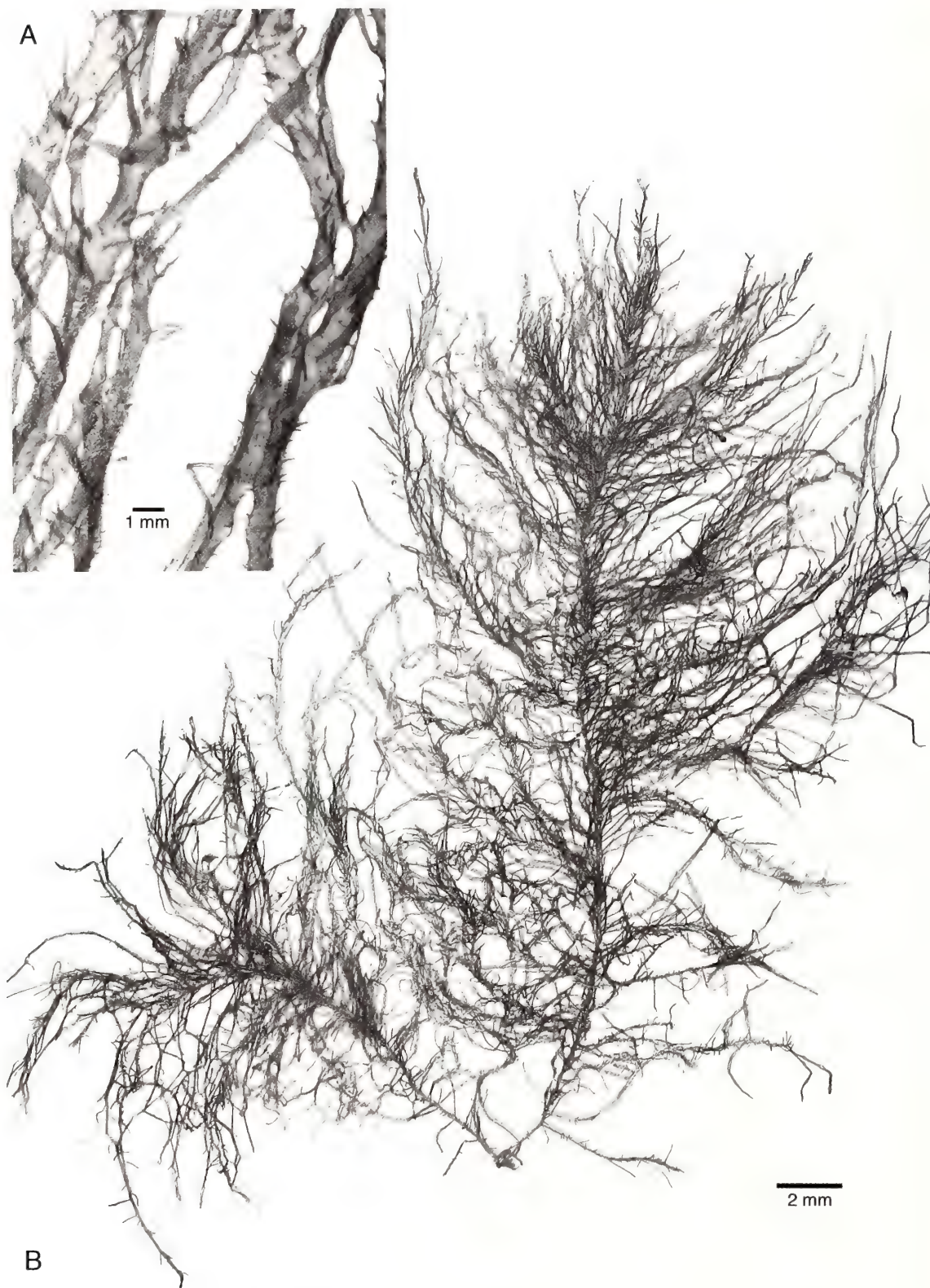


FIGURE 19. *Ulva acanthophora*: A. Close-up of spiny axes and branches (JN-5455). B. Robust thallus with abundant lateral branches, branchlets, and spines (JN-383).

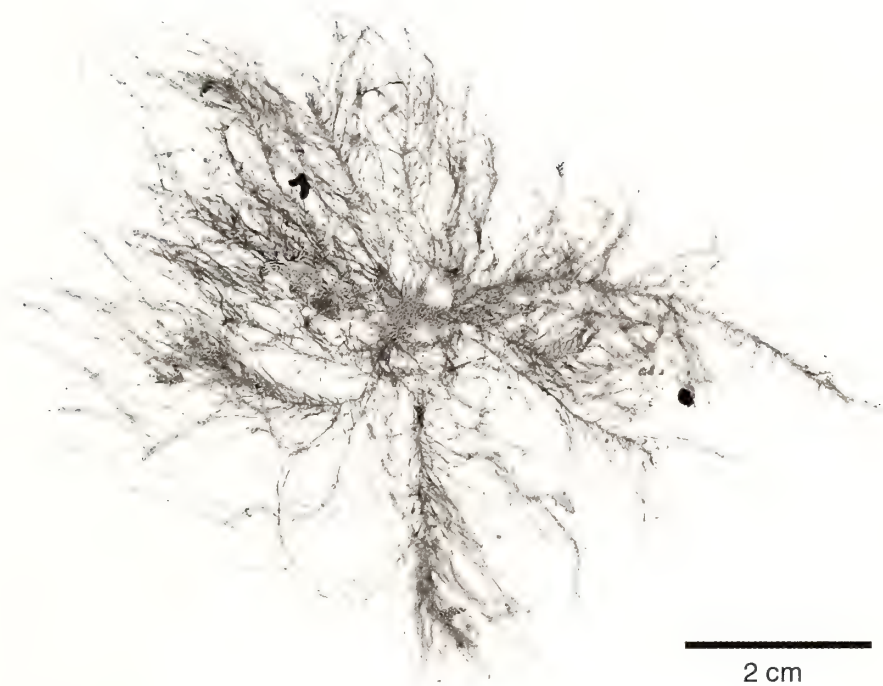


FIGURE 20. *Ulva clathrata*: Habit of extensively branched thallus (JN-4994).

1976a:73, fig. 27; Huerta-Múzquiz, 1978:339; Silva, 1979:340; R. Aguilar-Rosas, 1982:84; Ibarra-Obando and R. Aguilar-Rosas, 1985:96; De la Lanza et al., 1989:91; Mateo-Cid and Mendoza-González, 1991:26; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mateo-Cid et al., 1993:51; Servièze-Zaragoza et al., 1993:482; Mendoza-González et al., 1994:111; González-González et al., 1996:283; Riosmena-Rodríguez and Paul-Chávez, 1997:66; Mendoza-González and Mateo-Cid, 1998:24; Yoshida, 1998:34; Núñez-López et al., 1998:38; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Blomster et al., 1999:575, figs. 2, 10–16, Mateo-Cid et al., 2000a:69; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Cruz-Ayala et al., 2001:190; Hayden et al., 2003:288, tbl. 4; Abbott and Huisman, 2004:46, fig. 5A–C; R. Aguilar-Rosas et al., 2005b:35.

Enteromorpha crinita Link in Nees, 1820:2 [index]; Dawson, 1945b:22.

Enteromorpha clathrata var. *crinita* (Link in Nees) Hauck, 1884:429; R. Aguilar-Rosas, 1982:85; Sánchez-Rodríguez et al., 1989:39.

Ulva muscoides Clemente y Rubio, 1807:320; Cremades and Pérez-Cirera, 1990:490.

Enteromorpha muscoides (Clemente y Rubio) J. Cremades in Cremades and Pérez-Cirera, 1990:489; Silva et al., 1996a:737; Núñez-López et al., 1998:38; Blomster et al., 1999:575, figs. 1, 3–9, 22–25; Cruz-Ayala et al., 2001:190.

Enteromorpha plumosa sensu Setchell and Gardner, 1930:137 [non *Enteromorpha plumosa* Kützinger, 1843:300; which is now *Ulva paradoxa* C. Agardh, 1817:XXII].

Ulva ramulosa J. E. Smith, 1810:pl. 2137.

Enteromorpha ramulosa (J. E. Smith) Carmichael in W. J. Hooker, 1833:315; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Mendoza-González and Mateo-Cid, 1998:24.

Algae cylindrical to slightly compressed, up to 10 cm tall and 0.5–2.0 mm in diameter, and repeatedly branched, with numerous proliferations. Branches and ultimate branchlets end in multiseriate or uniseriate rows of cells. Cells in surface view, in distinct longitudinal rows in narrower portions, and either similarly ordered or more randomly arranged in broader older portions; cells 8–20 μm wide and 8–36 μm long, with a single chloroplast and 1 or more pyrenoids.

HABITAT. On rocks, mudflats and tidal platforms, in crevices, and in tide pools; generally in protected habitats; high to mid intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de La Paz; Punta Arena (vicinity of Cabo Pulmo). Pacific coast: Alaska to Oaxaca; Isla Clarion (Islas Revillagigedo); Isla Clipperton; Hawaiian Islands; Chile; China; Japan.

TYPE LOCALITY. Fehmarn, SW Baltic Sea (Roth, 1806) [neotype locality: Landskoma, Baltic Oresund (neotype illustrated by Bliding, 1963: fig. 69a–d)].

REMARKS. Surprisingly, *Ulva clathrata* has not yet been reported from the northern Gulf. Collections in the vicinity of Puerto Peñasco (JN-4994; US Alg. Coll. 310816) represent a northern extension from Puerto Escondido (Dawson, 1959a).

***Ulva compressa* Linnaeus**

Ulva compressa Linnaeus, 1753:1163; Linnaeus, 1755:433; Blomster et al., 1998:332, figs. 50 (typotype), 55–57; Hayden et al., 2003:289, tbl. 4; Mateo-Cid et al., 2006:48, 58; Pedroche et al., 2005:24; Pacheco-Ruiz et al., 2008:191, 201.

Enteromorpha compressa (Linnaeus) Link ex Nees, 1820:Index [2]; León-Tejera et al., 1993:199; González-González, 1993:443; Servièrre-Zaragoza et al., 1993:482; Leskinen and Pamilo, 1997:17; Bucio-Pacheco and Dreckmann, 1998:42; Yoshida, 1998:34; Paul-Chávez and Riosmena-Rodríguez, 2000:144; Abbott and Huisman, 2004:48, fig. 5D.

Enteromorpha compressa (Linnaeus) Greville, 1830:180, pl. 18: figs. 1–3; Setchell and Gardner, 1903: 213; Collins, 1909b:201; Setchell and Gardner, 1920b:251, pl. 14: figs. 7, 8, pl. 16: fig. 3; Setchell and Gardner, 1924a:716; Dawson, 1944:203; Dawson, 1949:236; Dawson, 1957b:7; Dawson, 1959a:4, 6, 11; Dawson, 1961b:373; Dawson, 1962b:228; Dawson, 1962c:278; Bliding, 1963:132, figs. 82–84; Dawson, 1966a:5; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Chávez B., 1972:268; Norris, 1973:3, 17; Norris, 1976a:74, fig. 29; Deviny, 1978:358; Huerta-Múzquiz, 1978:336; 338; Silva, 1979:340; Pedroche and González-González, 1981:63; Koeman and van den Hoek, 1982a:288, figs. 2–30; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; Mendoza-González and Mateo-Cid, 1986:419; Dreckmann et al., 1990:24; Mateo-Cid and Mendoza-González, 1991:27; Martínez-Lozano et al., 1991:23; Mendoza-González and Mateo-Cid,

1992:23; Mateo-Cid and Mendoza-González, 1992:24; Mateo-Cid et al., 1993:51; León-Tejera and González-González, 1993:497; León-Tejera et al., 1993:199; Mateo-Cid and Mendoza-González, 1994a:51; Mateo-Cid and Mendoza-González, 1994b:44; Mendoza-González et al., 1994:112; González-González et al., 1996:283; Mendoza-González and Mateo-Cid, 1996:74, 87, pl. 23: figs. 102, 103; Blomster et al., 1998:319, figs. 4–6, 10–15, 30–40, 55–57; L. Aguilar-Rosas et al., 2002:235; Dreckmann et al., 2006:153.

Algae mostly compressed, sometimes more or less tubular; up to 10 cm tall and mostly to 5 mm wide; upper portions usually sparsely branched (rarely unbranched); branches more slender near their branching origin and usually broadening distally; sometimes with microscopic, multiseriate or rarely uniseriate, branchlets; basal portion tapering to holdfast of rhizoidal cells. Cells in surface view, more or less quadrate, angular or rounded, 8–15 μ m in diameter; irregularly arranged throughout; with 1 or occasionally 2 pyrenoids.

HABITAT. On rocks, usually in exposed habitats; also in mudflats and estuaries, sometimes free-floating, rarely epiphytic; high to mid intertidal (also dredged 4–32 m; Dawson, 1944).

DISTRIBUTION. Gulf of California: Las Piedras del Burro to Bahía de La Paz. Pacific coast: Alaska to Costa Rica; Peru; Chile; Hawaiian Islands; China; Japan.

TYPE LOCALITY. Probably Bognor, Sussex, England (based on selection of lectotype illustration of Dillenius [1742:pl. 9: fig. 8] and typotype [see Stearn, 1957:129] by Blomster et al. [1998:332, figs. 50, 55–57]).

***Ulva flexuosa* Wulfen**

FIGURE 21A,B

Ulva flexuosa Wulfen, 1803:1; Hayden et al., 2003:289, tbl. 4; Pedroche et al., 2005:26; Servièrre-Zaragoza et al., 2007:8.

Conferva flexuosa Roth, 1800:188–190, *nom. illeg.* [since it is a homonym of *Conferva flexuosa* O. F. Müller, 1782:5].

Enteromorpha flexuosa (Wulfen) J. Agardh, 1883:126; Collins, 1909b:203; Setchell and Gardner, 1920b:255; Taylor, 1945:38; Dawson, 1957b:5; Bliding, 1963:73, figs. 38–41; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Chávez B., 1972:268; Huerta-Múzquiz and Garza Barrientos, 1975:6; Norris, 1976a:76, fig. 30; Deviny, 1978:358; Silva, 1979:340; Pedroche

and González-González, 1981:63; R. Aguilar-Rosas, 1982:84; Schnetter and Bula Meyer, 1982:15, pl. 1: figs. A–F; L. Aguilar-Rosas et al., 1985:125; Oliva-Martínez and Ortega, 1987:127, pl. 3: figs. 4a,b; Ortega et al., 1987:77, pl. 13: figs. 53–55; L. Aguilar-Rosas and Pacheco-Ruíz, 1989:81; Sánchez-Rodríguez et al., 1989:39; De Lara-Isassi et al., 1989:102; Dreckmann et al., 1990:24; Mateo-Cid and Mendoza-González, 1991:27; Mateo-Cid and Mendoza-González, 1992:24; Mateo-Cid et al., 1993:51; González-González, 1993:443; Servièrre-Zaragoza et al., 1993:482; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mendoza-González et al., 1994:112; González-González et al., 1996:284; Mendoza-González and Mateo-Cid, 1996:74, 87, pl. 24: figs. 104–106; Leskinen and Pamilo, 1997:17;

Bucio-Pacheco and Dreckmann, 1998:42; Yoshida, 1998:35; Mendoza-González and Mateo-Cid, 1998:24, 27; Servièrre-Zaragoza et al., 1998:169, 180; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; López et al., 2000:340; Cruz-Ayala et al., 2001:190; L. Aguilar-Rosas et al., 2002:235; Abbott and Huisman, 2004:48, fig. 6A–C; Wysor, 2004:215; Hernández-Herrera et al., 2005:146; Dreckmann et al., 2006:153.

Enteromorpha compressa var. *flexuosa* (Wulfen) Hamel, 1931a:65, fig. 48 (5,6).

Enteromorpha prolifera var. *flexuosa* (Wulfen) Doty, 1947:15; Dawson, 1961b:374.

Enteromorpha lingulata J. Agardh, 1883:143; Setchell and Gardner, 1930:137; Taylor, 1945:39; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126, 131; Huerta-Múzquiz

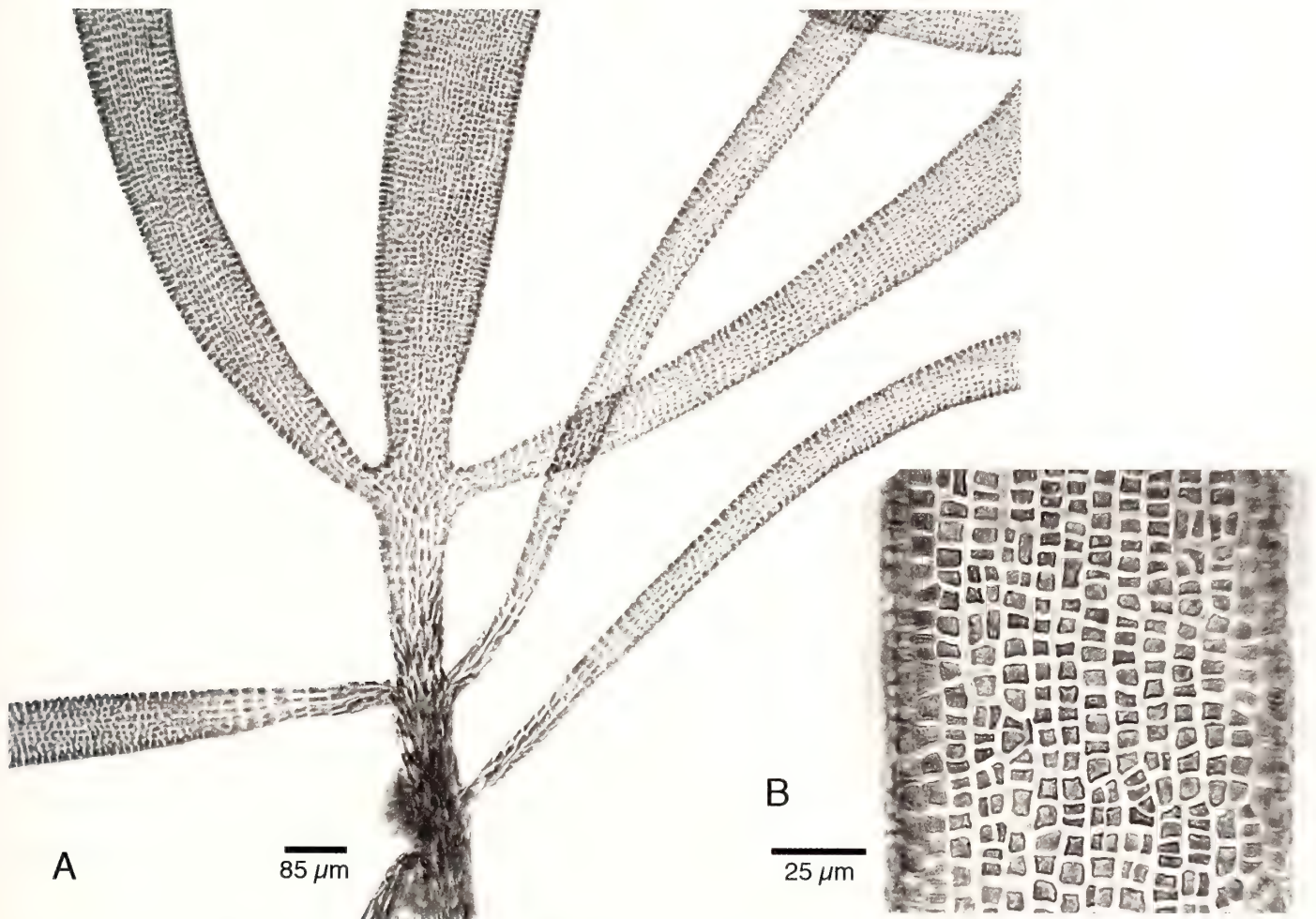


FIGURE 21. *Ulva flexuosa* (JN-4790): A. Lower portion of small thallus with several lateral branches and rhizoids growing downward toward the base. B. Surface view of cell arrangement in regular longitudinal and more or less transverse rows.

and Garza Barrientos, 1975:6; León-Tejera et al., 1993:199, 204; Mendoza-González and Mateo-Cid, 1998:24.

Enteromorpha tubulosa (Kützing) Kützing, 1856:11, pl. 32: fig. 2; Dawson, 1945b:59; Taylor, 1945:38, "prox."; Dawson, 1961b:374; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Chávez B., 1972:268; Huerta-Múzquiz, 1978:335, 338; Huerta-Múzquiz and Mendoza-González, 1985:42.

Enteromorpha intestinalis var. *tubulosa* Kützing, 1845:247.

Algae cylindrical to slightly compressed, up to 10 cm tall and 0.5–5.0 mm wide, usually unbranched or sometimes sparsely branched (rarely with secondary branches), and without proliferations. Cells in surface view in longitudinal rows and transverse rows (evident in younger, narrower portions; not always distinct in older or broader portions); angular, quadrate to elongate, 8–15 μm wide by 10–20 μm long, with a parietal chloroplast and 1–2(–6) pyrenoids. Transverse section of 1 cell layer, 20–30 μm thick; with cells 12–20(–30) μm tall by 9–20 μm wide.

HABITAT. On rocks; high to low intertidal.

DISTRIBUTION. Gulf of California: El Tornillal to La Paz. Pacific coast: British Columbia to Costa Rica; Panamá; Colombia; Ecuador; Galápagos Islands; Chile; Hawaiian Islands; Japan.

TYPE LOCALITY. Duino (NW of Trieste), Italy, Adriatic Sea.

Ulva intestinalis Linnaeus

FIGURE 22

Ulva intestinalis Linnaeus, 1753:1163; Linnaeus, 1755:418; Blomster et al., 1998:332, figs. 49 (typotype), 52–54; Hayden et al., 2003:289, tbl. 4; Hayden and Waaland, 2004:377, tbl. 3; Pedroche et al., 2005:27; Mateo-Cid et al., 2006:48; Pacheco-Ruíz et al., 2008:191, 201.

Enteromorpha intestinalis (Linnaeus) Link in Nees, 1820:Index [2], 5; Howe, 1911:490; Setchell and Gardner, 1920b:252; Dawson, 1944:203; Dawson, 1961b:373; Dawson, 1962c:278; Bliding, 1963:139, figs. 87–89; Dawson, 1966a:5; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Brusca and Thomson, 1975:42; Norris, 1976a:76, fig. 31; Huerta-Múzquiz, 1978:336, 338; Silva, 1979:340; L. Aguilar-Rosas et al., 1982:61; R. Aguilar-Rosas, 1982:84; Koeman and van den Hoek, 1982a:308, figs. 70–94; Littler and Arnold, 1982:309; L. Aguilar-Rosas and Bertsch, 1983:114, 119; L. Aguilar-Rosas et

al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:42; Ibarra-Obando and R. Aguilar-Rosas, 1985:96; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Tello-Velazco, 1986:73; L. Aguilar-Rosas and Pacheco-Ruíz, 1989:81; Sánchez-Rodríguez et al., 1989:39; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Dreckmann et al., 1990:24, 37; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; González-González, 1993:443; Mateo-Cid et al., 1993:51; Stout and Dreckmann, 1993:4; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517, 529; Mendoza-González et al., 1994:112; González-González et al., 1996:285; Mendoza-González and Mateo-Cid, 1996:74, 87, pl. 23: figs. 98–101; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Pacheco-Ruíz and Zertuche-González, 1996a:432; Leskinen and Pamilo, 1997:17; Bucio-Pacheco and Dreckmann, 1998:42; Yoshida, 1998:35; Mendoza-González and Mateo-Cid, 1998:24, 27; Blomster et al., 1998:319, figs. 1–3, 16–26, 27–29, 49, 52–54; Rodríguez-Morales and Siqueiros-Beltrones, 1999:30; L. Aguilar-Rosas et al., 2000:133; León-Tejera and González-González, 2000:327; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:49, fig. 7A–C; Riosmena-Rodríguez et al., 2005:101; Hernández-Herrera et al., 2005:146; R. Aguilar-Rosas et al. 2005b:35; Dreckmann et al., 2006:153.

Enteromorpha marchantiae Setchell et N. L. Gardner, 1924a:716, pl. 16: figs. 40–42.

Algae usually simple, tubular and smooth throughout (sometimes irregularly inflated and constricted), up to 15 mm in diameter; attenuated toward base, remaining tubular (rarely becoming slightly compressed) and broadening upward; rarely branched. Cells in surface view, irregularly arranged throughout; 5–10 μm wide and 5–12 (–17) μm long; with a single cup-shaped chloroplast and usually 1(–2) pyrenoid(s).

HABITAT. On rocks, occasionally epiphytic on other algae; high to low intertidal; also dredged 4–50 m (Dawson, 1944).

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía La Paz. Pacific coast: Alaska to Chiapas; Peru; Chile; Hawaiian Islands; Japan; China.

TYPE LOCALITY. "In Mari omni" (Linnaeus, 1753); probably Woolwich, River Thames, London, England (based on selection of lectotype illustration of Dillenius [1742:pl. 9: fig. 7] and typotype [see Stearn, 1957:129] by Blomster et al. [1999:332, figs. 49, 52–54]).

REMARKS. Although some specimens of *Ulva intestinalis* can sometimes be confused with morphologically



FIGURE 22. *Ulva intestinalis*: Cluster of tubular thalli; most unbranched, a few branched near base (JN-3327).

similar specimens of *U. compressa*, studies have shown them to be genetically distinct (Blomster et al., 1998; Hayden and Waaland, 2004).

***Ulva linza* Linnaeus**

FIGURE 23

Ulva linza Linnaeus, 1753:1163; Setchell and Gardner, 1920b:262, pl. 12: figs. 1–4; Levring, 1941:605; Smith, 1944:44, pl. 3: figs. 4, 5; Hayden et al., 2003:289, tbl. 4; Hayden and Waaland, 2004:378, tbl. 3; Mateo-Cid et al., 2006:48; Pacheco-Ruiz et al., 2008:191, 201.

Enteromorpha linza (Linnaeus) J. Agardh, 1883:134, pl. 4: figs. 110–112; Collins, 1909b:206; Howe, 1911:490; Doty, 1947:18, pl. 1: figs. 7–9; Dawson, 1961b:373; Dawson, 1966a:5; Norris, 1976a:76, fig. 32; Silva,

1979:340; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Mendoza-González and Mateo-Cid, 1992:23; Mateo-Cid et al., 1993:51; Servièrre-Zaragoza et al., 1993:482; González-González et al., 1996:285, 371; Pacheco-Ruiz and Zertuche-González, 1996a:432; Yoshida, 1998:36, pl. 1-3: fig. G; Mendoza-González and Mateo-Cid, 1998:24; L. Aguilar-Rosas et al., 2000:133, 137; L. Aguilar-Rosas et al., 2002:235; Abbott and Huisman, 2004:50, fig. 7D; R. Aguilar-Rosas et al., 2005b:36.

Algae linear to lanceolate, unbranched blades, up to 40 cm long and up to 10 cm wide; composed of a flattened upper portion of 2 cell layers, with margins usually hollow and 1 cell thick; margins smooth or sometimes ruffled; and a lower portion that gradually tapers downward to a tubular, hollow monostromatic basal portion. Cells with a single cup-shaped chloroplast and usually 1 pyrenoid. Cells in surface view irregularly arranged in upper flat portions, 10–20 μm in diameter; cells in longitudinal rows in basal portions, elongated, up to 35 μm long. Cells in trans-section rectangular, up to 20 μm tall and to 35 μm wide.

HABITAT. On sand/mud covered rocks and shells in drainage channels of estuaries; occasionally in tide pools and shaded habitats; and epiphytic on crustose corallines (L. Aguilar-Rosas et al., 2000); mid to low intertidal.

DISTRIBUTION. Gulf of California: Las Piedras del Burro to La Paz. Pacific coast: Alaska to Baja California; Jalisco; Oaxaca; Chile; Juan Fernandez Island; Hawaiian Islands; Japan.

TYPE LOCALITY. “*In Oceano*” (Linnaeus, 1753:1163); Sheerness, Kent, England (Hayden et al., 2003:289).

REMARKS. On the basis of molecular analysis, Hayden and Waaland (2004) noted that northeast Pacific “*Ulva linza*” and European *U. linza* (Tan et al., 1999) may be different taxa. It will be interesting to see the results of comparative molecular analyses of the Gulf “*U. linza*,” Pacific “*U. linza*,” and European *U. linza* (type or type locality), to test their taxonomic status and phylogenetic relationships.

***Ulva radiata* (J. Agardh) Hayden, Blomster, Maggs, P. C. Silva, Stanhope et Waaland**

Enteromorpha radiata J. Agardh, 1883:156; Koeman and van den Hoek, 1982b:54, figs. 54–78.

Ulva radiata (J. Agardh) Hayden, Blomster, Maggs, P. C. Silva, Stanhope et Waaland, 2003:290, tbl. 4.



FIGURE 23. *Ulva linza*: Thalli of three unbranched blades, widening upward; flattened upper portion with tubular margins, above a short tubular basal portion (JN-3694).

Enteromorpha prolifera subsp. *radiata* (J. Agardh) Bliding, 1963:56, figs. 25–28.

Enteromorpha prolifera sensu Setchell and Gardner, 1920b:254; Setchell and Gardner, 1924a:715;

Dawson, 1944:204; Doty, 1947:14; Glynn and Stewart, 1973:216; Norris, 1976a:77, fig. 33; Pedroche and González-González, 1981:63; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González

and Mateo-Cid, 1986:419; Martínez-Lozano et al., 1991:23; Servière-Zaragoza et al., 1993:482; González-González et al., 1996:286; Pacheco-Ruíz and Zertuche-González, 1996a:432; Cruz-Ayala et al., 2001:190; Pedroche et al., 2005:32; Pacheco-Ruíz et al., 2008:201 [non *Enteromorpha prolifera* (O. F. Müller) J. Agardh, 1883:129; which is *Ulva prolifera* O. F. Müller, 1778:7, fig. 1].

Ulva prolifera sensu Hayden and Waaland, 2004:377, tbl. 3 [non *Ulva prolifera* O. F. Müller, 1778:7].

Enteromorpha tubulosa sensu Setchell and Gardner, 1924a:716 [non *Enteromorpha tubulosa* (Kützing) Kützing, 1856:11; *E. intestinalis* var. *tubulosa* Kützing, 1845: 247; which is *Ulva flexuosa* Wulfen, 1803:1].

Algae with a distinct, cylindrical to compressed main axis, variable in width from very slender (hairlike) filaments to broad, expanded or convoluted masses; usually with numerous lateral branches (rarely sparingly branched). Cells with a single chloroplast, usually with only 1 pyrenoid; in surface view in more or less longitudinal series (usually distinct in some portions); angular, quadrate to polygonal, (10–)12–18 µm wide, becoming elongated near base, 10–18 µm wide by 12–20(–34) µm long. Cells in transection, 10–18 µm wide by 15–30 µm tall.

HABITAT. On rocks, forming mats on mudflats or free-floating; usually in sheltered bays or estuaries; intertidal.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles to Bahía La Paz. Pacific coast: Washington to southern California; Jalisco; Panamá.

TYPE LOCALITY. Arctic Norway (Bliding, 1963).

REMARKS. Gulf of California specimens are tentatively referred to *Ulva radiata*. This species is probably more widely distributed in the Gulf of California than

current records indicate. Bliding (1963, as “*E. prolifera* subsp. *radiata*”) proposed that *E. prolifera* and *E. radiata* were different taxa. Hayden and Waaland (2004) found the Pacific coast “*U. prolifera*” (Washington to southern California) was only distantly genetically related to European *U. prolifera* (Blomster et al., 1998) and hypothesized that the Pacific Northwest material identified as “*U. prolifera*” was *U. radiata*, noting this needed to be tested with comparative molecular data from the European *U. radiata*. Comparisons of Gulf “*U. radiata*” with *U. radiata* from Europe (type locality: Arctic Norway) and the western Pacific are needed to evaluate its taxonomic status.

CLADOPHOROPHYCEAE

Cladophorophyceae C. Hoek, D. G. Mann et Jahns, 1995:408, *nom. invalid.* [see McNeill et al., 2006:Art. 36.2; Pröschold and Leliaert, 2007:130].

Algae are uniseriate unbranched or branched filaments composed of multinucleate cells, with thalli ranging from simple filaments to structurally more complex forms. Cells of sporophytes and gametophytes are multinucleate and with numerous chloroplasts that form a parietal network or a more or less continuous layer. Some of the chloroplasts may also have a single pyrenoid. The principal polysaccharide of the cell wall is crystalline cellulose.

Life histories for many of the species are isomorphic. Sporophytes produce quadriflagellate zoospores that develop into gametophytic thalli. Gametophytes produce biflagellate isogametes or anisogametes. After fusion of two gametes, the zygote develops into a diploid sporophyte.

Two of the orders are present in the northern Gulf of California.

KEY TO THE ORDERS OF CLADOPHOROPHYCEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae unbranched or branched filaments of terete cells throughout; tenacular cells absent; sequential formation of laterals at nodes; cell division by centripetal crosswall formation **Cladophorales**
- 1b. Algae of diverse forms: large siphonous, tubular cells or inflated, clavate, or globose cells; tenacular cells present; simultaneous development of laterals at nodes; cell division lenticular or segregative **Siphonocladales**

CLADOPHORALES

Cladophorales Haeckel, 1894:302.

Cladophorales G. S. West, 1904:56; van den Hoek, 1984:157–178.

Algae are filamentous and may be (1) simple and unbranched or with few to many branches, or (2) branched filaments with few to many lateral branches that unite to

form a network. Most are attached to the substratum by rhizoids, although some may become unattached and free-floating. The cells of the filaments have crosswalls and are multinucleate, with one or more discoid or reticulate chloroplasts and usually one or more pyrenoids. Growth is apical or intercalary. Cell division is by nonsynchronous centripetal invagination, in which the parent wall divides into more or less equal halves (= “*Cladophora*-type” of cell division).

Vegetative propagation by fragmentation is known for many of the species. The life histories, where known, are isomorphic (with gametophytes and sporophytes of similar morphologies). Sporophytes produce biflagellate or quadriflagellate zoospores in sporangia derived from vegetative cells. Gametophytes produce biflagellate isogametes or anisogametes.

REMARKS. There have been different opinions on whether the Cladophorales should also include the Siphonocladales (e.g., van den Hoek, 1984; Bakker et al., 1994; Hanyuda et al., 2002; Abbott and Huisman, 2004; Wynne, 2005), or if the two should be kept as separate orders (Womersley, 1984; Leliaert et al., 2003; Kraft, 2007) with the type of cell division being a principle taxonomic character. The use of families in the Cladophorales/Siphonocladales complex is also problematic as there seems to be no phylogenetic basis that supports the currently accepted families (Leliaert et al., 2007). For now, the families are treated herein in these two orders. Members of the Cladophorales are mostly marine (although a few, e.g., *Cladophora*, also have freshwater species) and distributed from sub-boreal to tropical seas, and members of the Siphonocladales are exclusively marine and subtropical to tropical.

KEY TO THE GENERA OF CLADOPHORACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments sparsely to densely branched, to 1 or more orders *Cladophora*
 1b. Filaments simple and unbranched or with short rhizoidal branches 2
 2a. Filaments unattached, entangled or free-floating; or if attached, by short rhizoidal branches along their length
 *Rhizoclonium*
 2b. Filaments attached by a discoid basal cell or by rhizoids extending only from the basal cell *Chaetomorpha*

***Chaetomorpha* Kützing**

Chaetomorpha Kützing, 1845:203.

Algae are uniseriate, unbranched filaments that grow singularly or in clumps and may be free-floating or attached by a discoid basal cell or by nonseptate rhizoidal processes from an elongate basal cell. Growth is by intercalary cell division only. Cells of the filaments can be shorter or up to 10 times longer than wide, and rectangular, isodiametric, or cylindrical to barrel-shaped. Cells are multinucleate, with a parietal or reticulate chloroplast and many pyrenoids.

Vegetative reproduction is by fragmentation. Life histories are presumed to be an isomorphic alternation of stages. Sporangia are formed in undifferentiated cells and

There is one family, well represented, in the northern Gulf of California.

CLADOPHORACEAE

Cladophoraceae W. Wille in Warming, 1884:30.

Algae in this family are filamentous, uniseriate, branched or unbranched, and vary in color from light to dark green. Cells are multinucleate, with parietal chloroplasts containing few to many pyrenoids.

Asexual reproduction for many is by fragmentation. Sexual reproduction, where known, is isogamous.

REMARKS. In the northern Gulf of California the family is represented by three genera, *Chaetomorpha*, *Cladophora*, and *Rhizoclonium*. However, the taxonomic distinction of the unbranched genera *Rhizoclonium* and *Chaetomorpha* is questionable (Blair et al., 1982; Blair, 1983; Silva et al., 1996a), with taxonomy based solely on filament diameter, cell sizes, and nature of the holdfasts. The generic and species concepts need further study and phylogenetic testing.

produce quadriflagellate zoospores (probably meiospores). Sexual reproduction is isogamous, with gametangia (also formed in an undifferentiated cell) producing biflagellate isogametes. Isogametes have also been reported to develop parthenogenetically.

REMARKS. Five species have been reported to occur only in the southern Gulf (Dawson, 1949; Dawson, 1950c; Huerta-Múzquiz and Mendoza-González, 1985; R. Aguiar-Rosas and Machado-Galindo, 1990; Riosmena-Rodríguez and Paul-Chávez, 1997; Pedroche et al., 2005): *C. linoides* Kützing (1847), *C. minima* Collins et Hervey (1917), *C. pachynema* (Montagne) Kützing (1847), *C. spiralis* Okamura (1903, 1912), and *C. javanica* Kützing (1847).

Of the four species that are known in the northern Gulf of California, three also occur in the southern Gulf.

KEY TO THE SPECIES OF *CHAETOMORPHA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments unattached, free-floating or lying on substratum, or entangled with other algae *C. linum* (in part)
 1b. Filaments attached by a basal cell or rhizoids from basal cell; forming clumps or tufts 2
 2a. Upper filament cells 400–900 μm wide, 1–4 times longer than wide; distinctive basal cell very long, up to 9 mm, usually with annular constrictions *C. antennina*
 2b. Upper filament cells narrower, 175–450 μm wide, only 0.5–2.5 times longer than wide; basal cell shorter, less than 4 mm, without annular constrictions 3
 3a. Cells wider than long, 250–280 μm wide by 125–148 μm long (0.5–0.6 times diameter); lowermost 1–2 basal cells 1.25 times longer than wide, up to 350 μm long *C. bangioides*
 3b. Cells longer than wide, 625–1100 μm long (0.75–2.5 times diameter), 250–450 μm wide; basal cell 3–5 times longer than wide 4
 4a. Filaments mostly curly; cells 175–450 μm wide, more or less squarish to slightly longer (0.75–1.5 times diameter); basal cell less than 5 times longer than wide. *C. linum* (in part)
 4b. Filaments straight; 240–400 μm wide; cells longer than wide (mostly 1.5–2.5 times diameter); basal cell up to 5–8 times longer than wide *C. aerea*

***Chaetomorpha aerea* (Dillwyn) Kützing**

FIGURE 24B

Conferva aerea Dillwyn, 1806:pl. 80.

Chaetomorpha aerea (Dillwyn) Kützing, 1849:379; Collins, 1909b:324; Hartmann, 1929:485; Dawson, 1944:208 (in part); Chávez B., 1972:268; Huerta-Múzquiz, 1978:338; Silva, 1979:342; Blair, 1983:187, figs. 5, 6; Oliva-Martínez and Ortega, 1987:128, pl. 4: fig. 2a–d; Ortega et al., 1987:78, pl. 14: figs. 65–67; Mateo-Cid and Mendoza-González, 1992:24; Serrière-Zaragoza et al., 1993:482; Mendoza-González et al., 1994:112; González-González et al., 1996:278; Pacheco-Ruiz and Zertuche-González, 1996a:432; Yoshida, 1998:54; L. Aguilar-Rosas et al., 2000:133; Abbott and Huisman, 2004: 65, fig. 17; Pedroche et al., 2005:34; Pacheco-Ruiz et al., 2008:201.

Chaetomorpha linum sensu Abbott and Hollenberg, 1976:101 [in part] [non *Chaetomorpha linum* (O. F. Müller) Kützing, 1845:204].

Tufts of erect, straight, uniseriate filaments, up to 4 (or more) cm tall, attached to substrate by an elongate basal cell with a disc-shaped holdfast. Upper to lower cells of more or less same diameter throughout, (125–)240–400 μm in diameter, often more or less squarish to slightly elongate, 1.0–2.0 times longer than wide; lowermost cells, 1.0–2.5 times longer than wide. Basal cell (nonannulate) of

similar diameter to cells above, but much longer, (4–)5–8 times longer than wide, up to 1.8 mm long.

Reproduction not observed in Gulf specimens. Fertile cells reported from elsewhere, up to 600 μm in diameter (Blair, 1983).

HABITAT. On rocks; high to mid intertidal.

DISTRIBUTION. Gulf of California: Puertecitos to Bahía de Los Ángeles. Pacific coast: central California to Nayarit; Peru; Chile; Hawaiian Islands; Japan.

SYNTYPE LOCALITIES. England and Wales, UK.

REMARKS. Some specimens of *Chaetomorpha aerea* (e.g., JN-5180a on US Alg. Coll. slide 4144; El Desemboque, Sonora) were particularly rich with microscopic endophytes and epiphytes, such as *Entocladia viridis*, that grew on, sometimes encircling, the cells of the basal region.

Some phycologists consider *Chaetomorpha aerea* and *C. linum* to be growth forms of a single species (e.g., Christensen, 1957; Burrows, 1991). However, herein these two are recognized as separate species (e.g., following Kornmann, 1972; Blair et al., 1982; Blair, 1983; Silva et al., 1996a), until further morphological and molecular systematic studies have been done on types and type-locality specimens of these species, along with needed comparisons to elucidate their relationship to Gulf of California “*C. aerea*.” Although crystalline cell inclusions are reported in *C. aerea* from other regions (Leliaert and Coppejans, 2004:202, fig. 47), they have not been observed in Gulf *C. aerea*.

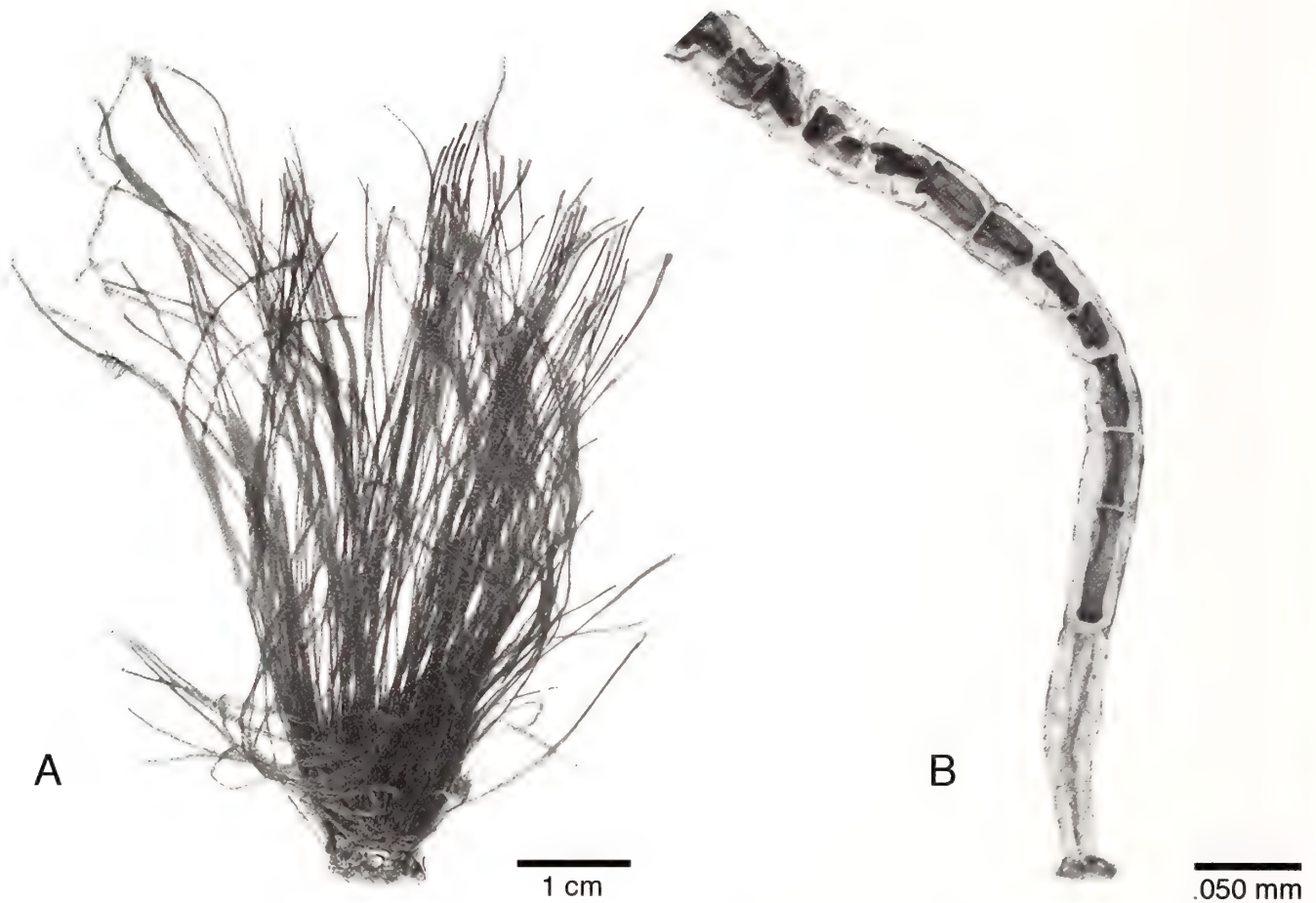


FIGURE 24. Species of *Chaetomorpha*. A. *Chaetomorpha antennina*: Clump of relatively stiff filaments (EYD-11023). B. *Chaetomorpha aerea*: Lower region of filament; long basal cell ending in disc-shaped base with short rhizoids (JN-5180a).

Chaetomorpha antennina
(Bory de Saint-Vincent) Kützing

FIGURES 24A, 25B

Conferva antennina Bory de Saint-Vincent, 1804a:381;
 Bory de Saint-Vincent, 1804b:161.

Chaetomorpha antennina (Bory de Saint-Vincent) Kützing, 1847:166; Kützing, 1849:379; Collins, 1909b:324; Howe, 1914:37; Setchell and Gardner, 1920b:203; Setchell and Gardner, 1924a:713; Setchell and Gardner, 1930:136; Dawson, 1944:207; Dawson, 1945b:59; Taylor, 1945:52; Dawson, 1949:245, 251; Dawson, 1950c:149, figs. 6, 7; Dawson, 1951:52; Dawson, 1954a:3; Dawson, 1959a:9, 12; Dawson, 1959c:4; Dawson and Beaudette, 1959:18, 20; Dawson, 1961b:376; Dawson, 1961c:403, pl. 1: figs 7, 8; Dawson, 1962b:172, fig. 8 (right); Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Norris,

1973:3, 19; Abbott and Hollenberg, 1976:101, fig. 58; Huerta-Múzquiz, 1978:338–340; Stewart and Stewart, 1984:140; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; Mendoza-González and Mateo-Cid, 1986:419; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:39; Dreckmann et al., 1990:24, 37; Mateo-Cid and Mendoza-González, 1991:27; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid and Mendoza-González, 1992:24; González-González, 1993:443; Stout and Dreckmann, 1993:4; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:52; Mateo-Cid and Mendoza-González, 1994b:44; León-Tejera and González-González, 1994:493; Mendoza-González et al., 1994:112; González-González et al., 1996:278; Silva et al., 1996b:229, 234; Mendoza-González and Mateo-Cid, 1996:75, 87, pl. 25, figs. 109, 110; Pacheco-Ruíz and Zertuche-González, 1996a:432; León-Alvarez et al.,

1997:397; Galindo-Villegas et al., 1997:4; Mateo-Cid and Mendoza-González, 1997:56; Servièrre-Zaragoza et al., 1998:169, 176, 178; Bucio-Pacheco and Dreckmann, 1998:44; Aguila-Ramírez et al., 1998:511; Yoshida, 1998:54; Mendoza-González and Mateo-Cid, 1998:25, 27; Mendoza-González et al., 1999:61; León-Tejera and González-González, 2000:237; Mateo-Cid et al., 2000a:69; Carballo et al., 2002:752; Abbott and Huisman, 2004:66, fig. 18A–D; Pedroche et al., 2005:35–36; Hernández-Herrera et al., 2005:146; Dreckmann et al., 2006:154; Servièrre-Zaragoza et al., 2007:7; Pacheco-Ruíz et al., 2008:201.

Conferva media C. Agardh, 1824:100.

Cladophora media (C. Agardh) Kützing, 1849:380; Huerta-Múzquiz and Tirado-Lizárraga, 1970:120, 131, 135; Chávez B., 1972:268; Pedroche and González-González, 1981:64.

Cladophora pacifica Kützing, 1849:379 (see Collins 1909b:324; Howe, 1914:37).

Algae erect, tufted or clumped, of relatively stiff, uniseriate filaments, up to 10 cm tall, attached by an elongated basal cell with long slender rhizoids from proximal end. Upper cells 400–900 µm in diameter, 1–4 times as long as wide; basal cell of similar width but much longer, 5–9 mm in length. Basal cell usually with annular constrictions.

Fertile cells swollen and larger than vegetative cells.

HABITAT. On rocks, usually in shaded areas; high to low intertidal.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles to Bahía San Carlos; Isla San Ildefonso; Cabeza Ballena to Cabo Pulmo. Pacific coast: southern California to Chiapas; Isla San Benedicto (Islas Revillagigedo); Cliperton Island; El Salvador; Panamá; Galápagos Islands; Ecuador; Peru; Chile; Hawaiian Islands; China; Japan.

TYPE LOCALITY. Réunion Island (Bourbon Is.), Mascarene Islands, Indian Ocean.

Chaetomorpha bangioides E. Y. Dawson

FIGURE 25A

Chaetomorpha bangioides E. Y. Dawson, 1950c:149, figs. 8–10; Dawson, 1959a:7, 12; Dawson, 1961b:376; Espinoza-Ávalos, 1993:333; Servièrre-Zaragoza et al., 1993:479, 485; González-González, 1993:443; González-González et al., 1996:128; Servièrre-Zaragoza et al., 1998:169, 180; Pedroche et al., 2005:36.

Algae tufted, up to 1 cm tall; of uniseriate more or less contorted filaments and attached by a small, conical

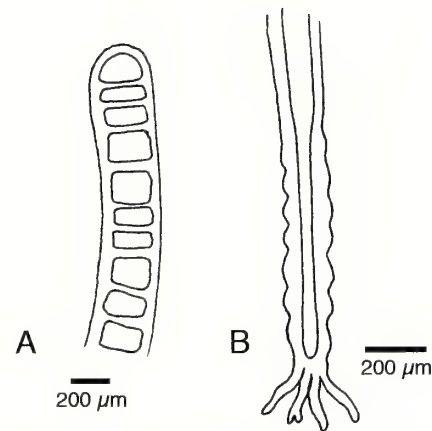


FIGURE 25. Species of *Chaetomorpha*. A. *Chaetomorpha bangioides*: Rectangular (wider than long) cells of different “*Bangia*-like” shapes in upper part of filament (after Dawson, 1950c:fig. 10). B. *Chaetomorpha antennina*: Basal cell, typically very long, with short attachment rhizoids, and cell wall with annular constrictions.

holdfast of coalesced rhizoids issued from the primary basal cell. Cells wider than long (more or less rectangular in lateral view), 250–280 µm in diameter, shorter in length (mostly 0.5–0.6 times diameter); lowermost 1–2 cells of similar diameter as upper cells, but slightly longer (up to 350 µm in length). Cell walls thick, up to 60 µm.

Reproduction unknown.

HABITAT. On rocks; intertidal.

DISTRIBUTION. Gulf of California: Isla Patos; Puerto Escondido. Pacific coast: Nayarit to Jalisco.

TYPE LOCALITY. Isla Patos, off Isla Tiburón, Gulf of California.

REMARKS. *Chaetomorpha bangioides* is named for the resemblance of its filament cells to those of *Bangia fuscopurpurea*. It differs from other Gulf of California species of *Chaetomorpha* in the shape of its cells, rectangular with the diameter wider than the length, and the absence of a very long or otherwise distinctive basal cell (Dawson, 1950c). This species remains poorly known and in need of further collection and study.

Chaetomorpha linum (O. F. Müller) Kützing

Conferva linum O. F. Müller, 1778:7, pl. 771; fig. 2.

Chaetomorpha linum (O. F. Müller) Kützing, 1845:204; Dawson, 1949:229; Dawson, 1959a:12; Dawson, 1961b:377; Devinny, 1978:358; L. Aguilar-Rosas et al., 1982:54, 61; L. Aguilar-Rosas and Bertsch, 1983:115, 121; Blair, 1983:178, figs. 1, 2a; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and

Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mendoza-González and Mateo-Cid, 1986:419; Ortega et al., 1987:79, 90, pl. 15: fig. 68; L. Aguilar-Rosas and Pacheco-Ruíz, 1989:81; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Stewart, 1991:29; Mateo-Cid and Mendoza-González, 1991:27; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid and Mendoza-González, 1992:24; Mateo-Cid et al., 1993:51; León-Tejera and González-González, 1993:497; Servièrre-Zaragoza et al., 1993:482; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mateo-Cid and Mendoza-González, 1994b:34, 44; Mendoza-González et al., 1994:112; González-González et al., 1996:278; Yoshida, 1998:56; Servièrre-Zaragoza et al., 1998:169, 177, 180; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; L. Aguilar-Rosas et al., 2000:133, 134; L. Aguilar-Rosas et al., 2002:235; Wysor, 2004:216; Pedroche et al., 2005:38–39; Riosmena-Rodríguez et al., 2005:101; Hernández-Herrera et al., 2005:146.

Chaetomorpha aerea f. *linum* (O. F. Müller) Collins, 1909b:325.

Chaetomorpha aerea sensu Dawson, 1944:208 [in part] [non *Chaetomorpha aerea* (Dillwyn) Kützing, 1849:379].

Algae of mostly curved to curled, uniseriate filaments, up to 5 (or more) cm long, usually entangled and unattached or occasionally found attached to substrate by an elongated, lobed basal cell. Upper cells cylindrical to barrel-shaped, (175–)200–450 µm in diameter, and not as long as wide or only slightly longer (length 0.75–1.5 times the width); basal cells, when present, 3–8 times longer than wide.

Reproductive cells barrel-shaped to subglobose, 400–600 µm in diameter.

HABITAT. Estuarine habitats and mangrove lagoons; mid intertidal to shallow subtidal (also dredged; Dawson, 1944).

DISTRIBUTION. Gulf of California: Puertecitos to La Paz. Pacific coast: Alaska to Baja California; Sinaloa to Colima; Oaxaca; Panamá; Chile; Japan.

SYNTYPE LOCALITIES. Nakskov Fjord and Rødby Fjord, Denmark.

REMARKS. The species *Chaetomorpha linum* and *C. aerea* have long been problematic and often confused (Blair, 1983), and Gulf of California specimens referred to either of these species should be reexamined to determine if only one or both taxa occur in the northern

Gulf of California. See also comments herein on *Chaetomorpha aerea* under Remarks for that species.

***Cladophora* Kützing**

Cladophora Kützing, 1843:262

Algae consisting of uniseriate filaments, sparsely to profusely branched; usually erect and attached by rhizoids from basal cells; or sometimes free-floating, forming small to large filamentous masses. Branching is often up to several orders, most with variation in pattern of branching and in diameter (often decreasing in diameter upward). Cells are cylindrical, multinucleate, and with numerous small chloroplasts (usually form a parietal reticulum) and pyrenoids. Cell division is apical or intercalary or sometimes both.

Vegetative reproduction by fragmentation occurs in many species. Life histories are an alternation of isomorphic generations. The terminal and subterminal cells of the filaments become the reproductive cells. Sporophytic reproduction is usually by the formation of quadriflagellate or biflagellate zoospores. Gametophytes produce biflagellate isogametes.

REMARKS. The Gulf species of *Cladophora* are in need of critical study. Their taxonomy, based primarily on characters such as habit, cell diameter and length/width ratio, and type and degree of branching, is complicated by a high degree of variability of their relatively simple morphologies. Another character, considered to have systematic value, is the presence or absence of crystalline cell inclusions (Leliaert and Coppejans, 2004). Comparative morphological studies of Gulf specimens of *Cladophora* and type specimens (such as those of van den Hoek, 1963, 1982; Söderström, 1963; Sakai, 1964; van den Hoek and Womersley, 1984; van den Hoek and Chihara, 2000) and molecular and phylogenetic analyses are needed to test their taxonomic status.

Five taxa are recorded in the southern Gulf: *Cladophora lehmanniana* (Lindenberg) Kützing (1843) by Dawson (1959a, as “*C. utriculosa* Kützing”), *C. glomerata* (Linnaeus) Kützing (1843) by Huerta-Múzquiz and Mendoza-González (1985), *C. glomerata* var. *crassior* (C. Agardh) van den Hoek (1963) by Huerta-Múzquiz and Mendoza-González (1985, as “*C. crispata*”), *C. rivularis* (Linnaeus) van den Hoek (1963) by Huerta-Múzquiz and Mendoza-González (1985, as “*C. insignis*”), and *C. stimpsonii* Harvey (1860; Dawson, 1959b) by Rocha-Ramírez and Siqueiros-Beltrones (1991).

A highly diverse genus, with 11 species of *Cladophora* currently recognized in the northern Gulf of California.

KEY TO THE SPECIES OF *CLADOPHORA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Basal portion procumbent, of densely entangled horizontally low-growing filaments; upper portion of erect filaments *C. columbiana*
- 1b. Basal and upper portions erect; of delicate to coarse filaments 2
- 2a. Cells of basal region with rhizoids that have cell walls with annular constrictions (occasionally some basal cells also with annular constrictions) *C. prolifera*
- 2b. Cells of basal region with rhizoids that lack annular constrictions or completely without rhizoids 3
- 3a. Cell diameter of main branches over 200 μm 4
- 3b. Cell diameter of main branches less than 200 μm 7
- 4a. Basal cells without downward growing rhizoids; filaments branched mostly to one side; branchlets usually strongly incurved or curled *C. vagabunda*
- 4b. Basal cells with downward growing rhizoids; filaments branched otherwise; branchlets not curled 5
- 5a. Branched sparingly, dichotomous in lower portions; secund to pectinate (occasionally opposite or rarely alternate) in upper portions *C. macdougallii*
- 5b. Branched mostly dichotomously to trichotomously throughout 6
- 6a. Stiff tufts; filament cells much longer than wide, lower cells 300–500 μm wide, 20–30 times longer than wide; upper cells 100–150 μm wide, 4–10 times longer than wide *C. graminea*
- 6b. Lax tufts (not stiff), branching divaricate; cells only 2–4 times longer than wide and smaller diameter throughout; lower cells 190–240 μm wide; upper cells 25–40 μm wide *C. hesperia*
- 7a. Branching dichotomous or trichotomous, becoming irregularly alternate to pectinate above; cells 120–180(–200) μm in diameter in lower portions, narrowing above *C. microcladioides*
- 7b. Branching subdichotomous, irregular, alternate or secund; cells of smaller diameter, 20–60(–85) μm 8
- 8a. Upper main axes subdichotomously, irregularly or unilaterally branched; branches formed at distal end of cells; cells of similar diameter, 20–30(–40) μm , throughout *C. albida*
- 8b. Upper axes subdichotomously and/or secondly branched; lower cells larger than 30 μm in diameter 9
- 9a. Branched sparingly (widely spaced), subdichotomously; branches of different lengths intermixed; lower cells 50(–85) μm wide (5–6 times as long) *C. sericea*
- 9b. Branched more regularly; subdichotomously below to secund above; lower cells less than 60 μm wide (3–5 times as long) 10
- 10a. Dense short tufts (<4mm tall) of stiff filaments; cells mostly 4–5 times longer than wide throughout (longest in lower cells) *C. tiburonensis*
- 10b. Delicate hairlike filaments to 2 cm tall; lower cells 3–4 times longer than wide, upper cells 1–2 times longer than wide *C. montagneana*

***Cladophora albida* (Nees) Kützing**

FIGURE 26A

Annulina albida Nees, 1820:Index [1] [see Silva et al., 1996a:769].

Cladophora albida (Nees) Kützing, 1843:267; León-Tejera et al., 1993:199; González-González, 1993:443; Servièrre-Zaragoza et al., 1993:481; Silva et al., 1996a:769; González-González et al., 1996:129, 368; Yoshida, 1998:60; Nuñez-López et al., 1998:39; van den Hoek and Chihara, 2000:122, figs. 55–59, 63B,D; Pedroche et al., 2005:40.

Conferva albida Hudson, 1778:595, *nom. illeg.* [since it is a later homonym of *Conferva albida* Forsskål, 1775:XII].

Cladophora albida (Hudson) Kützing, 1843:267; Kützing, 1849:400; Kützing, 1854:pl. 15; Collins, 1909b:336; Setchell and Gardner, 1920b:218; Yamada, 1928:fig. 1; Dawson, 1944:209; Söderström, 1955:275, figs. 1–6; Dawson, 1959a:12; Dawson, 1960a:31; Dawson, 1961b:377; Dawson, 1961c:403, pl. 2: figs. 1, 2; Dawson, 1962b:182, fig. 32; van den Hoek, 1963:94, pl. 20: figs. 241–243, pl. 21: figs. 244, 246–257, pl. 22: figs. 258–279, pl. 23: figs. 280–297, pl. 24: figs. 298–316; Söderström, 1963:65, figs. 55–61; Sakai, 1964:30,

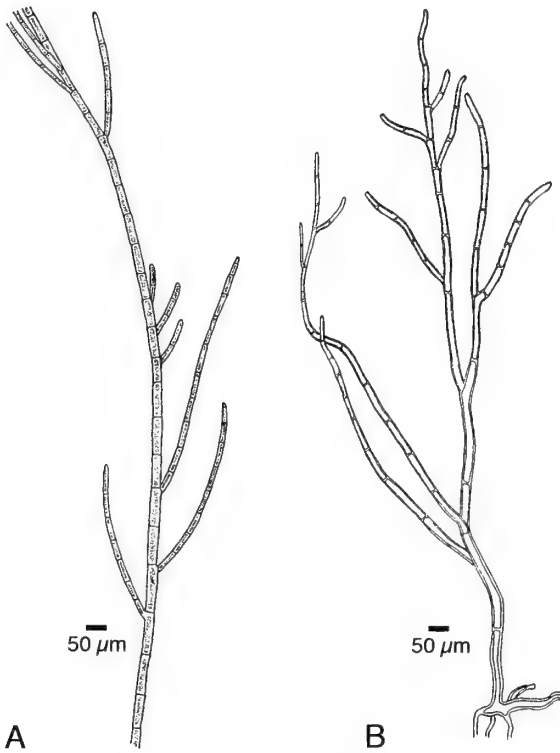


FIGURE 26. Species of *Cladophora*. A. *Cladophora albida*: Portion of a sparsely branched axis (after Dawson, 1962b:fig. 32). B. *Cladophora tiburonensis*: Habit of individual frond from short dense tuft (after Dawson, 1944: pl. 31, fig. 1).

Algae small tufts up to 1 cm tall, of delicate filaments with main axes closely and pseudodichotomously branched, mostly 1–2 orders. Branches formed at distal end of cells; usually 1 per cell. Filaments thin, of similar diameter throughout; mostly 20–30(–40) μm in diameter; cells (2–)4–5 times as long as wide. Cells with a reticulate chloroplast and numerous pyrenoids.

HABITAT. On shaded or exposed rocks, also epiphytic on *Cladophora microcladioides* and epizoic on a parrotfish beak; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles to Bahía Kino; Puerto Escondido; Cabo San Lucas. Pacific coast: British Columbia to Chiapas; El Salvador; Colombia; Japan.

TYPE LOCALITY. Isle of Selsey, England.

REMARKS. Not well known in the Gulf, *Cladophora albida* has been found epiphytic on *C. microcladioides* in the vicinity of Bahía Kino (Dawson, 1944) and Bahía de Los Ángeles (Pacheco-Ruíz and Zertuche-González, 1996a) and growing on the beak of a parrotfish taken at Puerto Escondido (Dawson, 1959a). A specimen from Cabo San Lucas (EYD-3203 [HAFH now UC]) represents a southern record for the Gulf.

Cladophora columbiana Collins

FIGURE 27A

Cladophora columbiana Collins in Setchell et N. L. Gardner, 1903:226; Dawson, 1944:210 [with doubt]; Dawson, 1961b:378; Abbott and Hollenberg, 1976:105, fig. 63; Devinny, 1978:358; L. Aguilar-Rosas et al., 1985:125; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mendoza-González and Mateo-Cid, 1986:419; R. Aguilar-Rosas et al., 1990:123; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Martínez-Lozano et al., 1991:22; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517, 526; González-González et al., 1996:129; Mendoza-González et al., 1999:61; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Pedroche et al., 2005:42; Riosmena-Rodríguez et al., 2005:101.

Cladophora trichotoma sensu Collins, 1909b:349; Howe, 1911:492; Setchell and Gardner, 1920b:210, pl. 16: fig. 2; Smith, 1944:58, pl. 7: fig. 2; Dawson, 1945b:64; Dawson, 1949:219, 222, 228; Huerta-Múzquiz and Mendoza-González, 1985:42; González-González et al., 1996:131 [non *Cladophora trichotoma* (C. Agardh) Kützing, 1849:414; basionym: *Conferva trichotoma*

figs. 10, 11, pl. 17: fig. 1; Söderström, 1965:173, 181; Abbott and Hollenberg, 1976:104, fig. 62; Devinny, 1978:358; Ortega et al., 1987:79, 90, pl. 16: figs. 72, 73; Schnetter and Bula Meyer, 1982:24, pl. 3: figs. D–F; van den Hoek, 1982:100, pl. 15: figs. 133–137, pl. 16: fig. 144; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mateo-Cid and Mendoza-González, 1991:27; Stewart, 1991:30; Mendoza-González and Mateo-Cid, 1992:24; León-Tejera et al., 1993:199; Mendoza-González and Mateo-Cid, 1996:75, 87, pl. 25: figs. 111–113; Pacheco-Ruíz and Zertuche-González, 1996a:432; Dreckmann et al., 2006:154; Pacheco-Ruíz et al., 2008:201.

Conferva hamosa Kützing, 1843:267.

Cladophora bertolonii var. *hamosa* (Kützing) Ardissonne, 1887:242; Huerta-Múzquiz and Mendoza-González, 1985:42.

Cladophora magdalenae Harvey, 1851:pl. 355A; Dawson, 1949:230.

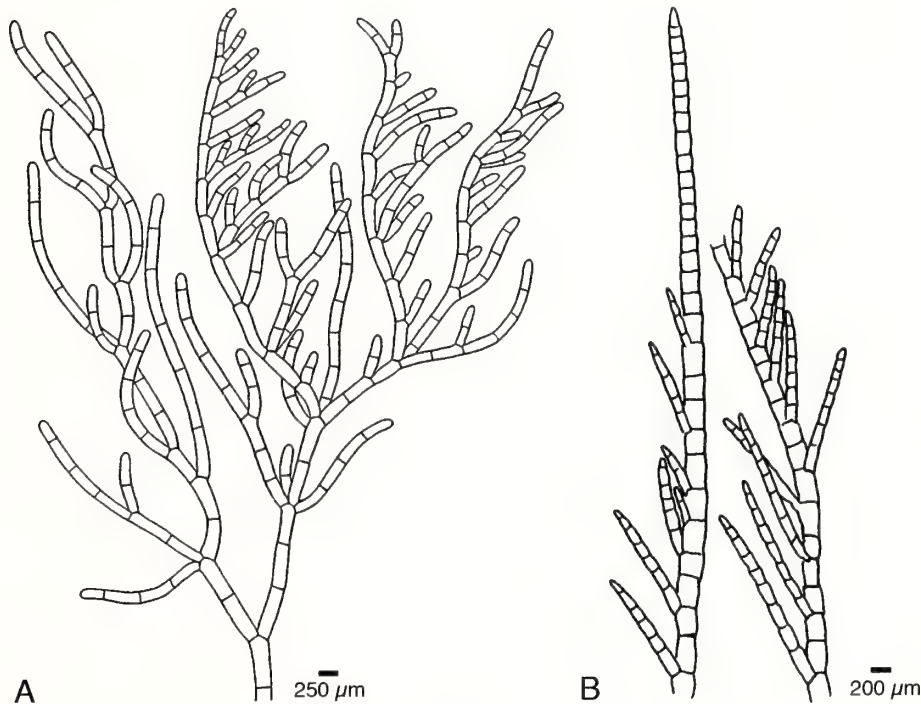


FIGURE 27. Species of *Cladophora*. A. *Cladophora columbiana*: Branching habit of a few upper branches (after Setchell and Gardner, 1920b: pl. 16, fig. 2). B. *Cladophora macdougalii*: Portion of two filaments, apical region (left) and upper portion (right) (after M. Howe, 1911: pl. 33, fig. 7).

C. Agardh, 1824:121, which is *Cladophora pellucida* (Hudson) Kützing, 1843:271; basionym: *Conferva pellucida* Hudson, 1762:483 (see van den Hoek, 1963:215)].

Algae cushionlike or forming low-growing mats of entangled filaments, 3–5 cm tall; attached by rhizoids from cells of basal filaments and from lower cells of erect filaments; lower basal filaments growing more or less horizontal; upper filaments erect, unbranched to sparsely branched in lower portion, becoming dichotomously or trichotomously to irregularly branched upward; with a blunt terminal cell. Cells cylindrical; in main axes 150–250(–300) µm in diameter, and 400–1500 µm long; apical cells narrower (90–)130–170 µm in diameter.

HABITAT. On rocks or other hard substratum; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; Bahía del Rincón to La Paz. Pacific coast: Alaska to Bahía Tortugas, Baja California Sur.

TYPE LOCALITY. Port Renfrew, Vancouver Island, British Columbia, Canada.

Cladophora graminea Collins

FIGURE 28A,B

Cladophora graminea Collins, 1909a:19, pl. 78: fig. 6; Setchell and Gardner, 1920b:211; Dawson, 1944:210; Smith, 1944:59, pl. 7: fig. 1; Dawson, 1945b:64; Dawson, 1949:222, 245; Dawson, 1951:52; Dawson et al., 1960a:26, pl. 1: fig. 6; Dawson et al., 1960b:5, 7–9, 12; Dawson, 1961b:377; Dawson, 1966a:6; Dawson and Neushul, 1966:174; Abbott and Hollenberg, 1976:105, fig. 64; Huerta-Múzquiz, 1978:336; Deviny, 1978:358; Littler and Littler, 1981:151, 153; Schnetter and Bula Meyer, 1982:25, pl. 3: figs. A–C; L. Aguilar-Rosas and Bertsch, 1983:116, 121; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; R. Aguilar-Rosas et al., 1990:123; Stewart, 1991:31; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mateo-Cid and Mendoza-González, 1994a:57; González-González et al., 1996:130; Pacheco-Ruíz and Zertuche-González, 1996a:432; Núñez-López et al., 1998:39; Pedroche et

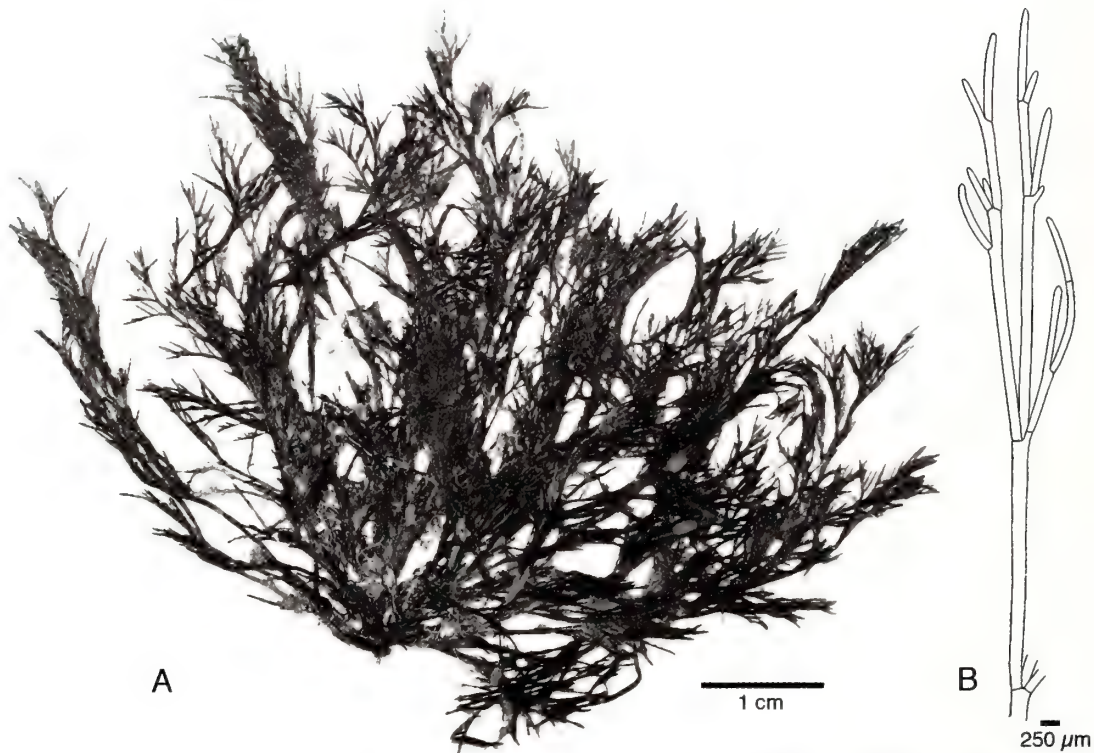


FIGURE 28. *Cladophora graminea*: A. Habit (JN-3118). B. Axis of long cells, slightly tapering in diameter to the apices (from Collins, 1909a: pl. 78, fig. 6).

al., 2005:43; Mateo-Cid et al., 2006:48; Pacheco-Ruíz et al., 2008:201.

Algae in tufts, up to 8(–18) cm tall; relatively stiff, coarse, dark green to blackish-green; dichotomously or trichotomously branched, sometimes becoming alternate in upper portions. Branch divisions at more or less same angle throughout; branches usually curving in same direction. Cells very long in relation to diameter, in lower portions up to 300 μm in diameter, and 20–30 times as long as wide; in upper branches 100–150 μm in diameter, and 4–10 times as long as wide.

HABITAT. On rocks, in shaded areas, crevices or under other larger algae; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas. Pacific coast: Oregon to Isla Magdalena (Baja California Sur); Colombia.

TYPE LOCALITY. Pacific Grove, Monterey County, California.

REMARKS. Dawson (1944, 1966a) referred his Gulf specimens to *Cladophora graminea* with doubt. However, the Gulf specimens, with their long cell length to width ratio, seem to agree with Pacific coast *C. graminea* and thus, for now, are retained under this name.

***Cladophora hesperia* Setchell et N. L. Gardner**

FIGURE 29A,B

Cladophora hesperia Setchell et N. L. Gardner, 1924a:713, pl. 13: fig. 17; Dawson, 1944:211; Dawson, 1949:247; Dawson, 1952:431; Dawson, 1954e:323; Dawson, 1961b:377; Dawson, 1966a:6; Stewart, 1982:54; Huerta-Múzquiz and Mendoza-González, 1985:42; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; González-González et al., 1996:130; Rodríguez-Morales and Siqueiros-Beltrones, 1999:17, 22; L. Aguilar-Rosas et al., 2000:133; Paul-Chávez and Riosmena-Rodríguez, 2000:146; L. Aguilar-Rosas et

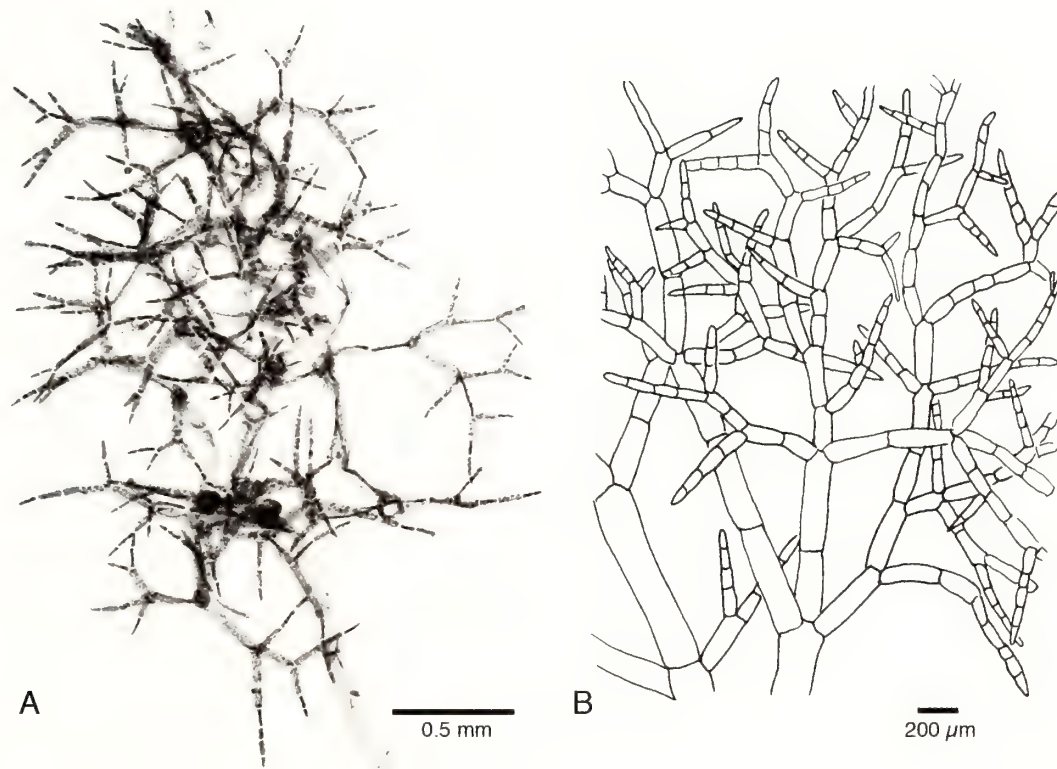


FIGURE 29. *Cladophora hesperia*: A. Branches widely divaricate and decreasing in diameter with each successive branch order (EYD-832). B. Branching habit of upper branches (after Setchell and Gardner, 1924a: pl. 13, fig. 17).

al., 2002:235; Pedroche et al., 2005:44; Mateo-Cid et al., 2006:48, 58.

Algae forming dense clumps or sometimes spreading thin mats, up to 1.5 cm tall, light green, abundantly and densely dichotomously to trichotomously branched, up to 6 orders, divaricate (branching at a wide angle) from the upper end of cells. Main branches of more or less uniform width, 190–240 μm in diameter; at each branch fork diameter becomes reduced upward; short branchlets of the fourth to sixth order much narrower, mostly 25–40 μm in diameter; tapering to blunt apices. Cells mostly 2–4 times as long as wide (up to 1 mm in length).

HABITAT. On mudflats and rocks, usually among other turf-forming algae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Piedras de La Salina to Bahía Kino; Bahía San Gabriel, Isla Espiritu Santo to Cabo San Lucas. Pacific Mexico: Punta Norte, Isla Cedros (Baja California) to Velero Point (~10 miles [16 km] west of Punta Malarrimo), Bahía Sebastián Vizcaíno (Baja California Sur); Mazatlán (Sinaloa).

TYPE LOCALITY: “Muddy habitat, at the southern extremity of Lower California [Baja California Sur]” (Setchell and Gardner, 1924a:714); given as “distrito de Cabo San Lucas” by Pedroche et al. (2005:44).

REMARKS. Originally described from the southern Gulf of California, *Cladophora hesperia* has also been reported from Pacific Mexico (Dawson, 1954e).

***Cladophora macdougalii* M. Howe**

FIGURE 27B

Cladophora macdougalii M. Howe, 1911:491, pl. 33: fig. 7; Collins, 1912:96; Setchell and Gardner, 1920b:214; Dawson, 1944:211; Dawson, 1961b:378; Hommersand, 1972:70; Espinoza-Ávalos, 1993:333; González-González et al., 1996:130; L. Aguilar-Rosas et al., 2000:129, 133; Pedroche et al., 2005:45.

Algae in tufts, coarse and rigid, yellow to dark green, up to 17 cm tall; branched sparingly dichotomously

below, and in upper portions usually secund to pectinate, or occasionally opposite or rarely alternate. Cells of main filaments 135–310 μm in diameter, 6–15 times as long as wide; cells of upper segments 75–110 μm in diameter, 1–4 times as long as wide; apical cells subacute or blunt.

HABITAT. Tidal flats and rocks; probably mid tidal.

DISTRIBUTION. Gulf of California: El Machorro; San Felipe to Puertecitos.

TYPE LOCALITY. San Felipe, Baja California, Gulf of California.

REMARKS. Thus far, *Cladophora macdougallii* is only known from the type and the more recent collections of L. Aguilar-Rosas et al. (2000). Although Collins (1912) noted that *C. macdougallii* was “quite close” to California specimens identified as “*C. ovoidea*” and Setchell and Gardner (1920b) considered Californian “*C. ovoidea*” close to illustrations of Kützing (1853:pl. 92: fig. 1), Dawson (1944) later preferred to keep these two separate. Further, the type material of European *C. ovoidea* Kützing (1843) is now considered to be a synonym of *C. sericea* (Hudson) Kützing (1843; see van den Hoek, 1963, 1982), and the California “*C. ovoidea*” sensu Collins (1909b, 1912) and Smith (1944) was recognized as a separate species, *C. sakaii* I. A. Abbott (1972). (Note that this is a replacement name since the earliest name, *C. densa* W. H. Harvey (1860; Dawson, 1959b), is a later homonym of *C. densa* (Roth) Kützing, 1845.) The lowermost basal portions of *C. macdougallii* have smooth cell walls, distinguishing them from those of *C. sakaii*, which have annular constrictions (see Abbott and Hollenberg, 1976:fig. 66).

For now, *C. macdougallii* is still recognized as a species, and will be until more Gulf collections have been made and morphological and molecular analyses have been completed and compared to other known species.

***Cladophora microcladioides* Collins**

FIGURE 30A,B

Cladophora microcladioides Collins, 1909a:17, pl. 78: figs. 2, 3; Setchell and Gardner, 1920b:212, pl. 13: fig. 2; Dawson, 1944:209; Smith, 1944:59, pl. 7: fig. 3; Dawson, 1945b:60, 64; Doty, 1947:23; Dawson, 1949:222, 224, 225; Dawson, 1961b:378; Dawson, 1962c:278; Dawson, 1966a:6; Abbott and Hollenberg, 1976:106, fig. 65; Devanny, 1978:538; R. Aguilar-Rosas, 1982:84; L. Aguilar-Rosas and Bertsch, 1983:116, 121; Stewart and Stewart, 1984:140; Huerta-Múzquiz and

Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Huerta Muzquiz, 1978:336; Mendoza-González and Mateo-Cid, 1986:419; Sánchez-Rodríguez et al., 1989:39; Dreckmann et al., 1990:24, 37; Mateo-Cid and Mendoza-González, 1991:27; Stewart, 1991:31; González-González, 1993:443; Mateo-Cid et al., 1993:51; León-Tejera et al., 1993:199, 204; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mateo-Cid and Mendoza-González, 1994a: 52, 61; Mendoza-González et al., 1994:103, 112; González-González et al., 1996:130; Pacheco-Ruíz and Zertuche-González, 1996a:432; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Bucio-Pacheco and Dreckmann, 1998:43; Núñez-López et al., 1998:39; Mendoza-González et al., 1999:61; Rodríguez-Morales and Siqueiros-Beltrones, 1999:17, 22; L. Aguilar-Rosas et al., 2000:133; León-Tejera and González-González, 2000:327; López et al., 2000:339; Paul-Chávez and Riosmena-Rodríguez, 2000:146; L. Aguilar-Rosas et al., 2002:235; Wysor, 2004:217; R. Aguilar-Rosas et al., 2005b:36; Hernández-Herrera et al., 2005:146; Pedroche et al., 2005:45; Riosmena-Rodríguez et al., 2005:101; Mateo-Cid et al., 2006:48; Pacheco-Ruíz et al., 2008:201.

Algae loosely tufted, up to 10 cm tall or more. Lower filaments 120–170(–200) μm in diameter with cells 3–4(–5) times as long as wide; becoming narrower above, 60–120 μm in diameter, with cells 2–4 times as long as wide; ultimate branchlets 30–50 μm in diameter and tapered slightly to rounded apices. Branching dichotomously or trichotomously from main axis, becoming irregularly alternate to pectinate above; lateral branches progressively shorter toward apex, with shorter secund branchlets along adaxial side; ultimate branchlets sometimes recurved.

HABITAT. On rocks; mid intertidal to shallow subtidal to 4(–32) m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific coast: Alaska to Michoacán; Oaxaca; Panama.

TYPE LOCALITY. San Pedro, Los Angeles County, California.

***Cladophora montagneana* Kützing**

Cladophora montagneana Kützing, 1849:415; van den Hoek, 1982:105, figs. 145–173; van den Hoek and Womersley, 1984:204, figs. 66B, 67E–I; Bucio-Pacheco and Dreckmann, 1998:43; Pedroche et al., 2005:46.



FIGURE 30. *Cladophora microcladioides*: A. Branching pattern of an upper branch (after Setchell and Gardner, 1920b: pl. 13, fig. 2). B. Upper lateral branches with pectinate branching pattern (EYD-2928).

Conferva brachyclados Montagne, 1837:349; Montagne, 1842a:13, pl. 4 [type of *Cladophora montagneana*; see van den Hoek, 1982:105].

Cladophora brachyclados (Montagne) Harvey, 1858:81.

Cladophora delicatula Montagne, 1850:302; Kützing, 1856: pl. 1: fig. 2; Dawson, 1944:210; Dawson, 1961b:377; Dawson, 1966a:5 [with a query]; González-González et al., 1996:281; Bucio-Pacheco and Dreckmann, 1998:44; Wysor, 2004:217; Mateo-Cid et al., 2006:48 [with a query].

Algae delicate hair-like tufts, of narrow filaments up to 2 cm long; branching often widely spaced, pseudodichotomous to irregular, sometimes in unilateral rows; attached by branched basal rhizoids. Cells of main axis and lower branches usually 40–50 μm in diameter and 3–4(–5) times longer than wide (mostly up to 200 μm long); upper cells shorter in length than lower cells, 18–25(–30) μm in diameter, and 1–2 times longer than wide.

HABITAT. On rocks and tidal flats; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Rio Mayo. Pacific coast: Michoacán; Panama.

TYPE LOCALITY. Cuba.

REMARKS. Collections of *Cladophora montagneana* in the vicinity of Puerto Peñasco were referred to this species with a query by Dawson (1966a, as “*C. delicatula*”). Although this species has been reported as “*C. delicatula*,” on the Pacific coast from Oregon to southern California (Doty, 1947; Dawson, 1961b), Abbott and Hollenberg (1976:105) concluded that Pacific specimens identified as “*C. delicatula sensu Collins (1909b; Smith, 1944)*” were misidentified and were another species, *C. albida*. Thus, the presence of *C. montagneana* in the northern Gulf needs to be verified. Crystalline cell inclusions were found in *C. montagneana* from Tanzania (Leliert and Coppejans, 2004:202, fig. 48), but have not been reported in the Gulf “*C. montagneana*.”

The name *C. montagneana* given by Kützing (1849) was necessary since a new combination of the earliest name for this taxon, *Conferva brachyclados* Montagne (1837),

would have created a later homonym of *Cladophora brachyclados* (Kützing) Kützing (1845; basionym: *Conferva crispata* var. *brachyclados* Kützing, 1834).

***Cladophora prolifera* (Roth) Kützing**

Conferva prolifera Roth, 1797:182, pl. III: fig. 2.

Cladophora prolifera (Roth) Kützing, 1843:271; Kützing, 1853:24, pl. 82: fig.3; Taylor, 1945:57; Dawson, 1949:230; Dawson, 1957b:8; Dawson, 1961b:378; Chávez B., 1972:268; van den Hoek, 1963 [in part, excluding *C. rugulosa*]:208, pl. 51: figs. 677–682, pl. 52: fig. 686; van den Hoek, 1982:166, pl. 32: figs. 318–327; Mateo-Cid and Mendoza-González, 1991:27; Mateo-Cid and Mendoza-González, 1991:24; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid and Mendoza-González, 1992:24; Mateo-Cid et al., 1993:51; González-González, 1993:443; Stout and Dreckmann, 1993:4; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994b:34; Mendoza-González et al., 1994:112; González-González et al., 1996:369; Bucio-Pacheco and Dreckmann, 1998:43; Mendoza-González and Mateo-Cid, 1998:25, 27; L. Aguilar-Rosas et al., 2000:129, 133, 134; van den Hoek and Chihara, 2000 [excluding *C. rugulosa*]:52, fig. 22; Mateo-Cid et al., 2000a:61, 69; L. Aguilar-Rosas et al., 2002:235; Leliaert and Coppejans, 2003:56, figs. 6A–C, 7; Leliaert, 2004:32, figs. 6A–C, 7; Pedroche et al., 2005:47; Mateo-Cid et al., 2006:58.

Algae dark green, forming dense tufts of branched filaments, up to 3 cm tall; above a distinctive stipe-like region of entangled, simple to branched, rhizoids (with annular constrictions) that descend from lower portions of basal cells, and form a rhizoidal attachment mat. Branches develop on apical end of axis and branch cells. Cells of main axes, branches, and basal cells (often with annular constrictions), 150–300 μm in diameter and 7–10 times as long as wide (1050–3000 μm in length); apical cells, 95–220 μm in diameter and 2.5–8 times as long as wide (320–1760 μm in length), with rounded tip. Rhizoids simple or branched, 40–100 μm in diameter, with characteristic annular constrictions.

HABITAT. On rocks and in tide pools, generally in shady areas; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Tornillal to Bahía Concepción; Cabo Pulmo. Pacific coast: Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur to Oaxaca; Costa Rica; Ecuador; Galápagos Islands; China (Hainan Island); Taiwan; Japan; Vietnam.

TYPE LOCALITY. “*In mare Corsicam*” (Roth, 1797). Lectotype: Miramare, Trieste, Italy (van den Hoek, 1963).

REMARKS. *Cladophora prolifera* has been recently reported in the Gulf of California (Mateo-Cid et al., 1993; L. Aguilar-Rosas et al., 2000, 2002). The description follows that of van den Hoek and Chihara (2000), who noted this species was predominately subtidal and widely distributed in tropical to warm-temperate waters of the Atlantic, Pacific, and Indian Oceans. Leliaert and Coppejans (2004:202) have reported another taxonomic feature, crystalline cell inclusions, in *C. prolifera* from Turkey. The relationship of *C. prolifera* to a similar species, *Cladophora rugulosa* G. Martens (1868) has been uncertain, e.g., the latter was considered to be a synonym of *C. prolifera* by van den Hoek (1963). Recently, Leliaert and Coppejans (2003; see also Leliaert, 2004) provided morphological evidence that these species are distinct, thus supporting others who have kept them as separate species (e.g., Papenfuss, 1943; Sakai, 1964; Papenfuss and Chihara, 1975; Yoshida, 1998).

***Cladophora sericea* (Hudson) Kützing**

Conferva sericea Hudson, 1762:485.

Cladophora sericea (Hudson) Kützing, 1843:264; van den Hoek, 1963 [in part]:77, pl. 17: figs. 184–189, pl. 18: figs. 190–209, pl. 19: figs. 210–226, 245; Abbott and Hollenberg, 1976:108, fig. 67; van den Hoek, 1982:93, pl. 15: figs. 138–143; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruía, 1986:77; Dreckmann et al., 1990:24, pl. 2: fig. 4; Mateo-Cid and Mendoza-González, 1991:27; Stewart, 1991:31; Mateo-Cid and Mendoza-González, 1991:27; Mateo-Cid and Mendoza-González, 1992:24; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:52; Mendoza-González et al., 1994:112; González-González et al., 1996:281, 410; Mendoza-González and Mateo-Cid, 1996:75, 87, pl. 26: figs. 114–118; Galindo-Villegas et al., 1997:2, 4; Mateo-Cid and Mendoza-González, 1997:60, pl. 8: figs. 32, 33; Bucio-Pacheco and Dreckmann, 1998:43; Núñez-López et al., 1998:39; Mendoza-González and Mateo-Cid, 1998:25; Mateo-Cid et al., 2000a:59, 69; Abbott and Huisman, 2004:77, fig. 22E; Pedroche et al., 2005:48; Dreckmann et al., 2006:154.

Conferva rudolphiana C. Agardh, 1827:636.

Cladophora rudolphiana (C. Agardh) Kützing, 1843:268; Collins, 1909b:336; Setchell and Gardner, 1920b:218; Dawson, 1944:209; Dawson, 1957b:8; Dawson, 1961b:378; González-González et al., 1996:131.

Cladophora gracilis sensu Doty, 1947:23; Dawson, 1961b:377; Sakai, 1964:33–38 [non *Cladophora gracilis* Kützing, 1845:763 (note that *Cladophora gracilis* (A. W. Griffiths ex Mackay) Kützing, 1845:215 is *nom. illeg.* since the basionym *Conferva gracilis* A. W. Griffiths ex Harvey, 1835:304 is also *nom. illeg.* as it is a later homonym of *Conferva gracilis* Wulfen, 1803:21; thus, the correct new name is *Cladophora gracilis* Kützing, 1845:763, which is now a synonym of *Cladophora flexuosa* (O. F. Müller) Kützing, 1843:270; basionym: *Conferva flexuosa* O. F. Müller, 1782: 5, pl. 882 (see Söderström, 1963, 1965; Bot et al., 1989; Silva et al., 1996a; van den Hoek and Chihara, 2000:164)].

Algae up to 5 cm tall, filaments of main axis branched sparingly, widely spaced, branches of different lengths intermixed; cells of axis 50(–85) μm in diameter and 5–6 times as long as wide (250–510 μm in length); cells of ultimate branches narrower, 20–30 μm in diameter and 5–7 times as long as wide (100–210 μm in length).

HABITAT. On rocks in tidal creeks and epiphytic on drift *Gracilaria*; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Empalme, Guaymas; Punta Arena to Cabo Pulmo. Pacific coast: Alaska to Chiapas; Costa Rica; Hawaiian Islands.

TYPE LOCALITY. Isle of Sheppey, Kent, England.

***Cladophora tiburonensis* E. Y. Dawson**

FIGURE 26B

Cladophora tiburonensis E. Y. Dawson, 1944:211, pl. 31: figs. 1–3; Dawson, 1949:247; Dawson, 1961b:378; Espinoza-Ávalos, 1993:333; González-González et al., 1996:131; Pedroche et al., 2005:48.

Algae forming dense tufts of short stiff filaments, up to 4 mm tall, branching subdichotomous to secund; branch diameter gradually decreasing upward. Basal cells up to 60 μm in diameter; upper cells about 25 μm in diameter; cells mostly 4–5 times as long as wide, occasionally much longer below.

Fertile cells 40–70 μm in diameter, conspicuously shorter and swollen compared to slender vegetative cells.

HABITAT. In tide pools; mid to low intertidal.

DISTRIBUTION. Gulf of California: Isla Turners; Mazatlán, Sinaloa.

TYPE LOCALITY. Isla Turners, off southeast end of Isla Tiburón, Las Islas de la Cintura, Gulf of California.

REMARKS. *Cladophora tiburonensis* is not well known. Dawson (1944), while noting its resemblance to *C. graminea* Collins (1909a), set it apart on the basis of its minute size and stiff habit. It is retained here to point out that its taxonomic status needs to be investigated.

***Cladophora vagabunda* (Linnaeus) van den Hoek**

Conferva vagabunda Linnaeus, 1753:1167; van den Hoek, 1963: pl. 36: figs. 470, 471 [type illustrations].

Cladophora vagabunda (Linnaeus) van den Hoek, 1963:144, pl. 33: figs. 434, 436–439; pl. 36: figs. 470–490, pl. 37: 491–503, pl. 39: 505–514; Schnetter and Bula Meyer, 1982:26, pl. 3: figs. H, I; van den Hoek, 1982:137, figs. 264–294; Mateo-Cid and Mendoza-Gonzalez, 1991:27; Mateo-Cid and Mendoza-González, 1992:24; Servière-Zaragoza et al., 1993:482; van den Hoek and Chihara, 2000:180, figs. 76–81; L. Aguilar-Rosas et al., 2002:235; Leliaert and Coppens, 2003:70, figs. 14A,B, 15; Abbott and Huisman, 2004:79, figs. 24A–D; Leliaert, 2004:47, figs. 14A,B, 15; Pedroche et al., 2005:49; Hernández-Herrera et al., 2005:307; Mateo-Cid et al., 2006:58.

Conferva expansa Mertens ex Jürgens, 1817:Decade 5: [exsiccate] No. 8.

Cladophora expansa (Mertens ex Jürgens) Kützing, 1843:265; Chávez B., 1972:268.

Conferva fascicularis Mertens ex C. Agardh, 1824:114.

Cladophora fascicularis (Mertens ex C. Agardh) Kützing, 1843:268; Collins, 1909b:345; Chapman, 1956:447, fig. 98; Sakai, 1964:25, fig. 8A–D, pl. 4: fig. 1; Yoshida, 1998:62.

Cladophora uncinella Harvey, 1860:334; Dawson, 1959b:28; Sakai, 1964:60, fig. 28, pl. 11: fig. 1; Yoshida, 1998:70; van den Hoek and Chihara, 2000:182.

Algae erect tufts, up to 5 cm tall, main axes pseudodichotomously to pseudotrictotomously branched, up to 3 orders; branchlets sometimes straight filaments, but usually clusters of short, secund or recurved branchlets, with relatively straight to curled apical cell ends; attached by branched rhizoids from basal end of lower cells, which may partly coalesce. Main filaments 140–260(–300) μm in diameter and (3–)4–8 times longer than wide; apical cells much smaller, (20–)30–50 μm in diameter and 2–6(–9) times longer than wide. Cell walls of upper cells mostly 1.0–2.0 μm thick; much thicker in lower cells, up to 20 μm thick.

HABITAT. On rocks, limestone-clay ledges, and mudflats and in tide pools, lagoons, and salt marshes;

sometimes unattached and floating or may be epiphytic or entangled with other algae or aquatic plants; high to low intertidal.

DISTRIBUTION. Gulf of California: Piedras de La Salina to Puerto Peñasco. Pacific coast: Nayarit to Guerrero; Colombia; Hawaiian Islands; Japan; Korea; China; Vietnam.

TYPE LOCALITY. Selsey, Sussex, England (lectotype; van den Hoek, 1963).

REMARKS. *Cladophora vagabunda* and a few other taxa sensu van den Hoek (1963) were considered to be forms of a single species, *C. flexuosa* (O. F. Müller) Kützing (1843), by Söderström (1965). Since then, however, *C. vagabunda* has continued to be recognized as a distinct taxon (e.g., Silva et al., 1996; Leliaert, 2004). DNA-DNA hybridization experiments of Bot et al. (1990) and molecular analysis of Bakker et al. (1995) on widely geographically separated isolates of *C. vagabunda* have shown considerable divergence, with at least four cryptic species. Specimens of Gulf *C. vagabunda* need to be similarly tested to elucidate their taxonomic status.

***Rhizoclonium* Kützing**

Rhizoclonium Kützing, 1843:261.

Algae are uniseriate, slender, cylindrical filaments, up to 60 µm in diameter, that are unbranched and may lack or have one- to few-celled rhizoidal laterals. They are either attached by a lobed holdfast or lay unattached on hard substratum or, more commonly, on mud or sand

flats. Cells are mostly several times longer than wide and contain numerous nuclei and a parietal, reticulate chloroplast with pyrenoids.

Vegetative reproduction is by fragmentation of the filaments. It is also by akinetes that are formed within some of the cells as they swell and thicken. Life histories, where known, are an alternation of isomorphic generations. Asexual reproduction is by biflagellate or quadri-flagellate zoospores. Sexual reproduction is by biflagellate isogametes.

REMARKS. *Rhizoclonium* occurs worldwide in fresh, brackish, and marine waters. The generic distinction of *Rhizoclonium* and *Lola* A. Hamel et G. Hamel (1929) is tenuous and needs to be investigated. For example, the only character separating them is isogamous reproduction in *Rhizoclonium* and anisogamous reproduction in *Lola*. Likewise, the generic differences between *Rhizoclonium* and *Chaetomorpha*, as well as their species separation, can be difficult. The morphological characters used, i.e., filament diameter, length/width ratio of cells, the absence or presence of attachment structures, and the absence or presence and number of lateral rhizoidal filaments, have been shown to be highly variable (e.g., Koster, 1955; Nienhuis, 1975; Nienhuis and de Bree, 1981; Blair, 1983). Setchell and Gardner (1920b) concluded that the only useful taxonomic character was filament cell diameter.

One species has been reported in the southern Gulf: *Rhizoclonium hieroglyphicum* (C. Agardh) Kützing (1845) by Huerta-Múzquiz and Mendoza-González (1985).

There are two species and two varieties known in the northern Gulf of California.

KEY TO THE SPECIES OF *RHIZOCLONIUM* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Uniseriate filaments mostly straight; cells mostly greater than 30 µm in diameter, up to 75 µm wide; filament cells either without or with short rhizoidal proliferations of only a single cell *R. tortuosum*
- 1b. Uniseriate filaments mostly twisted or curly; cells mostly less than 30 µm in diameter (occasionally up to 45 µm); filament cells either without or with tapering rhizoidal proliferations of 2–5 (or more) cells long.....2
- 2a. Cells mostly 20–30(–45) µm in diameter and 20–60(–90) µm long; filaments sometimes with few rhizoids
..... *R. riparium* var. *riparium*
- 2b. Cells smaller in diameter, usually 8–12(–20) µm, 24–50(–70) µm long; filaments rarely with rhizoids
..... *R. riparium* var. *implexum*

Rhizoclonium riparium* (Roth) Harvey var. *riparium

Conferva riparia Roth, 1806:216; Koster, 1955:336, fig. 1.
Rhizoclonium riparium (Roth) Harvey, 1849:238, pl. CCXXXVIII; Setchell and Gardner, 1920b:182; Smith,

1944:63, pl. 7: fig. 4; Taylor, 1945:55; Doty, 1947:27; Hollenberg, 1948:155; Dawson, 1961b:376; Scagel, 1966:74, fig. 18A–F; Nienhuis, 1975:84–88, figs. 35–60; Abbott and Hollenberg, 1976:92, fig. 46; Zedler, 1980:124; Nienhuis and de Bree, 1981:434; R. Aguilar-Rosas, 1982:84; Zedler, 1982:41; Schnetter and

Bula Meyer, 1982:18, pl. 1: figs. Q–S, pl. 2: figs. A, B; Blair, 1983:203; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1986:419; Mateo-Cid and Mendoza-González, 1991:27; Stewart, 1991:32; Mateo-Cid and Mendoza-González, 1992:25; León-Tejera et al., 1993:199; Servièze-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994b:44; Mendoza-González et al., 1994:112; Pedroche et al., 1995:112; González-González et al., 1996:289; Mendoza-González and Mateo-Cid, 1996:76, 88, pl. 27: fig. 122; Sánchez-Lizaso and Riosmena-Rodríguez, 1997:56; Núñez-López et al., 1998:39; L. Aguilar-Rosas et al., 2000:133; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:83, fig. 25D; Wysor, 2004:218; Pedroche et al., 2005:50; Hernández-Herrera et al., 2005:146; Dreckmann et al., 2006:154.

Algae unbranched, uniseriate filaments of cylindrical cells, mostly 1–2 times longer than wide (sometimes up to 6 times); (10–)15–30(–45) μm in diameter by 15–90(–270) μm long; without or with a few short rhizoidal proliferations of 2–5 (or more) cells; often unattached. Chloroplast reticulate, with 6 or more pyrenoids.

Vegetative reproduction by fragmentation. Reproduction not reported in Gulf specimens. Reproduction has been reported in Europe. Asexual reproduction is by biflagellate and quadriflagellate zoospores, and sexual reproduction by isogamous gametes (Nienhuis, 1975).

HABITAT. Entangled with other algae or aquatic plants, in tide pools, or on sand flats and mudflats of salt marshes, lagoons, and estuaries; or free-floating and unattached (also reported as epiphytic on *Gelidium johnstonii* and *Spyridia filamentosa*; L. Aguilar-Rosas et al., 2000); high to low intertidal.

DISTRIBUTION. Gulf of California: Puertecitos to Punta Arena (north of Cabo Pulmo). Pacific coast: Alaska to Chiapas; Panama; Colombia; Galápagos Islands; Chile; Hawaiian Islands; China; Japan.

TYPE LOCALITY. Norderney, East Frisian Islands, Germany.

***Rhizoclonium riparium* var. *implexum*
(Dillwyn) Rosenvinge**

Conferva implexa Dillwyn, 1809:46, (Suppl.) pl. B; Koster, 1955:336, fig. 2.

Rhizoclonium riparium var. *implexum* (Dillwyn) Rosenvinge, 1893:915, fig. 34; Taylor, 1945:55; Silva

et al., 1996a:786; Mateo-Cid et al., 2000a:69; León-Tejera and González-González, 2000:327; Pedroche et al., 2005:50; Servièze-Zaragoza et al., 2007:8.

Rhizoclonium implexum (Dillwyn) Kützing, 1845:206; Setchell and Gardner, 1920b:183; Smith, 1944:62, pl. 8: fig. 3; Taylor, 1945:55; Koster, 1955: 344, 348; Dawson, 1961b:375; Scagel, 1966:73, pl. 33A,B; Abbott and Hollenberg, 1976:92, fig. 45; Huerta-Múzquiz and Mendoza-González, 1985:42; Mendoza-González and Mateo-Cid, 1985:22; Mendoza-González and Mateo-Cid, 1986:419; Mateo-Cid and Mendoza-González, 1994a:57; González-González et al., 1996:138; Galindo-Villegas et al., 1997:2, 4; Yoshida, 1998:72; Abbott and Huisman, 2004:82, fig. 25C.

Lola implexa (Dillwyn) G. Hamel, 1931a:120, fig. 37 (6–7); Ortega et al., 1987:78, pl. 14: figs. 60–62; Perrot, 1965:506; González-González et al., 1996:137.

Rhizoclonium kernerii Stockmayer, 1890:582; Collins, 1909b:329; Setchell and Gardner, 1920b:185; Taylor, 1945:55; Dawson, 1961b:375; González-González, 1993:443; Ortega et al., 1987:77, pl. 13: figs. 58, 59; Servièze-Zaragoza et al., 1993:485; González-González et al., 1996:289; Servièze-Zaragoza et al., 1998:169.

Rhizoclonium kochianum Kützing, 1845:206; Dawson, 1959a:12; Dawson, 1960a:31; Dawson, 1961b:376; Earle, 1972:85; González-González et al., 1996:139.

Algae unbranched, uniseriate filaments of cylindrical cells, mostly 3–5 times longer than wide, (8–)10–12(–20) μm in diameter by (24–)30–50(–70) μm long; mostly lacking or rarely with short, rhizoidal proliferations. Chloroplasts reticulate, with numerous pyrenoids.

HABITAT. Epiphytic or entangled with other algae or plants, on rocks, in tide pools, or on sand and mudflats of salt marshes, lagoons, and estuaries; or unattached and free-floating; high to low intertidal.

DISTRIBUTION. Gulf of California: Guaymas to Punta Arena (north of Cabo Pulmo). Pacific coast: Alaska to Oaxaca; Isla Clarión (Islas Revillagigedo); Panama; China; Japan; Hawaiian Islands; Galápagos Islands.

TYPE LOCALITY. Bantry, Ireland.

REMARKS. The taxonomy of *Rhizoclonium implexum* has been diversely interpreted. Koster (1955) placed *R. kernerii* and *R. kochianum* in synonymy with *R. implexum* and also questioned whether *R. implexum* was distinct from *R. riparium* or if the two were one highly variable species. Since then, these latter two have been variously treated: as separate species (e.g., Abbott and Hollenberg, 1976; Womersley, 1984; Yoshida, 1998; Abbott and Huisman, 2004); as a single species with a variety,

R. riparium var. *implexum* (Dillwyn) Rosenvinge, 1893 (e.g., Silva et al., 1996a; Pedroche et al., 2005); and as an unnamed form of *R. riparium* (Blair, 1983). Herein, while treated as a single species following Nienhuis (1975), Nienhuis and de Bree (1981), Blair (1983), Burrows (1991), and John et al. (2004), the two varieties are recognized until further studies can be done.

Rhizoclonium tortuosum (Dillwyn) Kützing

FIGURE 31

Conferva tortuosa Dillwyn, 1805:pl. 46.

Rhizoclonium tortuosum (Dillwyn) Kützing, 1845:205; Setchell and Gardner, 1920b:185; Chapman, 1939:19; Doty, 1947:25; Dawson, 1961b:376; Blair, 1983:198, figs. 12, 13; Hoffman and Santelices, 1997:91, fig. 19; Bucio-Pacheco and Dreckmann, 1998:44; Pedroche et al., 2005:51.

Chaetomorpha tortuosa (Dillwyn) Kleen, 1874:45; Scagel et al., 1989:62.

Lola tortuosa (Dillwyn) Chapman, 1953:65; Chapman, 1956:463.

Rhizoclonium lubricum Setchell et N. L. Gardner in N. L. Gardner, 1919:492, pl. 42: fig. 5A,B; Setchell and Gardner, 1920b:185, pl. 9: fig. 5a,b; Taylor, 1945:56; Doty, 1947:26.

Lola lubrica (Setchell et N. L. Gardner in N. L. Gardner) A. Hamel et G. Hamel, 1929:1094; Hamel, 1931a:118, fig. 37 (1–5); Dawson, 1944:208; Dawson, 1961b:376; Abbott and Hollenberg, 1976:92, fig. 47; Ortega et al., 1987:78, pl. 14: figs. 63, 64; Scagel et al., 1989:74; Stewart, 1991:32; González-González et al., 1996:137; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Pedroche et al., 2005:49.

Rhizoclonium riparium f. *validum* Foslie in Wittrock et Nordstedt, 1884:No. 624; Foslie, 1890:139.

Algae of slippery filaments, up to 40 cm long, often entangled or forming free-floating mats; composed of unbranched filaments, (25–)30–75 μm in diameter; newer cells (25–)35–100 μm long; mature cells 120–300 μm long; attached by simple short rhizoids. Cells with a reticulate chloroplast, and numerous pyrenoids; cell wall 0.2 μm thick.

Vegetative reproduction by fragmentation. Reproduction not observed in Gulf material. A life history involving an isomorphic alternation of generations has been reported, with asexual reproduction by quadriflagellate zoospores, and sexual reproduction that is anisogamous,

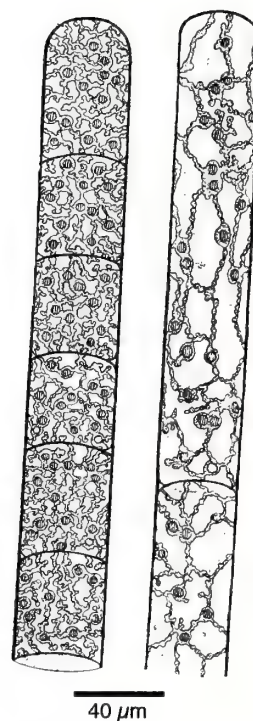


FIGURE 31. *Rhizoclonium tortuosum*: Terminal portion of young filament with short segments (left) and terminal portion of filament with long segments (right) (after Gardner, 1919: pl. 42, fig. 5A,B).

with biflagellate gametes (Hamel and Hamel, 1929; Blair, 1983).

HABITAT. On rocks or other hard substrata, often entangled with other algae; on mud-sand flats in lagoons and shallow bays; or sometimes unattached and free-floating; mid to low intertidal.

DISTRIBUTION. Gulf of California: Guaymas; Bahía San Gabriel; Isla Espíritu Santo; Laguna de Agiabampo (Sonora). Pacific coast: Alaska to Michoacán.

TYPE LOCALITY. Lectotype: Swansea, Glamorgan, Wales, UK (Blair, 1983:198).

REMARKS. *Rhizoclonium tortuosum* has been variously treated; some recognize it as a distinct species, others recognize it as part of a species complex. For example, Burrows (1991) considered *R. riparium* to be a single species conspecific with *R. tortuosum* and *R. implexum*. Herein, *R. tortuosum* is tentatively recognized as a separate species until detailed comparative morphological studies and molecular analyses have been conducted on Gulf material for comparisons to the European types of these taxa (see Silva et al., 1996a:936 for discussion of nomenclature and taxonomic problems of *R. tortuosum*).

SIPHONOCLADALES SENSU STRICTO

Siphonocladales (Blackman et Tansley) Oltmanns, 1904: 134.

Algae are of various forms, composed of large tubular, siphonous, or vesiculate cells that are formed by either lenticular cells, or by internal segregative cell division (not always obvious). In segregative division the protoplast cleaves into protoplasmic spheres, which, in turn, may either form new cell walls, remain in the parental cell, or be released as vegetative propagules. Endogenous expansion of these spheres within the parental vesicle results in the formation of pseudoparenchymatous tissue (e.g., *Dictyosphaeria*). Cells divide in some members by centripetal invagination of cell walls, but with new branches that remain in open connection (i.e., lack septa) at the base of the parent cell (e.g., *Cladophoropsis*). New lateral branches may also arise in some genera by expansion of lenticular cells; i.e., septa are initiated prior to elongation

of the vesicular branch on the surface of the parent vesicle (e.g., *Valonia*).

Cells are cylindrical or inflated, globose, clavate, or vesiculate. There is simultaneous formation of laterals at nodes (rather than sequential), and branching can be in three directions. Tenacular cells that are formed are one of four different kinds, and secondary anastomoses are usually formed.

REMARKS. The taxonomy of the families, as well as their generic composition, of the Cladophorales-Siphonocladales complex is unresolved (see Leliaert et al., 2003, 2007, and Remarks under Cladophorales herein). Although segregative cell division is a primary characteristic of the families Siphonocladaceae and the Boodleaceae, it has not been reported or described for all the genera generally considered to be members of these families.

Three of the currently accepted families in the Siphonocladales are represented in the northern Gulf of California.

KEY TO FAMILIES OF SIPHONOCLADALES IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli erect, of relatively large, elongated cylindrical cells that bear irregularly to regularly, radially arranged lateral or whorled branches **Siphonocladaceae**
 1b. Thallus a large individual vesicle; or cushionlike, of simple to branched, cylindrical to clavate, siphon cells 2
 2a. Thalli variable, filamentous to netlike; of branched, cylindrical or siphon cells secondarily attached to each other; cells formed either by segregative division or by centripetal invagination of cell walls **Boodleaceae**
 2b. Thallus a single globose vesicle, or composed of elongate siphon cells, some with branches, usually entangled; main axis not distinct; growth by lenticular cells **Valoniaceae**

BOODLEACEAE

Boodleaceae Børgesen, 1925:19, 24.

Algae are of various morphologies; mostly, they are tufts, clumps, or mats of clavate, cylindrical, or filiform cells with vesicular branches that often become constricted near their base, and are usually attached to the substratum by rhizoids. Development of new cells, forming laterals or branches, is primarily by segregative cell division, i.e., cytoplasm divides into portions that expand into protrusions before a cell wall is formed, or, in some, is by centripetal invagination of the cell walls. Some may also initiate new growth by the formation of lenticular cells. Cells are multinucleate with reticulate chloroplasts that lack pyrenoids. Crystalline cell inclusions may be present or absent.

Reproduction is poorly known. Life histories, in those studied, are an alternation of isomorphic generations.

Biflagellate and quadriflagellate zoospores have been observed in only a few of the genera. Sexual reproduction, where known, is by biflagellate isogametes.

REMARKS. Members of the Boodleaceae found in the Gulf of California have usually been referred to the Siphonocladaceae (e.g., Pedroche et al., 2005). However, the type genus, *Siphonocladus* F. Schmitz (1879), does not group with the other genera generally assigned to the family in molecular phylogenetic analyses (Leliaert et al., 2003; Leliaert and Coppejans, 2006). Although some genera such as *Phyllodictyon* have been included in the Anadyomenaceae Kützing (1843), there is no phylogenetic support for this, and that family is restricted to the genera *Anadyomena* J. V. Lamouroux (1812) and *Microdictyon* Decaisne (1841) as originally proposed by Kützing (Leliaert et al., 2007). Therefore, as noted by Kraft (2007) and Leliaert (University of Ghent, personal communication, 2008), the family Boodleaceae is available for the genera

other than *Siphonocladus*, *Anadyomena*, and *Microdictyon*. Herein the Boodleaceae is interpreted to include *Boodlea*, *Struvea*, *Cladophoropsis*, and *Phyllodictyon*.

Two genera of this family have been recorded for the southern Gulf: *Struvea* Sonder (1845) by Huerta-Múzquiz and Mendoza-Gonzalez (1985, as "*Struvea* sp.") and

Boodlea (Dickie) G. Murray et DeToni (in Murray, 1889) with the report of *B. composita* (Harvey) Brand (1904) by Mateo-Cid et al. (1993) and Mendoza-González et al. (1994).

Two of the genera are known in the northern Gulf of California.

KEY TO THE GENERA OF BOODLEACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae of terete, branched filaments (not netlike); branches formed singly on distal end of filament and elongate without forming a basal crosswall (septae) *Cladophoropsis*
 1b. Algae a simple or branched stalk(s) with an upper netlike portion (formed by attachment of tenacular cells of tips of apical cells of lateral branches to adjacent filaments); or the upper portion only partially netlike (reduced or incomplete or sometimes lacking) *Phyllodictyon*

Cladophoropsis Børgesen

Cladophoropsis Børgesen, 1905:288.

Algae generally form green, cushionlike turfs or mats of interweaving filaments, usually lack a distinct axis, and attach to substratum by branched septate rhizoids, adherent cell walls, or hapteroid cells. The filaments, more or less uniform in diameter, have irregularly spaced, usually sparse, lateral branches. Laterals are produced from nonseptate protrusions at the distal end of intercalary and apical cells that elongate to various lengths and gradually taper toward the apex. Septa (crosswalls), although initially lacking, can develop secondarily at intercalary and branch points. Cells are multinucleate, with numerous discoid chloroplasts, each has a single pyrenoid; crystalline inclusions present. Cells divide by centripetal invagination of cell walls. Growth is by apical and intercalary cell division. Annular constrictions and lenticular cells are absent. Rhizoids, produced above the septum, can become well developed and produce new axes. Adventitious rhizoids develop where branches come in contact with the substratum.

Propagation is by aplanospores, probably produced by segregative division. Life histories are presumed to be a biphasic alternation of generations.

REMARKS. Generic limits of *Cladophoropsis* are unclear, and only a few of the described species are apparently distinctive. The taxonomy is complicated by having few morphological characters, two of which, growth form and branching pattern, are environmentally influenced (e.g., Leliaert et al., 2003). There has also been confusion in the interpretation of septate and nonseptate lateral branches. Further problems were found in the species sampling in phylogenetic studies (Kooistra et al., 1993). Leliaert and Coppejans (2004) noted the absence or presence of different morphological types of crystalline cell inclusions to be of systematic value at the species level.

One species, *Cladophoropsis membranacea* (Hofman Bang ex C. Agardh) Børgesen (1905; Leliaert and Coppejans, 2006), has been reported in the southern Gulf (Huerta-Múzquiz and Mendoza-González, 1985), and Pacific Mexico (Dawson, 1960a, as "*Cladophora membranacea*"; see also Dawson, 1961b; Huerta-Múzquiz and Garza-Barrientos, 1975; Pedroche et al., 2005).

Two species are known in the northern Gulf of California.

KEY TO THE SPECIES OF *CLADOPHOROPSIS* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments relatively slender, 65–100(–125) μm in diameter; cells very long, up to 15 μm , 30–100 times longer than wide *C. gracillima*
 1a. Filaments much wider, usually over 350 μm in diameter; cells of main filaments not as long, 2.3–18 times longer than wide *C. macromeres*

***Cladophoropsis gracillima* E. Y. Dawson**

FIGURE 32A–C

Cladophoropsis gracillima E. Y. Dawson, 1950c:149, 151, figs. 12, 13; Dawson, 1957b:7; Dawson, 1960a:32; Dawson, 1961b:379; Dawson, 1962b:228; Dawson, 1966a:6; González-González et al., 1996:131; Rodríguez-Morales and Siqueiros-Beltrones, 1999:17; Leliaert, 2004:237, figs. 77 (isotype), 78; Pedroche et al., 2005:52; Mateo-Cid et al., 2006:48, 58.



FIGURE 32. *Cladophoropsis gracillima*: A–C. Drawings of type specimen (EYD-3233; after Dawson, 1950c: figs. 12–13). A. Upper portion of a branched filament showing the manner of septation of branches. B, C. Small portions of a skein-like alga showing extremely long cells and infrequent branching.

Algae loosely filamentous tufts, of sparsely, irregularly branched, cylindrical filaments, 2–4 cm long; entangled by creeping or entwining branches to other algae and attached by rhizoids to substratum. Chloroplast a slightly open to dense, parietal reticulatum with 1–4 pyrenoids. Cells very long, (0.3–)1.0–15 mm in length (30–100 times longer than wide), with diameter in cells of main filaments (50–)65–120(–130) µm; in basal cells 50–160 µm; and in apical cells (60–)80–120(–135) µm. Branches arising beneath a septum of the filament cell and usually remain in open connection between the branch cell and filament. Cell walls 2 µm thick.

Reproduction unknown for this species.

HABITAT. On rocks and in tide pools, usually entangled with other small algae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Puerto Refugio, Isla Ángel de la Guarda; Calerita (vicinity of La Paz) to Punta Palmilla. Pacific coast: Costa Rica.

TYPE LOCALITY. Punta Palmilla, Baja California Sur.

REMARKS. Dawson (1950c) separated *Cladophoropsis gracillima* from the morphologically similar species on the basis of its entangled habit, slender filaments, and much longer cells (30–100 times longer than diameter). Crystalline cell inclusions were briefly noted in a list as present in *C. gracillima* (Leliaert and Coppejans, 2004:202). This apparently was an error since Leliaert (2004:239) and Leliaert and Coppejans (2006:670) considered *C. gracillima*, because of its lack of crystalline inclusions and absence of tenacular cells, to be of uncertain taxonomic affinity. When more Gulf specimens are collected, studies are needed to evaluate the distinctiveness and phylogenetics of this taxon.

***Cladophoropsis macromeres* W. R. Taylor**

Cladophoropsis macromeres W. R. Taylor, 1928:64, pl. 4: figs. 15, 16; Mendoza-González and Mateo-Cid, 1986:419; González-González et al., 1996:281; Leliaert, 2004:116, figs. 3C,D, 5A,B, 8A–E; Pedroche et al., 2005:52; Leliaert and Coppejans, 2006:662, figs. 3, 4, 18–22.

Algae of cylindrical, loosely branched entangled filaments, forming mats up to 15 cm wide and 2–15 cm thick; usually found free floating or lying unattached on substratum. Main filaments (280–)350–510 µm in diameter; cells 2.3–18 times longer than wide, with cells walls up to 10 µm thick; upper filaments narrower, (140–)280–360(–400)

µm in diameter with cells up to 60 times longer than wide, and cell walls 2–4 µm thick. Branching mostly irregular, sometimes unilateral in upper portions. Chloroplasts polygonal to rounded in parietal reticulum, usually with a single large pyrenoid. Prismatic calcium oxalate crystals present in most cells.

HABITAT. Free-floating or cast ashore on sand flats or mudflats; sometimes entangled with other algae or aquatic plants; in protected tide pools or shallow waters; intertidal.

DISTRIBUTION. Gulf of California: Guaymas.

TYPE LOCALITY. Fort Jefferson on Garden Key, Dry Tortugas National Park, Monroe County, Florida.

REMARKS. *Cladophoropsis macromeres*, a western Atlantic species, is known in warm, calm, shallow waters (Taylor, 1960; Wynne, 2005); the description is based on Leliaert and Coppejans (2006). It has been recorded once in the northern Gulf from drift material (Mendoza-González and Mateo-Cid, 1986), and more collections would be helpful to verify its presence in the Gulf of California.

***Phyllodictyon* J. E. Gray**

Phyllodictyon J. E. Gray, 1866:70.

Algae are erect, of one or more reticulate (netlike) blades, above a monosiphonous (rarely branched) stalk that is attached by basal rhizoids. Blades are complanate, with an apical, uniaxial orientation that is maintained throughout development with primary and secondary laterals arising from opposite, astipitate protrusions along distal sides of previously cut-off segments. The distinctive network of the blade is formed as the initial laterals and subsequent higher-order distichously arranged laterals

develop by nonsynchronous centripetal wall invaginations (*Cladophora*-type cell division). Intercalary cell divisions are common. Tenacular cells on the apices of second- and third-order (rarely more) laterals may contact and fuse with adjacent laterals to form the filament network of the blade. Cells are multinucleate and have numerous discoid chloroplasts, each with a single pyrenoid.

Life histories are not known, but zoospores have been reported.

REMARKS. *Phyllodictyon* and the similar-looking genus *Struvea* Sonder (1845) are differentiated from each other primarily by their mode of cell division: “*Cladophora*-type” in *Phyllodictyon* versus the segregative cell division in *Struvea* (Kraft and Wynne, 1996), a generic distinction initially supported by molecular evidence (e.g., Kooistra et al., 1993; Bakker et al., 1994). However, Leliaert and Coppejans (2007) noted that while *Phyllodictyon*, *Struvea*, *Cladophoropsis*, *Chamaedoris* Montagne (1842b), *Boodlea* G. Murray et G. B. De Toni (in Murray, 1889), and *Struveopsis* Rhyne et Robinson (1969) were all nonmonophyletic genera and their generic separation was problematic, that for now and for practical utility, they should be distinguished by their considerable and consistent habit (morphological) differences.

One species, *Phyllodictyon anastomosans* (Harvey) Kraft et M. J. Wynne (1996) has been reported in the southern Gulf (Rocha-Ramírez and Siqueiros-Beltrones, 1991; Mateo-Cid et al., 2000a; both as “*Struvea anastomosans*”), and Pacific Mexico (Dawson, 1949, 1950d, as “*S. delicatula*”; Chávez B., 1972, Huerta-Múzquiz, 1978, Mateo-Cid and Mendoza-González, 1991, Mateo-Cid and Mendoza-González, 1992, León-Tejera et al., 1993, and González-González, 1993, all as “*S. anastomosans*”; and Mendoza-González and Mateo-Cid, 1998).

Two of the species are known in the Gulf of California.

KEY TO THE SPECIES OF *PHYLLODICTYON* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae with narrow main axes, 200–380 µm diameter, and upper netlike blades; tenacular cells at tips of apical cells and at base of main axial cells; lenticular cells absent. ***P. pulcherrimum***
- 1b. Algae with broader main axes, 950–1120 µm in diameter, upper bladelike portion either lacking or reduced (partial); tenacular cells only at tips of apical cells; lenticular cells present ***P. robustum***

***Phyllodictyon pulcherrimum* J. E. Gray**

FIGURE 33

Phyllodictyon pulcherrimum J. E. Gray, 1866:70; Kraft and Wynne, 1996:131–135, 139, figs. 26–28; John et al., 2004:23; Leliaert, 2004:fig. 52 (holotype); Pedroche et al., 2005:54; Leliaert et al., 2008:8, 10, tbl. 3.

Struvea pulcherrima (J. E. Gray) Murray et Boodle, 1888:281; Schneider and Searles, 1991:80, fig. 70.

Cladophoropsis pulcherrima (J. E. Gray) Leliaert et Coppejans in Leliaert, 2004:192, *comb. nov. prov.*, figs. 5C,D, 52–55.

Struvea ramosa Dickie, 1874b:316; Dawson, 1966b:55, fig. 1B; González-González et al., 1996:139.

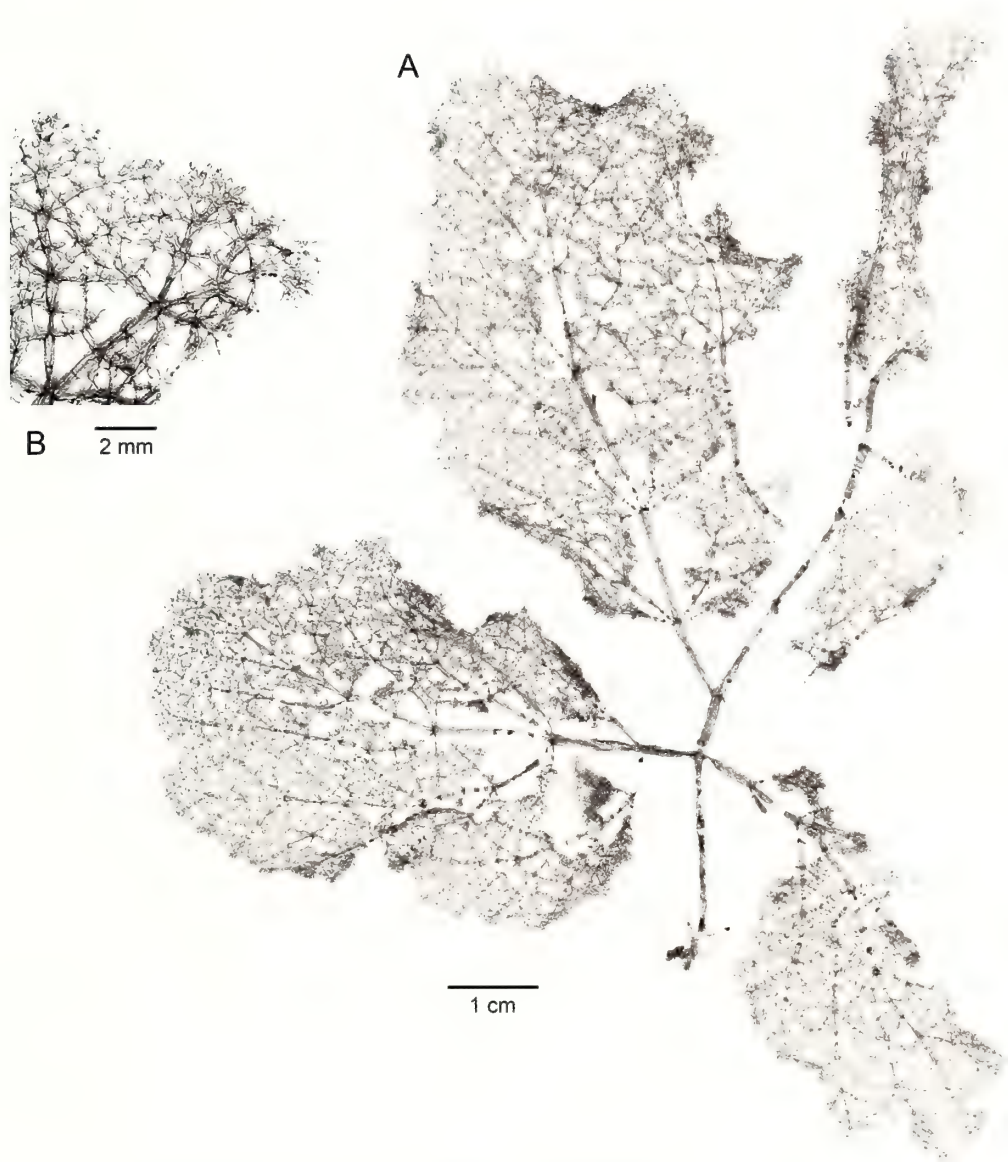


FIGURE 33. *Phyllocladion pulcherrimum*. A. Axis with several well-developed open reticulate fronds above a monosiphonous stalk (EYD-25872). B. Portion of net-like blade.

Algae erect, up to 20 cm tall, with reticulate blade(s) above a monosiphonous stalk, up to 1.5 mm in diameter, and attached below by branching, basal rhizoids. Lower portion of stalk usually unbranched; upper portion with a series of opposite branches, up to 3 orders, that form net-like blades, up to 12 cm long and up to 10 cm wide. Main axes 200–380 μm in diameter. Lateral branches, developed below a septum at distal end of axis cell, with up to 6 branches per cell. Tenacular cells abundant at tips of apical cells, and base of cells on main axes. Lenticular cells absent.

HABITAT. On rock; subtidal, 17 m depth.

DISTRIBUTION. Gulf of California: Punta Concepción.

TYPE LOCALITY. Gulf of Mexico.

REMARKS. The phylogenetic relationship of the western Atlantic *Phyllocladion pulcherrimum* (type locality Gulf of Mexico) to Gulf of California *P. pulcherrimum* should be tested. Calcium oxalate crystalline cell inclusions, thought to be of systematic value, have been described in *P. pulcherrimum* from other regions (Leliaert and Coppejans, 2004; Leliaert et al., 2008) but are not reported in Gulf of California *P. pulcherrimum*.

Phyllocladon robustum
(Setchell et N. L. Gardner) Leliaert et Wysor

FIGURE 34A-E

Cladophoropsis robusta Setchell et N. L. Gardner, 1924a:714, pl. 13: fig. 16 [holotype specimen only; see Leliaert et al., 2008:3–4, 9, figs. 2, 3, 15, 16, 23 (illustrations of holotype)]; Dawson, 1944:206; Dawson, 1957b:8; Dawson, 1961c:404, pl. 4: fig. 3, pl. 5: fig. 6; Dawson, 1962b:228; Chávez B., 1972:268; Mendoza-González and Mateo-Cid, 1986:419; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mateo-Cid and Mendoza-González, 1992:24; Mateo-Cid et al., 1993:51; Servièrre-Zaragoza et al., 1993:482; González-González et al., 1996:131; Servièrre-Zaragoza et al., 1998:168.

Cladophoropsis? *robusta* sensu Dawson, 1959a:9–11, fig. 3A; Dawson, 1961b:379.

Phyllocladon robustum Leliaert et Wysor in Leliaert et al., 2008:230, figs. 1–46.

Struveopsis robusta (Setchell et N. L. Gardner) Rhyne et H. Robinson, 1969:470; Stout and Dreckmann, 1993:6, 17; Kraft and Wynne, 1996:140; Pacheco-Ruíz and Zertuche-González, 1996a:432; Bucio-Pacheco and Dreckmann, 1998:42; L. Aguilar-Rosas et al., 2000:129, 133; Mateo-Cid et al., 2000a:69; L. Aguilar-Rosas et al., 2002:235; Wysor, 2004:219, fig. 7; Pedroche et al., 2005:54; Mateo-Cid et al., 2006:58.

Pseudostruvea robusta (Setchell et N. L. Gardner) Egerod, 1975:47; Espinoza-Ávalos, 1993:333; González-González et al., 1996:138; Pacheco-Ruíz and Zertuche-González, 1996a:432; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Cruz-Ayala et al., 2001:190; Pacheco-Ruíz et al., 2008:202.

Willella mexicana E. Y. Dawson, 1950c:151, fig. 11 (holotype); Papenfuss and Egerod, 1957:83; Dawson, 1957b:8; Dawson, 1959a:11–12; González-González et al., 1996:141; Leliaert, 2004:49; Leliaert and Coppejans, 2006:673; Leliaert et al., 2008: figs. 4 (holotype), 5–7 (isotype).

Cladophoropsis mexicana (E. Y. Dawson) Leliaert et Coppejans in Leliaert, *comb. nov. prov.*, 2004:184, fig. 47.

Algae erect, 2–4(–5) cm tall, highly variable in morphology; usually of few to several, monosiphonous main axes, unbranched to laterally branched up to 3 orders; attached below by entangled basal rhizoids. Main axes diameter 370–900(–1300) μm , increasing upward; branch diameter mostly 600–900 μm ; apical cells with rounded tips, 950–1120 μm in diameter, 1.5–3.2 mm in length.

Lower portion of main axis (stipitate), usually unbranched in first 1.0–2.5 cm; upper portion either remaining unbranched or becoming bladelike, with few, paired lateral branches, developed below a septum at distal end of axis cell, 2–4 mm in length, of (1–)3–6 cells, with up to 4 branches per cell. Septa either absent or present after growth of a few millimeters in length. Tenacular cells, apparently rare, at tips of apical cells; abundant on rhizoidal cells in culture (Leliaert et al., 2008). Lenticular cells present. Calcium oxalate crystals present in most cells; usually rectangular, polygonal or irregular, 8–40(–60) μm wide, with dentate margins; rarely octahedral.

Reproductive cells, with numerous raised pores, develop from rows of 2–4 slightly swollen apical cells (after Leliaert et al., 2008).

HABITAT. Growing on rocks or sometimes sponges; in tidepools and low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Gorda to Bahía La Paz; Cabo Pulmo. Pacific coast: Nayarit to Oaxaca; El Salvador; Costa Rica; Panamá.

TYPE LOCALITY. Punta Colorado (adjacent to Bahía Bocochoibampo), vicinity of Guaymas, Sonora, Gulf of California.

REMARKS. Since its original description from the Gulf of California, *Cladophoropsis robusta* has a notable history of taxonomic changes in generic placement. Papenfuss and Egerod (1957) suggested that *C. robusta* could be a *Willella* Børgesen (1930). Dawson (1959a:12, as “*C.? robusta*”) disagreed and noted in the type of *C. robusta*, “lens-shaped incipient branchlets” before branch formation that were “somewhat suggestive of *Struvea*” in the similar way its branches were cut off by a “lens-like cell” (lenticular cells). Dawson questioned its generic placement and concluded that *C.? robusta* and *Willella mexicana* Dawson (1950c) were the same species, more closely allied with *Valoniopsis* than to *Willella*. Subsequently, *C. robusta* was transferred to other genera, *Struveopsis* by Rhyne and Robinson (1969) and then later to *Pseudostruvea* by Egerod (1975).

Leliaert (2004) and Leliaert and Coppejans (2006) initially observed the holotype of *C. robusta* (CAS now UC) was not in agreement with the original description or illustration of Setchell and Gardner (1924a:714, pl. 13: fig. 16) and noted the type to be “*Valoniopsis pachynema*.” They further suggested that most records published as “*C. robusta*” were *Willella mexicana*. Most recently, Leliaert et al. (2008) reported re-examination of the holotype of *C. robusta* showed it to have tenacular cells at tips of some branches and that the branches developed exclusively

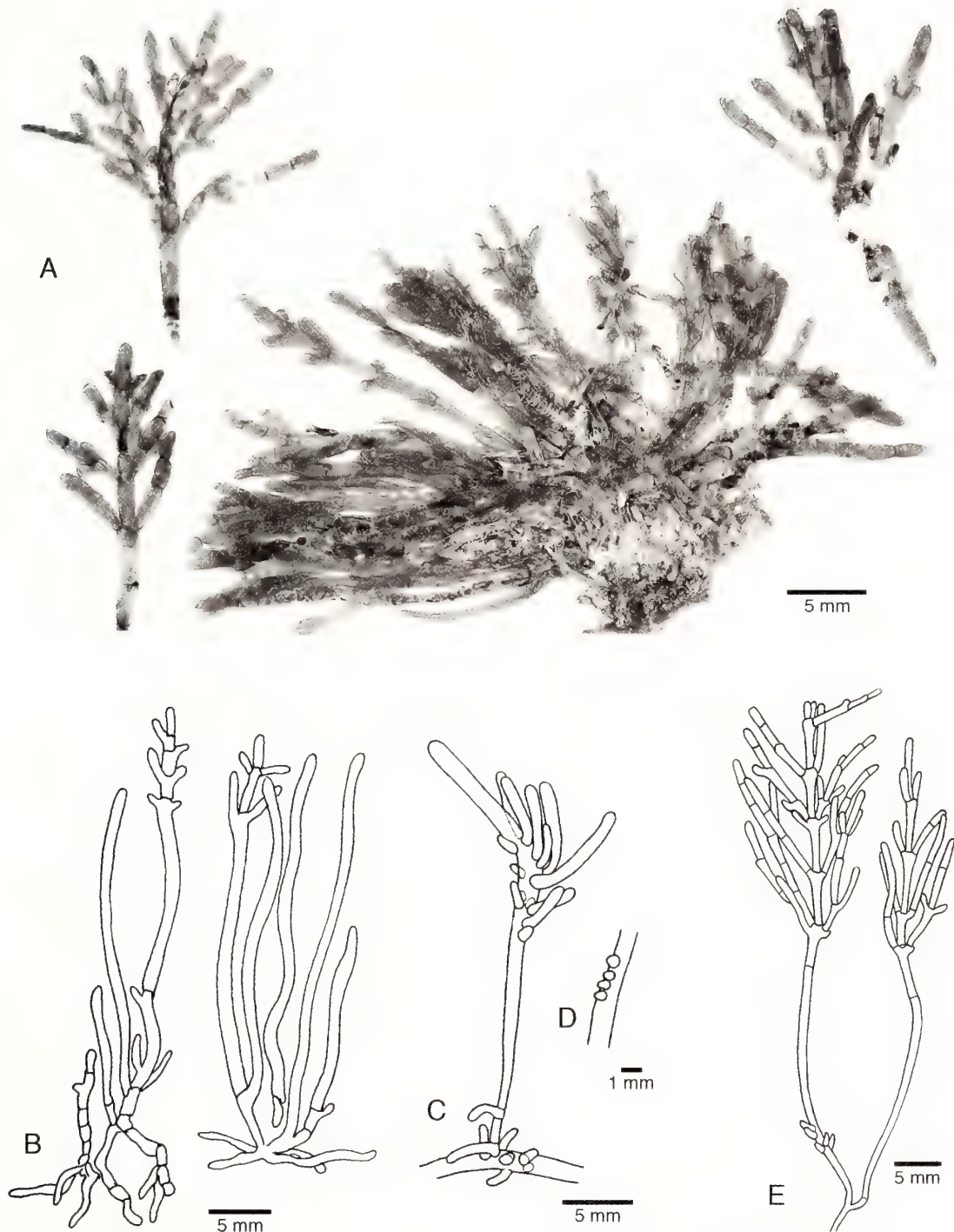


FIGURE 34. *Phyllocladion robustum*: A. Clump with some axes separated to show branching pattern (EYD-18555). B–D. Holotype of *Cladophoropsis robusta* (I. M. Johnston-135): B. Two specimens, axes with a few short, opposite branches near apices (after Setchell and Gardner 1924a: pl. 13, fig. 16). C. Prostrate and erect axes of another specimen with branches developing from lenticular cells. D. Close-up of lenticular cell buds on lower portion of an axis (C, D, after Leliaert et al., 2008:figs. 2, 3). E. Branching pattern of frond (after Dawson, 1950c:fig. 11; holotype of *Willella mexicana*, EYD-1789).

by lenticular cells, which together with its lack of “blades,” gave it a “*Valoniopsis*-like” appearance. They also found an isotype specimen of *W. mexicana* to have some branches initiated by lenticular cells and tenacular cells at tips of some apical cells. Results from their critical examination of type material, morphological and culture studies, and molecular analyses resolved the generic status of *C. robusta* as belonging to *Phyllocladon*, and supported *P. robustum* and *W. mexicana* as being a single species (Leliaert et al., 2008).

SIPHONOCLADACEAE

Siphonocladaceae F. Schmitz, 1879:20, as “Siphonocladaceae.”

Algae are erect and either are turfs or clumps of axes with irregular to regular, radially arranged branches that are composed of relatively large, branched, elongated cylindrical to clavate, siphon cells (e.g., *Siphonocladus*). Other members are initially or may remain solid or hollow, more or less spherical thalli that often develop into irregular or lobed shapes or can become open and sheet-like and are composed of large, globose cells that produce a pseudoparenchymatous structure (e.g., *Dictyosphaeria*). Tenacular cells occur in some and may function as structural support or as adventitious rhizoids. Cell division is exclusively segregative in main axes and branches of turf-branched forms and in the spherical to lobed forms. There can also be cell division by centripetal invagination in the rhizoids. Cells are multinucleate, with a reticulate chloroplast or numerous chloroplasts that either lack pyrenoids or have one or more pyrenoids.

Vegetative reproduction in some is by fragmentation. Life histories, where known, are an isomorphic alternation of generations, involving quadriflagellate zoospores, and isogamous biflagellate gametes. (However, at least one, *Siphonocladus pusillus*, has been suggested to have a macrodiploid phase, with the gametes being the only haploid phase [Jónsson and Puisseaux-Dao, 1959].)

REMARKS. Which genera comprise the Siphonocladaceae, as well as the family’s relationship to other families of Cladophorales-Siphonocladales complex, is in a state of flux (Leliaert et al., 2003; Kraft, 2007). Herein the taxonomy of the family and order is based on the genus *Siphonocladus* F. Schmitz (1879; Børgesen, 1905; generic type: *Siphonocladus wilbergii* F. Schmitz (1879); now = *S. pusillus* (C. Agardh ex Kützing) Hauck, 1884; basionym: *Valonia pusilla* C. Agardh ex Kützing, 1849). The family also includes the genera *Dictyosphaeria* and *Ernodesmis*.

Although not yet reported in the northern Gulf, one genus, *Dictyosphaeria* Decaisne (1842a; Decaisne ex

Endlicher, 1843), is represented in the southern Gulf by reports of three species: *D. versluysii* Weber-van Bosse (1905) by Dawson (1944), Rodríguez-Morales and Siqueiros-Beltrones (1999), and Paul-Chávez and Riosmena-Rodríguez (2000); *D. australis* Setchell (1926) by Dawson (1949); and *D. cavernosa* (Forsskål) Børgesen (1932) by Anaya-Reyna and Riosmena-Rodríguez (1996) and Riosmena-Rodríguez et al. (2005).

One of the genera is found in the northern Gulf of California.

Ernodesmis Børgesen

Ernodesmis Børgesen, 1912b:259.

Algae forming bushy clumps composed of elongate cells, with a primary upright clavate cell (or basal stalk) that is attached below by a holdfast of rhizoids and bears a distal whorl of branches. Whorl clusters are composed of 3–10 siphon branches. Each siphon branch of the whorl can initiate new branches at its apex, and in turn, each of these individual whorl branches can produce another whorl of siphon branches; this process may be repeated to produce several orders of whorled clusters. Secondary adventitious holdfasts may develop at the base of older branches, where they come in contact with the substratum. New uprights are produced from well-developed rhizoids. Tenacular cells are sparse, occurring only at junction of branch cells. Annular constrictions present on the basal stalk may also be present on the lower part of the branches. Cells are multinucleate, with numerous plate-like chloroplasts that form a reticulum, and contain 1 pyrenoid. Segments developed by lenticular cell division and sometimes also by segregative division in main stalks and by centripetal invagination in the rhizoids.

Vegetative reproduction is by fragmentation. Reproduction and life histories are poorly known.

REMARKS. The familial placement of *Ernodesmis* within the Cladophorales-Siphonocladales complex is uncertain. Solely on a morphological basis it would seem that *Ernodesmis* could be related to *Valonia* and *Valoniopsis* and therefore would be in the family Valoniaceae. However, the molecular analysis (Leliaert et al., 2003) supported a phylogenetic relationship of *Ernodesmis* to *Siphonocladus*, as earlier observed by Børgesen (1913). Thus, for now, *Ernodesmis* is tentatively considered a member of the Siphonocladaceae.

A monotypic genus of the Caribbean and known throughout the western Atlantic, the one species has also been reported in the Gulf of California.

***Ernodesmis verticillata* (Kützing) Børgesen**

FIGURE 35

Valonia verticillata Kützing, 1847:165.

Ernodesmis verticillata (Kützing) Børgesen, 1912b:259, figs. 10–12; Børgesen, 1913:66, figs. 52–54; Dawson, 1949:244; Dawson, 1959a:4, 8, 11; Dawson, 1961b:379; Dawson, 1966a:6; Dawson, 1966b:55; Papenfuss and Chihara, 1975:309, figs. 1–3; Huerta-Múzquiz and Garza-Barrientos, 1975:4; Huerta-Múzquiz and Mendoza-González, 1985:44; Mateo-Cid et al., 1993:51; González-González et al., 1996:286; La Claire et al., 1997:831; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Mateo-Cid et al., 2000a:61, 70; Pedroche et al., 2005:55; Mateo-Cid et al., 2006:49, 58; Servièrre-Zaragoza et al., 2007:7.

Algae light green tufts, up to 2.5 cm (sometimes more) tall; thallus a single elongate, cylindrical stalk cell, 10–20 mm in length and up to 2.5 mm in diameter, that bears a whorl of cylindrical branches at its apex. Each branch of the initial whorl, in turn, bears another whorl of similar but smaller cells; and this whorl pattern may repeat itself up to 6 times.

HABITAT. On rocks, usually in shaded areas, in crevices, tidepools, and lagoons; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific coast: Isla Socorro (Islas Revillagigedo).

TYPE LOCALITY. St. Croix, U.S. Virgin Islands.

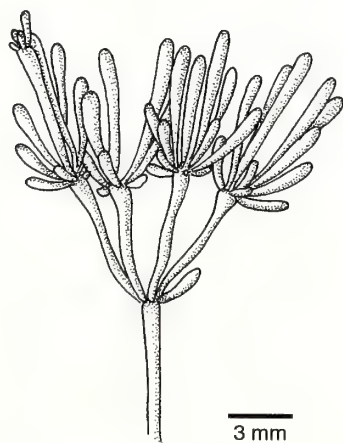


FIGURE 35. *Ernodesmis verticillata*: Upper portion showing successive series of whorled branches (after Børgesen, 1913:fig. 52).

REMARKS. Crystalline cell inclusions have been reported in specimens of Caribbean *Ernodesmis verticillata* from the type locality and in Gulf of California specimens from Punta Palmilla, Baja California Sur (Leliaert and Coppejans, 2004).

VALONIACEAE

Valoniaceae Kützing, 1849:507.

Members of this family lack a distinct central axis and are either relatively simple forms ranging from single giant vesicular cells to aggregations of vesicles, siphons, or cylindrical cells, or are more complex forms that produce clusters of elongated vesicles or cells from the primary vesicle. Growth is by lenticular cell division in which lenticular segments are formed inside the vesicles. These segments may either remain lenticular, or expand outward to develop branches (i.e., septa are initiated prior to elongation of the vesicular branch on the surface of the parent vesicle, e.g., *Valonia*) or may develop hapteroid cells that attach the alga to the substratum or adjacent vesicles.

Although biflagellate and quadriflagellate swimmers have been observed, for most species the life histories are not completely known. Sexual reproduction is only known in *Valonia macrophysa* Kützing (1843) and involves biflagellate isogametes with an isomorphic alternation of generations (Chihara, 1953, 1959).

One genus in the family, *Valonia* C. Agardh (1823), is recorded in the southern Gulf on the basis of the reports of *V. macrophysa* Kützing (1843) by Huerta-Múzquiz and Mendoza-González (1985) and Rodríguez-Morales and Siqueiros-Beltrones (1999).

One genus is known in the northern Gulf of California.

***Valoniopsis* Børgesen**

Valoniopsis Børgesen, 1934:10.

Algae forming cushion-like mats, composed of interwoven club-shaped, filiform, or elongated cylindrical siphons (cells) that initially grow more or less perpendicular to the substratum, then become repent and entangled, and attach by adventitious rhizoids that develop from the tips of downward arching branches that come in contact with the substratum. Branching is unilateral, pseudo-dichotomous or irregular, and obscures apical orientation. Well-developed attachment rhizoids can give rise to new erect segments. Siphons with one to several (1–)2–3 branches that are developed from cell division by lenticular cells (not from protrusions) distally and laterally on

the siphons; septa are formed only at branch base. Annular constrictions and tenacular cells are absent. Cells with numerous discoid chloroplasts, each with single pyrenoid covered with a starch sheath and bisected by traversing thylakoids. Cell division in the rhizoids is by centripetal invagination.

Reproduction is apparently unknown. Life histories are presumed to be similar to other algae of the Siphonocladales.

REMARKS. *Valoniopsis* can sometimes be confused with *Cladophoropsis*, but *Valoniopsis* has lenticular

cells and septa at branches, whereas *Cladophoropsis* has no lenticular cells and mostly nonseptate (occasionally septate) branches. The distinction between *Valoniopsis* and some species of *Valonia* is less certain, and the validity of their generic separation is debatable (Abbott, 1986; Kraft, 2000; Abbott and Huisman, 2004). Biochemically, both genera produce similar amino and fatty acids (Sivalingam, 1989).

There are only two known species of *Valoniopsis*, and both occur in the northern Gulf of California. One is an endemic species in the Gulf of California, and the other is a widespread tropical-subtropical species.

KEY TO THE SPECIES OF *VALONIOPSIS* OF THE NORTHERN GULF OF CALIFORNIA

- 1a. Lateral branches of the siphons, mostly 300–400 μm in diameter, and constricted at branch junctions *V. hancockii*
 1b. Lateral branches of the siphons, mostly 450–1000 μm in diameter, and not constricted at branch junctions
 *V. pachynema*

Valoniopsis hancockii E. Y. Dawson

FIGURE 36A

Valoniopsis hancockii E. Y. Dawson, 1944:207, pl. 31: fig. 9; Dawson, 1961b:379; Abbott, 1986:164; Espinoza-Ávalos, 1993:333; González-González et al., 1996:140; Pedroche et al., 2005:56; Pacheco-Ruiz et al., 2008:202.

Algae green, usually cushionlike, of small entangled masses of cylindrical, coenocytic siphons (filaments), with only occasional septa, mostly at branches. Prostrate siphons very crooked, 125–250 μm in diameter; ascending siphons straighter, 300–400 μm in diameter, with infrequent short lateral branches of about the same diameter that are sharply constricted at their base; apices broadly rounded.

HABITAT. On sand and rocky shores, low intertidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda.

TYPE LOCALITY. Puerto Refugio, Isla Ángel de la Guarda, Islas de la Cintura, Gulf of California.

REMARKS. A northern Gulf endemic, *Valoniopsis hancockii* (currently known only from the type collection) is distinguished by siphons that only occasionally have septa and has basal constrictions of the branch siphons (filaments) (Dawson, 1944; Abbott, 1986). Morphological and molecular studies on further collections of *V. hancockii*, particularly from the type locality, are necessary before this taxon can be properly understood.

Valoniopsis pachynema (G. Martens) Børgesen

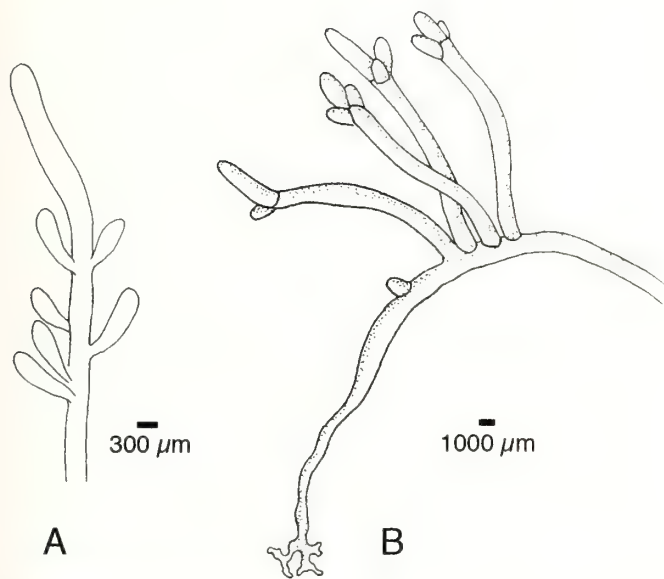
FIGURE 36B,C

Bryopsis pachynema G. Martens, 1868:24, pl. 4: fig. 2.
Valoniopsis pachynema (G. Martens) Børgesen, 1934:10, figs. 1, 2; Dawson, 1944:206; Dawson, 1949:234, 238; Dawson, 1951:54; Dawson, 1954e:324; Issac, 1957:85, pl. 28: figs. 6, 7; Papenfuss and Egerod, 1957:84; Dawson, 1959a:6, 12; Dawson, 1961b:379; Dawson, 1966a:6; Littler and Littler, 1981:151: tbl. 3, 152: fig. 4; Stewart, 1982:54; Littler and Littler, 1984:22; Abbott, 1986:163; Servière-Zaragoza et al., 1993:482; González-González et al., 1996:291; La Claire et al., 1997:831; Yoshida, 1998:51; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; L. Aguilar-Rosas et al., 2000:133; Kraft, 2000:580, fig. 27C,D; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Abbott and Huisman, 2004:93, fig. 32A; Mateo-Cid et al., 2006:48, 58; Pacheco-Ruiz et al., 2008:202.

Valonia pachynema (G. Martens) Weber-van Bosse, 1913:61.

Cladophoropsis robusta sensu Taylor, 1945:51 [see Dawson, 1959a:12] [non *Cladophoropsis robusta* Setchell et N. L. Gardner, 1924b:714, which is *Phyllocladon robustum* (Setchell et N. L. Gardner) Leliaert et Wysor in Leliaert et al., 2008:10].

Algae dark green, forming dense cushionlike clumps, up to 3 cm high and to 7 cm in diameter, irregularly branched near segment apices with 1 or more,



A

B

C

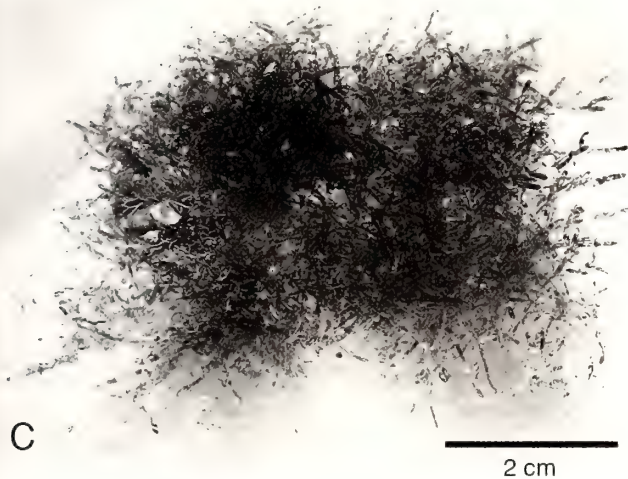


FIGURE 36. Species of *Valoniopsis*. A. *Valoniopsis hancockii*: Portion of type showing short branches with constrictions at their base (drawing of type specimen, EYD-[1940]-215, after Dawson, 1944: pl. 31, fig. 9). B. *Valoniopsis pachynema*: Portion showing branching and a branch bending downward with tip attaching to substratum by means of haptera (after Børgesen, 1934: pl. 13, fig. 1f). C. *Valoniopsis pachynema*: Clump of branched, cylindrical, siphonlike segments (photo of live specimen from Puerto Peñasco, Sonora, Mexico).

usually curved, branchlets, and attached below by rhizoids. Siphons coenocytic, cylindrical, (300–)450–1000 μm in diameter, interlaced and ascending. Branches with basal septa (lenticular crosswall); younger branches erect, older branches repent.

HABITAT. On rocks, occasionally entwined with other algae of turf communities; high to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Agua Verde; Isla Espíritu Santo to Bahía de La Paz. Pacific coast: Velero Point (south Bahía Sebastián Vizcaíno) and Punta Malarrimo, Baja California Sur; Isla Isabel, Nayarit; Hawaiian Islands; China; Japan.

SYNTYPE LOCALITIES. Benkulen and Pulau Tikus, near Bengkulu, Sumatra, Indonesia (*vide* Silva et al., 1996a).

REMARKS. Crystalline cell inclusions, considered to be of systematic value, have been reported in *Valoniopsis pachynema* from several locales in the Indian Ocean (Leliaert and Coppejans, 2004).

BRYOPSIDOPHYCEAE

Bryopsidophyceae Bessey, 1907:287.

Algae of this class are almost all exclusively marine and vary from relatively simple forms to structurally complex forms that are siphonous or tubular and coenocytic (i.e., lack cell walls and are multinucleate), with cytoplasm also containing numerous fusiform or ellipsoidal chloroplasts and a large central vacuole. Many are homoplastidic, with only chloroplasts that may contain or lack pyrenoids; others are heteroplastidic, with both chloroplasts and amyloplasts (colorless starch storage plastids). Cytoplasmic streaming occurs in the siphons, with organelles moving with the cytoplasm. Accessory pigments are siphonoxanthin and siphonein. Cell wall constituents are manna, xylan, and glucan (cellulose) in varying proportions; glucan is not in the crystalline form as found in members of the class Chlorophyceae Wille ex Warming (1884).

Reproduction is by biflagellate, quadriflagellate, or multiflagellate zoospores. In species that produce biflagella or quadriflagella, the flagella are in eleven and five o'clock positions, with overlapping basal bodies. Other members have stephanokont zoospores, i.e., multiple flagella arranged in whorls at the cell's anterior end. Sexual reproduction is anisogamous.

The class is usually considered to have a single order, Bryopsidales (e.g., Silva et al., 1996a; Abbott and Huisman, 2004; herein). However, some phylogenists consider the class to contain two orders and include the Halimadales C. van den Hoek, D. G. Mann et H. M. Jahns (1995).

BRYOPSIDALES

Bryopsidales J. H. Schaffner, 1922:133.

Codiales Setchell, 1929:584.

Caulerpales J. Feldmann, 1946:753.

Siphonales Warming, 1884:33, as "Siphoneae."

Algae are variable in shape and size, ranging from simple (unbranched) to branched and to complex systems of branching tubular siphons or filaments. Some form globose vesicles; others are of filaments or siphons that are freely branched or formed into thalli with distinctive morphologies. Most are attached by prostrate rhizoids. Transverse septa are generally lacking in vegetative portions but may be present at the base of reproductive sporangia or gametangia. Cells are coenocytic with numerous nuclei and chloroplasts that lack or contain pyrenoids. In some, the vegetative portion of the thallus is traversed by a system of internal strands of cell wall material (trabeculae) that form an elaborate network, thought to strengthen the outer siphon walls. All members possess two distinctive xanthophylls, siphonein and siphonoxanthin, which are not found in other members of the Chlorophyta.

Some reproduce vegetatively by rhizome-like structures, fragmentation, or propagules. Sporophytic repro-

duction is by multiflagellate zoospores or aplanospores, usually developed within morphologically differentiated sporangia. Sexual reproduction is isogamous, anisogamous, or oogamous, with gametangia producing biflagellate gametes.

REMARKS. Although the Bryopsidales is the more widely accepted name for this order (e.g., Silva et al., 1996a; Abbott and Huisman, 2004), the name Caulerpales has also been recently used (Graham and Wilcox, 1999; Lee, 1999). Members of this very large order are widespread in distribution and are particularly abundant in tropical to subtropical regions.

Phylogenetic analyses of the Bryopsidales suggested that the suborders Bryopsidineae Hillis-Colinvaux (1984) and Halimedineae Hillis-Colinvaux (1984) are distinct monophyletic lineages (Lam and Zechman, 2006). Family-level monophyly was supported for the Bryopsidaceae, Derbesiaceae and Codiaceae (Bryopsidineae), and the Caulerpaceae and Halimedaceae (Halimedineae), but not for the Udoteaceae (Lam and Zechman, 2006).

Five families are represented in the northern Gulf of California.

KEY TO THE FAMILIES OF BRYOPSIDALES IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae differentiated into three distinct portions: an erect, cylindrical to frondose upper portion; arising from prostrate, stolonlike runners; and attached by rhizoids at various points; not calcified **Caulerpaceae**
- 1b. Algae of various simple to structurally complex forms: filamentous or siphonous or vesiculate; not calcified or calcified 2
- 2a. Algae of coenocytic filaments, tubular cells or siphons or vesicles; not structurally complex; not calcified 3
- 2b. Algae multiaxial, of coenocytic filaments formed into complex thalli that are firm or spongy; calcified or not calcified 4
- 3a. Macrothalli filamentous, of one or more percurrent or non-percurrent axes with lateral branches; gametophytes and sporophytes isomorphic in some; others heteromorphic with filamentous macro-gametophytes, and micro-sporophytes of creeping prostrate filaments (protonema) **Bryopsidaceae**
- 3b. Heteromorphic macrothalli; sporophytes and gametophytes very different looking: sporophytes filamentous, without a percurrent axis, subdichotomously to irregularly branched; gametophytes a single vesicle **Derbesiaceae**
- 4a. Thalli not calcified; spongy; prostrate and cushionlike or erect, terete to flattened axes and branches; without segments. **Codiaceae**
- 4b. Thalli of calcified cylindrical to flattened segments that alternate with narrow, flexible noncalcified joints **Halimedaceae**

BRYOPSIDINEAE

Bryopsidineae Hillis-Colinvaux, 1984:287.

The suborder Bryopsidineae is characterized by homoplasty, the absence of a concentric lamellar system, and cell walls that are composed primarily of the polysaccharides, either mannan, or xylan and cellulose. Allelochemicals (secondary natural products) are generally absent. Reproduction is non-holocarpic. Reproductive structures usually have a septum (plug) at their base.

REMARKS. Species of the Bryopsidineae are tropical to subboreal in distribution. The suborder is represented by three families, Bryopsidaceae, Derbesiaceae, and Codiaceae, in the northern Gulf of California.

BRYOPSIDACEAE

Bryopsidaceae Bory de Saint-Vincent, 1829:203

Algae are coenocytic, siphonous filaments that are simple or sparsely to densely branched and are attached to

the substratum by a rhizoidal holdfast. Filamentous thalli lack internal trabeculae, may be with or without a distinct percurrent axis, and are branched pinnately, radially, or irregularly from a few to several orders. The main component of siphon walls is glucan (cellulose) and xylan in the gametophytes, while in the sporophytes it is mannan.

Reproduction can be by fragmentation, regeneration from extruded protoplasts, or parthenogenesis. Life histories, where known, generally involve filamentous phases: (1) an alternation of gametophytic *Bryopsis* and a sporophytic microthallus of creeping prostrate filaments (protonema), (2) an alternation of gametophytic “*Bryopsis*-like” phase with a filamentous *Derbesia* phase (i.e., *Bryopsidella* Feldmann ex H. Rietema, 1975), or (3) zygotes produced by *Bryopsis* that develop directly into another gametophyte. Stephanokont zoospores (with a ring or whorl of several flagella) are produced in differentiated sporangia with a basal septum in filamentous sporophytes. A few of the species are known to produce aplanospores.

Sexual reproduction is non-holocarpic. Gametophytic thalli can be either monoecious or dioecious. Biflagellate anisogametes are produced in the ultimate branchlets segregated from the rest of the filamentous thallus by a basal membrane.

One genus of the family, *Bryopsis*, is represented in the northern Gulf of California.

***Bryopsis* J. V. Lamouroux**

Bryopsis J. V. Lamouroux, 1809d:333.

Algae are erect, composed of a cylindrical, coenocytic, percurrent axial filament that is oppositely or more or less radially or irregularly branched, often appearing

featherlike, and attached below by rhizoids. Growth is indeterminate. Filaments are without septa and contain numerous disc-shaped chloroplasts, each containing 1 pyrenoid. Siphon walls of presumed sporophytes contain mannan, while those of gametophytes reportedly contain cellulose and xylan.

Asexual reproduction is by fragmentation, aplanospores, and regeneration from extruded protoplasts. Life histories generally involve an alternation of filamentous phases, with a feather-like or plumose gametophyte and either a sporophytic microthallus of creeping filaments (protonema) or an erect filamentous *Derbesia*-like phase. In some of the species cultured, filamentous or protonema sporophytes produced stephanokont zoospores that either developed into gametophytes or into a microthallus that produced anisogametes (Rietema, 1975; van den Hoek, 1981; Tanner, 1981). Sexual reproduction, with thalli being monoecious or dioecious, involves the tips of the ultimate branchlets that separate from the branch by formation of a basal septum, or plug, at maturity and develop into gametangia and produce biflagellate anisogametes.

REMARKS. The morphology of species of *Bryopsis* is so variable and sometimes overlapping (e.g., Womersley, 1984) that understanding the species limits will probably best be facilitated by molecular systematics. The Gulf of California species of *Bryopsis*, as well as those of the eastern Pacific, are in need of taxonomic, culture life history, molecular, and phylogenetic studies, such as the studies of Krellwitz et al. (2001).

One species, *B. muscosa* J. V. Lamouroux (1809b), has been reported in the southern Gulf by Dawson (1959a, 1961b).

Five other taxa, four species and one variety, are currently known in the northern Gulf of California.

KEY TO THE SPECIES OF *BRYOPSIS* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Main axes radially branched (sometimes irregular) *B. hypnoides*
- 1b. Main axes pinnately or oppositely branched in one plane or more or less in one plane (featherlike in appearance) 2
- 2a. Main axes with both determinate and longer indeterminate branchlets *B. salvadoreana*
- 2b. Main axes with only determinate branchlets 3
- 3a. Main axes over 400 μm in diameter (up to 1000 μm); lower portions without branches and upper portions with abundant, pinnately arranged branchlets *B. corticulans*
- 3b. Main axes smaller in diameter, 200–400 μm ; with frequent, occasional, or sparse branchlets limited to upper or terminal portions 4
- 4a. Main axes over 250 μm in diameter, up to 400 μm in diameter; ultimate branchlets opposite along sides of branches in one plane *B. pennata* var. *pennata*
- 4b. Main axes 210–250 μm in diameter; branchlets absent in lower portions; branchlets in upper portion usually sparse and more or less in one plane or partly radial *B. pennata* var. *minor*

***Bryopsis corticulans* Setchell**

Bryopsis corticulans Setchell in Collins, Holden, and Setchell, 1899: Exsiccate No. 626; Collins, 1909b:404; Setchell and Gardner, 1903:230; Setchell and Gardner, 1920b:160, pl. 15: figs. 4, 5, pl. 27; Smith, 1944:73, pl. 9: fig.3; Dawson, 1951:52; Dawson, 1961b:381; Abbott and Hollenberg, 1976:111, fig. 70; Devigny, 1978:358; Pedroche and González-González, 1981:64; L. Aguilar-Rosas and Bertsch, 1983:116; Mendoza-González and Mateo-Cid, 1986:419; Stewart, 1991:33; Servièrre-Zaragoza et al., 1993:481; González-González et al., 1996:126; Aguilar-Ramírez et al., 1998:511; Pedroche et al., 2005:57.

Algae tufted, up to 5–10(–20) cm tall; main axes 400–1000 µm in diameter; lower portions without branches, upper portions abundantly pinnately branched. Branches with downward growing rhizoids from their base; ultimate branchlets, 150–300 µm in diameter, abruptly constricted at base.

HABITAT. On rocks; mid to low intertidal.

DISTRIBUTION. Gulf of California: Bahía Kino. Pacific coast: southern British Columbia to Islas San Benito, Baja California; Jalisco.

TYPE LOCALITY. Pacific Grove, Monterey County, California (Smith, 1944).

REMARKS. *Bryopsis corticulans* is only known in the Gulf of California from the report of Mendoza-González and Mateo-Cid (1986). The description is based on Abbott and Hollenberg (1976). The species complex, comprising three morphologically similar taxa, *B. corticulans*, *B. hypnoides*, and *B. plumosa* (Hudson) C. Agardh (1822), needs to be studied to clarify the taxonomic status and relationship of these species to each other and to the Gulf *B. corticulans*.

***Bryopsis hypnoides* J. V. Lamouroux**

Bryopsis hypnoides J. V. Lamouroux, 1809d:333; Lamouroux, 1809b:135, pl. 1; fig. 2a,b; Setchell and Gardner, 1920b:159; Smith, 1944:73, pl. 9: fig. 2; Taylor, 1945:60 [with doubt]; Dawson, 1949:244; Dawson, 1961b:381; Abbott and Hollenberg, 1976:113, fig. 71; Huerta-Múzquiz, 1978:339; Pedroche and González-González, 1981:64; L. Aguilar-Rosas and Bertsch, 1983:116, 121; Huerta-Múzquiz and Mendoza-González, 1985:44; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mendoza-González and Mateo-Cid, 1986:420; Sánchez-Rodríguez et al., 1989:39; Dreckmann et al., 1990:24, pl. 2: fig. 2; Mateo-Cid and Mendoza-González, 1991:27;

Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid and Mendoza-González, 1992:25; Mateo-Cid et al., 1993:52; González-González, 1993:443; Servièrre-Zaragoza et al., 1993:481; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mateo-Cid and Mendoza-González, 1994a:52; Mateo-Cid and Mendoza-González, 1994b:45; Mendoza-González et al., 1994:103, 112; González-González et al., 1996:275, 365; Mendoza-González and Mateo-Cid, 1996:64, 67, 76, 88, pl. 28: figs. 126–128; Bucio-Pacheco and Dreckmann, 1998:43; Mendoza-González and Mateo-Cid, 1998:25; Servièrre-Zaragoza et al., 1998:168; Yoshida, 1998:139; L. Aguilar-Rosas et al., 2000:133, 134, 136, 137; Mateo-Cid et al., 2000a:70; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:96, fig. 33A; Wysor, 2004:219; Pedroche et al., 2005:58; Mateo-Cid et al., 2006:59; Dreckmann et al., 2006:154.

Algae tufted, up to 2–4 cm tall; main axes 200–250(–400) µm in diameter, branching often profuse, usually radial or sometimes irregular; branches become progressively narrower and smaller distally; ultimate branchlets up to 50 µm in diameter and up to 5 mm long, abruptly constricted at the base, and gradually tapered at upper end. Rhizoids grow downward from base of primary branches.

HABITAT. On rocks or shells; epiphytic on *Gelidium pusillum* (L. Aguilar-Rosas et al., 2000); mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas; Bahía Concepción to Cabo Pulmo. Pacific coast: British Columbia to Chiapas; Panama; Chile; Hawaiian Islands; Japan.

TYPE LOCALITY. Near Cette, Mediterranean coast of France.

REMARKS. Studies of *Bryopsis hypnoides* from California (Burr and West, 1970) and Europe (Rietema, 1975) showed them to be monoecious, whereas those of the northeastern United States were dioecious (Urban, 1969). *Bryopsis hypnoides* is part of a species complex that includes *B. corticulans* and *B. plumosa*; Gulf specimens need to be cultured and morphologically and molecularly analyzed in comparisons with type locality material of all three of these species to elucidate their taxonomy (see also Remarks under *B. corticulans*).

Bryopsis pennata* J. V. Lamouroux var. *pennata

FIGURE 37

Bryopsis pennata J. V. Lamouroux, 1809d:333, pl. 3, fig. 1 a,b; Egerod, 1952:370, fig.7; Dawson, 1957b:9;



FIGURE 37. *Bryopsis pennata*: Frond with distichous branching pattern giving a featherlike appearance (EYD-27451).

Dawson, 1959a:6, 8, 12, 14; Dawson, 1961b:381; Dawson, 1961c:404, pl. 4: fig.4; Dawson, 1966a:7; Huerta-Múzquiz, 1978:339; González-González, 1993:443; Servièrre-Zaragoza et al., 1993:481; González-González et al., 1996:275; Pacheco-Ruíz and Zertuche-González, 1996a:432; Mendoza-González and Mateo-Cid, 1998:25, 27; Mendoza-González et al., 1999:61; León-Tejera and González-González, 2000:327; Abbott and Huisman, 2004:98, fig. 33B; López et al., 2004:10; Wysor, 2004:219; Pedroche et al., 2005:58; Mateo-Cid et al., 2006:48, 59; Dreckmann et al., 2006:154.

Bryopsis plumosa var. *pennata* (J. V. Lamouroux) Børgesen, 1911:147; Dawson, 1944:212; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; León-Tejera and González-González, 1993:497; González-González et al., 1996:127.

Algae of 1 or more erect filaments, up to 5 cm tall; main axes and branches with more or less opposite branchlets of similar length in upper portions and in one plane (giving a lanceolate to oblong featherlike appearance); axes sometimes only sparsely branched; arising from a rhizoidal holdfast. Main axis 250–400 μm in diameter; branchlets 40–75(–150) μm in diameter and up to 2.0 mm long.

HABITAT. On rocks, usually in shaded areas, crevices, and tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific coast: Nayarit;

Guerrero to Oaxaca; Costa Rica; El Salvador; Panama; Chile; Hawaiian Islands.

TYPE LOCALITY. Antilles, West Indies.

***Bryopsis pennata* var. *minor* J. Agardh**

Bryopsis pennata var. *minor* J. Agardh, 1887:23; Silva et al., 1996a: 807; Bucio-Pacheco and Dreckmann, 1998:43; López et al., 2000:338; Mateo-Cid et al., 2000a:70; Pedroche et al., 2005:59; Pacheco-Ruíz et al., 2008:202.

Bryopsis pennatula J. Agardh, 1847:6; Kützing, 1856:27, pl. 76: fig. 2; Setchell and Gardner, 1920b:158; Taylor, 1945:61; Dawson, 1949:250, 251; Dawson, 1959a:12; Dawson, 1961b:381; Smith, 1969:624; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Abbott and Hollenberg, 1976:113, fig. 72; L. Aguilar-Rosas and Bertsch, 1983:116, 121; Stewart and Stewart, 1984:140; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:44; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Mendoza-González and Mateo-Cid, 1986:420; Sánchez-Rodríguez et al., 1989:38; Dreckmann et al., 1990:24, 37; Mateo-Cid and Mendoza-González, 1991:27; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Mendoza-González and Mateo-Cid, 1992:24; León-Tejera et al., 1993:199, 204; González-González, 1993:443; Stout and Dreckmann, 1993:5; Servièrre-Zaragoza et al., 1993:443; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; González-González et al., 1996:127; Mateo-Cid and Mendoza-González, 1994b:45; Mendoza-González et al., 1994:112; Mendoza-González and Mateo-Cid, 1996:77, 88, pl. 2: figs. 129–131; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Silva et al., 1996a:807; Galindo-Villegas et al., 1997:4; Aguila-Ramírez et al., 1998:511; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Paul-Chávez and Riosmena-Rodríguez, 2000:146; López et al., 2000:340; Carballo et al., 2002:753; Hernández-Herrera et al., 2005:146; Riosmena-Rodríguez et al., 2005:101; Lam and Zechman, 2006:671; Servièrre-Zaragoza et al., 2007:3, 7.

Algae of erect, cylindrical main axes, 210–250 μm in diameter, up to 3 cm tall; branchlets absent in lower portions; branchlets in upper portion sparse (often with only a few uppermost branchlets near the terminal portion) and more or less distichously or partially radially arranged, short, less than 1 mm long, 20–30 μm in diameter, strongly constricted at base, with rounded apices.

HABITAT. On rocks and in tide pools; high to low intertidal.

DISTRIBUTION. Gulf of California: Punta Cheuca, Sonora; Bahía de La Paz to Cabo Pulmo, Baja California Sur; Mazatlán, Sinaloa. Pacific coast: central California to Baja California; Nayarit to Chiapas; Galápagos Islands.

TYPE LOCALITY. San Agustín, Oaxaca, Pacific Mexico (Setchell and Gardner [1920b:159] noted "St. Augustin" as cited by Agardh (1847) was probably in the vicinity of Pochutla and Punta de Huatulco, Oaxaca [see also Liebmann, 1869:viii]).

REMARKS. Agardh (1887), in describing *Bryopsis pennata* var. *minor*, cited *B. pennatula* J. Agardh (1847) in the protologue, thus apparently reducing *B. pennatula* to a variety of *B. pennata*. Therefore, as noted by Silva et al. (1996a), these two taxon names have the same type, with *B. pennatula* being a synonym of *B. pennata* var. *minor*.

Specimens identified as "*B. pennatula*" from the Gulf of California and Pacific Mexico should be reexamined to verify they belong here.

***Bryopsis salvadoreana* E. Y. Dawson**

Bryopsis salvadoreana E. Y. Dawson, 1961c:405, pl. 5: fig. 2, pl. 6; Dawson, 1962b:228; Wýsor, 2004:221, figs. 11, 12.

Algae of erect dense tufts, (2-)3-5 cm tall; cylindrical main axes, 200-400 µm in diameter; with both determinate and indeterminate branchlets more or less distichously arranged; determinate branchlets constricted at base; indeterminate branchlets irregularly distichous, becoming long, 3-12 mm, and may further divide, upper portion sometimes with one or more divisions (some appearing lobed), apices rounded; attached by a dense basal mass of entangled rhizoids.

HABITAT. On boulders; intertidal.

DISTRIBUTION. Gulf of California: Isla Raza (Las Islas de la Cintura). Pacific coast: Punta Chiriquín and Isla Meanguera, El Salvador; Panama.

TYPE LOCALITY. Arrecife de Sacate, off Punta Chiriquín, Golfo de Fonseca, El Salvador.

REMARKS. Gulf of California specimens from Isla Raza (EYD-26103; US Alg. Coll.-37352) are tentatively referred to *Bryopsis salvadoreana*. Although they are similar to the type specimen of *B. salvadoreana* (EYD-21758; US Alg. Coll.-5162), the indeterminate branchlets of the Gulf material are not as abundant or apparently as well developed, and most are not as long and lack the fully developed upper divisions of the type. More Gulf collections and type locality material are needed for further

study, along with molecular analyses, to test their taxonomic and phylogenetic status.

DERBESIAEAE

Derbesiaceae Hauck, 1884:421.

Halicystaceae G. M. Smith, 1930:227, as "Halicystidaceae"; Smith, 1944:69; Papenfuss, 1955:129.

Algae of this family have two morphologically very different life history phases: a filamentous, siphonous sporophyte and vesiculate gametophytes. Sporangia with a basal septum are borne laterally on the sporophyte filaments and produce zoospores with numerous flagella (stephanokontic). Gametangia are formed in isolated portions of the cytoplasm inside the gametophytic vesicles and produce biflagellate anisogametes.

REMARKS. Although life histories for many species, including the generitype, involve an alternation of heteromorphic forms, variations in life histories of some species of *Derbesia* have also been reported: (1) macrogametes that develop new sporophytes by parthenogenesis, (2) development of vesicular phase directly from sporangia without the production of zoospores, (3) sporophytes that grow from zoospores, and (4) a haploid gametophyte that alternates with heterokaryotic sporophyte (the latter characterized by the presence of haploid nuclei from the two parents, e.g., *D. tenuissima* (Moris et De Notaris) P. Crouan et H. Crouan, 1867). Under these circumstances, nuclear fusion occurs in young sporangia shortly before meiosis and cleavage of zoospores.

One genus is known in the northern Gulf of California. A vesiculate "*Halicystis*-phase" is also reported in the northern Gulf. Its life history is unknown, but it may be involved with a *Derbesia* or possibly another genus (see below for various reported life histories).

***Derbesia* Solier**

Derbesia Solier, 1846:452; Solier, 1847:157.

Halicystis Areschoug, 1850:446.

Thalli are of two morphologically different forms. The sporophyte is composed of siphonous cylindrical filaments that are usually erect, and loosely unilaterally, irregularly or occasionally dichotomously branched, and attached by a prostrate system of irregularly branched rhizoidal filaments or lobed haptera. Although usually absent, simple or compound transverse septa sometimes develop in the siphonous filaments, mostly at base of branches. The

gametophytes are spherical to pyriform single-cell vesicles, “*Halicystis*-phase.” Both the filaments and vesicles are multinucleate and contain numerous disc-shaped or spindle-shaped small chloroplasts, which in some species have one to three pyrenoids, while other species are without pyrenoids.

Asexual reproduction can occur by fragmentation and proliferation of extruded protoplasts. The diploid, filamentous sporophyte, *Derbesia*-phase, produces stephanokont zoospores in modified lateral sporangia separated from the vegetative filament by a septum (or plug) or a double septum near their bases. A haploid vesicular gametophyte, *Halicystis*-phase, has been shown in the life histories for some species of *Derbesia*. A gametangium appearing as a transverse band within the vesicle develops biflagellate anisogametes that are released forcibly through papillae on the vesicle wall.

REMARKS. Filamentous species of *Derbesia* occur in the intertidal and down to 23 m depths of tropical to boreal seas worldwide. There are at least three types

of life histories known to involve species of *Derbesia*. Culture studies have shown life histories with a sporophytic filamentous *Derbesia*-phase and a gametophytic vesicular *Halicystis*-phase (Hollenberg, 1935, 1936; Kornmann, 1938; Drew, 1955; Page, 1970; Rietema, 1975). Sporophytic “*Derbesia*-like” phases have also been linked to the gametophytes of some species of *Bryopsis* (Hüstedde, 1964; Rietema, 1975), and apparent sporangia of a New England species of *Derbesia* developed directly into vesicular gametophytes without producing any zoospores (Sears and Wilce, 1970).

Two species and one unidentified species are reported in the southern Gulf: *Derbesia turbinata* M. Howe et Hoyt (1916) by Dawson (1966b), *D. hollenbergii* W. R. Taylor (1945) by Dawson (1959a), and “*Derbesia* sp.” by Rocha-Ramírez and Siqueiros-Beltrones (1991). The Gulf species of *Derbesia* need to be investigated morphologically, with culture studies and DNA analyses.

One species and one unidentified species of filamentous *Derbesia* are reported in the northern Gulf of California.

KEY TO THE DIFFERENT LIFE HISTORY PHASES OF *DERBESIA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Sporophyte (*Derbesia*): cylindrical, coenocytic filaments without a distinct percurrent axis; branched sparsely to moderately, predominately unilateral or sometimes irregular 2
- 1b. Gametophyte: a spherical vesicle (a single large cell), up to 15 mm in diameter, above a very short stalk *Halicystis*-phase
- 2a. Filaments branched mostly unilaterally; 50–65 µm in diameter *Derbesia marina*
- 2b. Filaments sparsely and irregularly branched; 40–70 µm in diameter *Derbesia* sp. A

***Derbesia marina* (Lyngbye) Solier**

FIGURE 38

Vaucheria marina Lyngbye, 1819:79, pl. 22A (sporophyte). *Derbesia marina* (Lyngbye) Solier, 1846:453; Solier 1847:157; Collins, 1909b:407, pl. 17: fig. 152; Setchell and Gardner, 1920:164, pl. 15: fig. 3; Smith, 1944:71, pl. 8: fig. 4; Dawson, 1956:34, fig. 15; Dawson, 1961b:380; Dawson, 1962c:278; Abbott and Hollenberg, 1976:115, fig. 73; Huerta-Múzquiz, 1978:336; Devinny, 1978:538; Kobara and Chihara, 1980:214, figs. 8–12; Kobara and Chihara, 1981:2, figs. 1–3, 7–20; Pedroche and González-González, 1981:64; Lewbel et al., 1981:165; Huerta-Múzquiz and Mendoza-González, 1985:44; Mendoza-González and Mateo-Cid, 1985:22; L. Aguilar-Rosas and Pacheco-Ruíz, 1986:77; Dreckmann et al., 1990:26, 37;

Mateo-Cid and Mendoza-González, 1991:24, 27; Mateo-Cid and Mendoza-González, 1992:25; Mateo-Cid and Mendoza-González, 1993:9–11; Mateo-Cid et al., 1993:52; Stout and Dreckmann, 1993:5; Mateo-Cid and Mendoza-González, 1994a:57; Mateo-Cid and Mendoza-González, 1994b:45; León-Tejera and González-González, 1994:492; Mendoza-González et al., 1994:113; González-González et al., 1996:293; Pacheco-Ruíz and Zertuche-González, 1996a:432; Mendoza-González and Mateo-Cid, 1996:76, 88, pl. 28: figs. 123–125; Bucio-Pacheco and Dreckmann, 1998:43; Mendoza-González and Mateo-Cid, 1998:25; Yoshida, 1998:144, fig. 1-13: E–G; Serviére-Zaragoza et al., 1998:169; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; López et al., 2000:339; Wysor, 2004:223; Riosmena-Rodríguez et al., 2005:101; Pedroche et al., 2005:60; Mateo-Cid et al., 2006:59; Dreckmann et al., 2006:154.

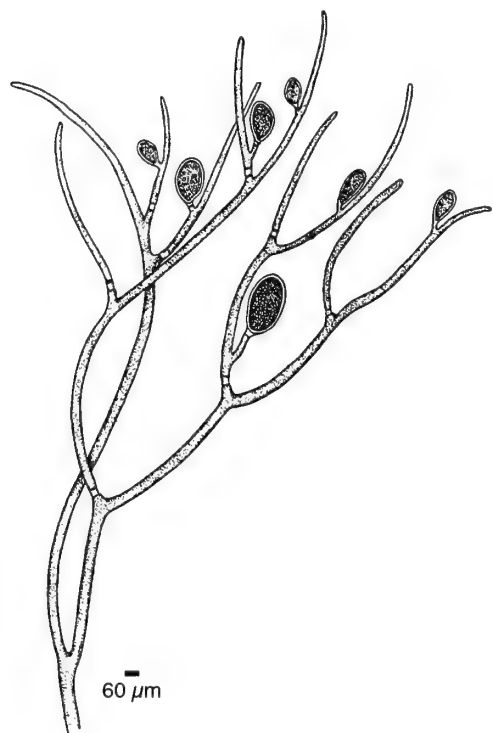


FIGURE 38. *Derbesia marina*: Sporophyte: Filaments bearing lateral sporangia, each with a single basal septum (after Collins, 1909b: pl. 17, fig. 152).

Derbesia vaucheriaeformis sensu Chávez B., 1972:268 [non *Derbesia vaucheriaeformis* (Harvey) J. Agardh, 1887:34].

Gastridium ovale Lyngbye, 1819:72, pl. 18: fig. B (gametophyte).

Halicystis ovalis (Lyngbye) Areschoug, 1850:447; Setchell and Gardner, 1920b:155, pl. 14: fig. 3; Hollenberg, 1935:782, pls.1–4; Smith, 1944:70, pl. 9: fig. 1; Dawson et al., 1960a:10, 14, pl. 1: fig. 5; Dawson et al., 1960b:5, 6, 8, 11, 13; Dawson, 1961b:380; Scagel, 1966:116, pl. 2: figs. A–F; Abbott and Hollenberg, 1976:115, fig. 75; Kobara and Chihara, 1980:214, figs. 1–7, 13; Lewbel et al., 1981:165; L. Aguilar-Rosas and Bertsch, 1983:116, 122; R. Aguilar-Rosas et al., 1990:123; Stewart, 1991:115; Mendoza-González and Mateo-Cid, 1992:24; Mateo-Cid et al., 1993:52; González-González et al., 1996:137; Pacheco-Ruíz and Zertuche-González, 1996a:432; L. Aguilar-Rosas et al., 2000:133; Pacheco-Ruíz et al., 2008:202.

Sporophytes small filamentous tufts, up to 15 mm tall; filaments of long, cylindrical coenocytic cells, 50–65 μm in diameter; branching mostly unilateral, with subacute

apices; attached by irregularly branched prostrate filaments. Chloroplasts without pyrenoids. Sporangia formed on ultimate branchlets, borne on a short pedicel with a crosswall at apex of pedicel; ovoid to pyriform, 150–200 μm long and 100–160 μm in diameter; producing zoospores.

Gametophytes (*Halicystis*-phase of *Derbesia marina*) erect, spherical vesicles, up to 15 mm in diameter; above a very short stalk attached to calcareous substratum by basal rhizoids that often penetrate it. Vesicle with a large vacuole, and peripheral cytoplasm containing multiple nuclei and numerous chloroplasts without pyrenoids. Vegetative reproduction by regeneration of new vesicles from apparently perennial attachment rhizoids. Sexual reproduction by biflagellate anisogametes, produced in separate gametophytic vesicles. Male vesicles develop slender gametes in brownish-green fertile areas of the cytoplasm. Female vesicles develop larger and rounder gametes in greenish-black fertile areas. Gametes forcibly released through 1 or more papillae (appearing as whitish dots) on the vesicle wall.

REMARKS. Culture life history studies have linked gametangial *Halicystis* to sporophytic *Derbesia* from the Pacific coast of North America (Hollenberg, 1935, 1936; Scagel, 1966), Japan (Kobara and Chihara, 1980, 1981), Europe (Kornmann, 1938; Feldmann, 1950; Eckhardt et al., 1986), and Bermuda (Page, 1970). Thus, species of *Halicystis* are usually referred to as the “*Halicystis*-phase of *Derbesia*.”

HABITAT. On rocks, epiphytic on crustose corallines; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Concepción; Bahía del Rincón to San Jose del Cabo; Matzatlán, Sinaloa. Pacific coast: Alaska to Baja California; Nayarit to Chiapas; Panama; Japan.

TYPE LOCALITY. Kivig, Strømø, Faeroe Islands, Denmark.

***Derbesia* sp. A**

Derbesia sp. of Dawson, 1966a:7; Mateo-Cid et al., 2006:48.

Algae forming small, filamentous tufts, up to 10 mm long, of filaments sparsely and irregularly branched, without a percurrent axis, and 40–70 μm in diameter. Siphonous cells with numerous chloroplasts that lack pyrenoids.

HABITAT. Growing on rocks or sometimes entangled on gorgonians; mid to low intertidal.

DISTRIBUTION. Gulf of California: Punta Pelicano, vicinity of Puerto Peñasco.

REMARKS. Although lacking a distinct main axis and reproductive structures, the material reported

as “*Derbesia* sp.” (Dawson, 1966a) somewhat resembles sparsely and irregularly branched forms of *Bryopsis pen-nata*. More collections, particularly fertile specimens, are needed to determine which species of filamentous *Derbesia* are present in the northern Gulf.

***Halicystis*-phase**

FIGURE 39A,B

“*Halicystis ovalis*” sensu Norris and Bucher, 1976:3, fig. 2.

Northern Gulf specimens: spherical vesicles, up to 10 mm in diameter, and dark emerald green. Vesicle above a very short stalk; lowermost portion of basal stalk attached to *Amphiroa* by rhizoidal growths.

HABITAT. Epiphytic on the articulated coral-line, *Amphiroa*; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Wil-lard (Bahía San Luis Gonzaga) to Bahía Concepción.

REMARKS. Although similar in morphology to the Pacific coast *Halicystis ovalis*-phase, the northern Gulf material referred to as “*Halicystis*-phase” were epiphytic on the articulated coralline, *Amphiroa vanbosseae* (Nor-ris and Bucher, 1976), whereas the Pacific coast *Halicystis ovalis*-phase of *Derbesia marina* (Abbott and Hollenberg, 1976; Scagel et al., 1989) and the Japanese *H. ovalis*-phase of *D. marina* and *H. parvula*-phase of *D. tenuissima*

(Kobara and Chihara, 1980) are only reported on crustose corallines.

The life history of Gulf of California *Halicystis*, or even if the vesicles are gametangial or sporophytic, is unknown. Thus far, known life histories that involve a “*Halicystis*” either have an alternate heteromorphic phase (which is either a *Derbesia* or an alternate that is another genus, i.e., not a *Derbesia*) or have a repeating life history of only *Halicystis*-forms (i.e., with no alternate phases). Therefore, Gulf of California *Halicystis*, including those of the southern Gulf (reported epiphytic on mangroves; Mateo-Cid et al., 1993, as “vesicular gametangium [of] *Derbesia marina*”), need to be tested for host specificity and need cul-ture studies to elucidate their life history and reproductive condition (whether gametangial, as generally presumed, or sporophytic), and molecular analyses to determine their taxonomic status and phylogenetic relationships.

CODIACEAE

Codiaceae Kützing, 1843:302, 308.

Thalli may be growing prostrate or erect, lack cal-cification, and are multiaxial, spongy, unbranched or branched, variable forms, that can be globose, cushion-like, cylindrical, compressed, flattened, or blade-like, and are attached by compacted masses of rhizoids. Internally the thalli are composed of branching, tubular, mostly

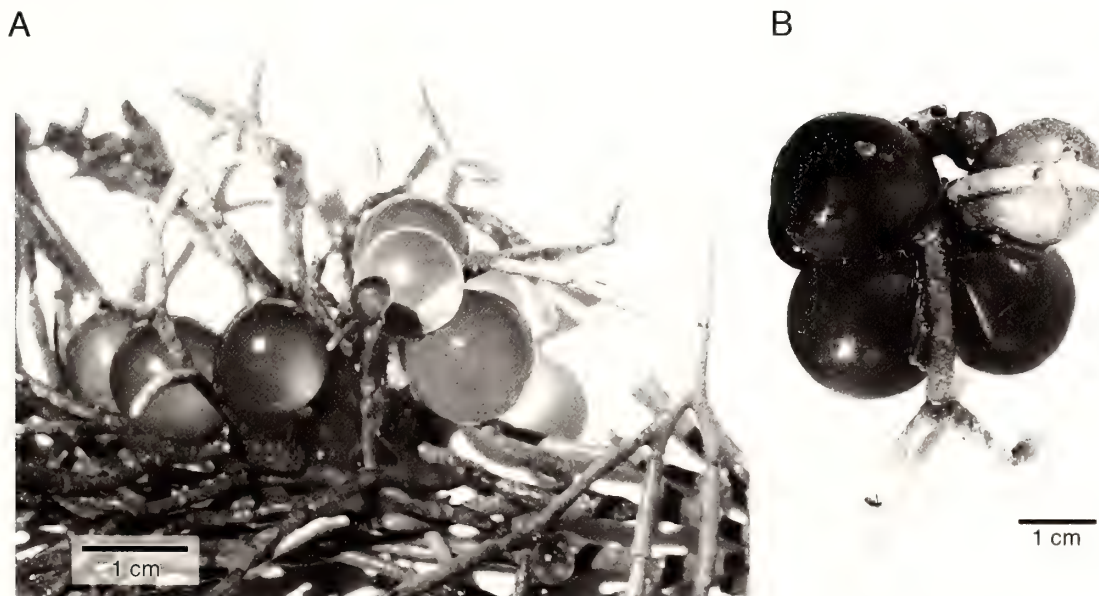


FIGURE 39. *Halicystis*-phase: A, B. Gametophytes: Globose, coenocytic thalli (JN-5732); epiphytic on the articulated coralline *Amphiroa*.

nonseptate, multinucleate filaments (siphons). Branching of the filaments (siphons) is mostly sympodial, with the outer branched filaments forming a cortical layer of utricles at the surface. Cells contain numerous small nuclei and discoid chloroplasts (without pyrenoids), and no amyloplasts, with cell walls containing mostly mannan. Accessory pigments include siphonoxanthin and siphonoin.

Asexual reproduction is by fragmentation or by parthenogenesis in some. Sexual reproduction is by biflagellate anisogametes. Gametangia are developed laterally on the utricles and cut off by a basal septum.

The family consists of five genera, with the species-rich genus *Codium* represented in the northern Gulf of California.

Codium Stackhouse

Codium Stackhouse, 1797:xvi, xxiv.

Algae are spongy, non-calcareous macrothalli of definite shapes, with species that are either prostrate or repent globose or pulvinate forms, or erect branching cylindrical, compressed, or complanate forms. Internally, the thalli are composed of branched filaments that are organized into a medulla of longitudinal, densely intertwined, colorless coenocytic filaments (medullary siphons) and an outer surface layer of inflated, cylindrical or clavate, photosynthetic utricles with an apical wall that is usually thickened and often ornamented in a characteristic pattern. Utricles are developed primarily by the enlargement of sympodial branches of medullary siphons and secondarily by budding or by production of additional utricle-forming medullary siphons from basal portion of existing utricles. Rhizoidal filaments (siphons), which grow into the medulla, are also produced from basal portion of the utricles. Colorless hairs are produced along the sides of the utricles, with a basal plug which remains as a prominent scar after the hair falls off.

Asexual reproduction is by parthenogenesis, fragmentation, or the cutting off of modified aborted gametangia. Species may be monoecious or dioecious. Gametangia are cylindrical or fusiform to ovate above a short pedicel with a basal plug and are borne laterally on the utricles. Biflagellate anisogametes are extruded in gelatinous masses upon rupture of the apices of the gametangia. Male gametes are very small, with one or two chloroplasts, and female gametes are much larger and have numerous chloroplasts. Life histories are not fully known. The zygote develops into an amorphous, prostrate vesicle that produces erect elongate vesicles; these, in turn, initiate primary utricle-producing siphons that eventually consolidate into a multiaxial thallus. Some species are known to have a filamentous derbesioid or vaucherioid (*Vaucheria*-like) stage in their life history (Fletcher et al., 1989; Yang et al., 1997).

REMARKS. *Codium* is a widespread genus with species occurring from the intertidal down to at least 70 m depths (Norris and Olsen, 1991). Although species are found in almost every sea (except the Arctic and Southern Ocean), the largest number of species of *Codium* are in subtropical to temperate regions.

Several species that were originally described from the Gulf of California (Setchell and Gardner, 1924a; Dawson, 1944) have been placed in synonymy with other species on the basis of comparative morphological studies (Pedroche et al., 2002). These species concepts need to be tested by molecular phylogenetic and morphological analyses. One species, *Codium picturatum* Pedroche et P. C. Silva (1996), described from Colima (Pacific Mexico), has also been reported from the southern Gulf, and includes records of "*C. setchellii*" (Pedroche et al., 2002, 2005; Riosmena-Rodríguez et al., 2005) (note "*C. setchellii*" of Dawson [1949] and Brusca and Thomson [1975] may also belong here).

Currently, there are three species known in the northern Gulf of California. Two of these are also known from the Pacific coast of Mexico, and one, *C. brandegeei*, is apparently a Gulf-endemic species.

KEY TO THE SPECIES OF *CODIUM* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli usually very long, up to 85 cm tall; axes and branches mostly cylindrical, branches often flattened at dichotomies; very large utricles, most greater than 900 μm in length *C. amplivesiculatum*
- 1b. Thalli shorter in overall length; axes and branches variable, of three forms: cylindrical throughout or cylindrical but compressed at the dichotomies or compressed but with cylindrical ultimate branches; utricles less than 900 μm (mostly 550–850 μm long) 2
- 2a. Utricles claviform, constricted below; utricle apices conical, hyaline, and very thick (up to 85 μm thick) *C. brandegeei*
- 2b. Utricles mostly cylindrical (if constricted, only slightly); utricle apices truncate or rounded (not conical), hyaline, and thinner (up to 46 μm thick) *C. simulans*

***Codium amplivesiculatum*
Setchell et N. L. Gardner**

FIGURES 40, 41A,B

- Codium amplivesiculatum* Setchell et N. L. Gardner, 1924a:709, pl. 15: figs. 28, 29, pl. 35; Dawson, 1944:217; Dawson, 1959a:7, 16; Dawson, 1961b:381; Norris, 1973:4, 17; Norris, 1985:208; Espinoza-Ávalos, 1993:333; González-González et al., 1996:132; Pacheco-Ruiz and Zertuche-González, 1996a:432; Núñez-López et al., 1998:39; Pedroche et al., 2002:40, figs. 42–53; R. Aguilar-Rosas et al., 2005b:36; Pedroche et al., 2005:69; Servière-Zaragoza et al., 2007:7; Pacheco-Ruiz et al., 2008:202; Riosmena-Rodríguez and Holguín-Acosta, 2008:1, figs. 1–12.
- Codium decorticatum* sensu Howe, 1911:494; Setchell and Gardner, 1930:130; Taylor, 1939:9; Huerta-M., 1978:339; Mateo-Cid and Mendoza-González, 1992:25 [in part; see Pedroche et al., 2005:72]; Mateo-Cid et al., 1993:52 [with a query]; González-González et al., 1996:369 [Gulf specimens only]; Silva et al., 1996b:235 [non *Codium decorticatum* (Woodward) M. Howe, 1911:494].
- Codium dichotomum* sensu Taylor, 1945:68; Dawson, 1949:229 [in part; see Pedroche et al., 2002:40] [non *Codium dichotomum* (Hudson) S. F. Gray, 1821:293].
- Codium fernandezianum* sensu Taylor, 1945:71 [in part; see Pedroche et al., 2002:40] [non *Codium fernandezianum* Setchell, 1937a:592].
- Codium longiramosum* Setchell et N. L. Gardner, 1924a:710, pl. 15: fig. 27, pl. 37; Taylor, 1945:70 [in part]; Dawson, 1961b:382; Dawson, 1966b:55; Stewart and Stewart, 1984:140; González-González et al., 1996:134.
- Codium magnum* E. Y. Dawson, 1950f:298, fig. 1; Dawson, 1961b:382; Dawson, 1962c:278, 280; Huerta-Múzquiz, 1978:336; Huerta-Múzquiz and Mendoza-González, 1985:44; Ibarra-Obando and R. Aguilar-Rosas, 1985:96; Mendoza-González and Mateo-Cid, 1985:22; Sánchez-Rodríguez et al., 1989:36, 38–39; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Mateo-Cid and Mendoza-González, 1994a:52; González-González et al., 1996:134; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Riosmena-Rodríguez et al., 2005:101.

Algae erect, mostly cylindrical, up to 85 cm tall (largest to 10 m in length; Pedroche et al., 2002); simple or branched dichotomously to subdichotomously (or

sometimes trichotomously); branches usually flattened at dichotomies; attached below by a spongy mass of rhizoidal filaments. Lower branches (6–)13–20 mm in diameter, often with long interdichotomies, up to 40 cm in length; dichotomies flattened, up to 10 cm wide. Upward branches gradually narrowing to apices, (1–)3–10 mm in diameter. Medullary filaments, 25–110 μ m in diameter, with lateral cell wall thickenings ('cellulose plugs'). Utricles cylindrical to clavate, (840–)1180–1930(–3025) μ m in length, and (140–)230–410(–655) μ m in diameter in upper portions, and near the base (40–)110–235(–385) μ m in diameter; utricle apices truncate or rounded, 4.5–8.0 μ m thick; utricle wall sides 1.5–2.3 μ m thick; hairs and scars present, never abundant, about 220 μ m below the apices.

Gametangia elongated, fusiform to ovate, wider at their base, (160–)255–340(–430) μ m long by (46–)90–140(–170) μ m in diameter; borne about (370–)450–600(–750) μ m below the utricle apex on short pedicel, up to 15 μ m long.

HABITAT. Attached or free-floating in esteros or lagoons; on rocks; low intertidal to shallow subtidal, usually 0.5 to 17 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Punta Arena (north of Cabo Pulmo). Pacific coast: Bahía de San Quintín to Bahía Magdalena; Isla Cedros; Isla Guadalupe; Isla Clarión and Isla Socorro (Islas Revillegigdo); Nayarit to Jalisco.

TYPE LOCALITY. Drift, most likely Isla Estanque (also known as Pond Island and Isla La Bibera); however, Setchell and Gardner (1924a:709) only stated "near south end of [Isla] Ángel de la Guarda, Gulf of California."

REMARKS. *Codium amplivesiculatum* is the largest species of *Codium*, and may be the largest green alga in the Gulf of California. Two other species, the Gulf of California *C. longiramosa* Setchell et N. L. Gardner (1924a) and the Pacific Baja California *C. magnum* E. Y. Dawson (1950f), were recently treated as synonyms of *C. amplivesiculatum* by Pedroche et al. (2002). Hommersand (1972) and Pedroche et al. (2005:70) noted that the problematic separation of the Gulf *C. amplivesiculatum* and the Japanese *C. cylindricum* Holmes (1896; Yoshida, 1998) and their phylogenetic relationship needs to be clarified.

***Codium brandegeei* Setchell et N. L. Gardner**

FIGURES 41C–F, 42

Codium brandegeei Setchell et N. L. Gardner, 1924a:712, pl. 14: figs. 25, 26, pl. 30; Dawson, 1944:215;



FIGURE 40. *Codium amplivesiculatum*: Habit of a large specimen (JN-5700).

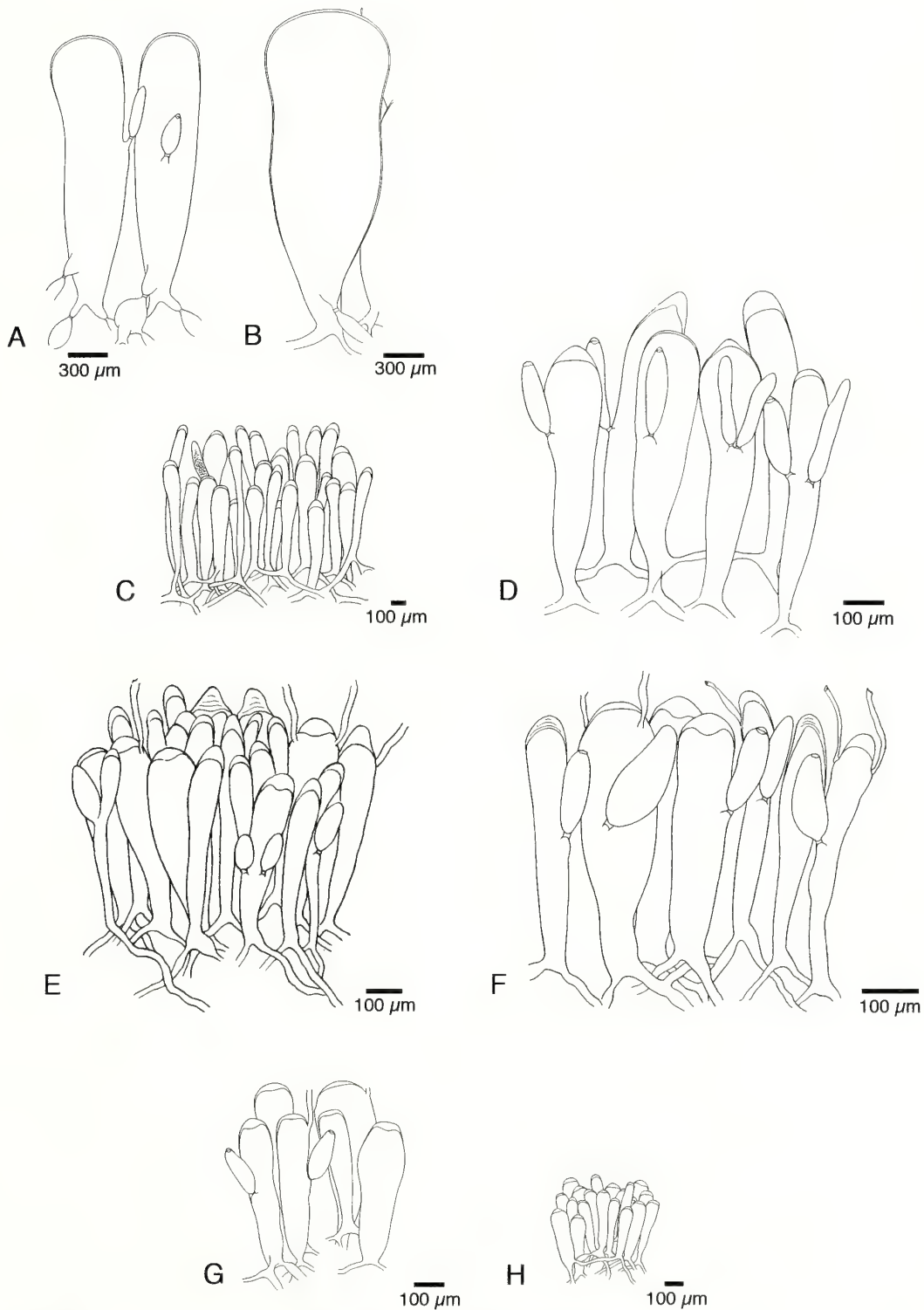


FIGURE 41. Species of *Codium*: Detail of utricles, some with gametangia and/or hairs, showing variation in shape and size. A, B. *Codium amplivesiculatum*: Large, wide utricles; (drawn from the type specimen, I. M. Johnston-74, after Setchell and Gardner, 1924a: pl. 15, figs. 28, 29). C–F. *Codium brandegeei*: Variation in utricles size: C, D. Utricles drawn from the type of the synonym *C. cervicorne* (Marchant-8, after Setchell and Gardner, 1924a: pl. 14, figs. 19, 20). E, F. Utricles of *C. brandegeei* (drawn from the type specimen, T. S. Brandegeee-28, after Setchell and Gardner, 1924a: pl. 14, figs. 25, 26). G, H. *Codium simulans*: Variation in utricles (drawn from the type specimen, I. M. Johnston-8, after Setchell and Gardner, 1924a: pl. 14, figs. 21, 22).

González-González et al., 1996:132; Pedroche et al., 2002:54–55, figs. 19, 66–80; Pedroche et al., 2005:70; Mateo-Cid et al., 2006:49, 59; Pacheco-Ruiz et al., 2008:202.

Codium anastomosans Setchell et N. L. Gardner, 1924a:711, pl. 16: figs. 36, 37; Dawson, 1944:218; Dawson, 1961b:381; Martínez-Lozano et al., 1991:22; Espinoza-Ávalos, 1993:333; González-González et al., 1996:132.

Codium cervicorne Setchell et N. L. Gardner, 1924a:712, pl. 14: figs. 19, 20, pl. 32b; Dawson, 1961b:381; Martínez-Lozano et al., 1991:22; González-González et al., 1996:132.

Codium cuneatum sensu Dawson, 1944:218 [non *Codium cuneatum* Setchell et N. L. Gardner, 1924a:708].

Codium macdougalii E. Y. Dawson, 1944:218, pl. 35: fig. 1; Dawson, 1961b:382; Dawson, 1966a:7; Dawson, 1966b:55; Norris, 1973:4, 17, 19; Espinoza-Ávalos, 1993:333; González-González et al., 1996:134; L. Aguilar-Rosas et al., 2000:133.

Codium reductum Setchell et N. L. Gardner, 1924a:707, pl. 14: figs. 23, 24, pl. 33; González-González et al., 1996:134.

Codium simulans sensu Dawson, 1944:216; Dawson, 1945a:22 [non *Codium simulans* Setchell et N. L. Gardner, 1924a:706].

Codium tomentosum sensu Mendoza-González and Mateo-Cid, 1986:420 [non *Codium tomentosum* Stackhouse, 1797:xxiv].

Algae erect, more or less cylindrical throughout, up to 15 cm tall; branching irregularly dichotomous; attached by discoid base of rhizoidal filaments. Branches cylindrical; in lower portions sometimes narrow and constricted at dichotomies; in midportions broadening; and in terminal portions sometimes swollen to club-shaped, up to 1.6 cm in diameter. Medulla filaments 23–45(–50) μm in diameter. Utricles slender, cylindrical to clavate, constricted below, giving upper portion spoon-shaped appearance, (460–)540–820(–1150) μm long by (70–)95–200(–290) μm in diameter, and in basal portion (30–)40–70(–112) μm in diameter; sometimes with secondary utricles; utricle apices blunt to dome shaped, outer end with hyaline, laminated, conical cell wall, (30–)50–85 μm thick; hairs and scars present.

Gametangia fusiform or cylindrical, (130–)200–270(–330) μm long by (40–)60–90(–125) μm in diameter; usually one per utricle, borne about (230–)280–390(–500) μm below the apices.

HABITAT. On rocks and tidal platforms, often exposed; mid intertidal to shallow subtidal, down to 10 m depths.

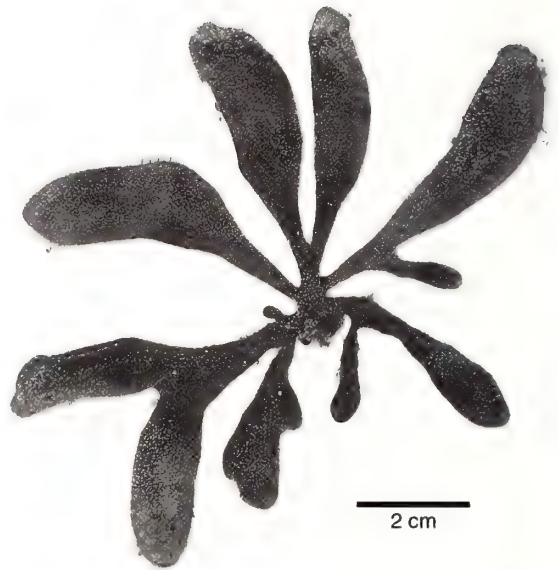


FIGURE 42. *Codium brandegeei*: Habit of “*C. macdougalii*-form” with swollen, club-shaped branches (JN-5020).

DISTRIBUTION. Gulf of California: Punta Pelicano (vicinity of Puerto Peñasco) to Guaymas; Bahía Concepción to Bahía de La Paz.

TYPE LOCALITY. “Probably at La Paz,” Baja California Sur, Gulf of California (Setchell and Gardner, 1924a).

REMARKS. *Codium brandegeei* is apparently endemic to the Gulf of California, as the Pacific Mexico reports of “*C. brandegeei*” from Nayarit and Jalisco (Servière-Zaragoza et al., 1993, as “*C. cervicorne*”) and Guerrero (Salcedo-Martínez et al., 1988, as “*C. cervicorne*”) were noted to be *C. isabellae* W. R. Taylor (1945) by Pedroche et al. (2005:71).

Although the Gulf *C. macdougalii* is now considered to be conspecific with *C. brandegeei* (Pedroche et al., 2002), in the field the “*C. macdougalii*-morph” can be distinguished from the other Gulf species of *Codium* by the broad, swollen, club-shaped upper portions of its branches (Figure 42).

***Codium simulans* Setchell et N. L. Gardner**

FIGURES 5B, 41G,H, 43

Codium simulans Setchell et N. L. Gardner, 1924a:706, pl. 14: figs. 21, 22, pl. 31; Setchell and Gardner, 1930:133; Dawson, 1944:216; Dawson, 1949:233–234, 237, 242; Dawson, 1959a:18; Dawson, 1961b:382; Norris,

- 1973:4, 17, 19; Brusca and Thomson, 1975:42; Huerta-Múzquiz, 1978:338; Littler and Littler, 1981:151, 153; Stewart and Stewart, 1984:140; Littler and Littler, 1984:15, 23, 25; Norris, 1985:209, fig. 16.2; Salcedo-Martínez et al., 1988:82; Rocha-Ramírez and Siqueiros-Beltrones, 1991:30; Martínez-Lozano et al., 1991:22; González-González et al., 1996:135; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Pacheco-Ruíz and Zertuche-González, 1996a:432; L. Aguilar-Rosas et al., 2000:133; Pedroche et al., 2002:61, figs. 65, 81–89; R. Aguilar-Rosas et al., 2005b:36; Pedroche et al., 2005:77; Hernández-Herrera et al., 2005:146; Riosmena-Rodríguez et al., 2005:101; Mateo-Cid et al., 2006:49, 59; Servièrre-Zaragoza et al., 2007:7; Pacheco-Ruíz et al., 2008:191, 202.
- Codium anastomosans* sensu Martínez-Lozano et al., 1991:22 [non *Codium anastomosans* Setchell et N. L. Gardner, 1924a:711; which is now *C. brandegeei* Setchell et N. L. Gardner, 1924a:712 (see Pedroche et al., 2005:780)].
- Codium cervicorne* sensu Martínez-Lozano et al., 1991:22; Servièrre-Zaragoza et al., 1998:168 [non *Codium cervicorne* Setchell et N. L. Gardner, 1924a:712 (see Pedroche et al., 2005:780)].
- Codium conjunctum* Setchell et N. L. Gardner, 1924a:706, pl. 15: figs. 32, 33, pl. 32a; Dawson, 1949:236, 238; Dawson, 1944:217; Sánchez-Vargas and Hendrickx, 1987:161; Salcedo-Martínez et al., 1988:82; González-González et al., 1996:132.
- Codium cuneatum* Setchell et N. L. Gardner, 1924a:708, pl. 16: figs. 34–35, pl. 34; Setchell and Gardner, 1930:133; Dawson, 1944:218; Dawson, 1945a:22; Dawson, 1949:227; Silva, 1951:99, pls. 3–6, figs. 23–32; Dawson et al., 1960a:10, 26, pl. 5: fig. 2; Dawson et al., 1960b:6–14; Dawson, 1961b:382; Dawson, 1966a:7; Dawson and Neushul, 1966:174; Chávez B., 1972:268; Guzmán del Prío et al., 1972:260; Norris, 1973:4, 18; Abbott and Hollenberg, 1976:116, fig. 76; Lewbel et al., 1981:165; L. Aguilar-Rosas and Bertsch, 1983:116, 122; Stewart and Stewart, 1984:140; Mendoza-González and Mateo-Cid, 1985:22; Huerta-Múzquiz and Mendoza-González, 1985:44; Mendoza-González and Mateo-Cid, 1986:420; Sánchez-Rodríguez et al., 1989:38, 39; R. Aguilar-Rosas et al., 1990:123; Mateo-Cid and Mendoza-González, 1991:27–28; Rocha-Ramírez and Siqueiros-Beltrones, 1991:18, 30; Martínez-Lozano et al., 1991:22; Mendoza-González and Mateo-Cid, 1992:24, 25; Mateo-Cid and Mendoza-González, 1992:25; Mateo-Cid et al., 1993:52; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:52; Mateo-Cid and Mendoza-González, 1994b:34; Mendoza-González et al., 1994:113; González-González et al., 1996:132; Pacheco-Ruíz and Zertuche-González, 1996a:432; Núñez-López et al., 1998:39; Cruz-Ayala et al., 1998:194; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Sánchez-Rodríguez et al., 2001:148; Pacheco-Ruíz et al., 2008:191.
- Codium dichotomum* sensu Taylor, 1945:68 [in part; see Pedroche et al., 2002:78] [non *Codium dichotomum* (Hudson) S. F. Gray, 1821:293].
- Codium latum* subsp. *palmeri* sensu Pedroche et al., 2002:34, figs. 33, 34, 37 [non *Codium latum* subsp. *palmeri* (E. Y. Dawson) P. C. Silva, 1962:208; basionym: *Codium palmeri* E. Y. Dawson, 1945a:23 (see Pedroche et al., 2005:76, 77)].
- Codium tomentosum* sensu Howe, 1911:493 [non *Codium tomentosum* (Hudson) Stackhouse, 1797:xxvii].
- Codium unilaterale* Setchell et N. L. Gardner, 1924a:710, pl. 15: figs. 30–31, pl. 36; Martínez-Lozano et al., 1991:22; González-González et al., 1996:135.
- Algae erect, up to 35 cm tall; branching dichotomous to subdichotomous; branches 4–15 mm in diameter and variable in shape, either cylindrical throughout; cylindrical, and only slightly flattened to cuneate at branch dichotomies (2.0–25 mm broad); or compressed, with only stipe and branch tips cylindrical; and attached by a disc of rhizoidal filaments. Medullary filaments 19–77 µm in diameter. Utricles cylindrical, subcylindrical to slightly claviform, (330–)450–800(–1300) µm long by (70–)200–250(–440) µm in diameter in upper portions and (30–)40–120(–385) µm in diameter near the base; apices of utricle smooth, mostly rounded, with hyaline, apical cell wall, 20–46 µm thick. Hairs or scars present, single to numerous, about 120 µm below the thickened distal end of the utricle.
- Gametangia, 1 or 2 per utricle, mostly subfusiform to fusiform, (130–)180–290(–330) µm long by (50–)60–110(–162) µm in diameter and usually narrowed at the base; borne on a short pedicel (up to 10 µm in length), (90–)230–350(–670) µm below utricle tip.
- HABITAT.** On rocks and tidal platforms, usually exposed; mid intertidal to shallow subtidal, down to 20 m depths.
- DISTRIBUTION.** Gulf of California: Puerto Peñasco to Cabeza Ballena. Pacific coast: Santa Cruz Island (California Channel Islands) to Guerrero; Isla Guadalupe; Isla Clarión (Islas Revillagigedo).
- TYPE LOCALITY.** Isla San Marcos, off the Baja California Sur coast between Caleta de San Lucas and Punta Chivato (separated by Canal de San Marcos [Craig Channel]), Gulf of California.

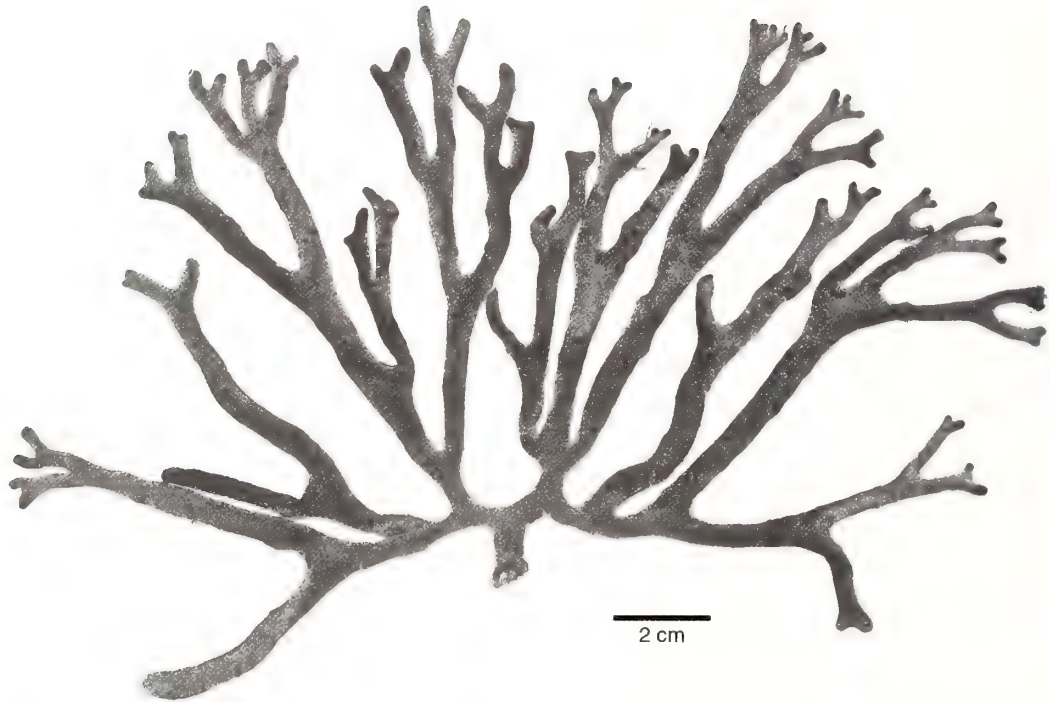


FIGURE 43. *Codium simulans*: Habit, with terete to slightly compressed axis and branches, flattened at dichotomies (JN-5713).

REMARKS. The most common species of *Codium* in the northern Gulf, *C. simulans* is found from February to September. Silva (1951:101, as "*C. cuneatum*") noted it "to be a unique species whose young stages are more or less rept, intricate, and basally anastomosing, but whose adult thalli are erect and openly branched... [and] degree and incidence of flattening are variable." As currently understood (Pedroche et al., 2002), *C. simulans* comprises a wide variety of different morphologies (many of which were previously separate species) that may be cylindrical throughout or mostly cylindrical but compressed at the dichotomies or mostly compressed with only the stipe and ultimate branches cylindrical.

Subtidal specimens of *Codium* sp. A (Figure 44; JN-5286) from Puerto Refugio (Isla Ángel de la Guarda) are somewhat similar to "*C. cuneatum*-form" of *C. simulans* but are much larger, wider and flattened throughout. While they are tentatively referred to this species, they should be further studied to see if they represent a new taxon.

Uncertain Record:
***Codium fragile* (Suringar) Hariot**

Acanthocodium fragile Suringar, 1868:258.
Codium fragile (Suringar) Hariot, 1889:32.

REMARKS. Although *Codium fragile* is widely reported on the Pacific coast from Alaska to Baja California (e.g., Abbott and Hollenberg, 1976; González-González et al., 1996; Scagel et al., 1989; Pedroche et al., 2005), its reported presence in the northern Gulf (Martínez-Lozano et al., 1991) needs to be verified.

HALIMEDINEAE

Halimedineae Hillis-Colvinaux, 1984:287.

The suborder Halimedineae is characterized by heteroplasty, presence of a concentric lamellar system, and cell walls that are composed primarily of xylan, with cellulose absent (or only barely present). Allelochemicals (secondary natural products) are usually present. Reproduction is mostly holocarpic (i.e., entire cytoplasm of the coenocytic thallus is transformed into gametes). Reproductive structures are usually without septa.

REMARKS. Species of the suborder Halimedineae are mostly tropical to subtropical, with a few temperate, in distribution. Many members are known to produce unique natural products, diterpenoid metabolites (Paul and Fenical, 1985, 1986).



FIGURE 44. *Codium* sp. A: Specimen somewhat similar to “*Codium cuneatum*-form” of *C. simulans*: Flat, with exceptionally broad axes, possibly a new species (JN-5286).

One of its families, the Udoteaceae J. Agardh (1887), is represented in the southern Gulf by two species *Chlorodesmis hildebrandtii* A. et E. S. Gepp (1911; see Dawson, 1959a, 1961b; González-González et al., 1996; Mateo-Cid et al., 2000a) and *Geppella decussata* E. Y. Dawson (1959a) described from Isla San Francisco (off south end of Isla San José, Baja California Sur). There is a problem with the generic placement of *G. decussata*, as the generic type of *Geppella* Børgesen (1940), *G. mortensenii* Børgesen, is now conspecific with *Rhipiliopsis mortensenii* (Børgesen) Fraghaly et Denizot (1979). Therefore, the generic status of the Gulf *G.?* *decussata* is uncertain (see also Tanaka and Itono, 1977; Dong and Tseng, 1983) and in need of reinvestigation.

Two families of the suborder Halimedineae, the Caulerpaeae and Halimedaceae, are represented in the northern as well as the southern Gulf of California.

CAULERPACEAE

Caulerpaeae Kützing, 1843:302, 307.

Algae are differentiated into distinct erect portions and prostrate, creeping stolon-like runners, that issue rhizoids that attach it to sand or hard substratum. The erect portions exhibit a great variety of forms and sizes, from tubular to foliose, and can be simple to much branched. The vegetative portions of these algae are coenocytic, multinucleate, and with two types of plastids, chloroplasts and amyloplasts. Structurally, there is an internal web or network of trabeculae that originate from the interior walls of the thallus and are unique to this family.

Asexual reproduction is by fragmentation and also by vegetative propagation of the stolons. Zooidangia are apparently known only in the non-holocarpic *Caulerpella*. Its reproductive structures are in external stalked-whorls, developed from the basal portion of a fertile branch that is separated from the lateral branch by a septum (crosswall). Spores are released via a discharge tube at apex of fertile branch. Sexual reproduction has been reported in a few species of holocarpic *Caulerpa* (e.g., Clifton and Clifton, 1999). The species of *Caulerpa* thus far studied are diploid, forming biflagellate anisogametes within the contents of the branches by the separation of the cytoplasm without development of septa (crosswalls). Anisogametes are released through superficial papillae.

REMARKS. The Caulerpaeae is composed of two genera. *Caulerpa* is found in tropical to subtropical seas worldwide and in temperate waters of the Southern Hemisphere, and *Caulerpella* Prud'homme van Reine et Lokhorst (1992) is found in tropical and subtropical seas.

One genus, *Caulerpa*, is known in the Gulf of California.

Caulerpa J. V. Lamouroux

Caulerpa J. V. Lamouroux, 1809d:332.

Algae included in *Caulerpa* are easily recognized by their differentiated fronds: erect upper branches of diverse morphologies that arise from prostrate, creeping stolons (rhizome-like runners), which are attached to the substratum at various points by groups of colorless rhizoids. The erect axes and branches are cylindrical to blade-like and simple or pinnately, radially, or bilaterally branched; their shape and pattern are species specific and may be elaborate and variable. The thallus is coenocytic throughout, i.e., multinucleate, with numerous chloroplasts and amyloplasts (specialized for starch accumulation), a cell wall principally of xylan, and an elaborate internal network of trabeculae (slender internal strands of cell wall material) that traverses the cytoplasm throughout the thallus, presumably structurally bracing the cell wall. Growth is apical and indeterminate.

Asexual reproduction is by fragmentation. Sexual reproduction, where known, is holocarpic (i.e., the entire cytoplasm is transformed into gametes), and the thallus remains unmodified, and no crosswalls are formed. Both dioecious and monoecious species are reported, with anisogametes extruded in gelatinous strands through papillae on the siphon wall.

REMARKS. Members of *Caulerpa* grow from the intertidal down to depths of at least 81 m (Littler et al., 1985, 1986; Norris and Olsen 1991). Exhibiting extreme morphological plasticity, their habit is influenced by both biotic and physical factors of their environment, e.g., light and water motion, which has resulted in numerous described subspecies, varieties, forms, or ecads. When wounded or grazed by herbivorous fish or invertebrates (e.g., sacoglossan molluscs) the thallus responds by extruding a yellowish gelatinous mass that hardens in a few minutes to form a wound plug (Dreher et al., 1978; Dawes and Goddard, 1978; Menzel, 1980, 1988). Several species produce secondary metabolites, caulerpin (Santos and Doty, 1968; Maiti et al., 1978) and caulerpicin (Doty and Aguilar-Santos, 1966; Mahendran et al., 1979; Nielsen et al., 1982; Vest et al., 1983) or caulerpenyne (Amico et al., 1978; Faulkner, 1984; Amade and Lemée, 1998), that serve as a chemical defense, making them unpalatable or even toxic to certain herbivores (e.g., Norris and Fenical, 1982; Paul and Fenical, 1986, 1987). Some species of sacoglossan mollusks, specialist herbivores, ingest,

transfer and store the natural products, along with the chloroplasts, of *Caulerpa*, in their tissues (e.g., Doty and Aguilar-Santos, 1970; Trench, 1973).

Three species and one variety are reported in the southern Gulf: *C. antoensis* Yamada (1940; = *C. arenicola* W. R. Taylor, 1950) by Huerta-Múzquiz and Mendoza-González (1985) and Rocha-Ramírez and Siqueiros-Beltrones (1991); *C. peltata* J. V. Lamouroux (1809c) by Dawson (1959a), Huerta-Múzquiz and Mendoza-González (1985), Rocha-Ramírez and Siqueiros-Beltrones (1991), and Mateo-Cid et al. (2000a); and *C. racemosa* (Forsskål) J. Agardh (1873) by Dawson (1944), Huerta-Múzquiz (1978),

Mendoza-González and Mateo-Cid (1986), Anaya-Reyna and Riosmena-Rodríguez (1996), Rodríguez-Morales and Siqueiros-Beltrones (1999, as "*C. racemosa* var. *uvifera*"), Paul-Chávez and Riosmena-Rodríguez (2000), and Riosmena-Rodríguez et al. (2005); and *C. racemosa* var. *turbinata* (J. Agardh) Eubank (1946) by Dawson (1944, as "*C. racemosa* var. *chemnitzia*"), Dawson (1949, 1959a), Huerta-Múzquiz and Mendoza-González (1985, as "*C. racemosa* var. *chemnitzia*"), Rocha-Ramírez and Siqueiros-Beltrones (1991), and Mateo-Cid et al. (2000a).

Three species are present in the northern Gulf of California.

KEY TO THE SPECIES OF *CAULERPA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Axes and branches flattened throughout, with primary branches and numerous pinnate (oppositely branched) branchlets. *C. mexicana* f. *pectinata*
- 1b. Axes, primary branches and branchlets cylindrical throughout 2
- 2a. Cylindrical erect axes with oppositely branched branchlets (featherlike appearance); branchlet apices acute, with pointed tip *C. sertularioides*
- 2b. Cylindrical erect axes simple and unbranched or sparsely and irregularly branched; 500–1000 µm in diameter; apices rounded or more or less clavate *C. vanbosseae*

Caulerpa mexicana f. *pectinata* (Kützinger) W. R. Taylor

FIGURE 45

Caulerpa pectinata Kützinger, 1849:495.

Caulerpa mexicana Sonder ex Kützinger f. *pectinata* (Kützinger) W. R. Taylor, 1960:141; Apartado et al., 2002:99, figs. 2, 5; Pedroche et al., 2005:64.

Caulerpa pinnata C. Agardh f. *pectinata* (Kützinger) Weber-van Bosse, 1898:291, pl. 24: fig. 3; Dawson, 1944:213; Dawson, 1961b:380; Dawson, 1966a:7; Dawson, 1966b:55, fig. 1A; González-González et al., 1996:127; Mateo-Cid et al., 2006:48; Pacheco-Ruíz et al., 2008:202.

Caulerpa crassifolia (C. Agardh) J. Agardh f. *pectinata* (Kützinger) Collins, 1909b:414.

Algae erect, with flat, fronds of pinnate branches, up to 5 cm tall, arising from a short stalk above the spreading stolon; attached below by rhizoids issued from stolons. Fronds simple or forked; branches lanceolate to oblong in shape, 2–5 cm long and narrow, up to 5 mm wide; composed of a flattened main axes and closely set, opposite flat short branchlets in one plane; branchlets not contracted at base, not closely adjacent, and curved slightly upward with acuminate tips.

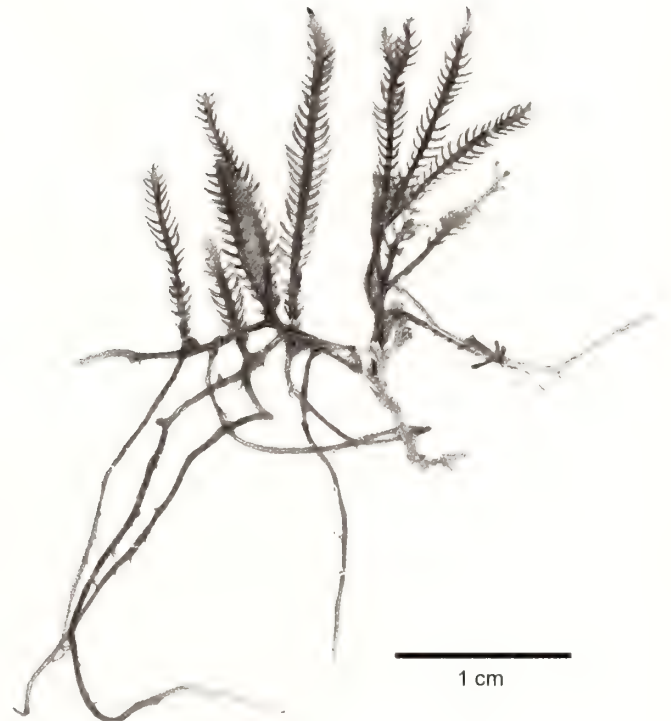


FIGURE 45. *Caulerpa mexicana* f. *pectinata*: Habit, narrow pinnate fronds; axes and branchlets are flattened (JN-5861).

HABITAT. On sand covered rock, tidal platforms and in tide pools; often under larger algae such as *Sargassum*; mid intertidal to shallow subtidal (also dredged in 12–22 m depths; Dawson, 1944).

DISTRIBUTION. Gulf of California: Puerto Peñasco; Puerto Refugio, in shallows of channel between Isla Mejía and Isla División (northwest end of Isla Ángel de la Guarda).

TYPE LOCALITY. La Guaira (La Guayra), seaport town for Caracas, Federal District, northern Venezuela.

REMARKS. Generally considered a tropical western Atlantic taxon (Taylor, 1960; Apartado et al., 2002), *Caulerpa mexicana* f. *pectinata* has also been reported in the northern Gulf by Dawson (1944, 1966a, 1966b, as "*C. pinnata* f. *pectinata*"). Gulf specimens need to be morphologically and molecularly compared with those of the western Atlantic, particularly with those from the type locality, to test their phylogenetic relationship.

***Caulerpa sertularioides* (S. G. Gmelin) M. Howe**

FIGURE 46A,B

Fucus sertularioides S. G. Gmelin, 1768:151, pl. 15: fig. 4.
Caulerpa sertularioides (S. G. Gmelin) M. Howe, 1905:576; Dawson, 1944:213; Taylor, 1945:63; Dawson, 1949:244–245; Dawson, 1959a:4, 6, 7, 14; Dawson, 1961b: 381; Huerta-Múzquiz and Tirado-Lizárraga, 1970:126; Huerta-Múzquiz and Tirado-Lizárraga, 1970:121–122, 127, 131, 134, 136; Chávez B., 1972:268; Earle, 1972:85; Huerta-Múzquiz, 1978:338, 340; Huerta-Múzquiz and Mendoza-González, 1985:44; Mendoza-González and Mateo-Cid, 1986:420; Ortega et al., 1987:80; Sánchez-Vargas and Hendrickx, 1987:161; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:39; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mateo-Cid and Mendoza-González, 1991:28; Martínez-Lozano et al., 1991:23; Mateo-Cid and Mendoza-González, 1992:25; León-Tejera and González-González, 1993:497; León-Tejera et al., 1993:199, 204; González-González, 1993:443; Mateo-Cid et al., 1993:52; Mendoza-González et al., 1994:113; González-González et al., 1996:277, 366–367; Anaya-Reyna and Riosmena-Rodríguez, 1996:862, 863; Galindo-Villegas et al., 1997:4; Mendoza-González and Mateo-Cid, 1998:25, 27–28; Yoshida, 1998:103; Cruz-Ayala et al., 1998:192; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Paul-Chávez and Riosmena-Rodríguez, 2000:146;

López et al., 2000:339; Mateo-Cid et al., 2000a:60, 70; Cruz-Ayala et al., 2001:190; Scrosati, 2001:722; Beltrán-Magallanes, 2002:44; Carballo et al., 2002:753; Abbott and Huisman, 2004:124, fig. 45B,C; Hodgson et al., 2004:32; López et al., 2004:10; Wysor, 2004:224; Riosmena-Rodríguez et al., 2005:101; Pedroche et al., 2005:67; Servière-Zaragoza et al., 2007:3, 7.

Algae with erect (feather-like) fronds, in the northern Gulf mostly less than 7.0 cm tall, arising from a short cylindrical stalk above the horizontal stolon, attached below by rhizoids. Fronds 2–7(–11) cm long and up to 1 cm wide, most simple and unbranched or occasionally branched; with a terete main axes bearing opposite cylindrical branchlets; branchlets not constricted at base, usually closely adjacent, and curved upward, with pointed tips.

HABITAT. In sandy habitats and in crevices and tide pools; attached to sand, on rocks or broken shells; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía San Carlos; Bahía Concepción to Punta Los Frailes; Mazatlán (Bahía de Altata to Estero del Urías), Sinaloa. Pacific coast: Bahía Magdalena, Baja California Sur; Islas Revilagigedo; Nayarit to Chiapas; Panama; Hawaiian Islands; China; Japan.

TYPE LOCALITY. “. . . *nonnisi* [only] in *coralliis americanis*” (Gmelin, 1768:151); “no definite locality is given” (Howe, 1905:576); “possibly tropical Atlantic America” (Hodgson et al., 2004:32).

REMARKS. Collections (US Alg. Coll.) from Bahía San Carlos (north of Guaymas, Sonora) establish *Caulerpa sertularioides* in the northern Gulf. Two forms of this species have been previously recorded in the southern Gulf *Caulerpa sertularioides* f. *brevipes* (J. Agardh) Svedelius (1906) has been reported in Laguna de Agiabampo, southern Sonora (Ortega et al. 1987), and *C. sertularioides* f. *longiseta* (Bory de Saint-Vincent) Svedelius (1906) from La Paz by Huerta-Múzquiz and Mendoza-González (1985) and Cruz-Ayala et al. (2001).

Ecological monitoring of *Caulerpa sertularioides* over 2 years in Bahía Balandra (vicinity of La Paz) by Scrosati (2001) showed a high population abundance during the relatively high temperatures of El Niño conditions and, in contrast, an absence during the relatively low temperatures of La Niña. Scrosati (2001) suggested that quantitative monitoring of Gulf of California seaweeds could be useful in predicting long-term effects of El Niño and La Niña on changes of marine algal distribution and abundance.

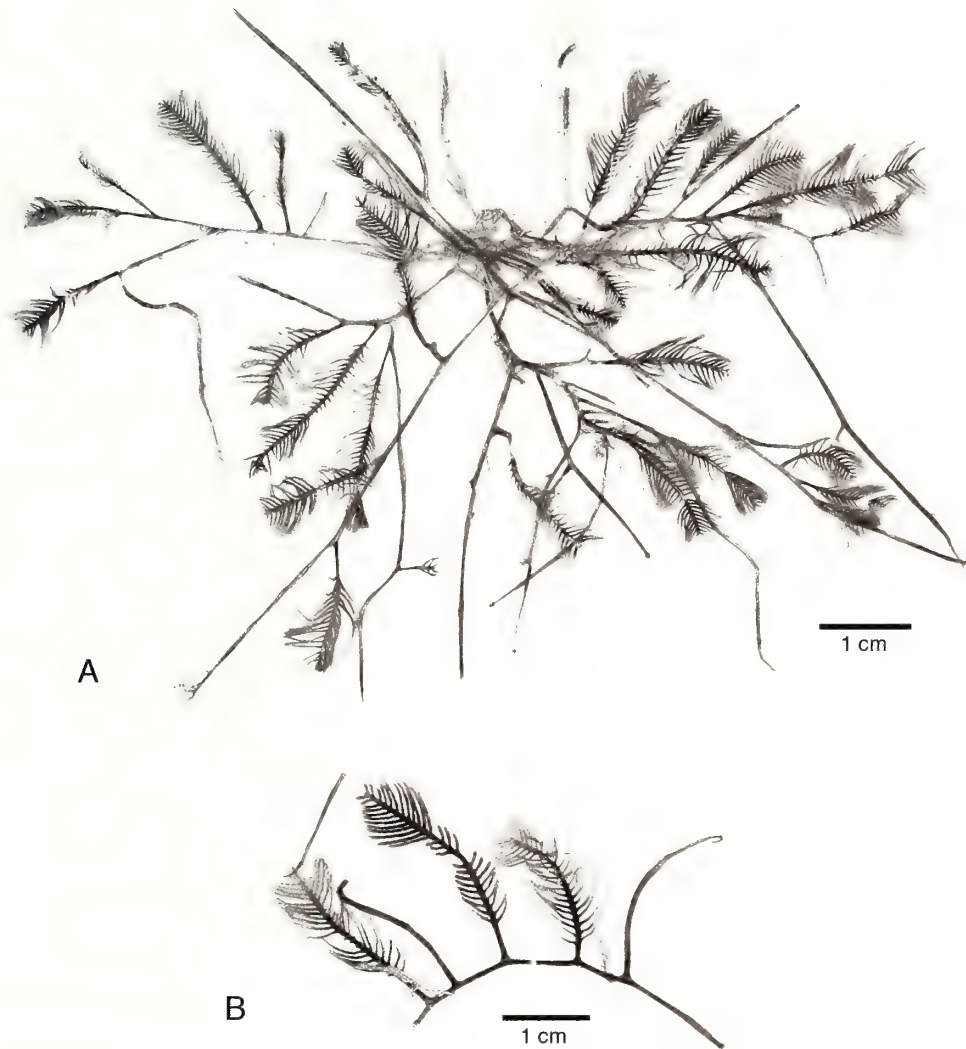


FIGURE 46. *Caulerpa sertularioides*: A. Habit (JN-4471). B. Prostrate stolons bearing erect axes with distichously arranged branchlets; both axes and branchlets are cylindrical (JN-4277).

***Caulerpa vanbosseae* Setchell et N. L. Gardner**

FIGURE 47A,B

Caulerpa vanbosseae Setchell et N. L. Gardner, 1924a:704, pl. 13: figs. 13–15; Dawson, 1944:212; Dawson, 1949:234; Dawson, 1959a:8–10, 14; Dawson et al., 1960b:13; Dawson, 1961b:381; Dawson, 1966a:7; Littler and Littler, 1984:15, 23; Sánchez-Rodríguez et al., 1989:38, 39; Mateo-Cid et al., 1993:52; González-González et al., 1996:127; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Cruz-Ayala et al., 2001:190; Pe-

droche et al., 2005:69; Mateo-Cid et al., 2006:48, 59; Pacheco-Ruíz et al., 2008:202.

Algae cylindrical throughout, erect portions simple and unbranched or irregularly branched (sometimes more or less alternately or oppositely branched); forming loosely entangled, sometimes spreading, clumps up to 6 cm tall; attached below by rhizoids issued from creeping stolons. Erect axes and branches, and horizontal stolons of more or less similar diameter, (400–)500–1000 μm in diameter. Terminal portions of axes and branches often more or less clavate or rounded. Reproduction not known.

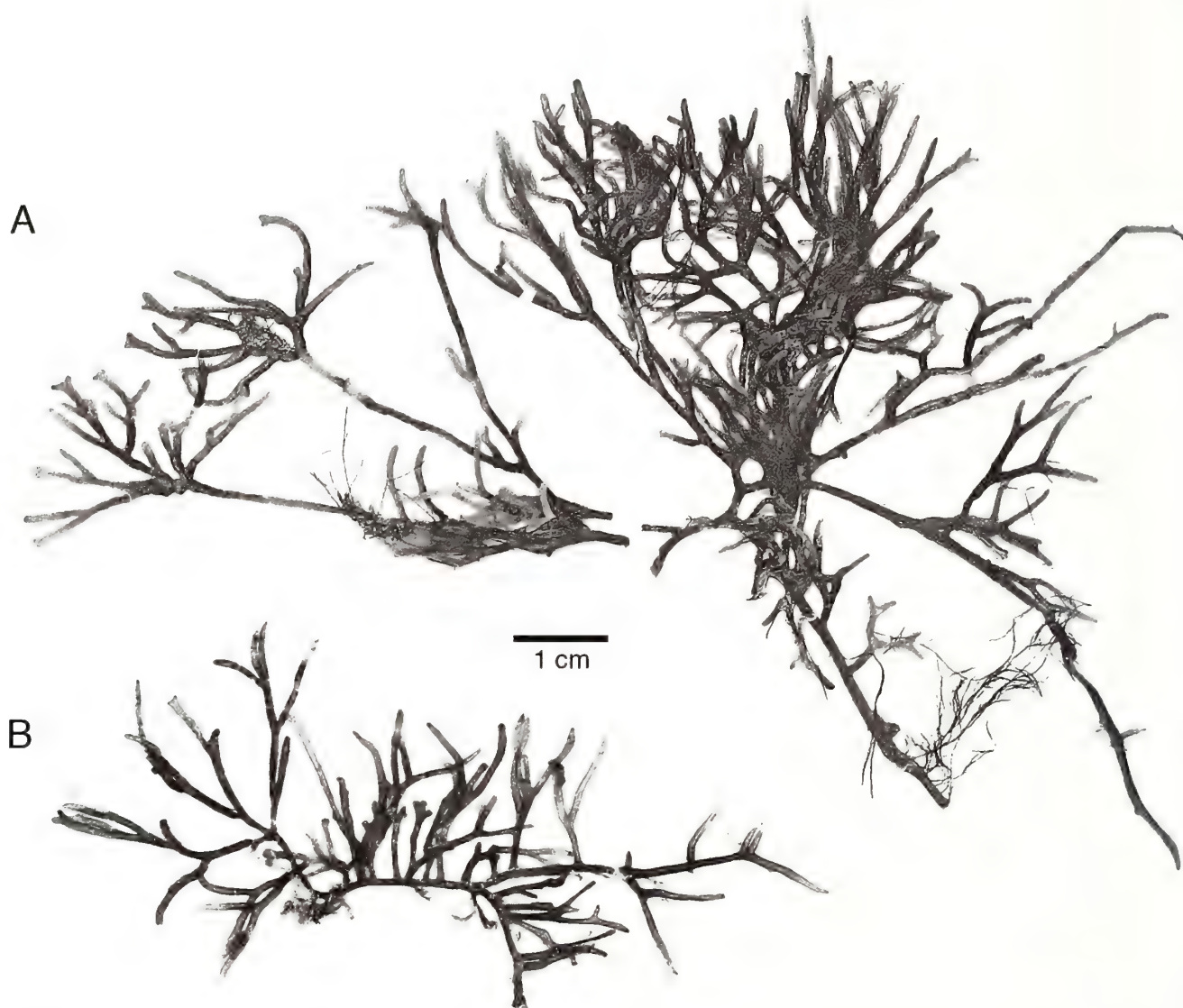


FIGURE 47. *Caulerpa vanbosseae*: Erect upper portions of simple to irregularly branched cylindrical axes, above horizontal, cylindrical, stolon-like rhizomes. A. Habit (JN-6562). B. Habit (JN-4981).

HABITAT. On rocks or broken shells, in crevices and tide pools; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía La Paz. Pacific coast: Punta Entrada (Bahía Magdalena) and Isla Santa Margarita (Bahía Las Almejas), Baja California Sur.

TYPE LOCALITY. Vicinity of La Paz, Baja California Sur, Gulf of California.

REMARKS. *Caulerpa vanbosseae* is apparently known only in the Gulf of California and Pacific Baja California Sur. A few specimens of Gulf *C. vanbosseae*

bear a morphological resemblance to some of the cylindrical, sparsely, irregularly branched forms of deep-water *C. ashmeadii* Harvey (1858) from the eastern Gulf of Mexico (US Alg. Coll.).

HALIMEDACEAE

Halimedaceae Link, 1832:115.

Most members of this family have a multiaxial construction, and most are calcified (aragonite mineral form

of calcium carbonate). Development is initially uniaxial; as more siphonous filaments are formed, they become consolidated into a multiaxial thallus, with a filamentous medulla and a cortex of utricles. Cells have numerous chloroplasts and leucoplasts, with xylan as a principal cell wall constituent.

Sexual reproduction is holocarpic. Biflagellate anisogametes are formed in differentiated gametangia that develop above the surface layer of the segments. Anisogametes are discharged through papillae.

A monotypic family; the single genus *Halimeda* is represented in the northern Gulf of California.

***Halimeda* J. V. Lamouroux**

Halimeda J. V. Lamouroux, 1812:186, as "*Halimedeae*."

Algae are erect or spreading and variously branched and are composed of articulated sequences of calcified segments that alternate with narrow, flexible noncalcified joints. Attachment to the substratum is by either a large, dense fibrous holdfast; a small holdfast of rhizoidal filaments; or by several rhizoidal masses developed from the segments or nodes. Calcified (aragonite) segments may be cylindrical, compressed or flat, or spherical, simple or lobed. Segments are internally composed of a multiaxial (rarely uniaxial), filamentous medulla that branches outward to form 2–6 layers of subsurface utricles and a surface layer of utricles. Outer surface utricles may be loosely to closely adherent. Growth is indeterminate. The flexible joints are composed of coenocytic medullary filaments that are closely parallel and remain separate or are fused in pairs, in small groups, or into a single group. Filaments contain numerous nuclei, chloroplasts and amyloplasts, and have cell walls primarily composed of xylan. Accessory pigments are siphonoxanthin and siphonein.

Asexual reproduction is by fragmentation. New thalli can also develop at ends of filaments that grow out of segments, as well as from filaments of basal stolons. Sexual reproduction, where known, is holocarpic. Biflagellate anisogametes are formed in gametangia on branched stalks grouped together on the surface of the calcified segments.

REMARKS. *Halimeda* is widely distributed in tropical to subtropical seas, from intertidal to depths of at least 150 m (Littler et al. 1985, 1986). *Halimeda* has long been known to play a critical role in the formation of tropical beach sands (van Overbeek and Crist, 1947). Growth patterns, calcification, and defense chemicals are synchronized on a daily cycle to maximize growth by avoiding some daytime herbivores (Hay, 1988, 1997b). Holocarpic

sexual reproduction of *Halimeda* also follows a diel pattern (Clifton, 1997; Hay, 1997a; Clifton and Clifton, 1999). Initiated after sunset, it is a brief phenomenon, with almost all of the alga's protoplasm put into gamete production. Overnight, the green calcified segments become white, with stalked green gametangia on their surface and edges, and right before dawn, the gametes are released, leaving behind the dead calcified structure.

Currently there is one species, *H. discoidea*, known in the northern Gulf of California.

One additional species, *Halimeda opuntia* (Linnaeus) J. V. Lamouroux (1816), is recorded in the southern Gulf (Rocha-Ramírez and Siqueiros-Beltrones, 1991).

***Halimeda discoidea* Decaisne**

FIGURE 48A–C

Halimeda discoidea Decaisne, 1842b:102; Collins, 1909b:400; Howe, 1911:492; Setchell and Gardner, 1920b:177, pl. 13: fig. 3; Setchell and Gardner, 1924a:704; Dawson, 1944:214; Taylor, 1945:73; Dawson, 1949:244, 245; Taylor, 1950:85, pl. 45: fig. 1; Dawson, 1957b:9; Dawson, 1959a:4, 6, 8, 18; Hillis, 1959:352, pl. 2: fig. 5, pl. 5: fig. 11, pl. 6: fig. 11, pl. 7: figs. 9, 10, pl. 8: figs. 5–8, pl. 11; Dawson, 1960c:97; Dawson et al., 1960b:13, 14; Dawson, 1961b:382; Dawson, 1961c:406, pl. 7: fig. 1; Dawson, 1962b:177, 229, fig. 22; Huerta-Múzquiz, 1978:338; Hillis-Colinvaux, 1980:136, fig. 41; Pedroche and González-González, 1981:64; González-González, 1993:443; Huerta-Múzquiz and Mendoza-González, 1985:44; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:39; Mateo-Cid and Mendoza-González, 1991:25; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Martínez-Lozano et al., 1991:22; Tsuda and Kamura, 1991:69, pl. 4: fig. 1; Mateo-Cid and Mendoza-González, 1992:25; León-Tejera et al., 1993:199, 202; Servière-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994b:45; León-Tejera and González-González, 1994:26; González-González et al., 1996:287; Bucio-Pacheco and Dreckmann, 1998:43, 45; Yoshida, 1998:114; Hillis et al., 1998:671; Mendoza-González and Mateo-Cid, 1998:26; Servière-Zaragoza et al., 1998:169, 179; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; López et al., 2000:339; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Abbott and Huisman, 2004:131, fig. 49B–E; López et al., 2004:10; Wysor, 2004:225; Hernández-Herrera et al., 2005:146; Pedroche et al., 2005:80; Riosmena-

A

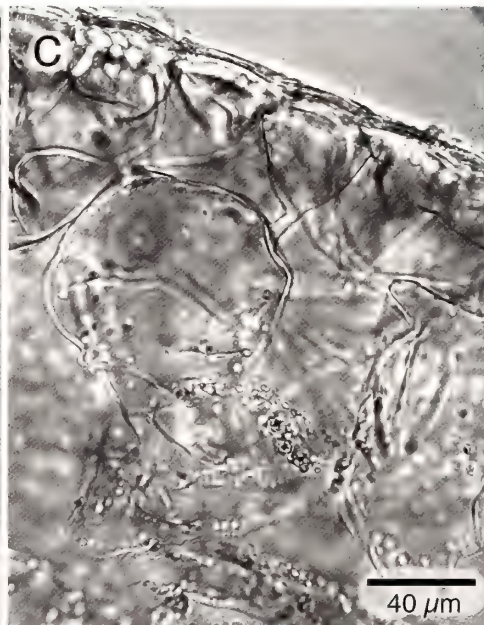
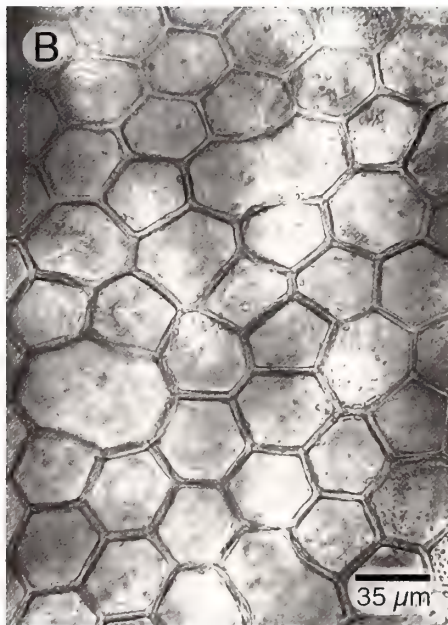
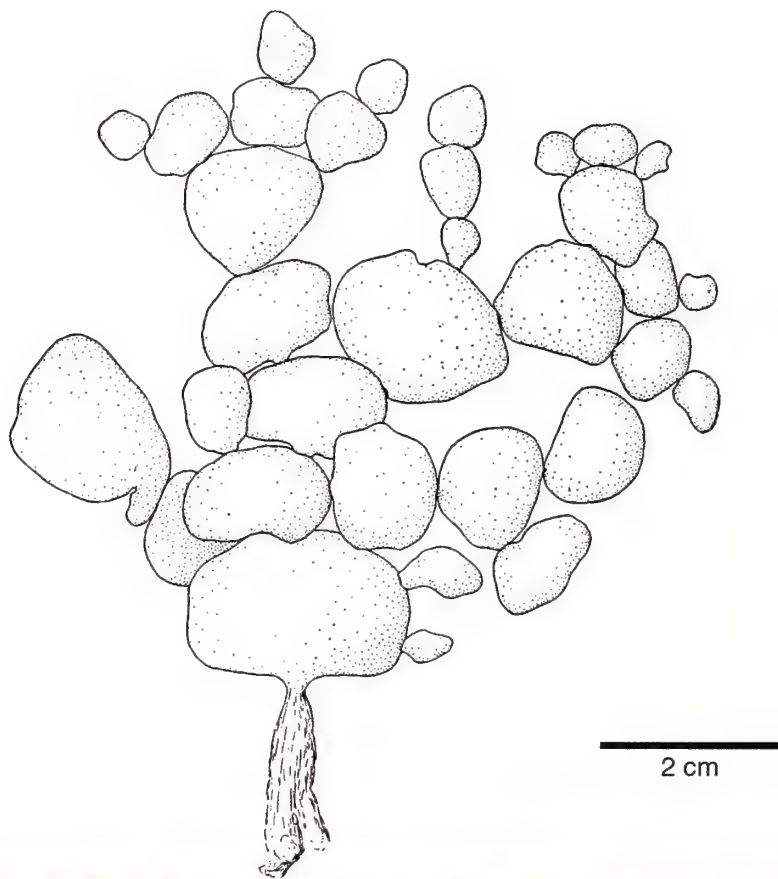


FIGURE 48. *Halimeda discoidea*: A. Habit (after Setchell and Gardner, 1920b: pl. 13, fig. 3). B. Surface view of decalcified segment with hexagonal pattern formed by abutting surface utricles; occasionally, two adjacent utricles merge across one of their facets, consequently forming polygons (EYD-25921). C. Section of segment showing large secondary utricle bearing smaller cup-shaped peripheral utricles (EYD-25921).

Rodríguez et al., 2005:101; Servièrre-Zaragoza et al., 2007:7; Pacheco-Ruíz et al., 2008:202.

Algae forming small clumps of subdichotomously to trichotomously branched fronds (branching in several planes), up to 10 cm high; of lightly to moderately calcified flat segments that alternate with very short noncalcified joints of entangled medullary filaments fused in pairs (rarely 3); attached below by a single, relatively small, mass of rhizoidal filaments. Flat segments variable in shape, mostly obovate to reniform, and 1.0–2.5 cm wide; upper segments usually flexible, leathery. Surface utricles forming hexagonal pattern in surface view; cup-shaped in transection, 25–45 µm in diameter; laterally adherent to adjacent surface utricles (even after decalcification) along their distal margins for 15–20 µm; borne on notably larger, inflated secondary internal utricles, 60–175 µm in diameter.

HABITAT. On rocks, and in crevices and tide pools; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda; Isla Partida; Guaymas to San Jose del Cabo. Pacific coast: Isla Socorro and Isla Clarion (Islas Revillagigedo); Isla Magdalena (southwest of Punta Entrada, Bahía Magdalena, Baja California) to Costa Rica; Panama; Hawaiian Islands; Bikini Island; China; Japan.

TYPE LOCALITY. “Not certain” (Silva et al., 1996a). Although the herbarium label (PC) indicates it was collected “Kamtschatka” (Russia) during the voyage of the exploring ship *Venus* (Decaisne, 1842b:102), Hillis (1959:352; see also Hillis-Colvinaux, 1980) noted that “at least the locality [is] incorrect,” as waters of the Kamchatka Peninsula are far too cold for this tropical to subtropical species.

REMARKS. In the Gulf of California, *Halimeda discoidea* is usually found in the warmer waters of the southern Gulf, but it is also known from a few collections in the northern Gulf.

DASYCLADOPHYCEAE

Dasycladophyceae C. van den Hoek, D. G. Mann et Jahns, 1995:436, *nom. invalid.* [see McNeill et al., 2006:Art. 36.2; Pröschold and Leliaert, 2007:130].

Algae of this class are exclusively marine, siphonous, and composed of a primary main axis or stalk that bears whorls of simple or branched laterals that are either free or joined distally to form a cortex. Each thallus is a single

coenocytic cell with a parietal layer of cytoplasm and a large central vacuole. Many are slightly to moderately calcified. Siphons contain numerous nuclei and fusiform to ellipsoid chloroplasts that do not have pyrenoids but, instead, often have storage grains of fructan and starch. These grains may also be found in the cytoplasm. Cytoplasmic streaming of the organelles, including chloroplasts, grains, and nuclei, occurs along numerous “lanes” (striae) that run parallel to the longitudinal axis of the cell. The cell wall of the vegetative thallus is composed of mannan, and the wall of the gametangial cyst is predominantly cellulose.

Life histories, where known, involve a haploid gametophytic stage, the macrothallus, that alternates with a zygote stage containing a giant diploid nucleus (the only diploid nucleus in the life history). Sexual reproduction is by fusion of biflagellated gametes. Gametes may be formed in gametangial cysts of lateral branches or in disc rays.

There is one order represented in the northern Gulf of California.

DASYCLADALES

Dasycladales Pascher, 1931:328.

Dasycladales Bessey, 1907: 287.

Structurally composed of coenocytic cells, these algae have radial symmetry and are often calcified and attached below by rhizoids. The siphonous main axis or stalk bears whorls of simple or divided laterals that can be free or united and are sometimes branched to several orders.

Reproduction is by operculate cysts that function as gametangia and are developed from a nucleus that has divided into numerous small secondary nuclei and presumably undergoes meiosis to produce gametes. These cysts release biflagellate isogametes, which upon fusion, form a quadriflagellate zygote. This zygote settles and develops into a siphonous system from which the primary axis develops.

REMARKS. The extensive fossil record of the Dasycladales is unique among the Chlorophyta. Most of the 150 genera of Dasycladales are fossils, extending back to the Ordovician (e.g., Pia, 1927; Nitecki, 1970). Currently, there are only 11 known living genera, of which three extend from the Cretaceous.

In the southern Gulf, one of its two families, the Dasycladaceae Kützing (1843), is represented by two genera, *Batophora* J. Agardh (1854) and *Neomeris* Lamouroux (1816), with records of *Batophora oerstedii* J. Agardh (1854; Ortega et al., 1987) and *Neomeris annulata* Dickie (1874a; Dawson, 1959a; Huerta-Múzquiz, 1978; Mateo-Cid et al., 2000a:70; Hinojosa-Arango and

Riosmena-Rodríguez, 2001; Riosmena-Rodríguez et al., 2005).

The Polyphysaceae of the Dasycladales is represented throughout the Gulf of California.

POLYPHYSACEAE

Polyphysaceae Kützing, 1843:302, 311.

Acetabulariaceae Nägeli, 1847:158, 252.

Algae a unicell, with a stalk bearing two kinds of whorled laterals that can be arranged in two different ways: (1) numerous whorls of hyaline branched laterals (may be pale green when immature) and a subterminal or terminal disc or cap of a whorl of gametangial rays (which may be lost after reproductive maturity and later replaced) or (2) alternating whorls of hyaline (or pale green) laterals and green discs or caps of gametangial rays. Gametangial rays with a circle of short protuberances (superior corona) on the upper side that bear hairs and/or scars after hairs are shed; rays may or may not have a ring of additional segments beneath (inferior corona), which if present, lacks hairs.

Reproduction is by gametes that develop in cysts within the gametangial rays of the cap or disc.

REMARKS. The Polyphysaceae was shown to be a monophyletic group distinct from the family Dasycladales (Olsen et al., 1994).

One of the genera, *Parvocaulis* S. Berger, Fettweiss, Gleissberg, Liddle, U. Richter, Sawitsky et Zuccarello (2003), has been reported in the southern Gulf with records of two species *Parvocaulis pusilla* (M. Howe) S. Berger et al. (2003) by Huerta-Múzquiz and Mendoza-González (1985), Rocha-Ramírez and Siqueiros-Beltrones (1991), and Baynes (1999) (all as "*Acetabularia pusilla* (M. Howe) Collins, 1909b") and *Parvocaulis parvulus* (Solms-Laubach) S. Berger et al. (2003) by Mateo-Cid et al. (2000a, as "*Acetabularia parvula* Solms-Laubach, 1895").

One genus, *Acetabularia*, is known in the northern Gulf of California.

Acetabularia J. V. Lamouroux

Acetabularia J. V. Lamouroux, 1812:185.

Algae are light to moderately calcified and are composed of an erect, siphonous stalk (up to 1 mm in diameter) above a lobed, rhizoidal base attached to solid substratum. The cylindrical stalk bears successive whorls of deciduous, branched sterile laterals (hairs) in its upper

portions that can leave scars, and at its upper end it bears, terminally or subterminally, one or more caps or discs of laterally joined rays. Near the base of each ray are borne small projections on the upper and lower surfaces: the projections form a whorl, the superior (apical) corona with colorless hairs and the inferior corona without hairs. Cytoplasm is peripheral and contains numerous discoid plastids and lacks pyrenoids and surrounds a large central vacuole. Chloroplast ultrastructure is variable and with or without stacked grana. Starch grains are in both the chloroplast and cytoplasm, but they are not membrane-bound in the latter. Vegetative cells have a single, diploid, primary nucleus in a branch of the rhizoid. Primary nuclear division is meiotic, followed by a series of mitotic divisions that form secondary nuclei that migrate up the stalk and establish themselves in the rays of the cap.

Asexual reproduction is by fragmentation or growth of new thalli from basal rhizoids or regeneration after wounding from grazing herbivores or physical force, such as wave action. Gametangial rays develop thick-walled, operculate cysts by uninucleate aggregations of cytoplasm, and subsequent division of the nuclei produces biflagellate isogametes. The thick-walled cysts are released from the rays and can survive for some time on their own. When conditions are suitable, an ostiole opens in the cyst, and the gametes swim out. Two gametes fuse to form the diploid zygote that settles and develops into a new thallus.

REMARKS. Species of *Acetabularia* are quite distinctive with a narrow stalk that bears a beautiful, delicate, parasol-like, discoid, or cup-shaped cap. They are found in tropical to subtropical seas, often in brackish to hypersaline shallow waters. On the basis of the pioneering studies of Woronine (1862) and De Bary and Strasburger (1877) the life history of *Acetabularia* has long been reported to be three years before the reproductive caps with cysts were formed, but more recently, Berger and Liddle (2003) showed the life history can be completed in one growing season.

Three western Atlantic species have also been reported in the southern Gulf of California: *Acetabularia farlowii* Solms-Laubach (1895) and *A. crenulata* J. V. Lamouroux (1816) were reported by Ortega et al. (1987) and Rocha-Ramírez and Siqueiros-Beltrones (1991). More recently, L. Aguilar-Rosas et al. (2006) added another species, *Acetabularia schenckii* K. Möbius (1889), to Bahía de La Paz and Sinaloa and also added new distribution records of *A. farlowii* to Sinaloa and Pacific Baja California.

One species is recorded in the upper Gulf of California.

***Acetabularia caliculus* J. V. Lamouroux in Quoy et Gaimard**

FIGURE 49A,B

Acetabularia caliculus J. V. Lamouroux in Quoy et Gaimard, 1824:621, pl. 90: figs. 6, 7; Yoshida, 1998:154; Berger et al., 2003:527, figs. 8, 31. As *Acetabularia* "*calyculus*": Dawson, 1954d:396, fig. 13h; Dawson, 1966a:8;

Dawson, 1966b:55; Valet, 1969:617, pl. 44: figs. 7–9; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127, 132, 136; Womersley, 1971:119, fig. 15; Huerta-Múzquiz, 1978:340; Womersley, 1984:295, figs. 101B, 102B–D; Huerta-Múzquiz and Mendoza-González, 1985:42; González-González et al., 1996:126; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Núñez-López et al., 1998:39; Rodríguez-Morales and Siqueiros-Beltrones, 1999:22; Paul-Chávez and Riosmena-Rodríguez,

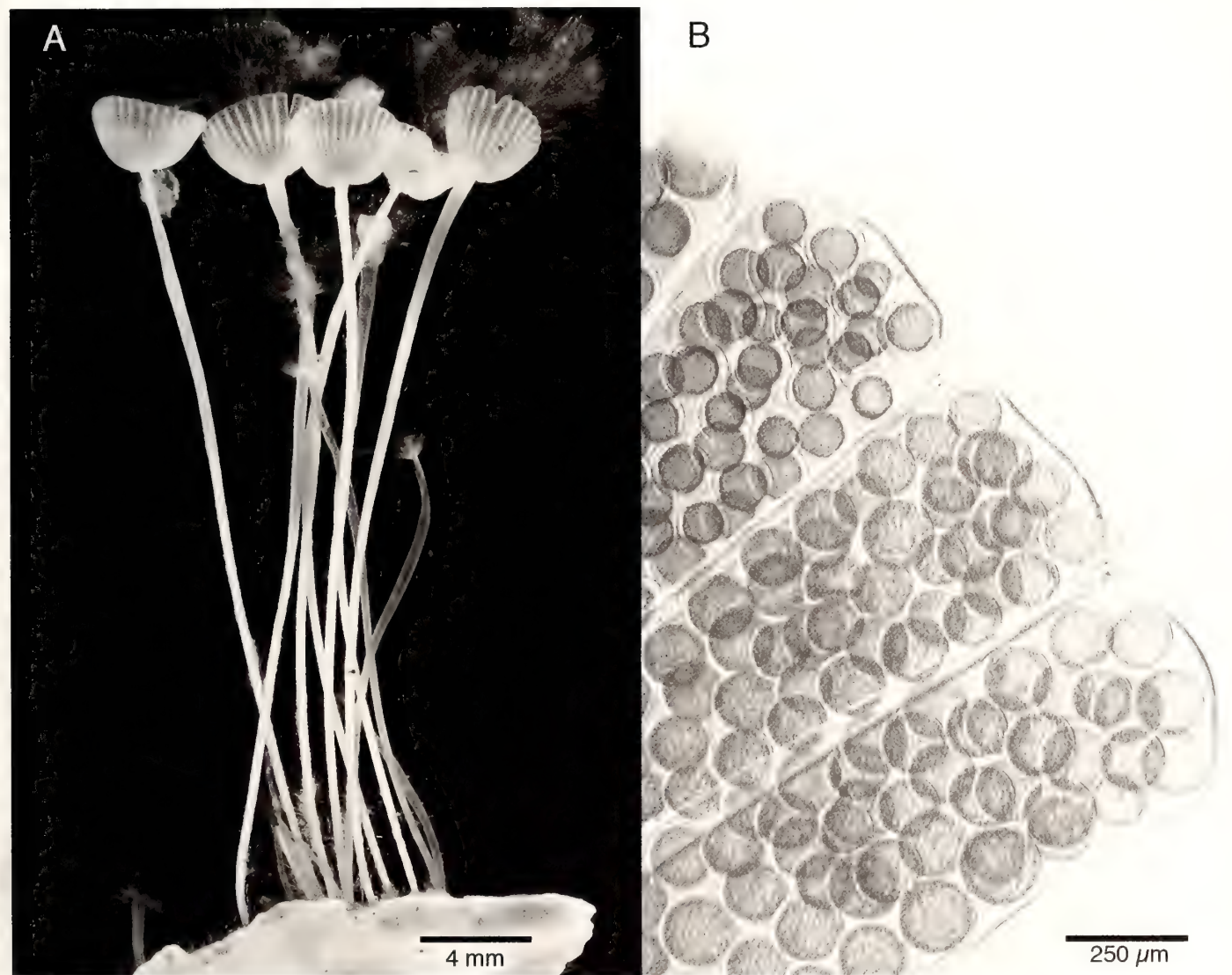


FIGURE 49. *Acetabularia caliculus*: A. Cluster of several mature thalli, with calcified stalk and cup-shaped disc of laterally adhering gametangial rays; some discs with central tuft of deciduous hairs (issued from the corona superior) still intact (liquid preserved; EYD-27569). B. Numerous spherical reproductive cysts enclosed in gametangial rays of mature disc; note smooth, truncate outer margin of each ray and faint seam of calcium carbonate along ray lateral margins (US Alg. Coll. slide 5533).

2000:146; Cruz-Ayala et al., 2001:190; Riosmena-Rodríguez et al., 2005:101; Pedroche et al., 2005:84; Mateo-Cid et al., 2006:48; Dreckmann et al., 2006:154.

Alga erect, usually growing in clusters, up to 3 cm tall; a rigid, thin cylindrical calcified stalk with several whorls of ephemeral branched laterals (green when young, later colorless) in upper portion and a subterminal, cup-shaped disc, 3–5(–7) mm in diameter; attached below by a rhizoidal base. Disc solitary of (20–)22–30 laterally adjoined rays; outer margin of rays truncate in most discs or knobbed in some discs. Corona superior with short blunt lobes that each bear 2–3(–4) branched colorless hairs or hair scars; inferior corona inconspicuous, each segment a single blunt lobe beneath the ray at the place of attachment.

When reproductive, each gametangial ray filled with 45–75 spherical cysts containing gametes; each cyst 100–150(–175) μm in diameter (US Alg. Coll.-95320, slide 5533).

HABITAT. Growing on shells in shell/sand and sand/mud bottoms of rapid flowing tidal channels; mid to low intertidal.

DISTRIBUTION. Gulf of California: Bahía Cholla (Choya), vicinity of Puerto Peñasco; Bahía La Paz. Pacific coast: Baja California Sur; Oaxaca to Chiapas; China; Japan.

TYPE LOCALITY. Baie des Chiens-Marins (Shark Bay), Western Australia.

REMARKS. *Acetabularia caliculus* is apparently known only from shallow bays in the Gulf of California. The outer margins of the disc rays in the northern Gulf specimens of *A. caliculus* (Figure 49B) are both truncate (in agreement with those reported by Berger and Kaever, 1992) and sometimes knobbed (as observed in *A. caliculus* of Lord Howe Island, Australia; Kraft, 2008: fig. 104C,D). Morphological and molecular studies, such as those of Olsen et al. (1994) and Berger et al. (2003), are needed to test the taxonomy and phylogenetics of Gulf *A. caliculus* in relation to those from the Western Australian type locality.

The original spelling of the species name, *caliculus* (Lamouroux in Quoy and Gaimard, 1824), agrees with the Latin usage (*calix* (L.), a small cup [Brown, 1956]); thus, it is not necessary to change the original spelling to Greek usage, i.e., *calyculus* (*calyx*, *kalyx* [Gr.]).

PART II: BROWN ALGAE

STRAMENOPILES

Stramenopiles D. J. Patterson, 1989:372.

Stramenopiles are a very large, extremely diverse, group of eukaryotes that range from the microscopic to the largest of all marine plants, and include autotrophs, heterotrophs, and mixotrophs. Most are planktonic or benthic and are found in terrestrial, freshwater, and marine environments, although a few are aerial and some are endosymbionts. The discovery that heterokont algae are related to some nonheterokont algae and to various nonphotosynthetic organisms (including some previously thought to be fungi or protozoa, such as protozoan-like unicells or loosely associated colonies, hypochoytrids, water molds, and downy mildews) has led to their being grouped together. The ancestor of the basal Stramenopiles may have been an alga, and then some groups could have arisen through plastid loss or, possibly, branched off before the appearance of plastids within the group. Plastid reduction as well as reacquisition has also occurred in some lineages. Stramenopiles are grouped together on the basis of their cytology and ultrastructure, supported by biochemical and molecular studies (e.g., Moestrup and Andersen, 1991; Williams, 1991a, 1991b; Leipe et al., 1994; Reith, 1995; Medlin et al., 1995, 1997; Saunders et al., 1997; Daugbjerg and Andersen, 1997; Delwiche, 1999; Patterson, 1989, 1999; Goertzen and Theriot, 2003; Andersen, 2004a, 2004b; Adl et al., 2005).

Members include both unicellular motile flagellates and multicellular organisms; typically, all members have cells or produce cells with heterokont flagella (two dissimilar flagella) at some point in their life history, e.g., zoospores or gametes. One of the flagella is an anterior tinsel flagellum with mastigonemes (unique three-parted, tubular hair-like structures) in two opposite rows. This feature, together with the flagella typically being supported by four microtubule roots in a distinctive pattern, and mitochondria with tubular cristae are defining characteristics of the Stramenopiles. Most members either have this tinsel flagellum or were derived from organisms that had this type of flagellum. The other flagellum is reverse-directed, smooth, and usually shorter or is reduced to a basal body in some. A few Stramenopiles do not produce cells with the typical

heterokont flagella, and the flagella have been altogether lost in a few lines, most notably the diatoms.

Photosynthetic Stramenopiles include microscopic biflagellated or nonflagellated unicellular, colonial, and loosely filamentous algae (e.g., chrysophytes, diatoms) and multicellular algae that range from siphonous filaments (e.g., *Vaucheria*) to the structurally complex kelps (e.g., *Macrocystis*, *Laminaria*). Some have siliceous scales and spines or silicate skeletons, and their species may also be found in the fossil record; others are without cell walls or scales, and a few may be amoeboid. Cells of stramenopile algae have chloroplasts containing chlorophyll *a* and chlorophylls *c*1 and *c*2 (some may also have *c*3) and, usually, the accessory pigments fucoxanthin, heteroxanthin, vaucheriaxanthin, or violaxanthin. Plastids have three thylakoids per lamellae, lack nucleomorphs, and are surrounded by four membranes; the outermost is continuous with the endoplasmic reticulum. Reserve polysaccharides include chrysolaminarin or laminarin, formed in vesicles outside of the plastid.

REMARKS. Classification systems have not always grouped the currently accepted members of the Stramenopiles together (for a review, see Hausmann et al., 2003), and they have been variously placed in the Chromista Cavalier-Smith (1981), Heterokonta Cavalier-Smith (1986), Heterokontophyta Ø. Moestrup (1992), and Protista or Protoctista (e.g., Whittaker, 1969; Margulis et al., 1990; Corliss, 1994; Cavalier-Smith, 1986, 1998; Margulis and Schwartz, 1998). Recently, Adl et al. (2005) recognized the Stramenopiles (Patterson, 1989, 1999) to comprise 20 groups within the Chromalveolata Adl et al. (2005), one of seven clusters of eukaryotes that represent the basic groups (or traditional kingdoms) in their nameless ranked higher-level classification.

One very large multicellular group of Stramenopiles, the Phaeophyceae, is well represented in the Gulf of California.

PHAEOPHYCEAE

Phaeophyceae Kjellman, 1891:176.

Melanophyceae Rabenhorst, 1863:274.

Fucophyceae Warming, 1884:38, as "Fucoideae."

Phaeophyceae Hansgirg, 1886:17, 27.

The Phaeophyceae (brown algae) are multicellular and exceptionally variable in form and size, ranging from microscopic to macroscopic, and include filamentous, crustose, tubular, globose, and foliose forms and very

large, structurally complex species. The 266 genera comprising the brown algae are almost all marine; only four to five genera occur in freshwater (Wehr and Sheath, 2003). The Phaeophyceae vary in color from light yellow-brown to dark blackish-brown, with a few that are chalky or whitish due to their surface calcification (e.g., some species of *Padina* and *Newbousia* [Kraft et al., 2004]). The class contains the largest of all the algae, with some species of the "giant kelp," *Macrocystis* C. Agardh (1820), up to 70(–100) m long (Foster and Schiel, 1985; Womersley, 1987). Most of the marine brown algae are benthic, often dominating intertidal and subtidal communities, and are found in depths down to 88 m (Littler et al., 1985, 1986); a few apparently live as free-floating forms, e.g., species of *Sargassum* in the Sargasso Sea.

Growth may be apical, intercalary, trichothallic, or diffuse. Phaeophycean hairs are often present. Cells are uninucleate, with the photosynthetic pigments in plastids containing thylakoids in groups of three and with or without a pyrenoid. Plastids are singular or present in various numbers and may be parietal, ribbonlike, or discoid; physodes (vesicles produced within the plastids) are usually present. The photosynthetic pigments, chlorophylls *a*, *c*1, and *c*2, are masked by the accessory pigments β carotene and the xanthophylls (particularly, fucoxanthin, violaxanthin, and diathoxanthin), thus giving the characteristic brown color to the group. Photosynthetic reserves include the soluble carbohydrates laminarin (a beta-linked polymer of glucose) and mannitol. Cell walls are firm and composed of two layers, the inner of cellulose microfibrils and a gelatinous outer layer that contains alginic acid and fucinic acid.

Life histories are either isomorphic, heteromorphic (usually with a larger sporophyte), or diplontic (meiosis to form gametes, e.g., *Fucus*). Sporophytes develop unilocular or plurilocular sporangia; the latter produce more than one spore. Sexual reproduction is isogamous, anisogamous, or oogamous, with parthenogenesis known in some species. Gametangia are typically plurilocular, with the exception being oogamous females. Motile cells (i.e., zoospores and gametes) have two laterally inserted, unequal-length flagella: the larger is anterior tinsel type, and the smaller is posterior whiplash type. However, in the Fucales, the flagella are more or less of equal length, and at least one group, the Dictyotales, produce nonmotile aplanospores and uniflagellate sperm that lack a posterior flagellum.

REMARKS. In the northern Gulf of California, the Phaeophyceae have about the same numbers of species as the green algae, but both have fewer species than the red algae. Ecologically, the brown algae generally comprise

the bulk of the northern Gulf's algal biomass, and seasonally, there is greater abundance and more species of brown algae during the winter and spring (see also McCourt, 1984a, 1984b; Huerta-Múzquiz and Mendoza-González, 1985; Pacheco-Ruíz and Zertuche-González, 1996b). Three northern Gulf regions that have high brown algal species richness are Puerto Peñasco (Norris, 1975), Bahía de Los Ángeles (Pacheco-Ruíz et al., 2008), and Bahía de La Paz (L. Aguilar-Rosas and R. Aguilar-Rosas, 1993).

In recent years, the presumed relationships among the brown algae have been somewhat uncertain (e.g., Saunders et al., 1992). The traditional concept, based on morphology and life histories, that the Ectocarpales are basal to the other brown algal orders (e.g., Kylin, 1933;

Papenfuss, 1951, 1955; van den Hoek et al., 1995) has not been supported by molecular analyses, and new systematic relationships have been proposed (e.g., de Reviere and Rousseau, 1999; Rousseau et al., 2001; Draisma et al., 2001, 2002, 2003). The Phaeophyceae, as presented herein, has several subdivisions to reflect the most recent contributions by Cho et al. (2006) and Phillips et al. (2008), which elucidate the evolutionary relationships among the brown algae. These subdivisions are grouped as orders, primarily on the basis of life histories and gene sequence data (see synopsis of ordinal characters given by Adl et al., 2005).

Members of nine of the orders of Phaeophyceae are represented in the northern Gulf of California.

KEY TO THE ORDERS OF THE PHAEOPHYCEAE FOR MEMBERS OCCURRING IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae crustose (in at least one of its life history phases); plastids without pyrenoids 2
- 1b. Algae not crustose; erect, filamentous, or cylindrical, compressed or flattened; plastids with or without pyrenoids 3
- 2a. Crusts discoid to spreading or initial crustose stage that develops into low-growing clumps of mostly horizontal, short branches; filamentous structure of 2–3 distinct layers; growth by terminal cells of horizontal and erect filaments or intercalary from basal meristems of cortical filaments **Ralfsiales**
- 2b. Crusts prostrate, encrusting, multilobed; thin; parenchymatous structure; growth by marginal row of apical cells (sporophyte) **Cutleriales, in part**
- 3a. Algae usually small tufts of uniseriate or multiseriate, unbranched to branched free filaments 4
- 3b. Algae not tufted; usually moderate to large size and various forms: cylindrical, compressed or flattened; simple to branched; or saccate, subglobose, or foliose; or frondose; some parenchymatous, others of loosely to densely compacted filaments 5
- 4a. Uniseriate filaments, simple to branched; growth apical or intercalary, localized or diffuse; ribbon-shaped or discoid plastids with pyrenoid **Ectocarpales, in part**
- 4b. Multiseriate branched filaments; growth by single conspicuous apical cell, initially divides transversely, followed by transverse division of subapical cells, then longitudinal divisions, and, in some, secondary transverse divisions; plastids discoid and no pyrenoids. **Sphacelariales**
- 5a. Growth trichothallic (apical meristem surmounted by filament or tuft of filaments) 6
- 5b. Growth not trichothallic; either intercalary, or by a single apical cell, or group or marginal row of apical cells 8
- 6a. Algae erect, flat, fan-shaped; growing margin fringed with trichothallic filaments (gametophytes) **Cutleriales, in part**
- 6b. Algae not fan-shaped; axes and branches either compressed to flat, narrow to broad, apical and lateral meristems with single trichothallic filament or terete (wiry) with apical tufts of trichothallic filaments and determinate branchlets with terminal tufts of filaments 7
- 7a. Algae wide, flat blades, simple to sparsely branched blades, or narrow, compressed axes and branches (>1.5 mm wide); growth from apical and lateral meristems with single terminal trichothallic filament **Desmarestiales**
- 7b. Algae thin, wiry, terete to subcylindrical axes and branches (<1 mm wide) with terminal tufts of trichothallic filaments and distinctive determinate branchlets with sporangial sori surrounding portion of branchlet below terminal tuft of hairs **Sporochnales**
- 8a. Growth intercalary; ribbon-shaped plastids with pyrenoid; internally centrally solid or hollow; medulla filamentous, surrounding a core of uniaxial or multiaxial filaments or of large parenchymatous cells **Ectocarpales, in part**
- 8b. Growth by conspicuous or inconspicuous apical cell or a group or row of apical cells; discoid plastids without pyrenoids; internally solid either, parenchymatous with medulla, cortex, and surface meristoderm, or medulla of filament-like hyphal cells and cortical assimilatory filaments, or large squarish to rectangular medullary cells and small cuboidal cortical cells 9

- 9a. Algae (Gulf members) of terete axes and branches, leaflike blades, and buoyant vesicles; internally with medulla, cortex, and surface meristoderm; apical cell sunken in terminal pit; gametangia in pitlike conceptacles within receptacles (reproductive branchlets); oogamous reproduction (sporangia lacking) **Fucales**
- 9b. Algae not differentiated as above; thallus flat, strap-shaped to bladelike; reproductive structures, including sporangia, on thallus surface (not in pitlike conceptacles) 10
- 10a. Algae with a single apical cell or group or marginal row of apical cells; medulla 1 or more layers of large cells, cortex of 1 or more layers of small cells; oogamous reproduction **Dictyotales**
- 10b. Algae with an inconspicuous apical cell; medulla of hyphael cells (filament-like), cortex of anticlinal rows of cuboidal cells; isogamous reproduction **Ishigeales**

ISHIGEALES

Ishigeales G. Y. Cho et S. M. Boo in G. Y. Cho et al., 2004:934.

Algae are terete, compressed, or foliose branched fronds that arise from a small holdfast or expanded crustose base. Growth is from a small inconspicuous meristematic apical cell. Anatomically, there is a distinct medulla of hyphael cells that connect to adjacent hyphael cells or to the inner cortical cells. The cortex is pseudoparenchymatous, composed of cells of assimilatory filaments. Cortical cells have several discoid plastids but lack pyrenoids (note that although rare, a “rudimentary pyrenoid” has been reported in *I. okamurae* [Cho et al., 2004:921, fig. 5d]). Phaeophycean colorless hairs, originating from the outer medullary cells, are clustered within pits (cryptostomata) on the thallus surface and project above it.

Members have an isomorphic life history. Terminal unilocular sporangia are developed by transformation of cells of the outermost cortical layer and produce spores. Uniseriate plurilocular sporangia (gametangia) that lack sterile terminal cells originate from the assimilatory filaments and produce isogametes.

REMARKS. Species of *Ishige* may grow attached to hard substrate or be epiphytic on other algae. The life history is presumed to be isomorphic (Tanaka, 1993; Hori, 1993; Cho et al., 2004; Kawai et al., 2005). In culture studies of *I. okamurae* from Japan, Ajisaka (1989) reported biflagellated spores, produced from plurilocular structures on the macrothalli, that developed into discs. The discs grew profusely branched filaments that later developed into the erect, dichotomously branched macrothalli. In contrast, Arasaki (1943, as “*I. foliacea*”) reported a heteromorphic life history in the culture study of Japanese *I. sinicola*; however, the culture may have been contaminated, making the results doubtful (see Kawai et al., 2005).

Currently, the Ishigeales contains one family. Recent molecular phylogenetic studies of Lim et al. (2007) showed

another genus, *Diplura* Hollenberg (1969; Tanaka and Chihara, 1981b), was also close to the Ishigeales and suggested that the genus be removed from the Ralfsiaceae (Ralfsiales) and placed in a new family within the Ishigeales.

The single family is represented in the northern Gulf of California.

ISHIGEACEAE

Ishigeaceae Okamura in Segawa, 1935:65.

Ishigeaceae is a monotypic family that has the characteristics of its only genus, *Ishige*.

REMARKS. Although the Ishigeaceae has been usually placed in the Chordariales (e.g., Yoshida, 1998), the family was shown to have a distant phylogenetic relationship with the Chordariales (or Ectocarpales sensu lato) and to have diverged early in the phaeophycean lineage (Kawai et al., 2005), basal to the other brown algal orders (Cho et al., 2004, 2006; Phillips et al., 2008). On the basis of its unique morphological, molecular, and ultrastructural features, Cho et al. (2004) established an order for the family.

The family is represented in the northern Gulf of California by one species of *Ishige*.

Ishige Yendo

Ishige Yendo, 1907:154.

Algae are erect, filiform, or compressed to complanate, dichotomously to subdichotomously branched fronds above a short stipe that is attached below by a discoid holdfast. Small hair pits (cryptostomata) are present on thallus surfaces, with phaeophycean hairs developing from the cells of the medulla, or lowermost cortical cells. Internally, the medulla is composed of intertwined, usually dense, colorless, hyphael cells (appearing filament-like), a subcortical layer of pseudoparenchymatous cells, and an

outer cortex of assimilatory filaments (rows of anticlinally arranged small pigmented cells). Pyrenoids are absent in *I. sinicola*, and in *I. okamurae* they are “rudimentary” (Cho et al., 2004) and very rarely observed (Hori, 1971).

Unilocular sporangia and uniseriate plurilocular sporangia are either on the same thallus or on separate thalli. Both structures are found in the upper portions of branch segments. The unilocular sporangia are terminal, developing from the outermost cells of assimilatory filaments. Plurilocular sporangia originate from the assimilatory filaments, lack any sterile terminal cells, and are in uniseriate rows within sori (reported from Japanese *I. foliacea* [Lee et al., 2003])

REMARKS. Although the external habit of *Ishige* is somewhat similar to some members of the Dictyotaceae, they are easily separated by their internal vegetative anatomy. Species of *Ishige* have a medulla of entangled hyphael cells (appearing filamentous) and a cortex of assimilatory filaments, whereas the medulla of members of the Dictyotaceae is composed of one or more layers of large cells and a cortical layer of one to several small cells.

Interestingly, of the three known species, the northern Gulf *I. sinicola* is found on hard substratum, whereas *I. foliacea* of eastern Asia (Japan, China, Taiwan and Korea), may be either epilithic or epiphytic on *I. okamurae* (Cho et al., 2004).

There is one species, apparently endemic, described from the northern Gulf of California.

***Ishige sinicola* (Setchell et N. L. Gardner)
Chihara**

FIGURE 50A,B

Polyopes sinicola Setchell et N. L. Gardner, 1924a:784, pl. 28; fig. 61, pl. 42b; Dawson, 1954c:267.

Ishige sinicola (Setchell et N. L. Gardner) Chihara, 1969:3, fig. 2; Hommersand, 1972:70; Littler and Littler, 1981:151, tbl. 3, figs. 4–6; González-González et al., 1996:153; Pacheco-Ruíz and Zertuche-González, 1996b:171; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2006:49, 58; Pacheco-Ruíz et al., 2008:203; Pedroche et al. 2008:59; K. M. Lee et al. 2009: [in press], fig. 3 A–E.

Carpopeltis sinicola (Setchell et N. L. Gardner) Kylin, 1956:221.

Ishige foliacea sensu Dawson, 1944:234, pl. 53; fig. 2; Dawson, 1954c:267; Dawson, 1960c:98; Dawson, 1961b:394; Dawson, 1966a:10; Norris, 1973:6 [non *Ishige foliacea* Okamura in Segawa, 1935:65; Okamura, 1936:239, figs. 130: 1, 2, 5, fig. 131; which is

Ishige okamurae sensu Yendo, 1907 (in part; only the foliose type):155, pl. II: figs. 1–3, 5, 6, 8; and non *Ishige okamurae* Yendo, 1907, as “*I. okamurai*” (only the filiform type):154].

Algae erect, dark brown to blackish-brown, with flat, straplike, regularly to irregularly dichotomously branched fronds, up to 10 cm tall and up to 6 mm wide; arising from a crustose holdfast. Branch segments, after the dichotomy either more or less same length or one longer than the other; branches becoming narrower in width upwards. Medulla dense; of colorless, entangled hyphael cells. Cortex of filaments of up to 10–13 small cuboidal cells in anticlinal rows; in transection, cortical filaments shorter near thallus apices, up to 50 µm thick, becoming thicker and of more cells below, 70–140 µm in middle portion and 120–165 µm thick near stipe. Cryptostomata are rare; they contain only a few phaeophycean hairs (produced from lowermost cortical cells), a small number of which may project above thallus surface. Pyrenoids absent.

Unilocular sporangia terminal on cortical filament (Dawson, 1944). Plurilocular sporangia unknown in northern Gulf material.

HABITAT. On rocks; midtidal to lowermost intertidal; occasionally in the shallow subtidal.

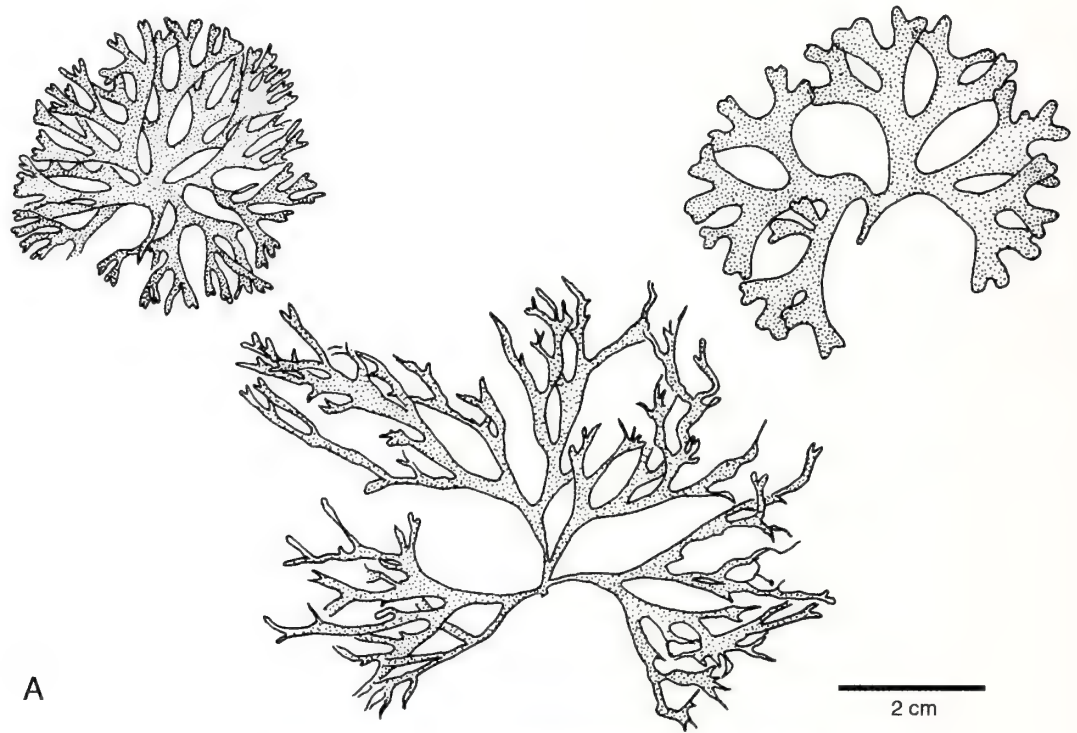
DISTRIBUTION. Gulf of California: Puerto Peñasco to Ensenada Bocoichampo (northeast of Guaymas).

TYPE LOCALITY. Isla Partida, Las Islas de la Cintura, Gulf of California.

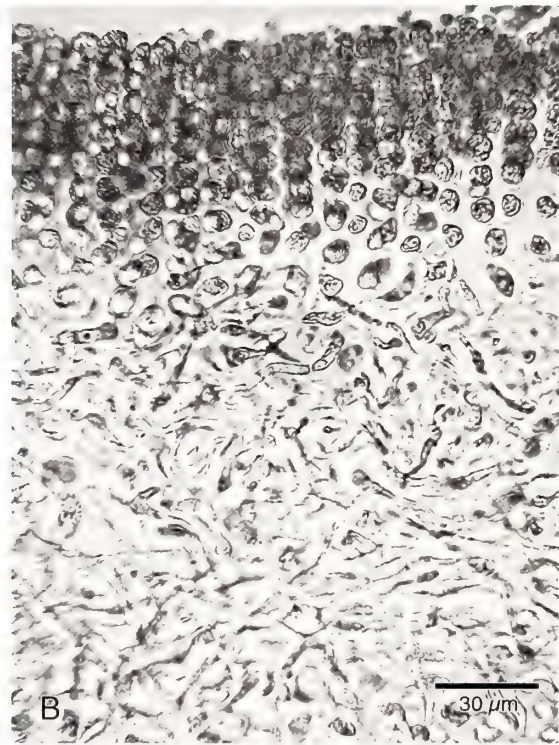
REMARKS. In Mexico, the distribution of *Ishige sinicola* is apparently restricted to the northern Gulf. According to Pedroche et al. (2008) the southern Gulf record from La Paz was erroneously attributed to Dawson (1960c) by Riosmena-Rodriguez and Paul-Chávez (1997). A perennial species, it is most abundant, with the broadest fronds, during the winter and least abundant, with the narrowest fronds, in summer (Dawson, 1941, 1944).

Dawson (1944, as “*I. foliacea*”) noted that northern Gulf and Japanese specimens were similar in habit, and later that another species, *Polyopes sinicola* Setchell et N.L. Gardner (1924a), was incorrectly described as a red alga and was actually the same as the Gulf *I. foliacea* (Dawson 1954c). Later Chihara (1969) made the combination *I. sinicola* (Setchell et N. L. Gardner) Chihara and considered it to be conspecific with *I. foliacea*.

Ishige sinicola was one of the Gulf species thought to have a disjunct distribution, known only in the Gulf of California and Japan/eastern Asia (Dawson, 1960c; Yoshida, 1998; Kitayama, 2006; Pedroche et al., 2008).



A



B

FIGURE 50. *Ishige sinicola*: A. Specimens illustrating variation in morphology (JN-2980, JN-4621, and JN-4166). B. Portion of a transection from lower part of frond; note medulla of entangled hyphael cells and anticlinal rows of cortical filaments (JN-5824).

Collections from Japan, Korea and the northern Gulf were recently studied by K. M. Lee et al. (2009). Their molecular analyses showed the northern Gulf *I. sinicola* to be distinct from *I. okamurae*, and those reported as "*I. sinicola*" from Japan (e.g., Yoshida, 1998) and Korea (E.-Y. Lee et al., 2003; Kawai et al. 2005) for which they reinstated *I. foliacea* (K. M. Lee et al. 2009). Other east Asian (western Pacific) records of "*I. sinicola*," such as those reported from China (Tseng, 1983) and Taiwan (Lewis and Norris, 1987) need to be investigated, and are probably *I. foliacea* as well.

SPHACELARIALES SENSU STRICTO

Sphacelariales Migula, 1908:173, 237.

Sphacelariales Oltmanns, 1922:83.

Algae are erect, terete, unbranched or branched filaments that are attached by a mono- or polystromatic discoid holdfast or creeping basal filaments (rhizoids or stolons) or aggregated cells endophytic in a host. Filaments are uncorticated in some species or corticated by rhizoidal growth in others. In the species that branch, there are few to many determinate or indeterminate branches. Growth is by a prominent apical cell that, at first, divides transversely to form a short apical region; below this region the cells longitudinally divide (except in *Sphacella*) to develop the characteristic pseudoparenchymatous filament. In some taxa these longitudinal segments may also undergo secondary transverse divisions and either do not enlarge or may continue to grow in length and width. Hairs are known in some. Cells contain several discoid chloroplasts without pyrenoids.

Vegetative reproduction can be by fragmentation or by propagules (specialized branchlets). Life histories, where known, are isomorphic or slightly heteromorphic. Sporophytic and gametophytic thalli are similar in appearance. Unilocular sporangia (zoidangia) produce zoospores, and neutral plurilocular sporangia produce neutral spores. Sexual reproduction is isogamous, anisogamous, or oogamous. Plurilocular gametangia produce isogametes or anisogametes. Unilocular oogonia develop an oogonium.

REMARKS. Most of the species are marine, with only one known from freshwater (Prud'homme van Reine, 1993). Three families are usually recognized in the Sphacelariales. On the basis of molecular and morphological analyses of members from these three families, Draisma et al. (2002) found problems in resolving their phylogenetic relationships and discussed alternative circumscriptions.

There is one family represented in the Gulf of California.

SPHACELARIAEAE

Sphacelariaceae Decaisne, 1842a:329, 341.

Algae are small to medium sized, usually erect, and filamentous, and may either be solitary individuals or form tufts or mats. Thalli arise from a rhizoidal or stoloniferous base or a mono- or polystromatic discoid holdfast. The filament-like main axes and branches are similar and either uncorticated or corticated. The cortication may be formed by rhizoids or by short branchlets growing from the axis. Growth of the erect filaments is by transverse division of the single apical cell, and in most genera, subsequent segments are formed by longitudinal divisions below the apical region in a regular and characteristic fashion. This produces few to many longitudinal cell walls in regular transverse tiers. Secondary transverse divisions occur in the longitudinal segments of some species. There is no secondary growth in the secondary segments.

Life histories, where known, are isomorphic or slightly heteromorphic. Reproduction is by unilocular and plurilocular sporangia, which are apparently rare. There is also vegetative reproduction by propagules (e.g., *Sphacelaria* subgen. *Propagulifera*) or fragmentation, and parthenogenesis has been reported from "neutral" plurilocular and unilocular gametangia. Species are dioecious (some probably are monoecious), with plurilocular gametangia that produce isogametes or anisogametes.

REMARKS. In contrast to *Sphacelaria*, the only other genus in the Sphacelariaceae, *Sphacella* Reinke (1890), is composed of only monosiphonous filaments (lacking longitudinal divided segments or secondary transverse divisions), but this genus has not been found in the Gulf of California.

One genus is represented in the northern Gulf of California.

***Sphacelaria* Lyngbye in Hornemann**

Sphacelaria Lyngbye in Hornemann, 1818:pl. 1600.

Sphacelaria Lyngbye, 1819:xxxii, 103.

Algae are erect, terete filaments that form small, sometimes bushy, tufts that grow on rocks attached by small discoid holdfasts or are epiphytic and attached by spreading or penetrating rhizoids. Filaments may be unbranched or sparsely to densely branched with determinate or indeterminate branches and with or without corticating rhizoids. Phaeophycean hairs are commonly found on some species but are absent on others. Growth is by a usually

conspicuous meristematic apical cell on the axes and lateral branches that at first divides transversely and later divides below the initial apical segments by longitudinal divisions that produce more and smaller cells in the tiers without increasing the filament diameter. Additionally, secondary transverse divisions may occur in the longitudinal segment cells of some species. Cells have numerous discoid plastids and are without pyrenoids.

Vegetative reproduction by propagules is common in some of the species (i.e., *S.* subgen. *Propagulifera*). The features of the propagules (e.g., various sizes, shapes, and numbers of the lateral apical cells and central apical cell) are important characters for discriminating the taxa and are generally species specific. Sporophytic and gametophytic algae are nearly identical in vegetative structure. Unilocular sporangia (zoidangia), neutral plurilocular sporangia, and plurilocular gametangia are on separate individuals, or several kinds may occur together on the same alga.

REMARKS. Three species are reported in the southern Gulf. *Sphacelaria brevicornis* Setchell et N. L. Gardner (1924a, as "*Sphacelaria brevicorne*") was described from La Paz and has again been reported from there (Huerta-Múzquiz and Mendoza-González, 1985). Dawson (1944), in agreement with Setchell and Gardner (1924a), noted *S. brevicornis* from Isla Espiritu Santo was similar to *S. cornuta* Sauvageau (1901). However, Prud'homme van Reine (1982) thought *S. brevicornis* was probably the same as *S. tribuloides* but later considered *S. brevicornis* to be of uncertain taxonomic position (Prud'homme van Reine, 1993). The others were *S. divaricata* Montagne (1849; Riosmena-Rodriguez and Paul-Chávez, 1997, as "*S. didichotoma*"), and an unidentified species, reported by Rocha-Ramírez and Siqueiros-Beltrones (1991, as "*Sphacelaria* sp.").

There are four species known in the northern Gulf of California.

KEY TO THE SPECIES OF *SPHACELARIA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Propagules slender (Y-shaped), the upper end with 2(-3) projecting, long, thin, cylindrical unbranched arms (*S.* subgen. *Propagulifera* sect. *Furcigeræ*) *S. rigidula*
- 1b. Propagules without projecting arms; stout, tribuliform (more or less triangular), broader at upper end with 1 central and 2-3 lateral rounded to pointed apical cells (*S.* subgen. *Propagulifera* sect. *Tribuloides*) 2
- 2a. Axes unbranched or sparsely branched; secondary transverse walls absent within longitudinal segment cells; mature propagules with protruding, relatively pointed lateral apical cells (conical horns) *S. tribuloides*
- 2b. Axes branched, often densely, in either the upper or lower portions; secondary transverse walls absent or present within longitudinal segment cells; propagules with nonprotruding to slightly protruding lateral apical cells 3
- 3a. Main axes usually without branches in lower portions, often dense with laterals above; secondary transverse cell walls occasional within longitudinal segments; propagules with round, conical, slightly protruding lateral apical cells [Figure 52A] *S. californica*
- 3b. Main axes densely branched from base, only sparsely branched above; secondary transverse cell walls absent; propagules with 2 rectangular, nonprotruding (to barely) protruding lateral apical cells [Figure 52B] *S. hancockii*

***Sphacelaria* subgen. *Propagulifera* sect. *Furcigeræ* Prud'homme van Reine**

Sphacelaria subgen. *Propagulifera* sect. *Furcigeræ*
Prud'homme van Reine, 1982:203.

Erect filaments are irregularly branched and arise above a monostromatic discoid base or stolons or rhizoids. Lateral branches are of similar morphology to the axes and have indeterminate growth. Propagules are cylindrical with long arms. The subapical cell is divided unequally and diagonally.

***Sphacelaria rigidula* Kützing**

FIGURE 51A-C

Sphacelaria rigidula Kützing, 1843:292; Kützing, 1855:25, pl. 86: fig. 1; De Toni, 1895a:50; Prud'homme van Reine, 1982:203, figs. 508-554; R. Aguilar-Rosas and Machado Galindo, 1990:188; Yoshida et al., 1990:281; Stewart, 1991:51; González-González, 1993:443; León-Tejera and González-González, 1993:498; León-Tejera et al., 1993:200; Mateo-Cid et al., 1993:50; Prud'homme van Reine, 1993:149; Servièrre-Zaragoza

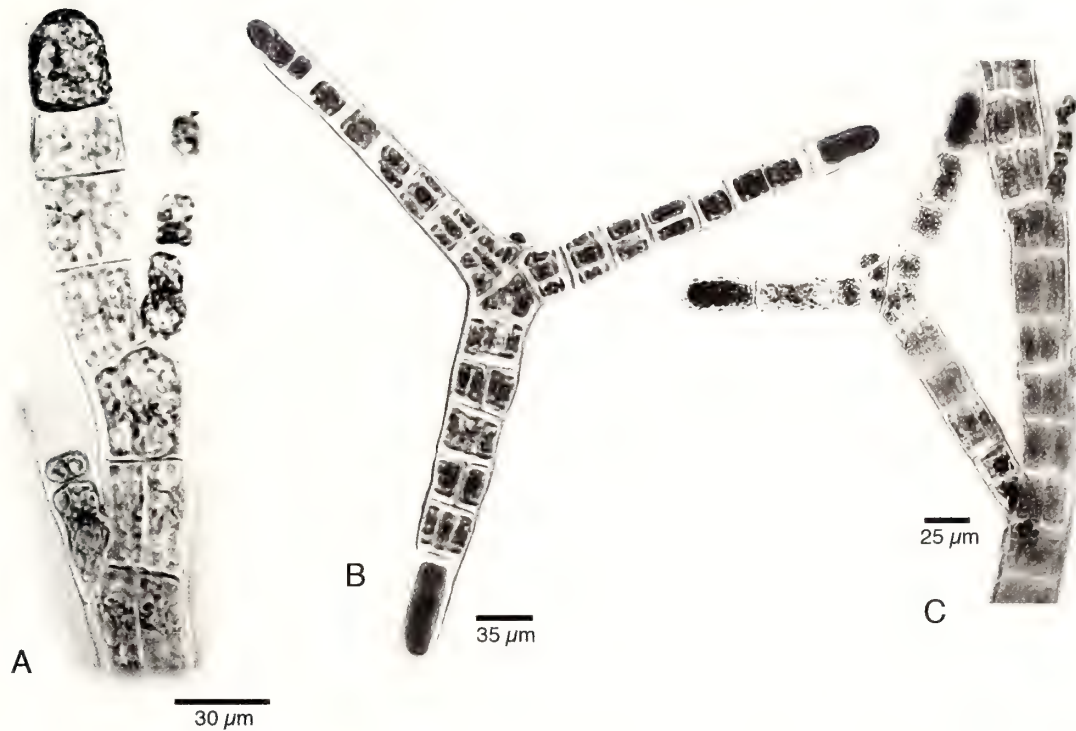


FIGURE 51. *Spacelaria rigidula*: A. Upper part of filament with prominent apical cell, below the secondary segments with longitudinal walls, and two phaeophycean hairs (JN-4041). B. Y-shaped mature propagule (JN-3271). C. Erect filament with young propagule and a phaeophycean hair (JN-3715).

et al., 1993:482; Kitayama, 1994:72, figs. 22–28; González-González et al., 1996:300; Yoshida, 1998:200, fig. 2-3 D; L. Aguilar-Rosas et al., 2000:132; Mendoza-González et al., 2000:27, figs. 34–37; L. Aguilar-Rosas et al., 2002:235; Lipkin and Silva, 2002:41; Abbott and Huisman, 2004:190, fig. 72C; López et al., 2004:10; R. Aguilar-Rosas et al., 2005b:35; Keum et al., 2005:4, figs. 1–12; Riosmena-Rodríguez et al., 2005:101; Mateo-Cid et al., 2006:49, 57; Servièrre-Zaragoza et al., 2007:8; Pedroche et al., 2008:33.

Spacelaria furcigera Kützing, 1855:27, pl. 90: fig. 2; Setchell and Gardner, 1924a:724, pl. 19: fig. 58; Setchell and Gardner, 1925:396, pl. 37: fig. 29; Setchell and Gardner, 1930:138; Dawson, 1944:224; Dawson, 1951:52; Dawson, 1954d:400, fig. 14h; Dawson, 1957b:9; Dawson, 1959a:18; Dawson, 1959c:4; Dawson et al., 1960a:10; Dawson, 1966a:10; Dawson and Neushul, 1966:174; van den Hoek and Flinterman, 1968:193; Abbott and Hollenberg, 1976:218, fig. 181; Pacheco-Ruíz, 1982:70; Stewart, 1982:54; Schnetter and Bula Meyer, 1982:59, pl. 8: fig. I; Stewart and

Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:44; Sánchez-Rodríguez et al., 1989:41; González-González et al., 1996:299; Hoffmann and Santelices, 1997:138, fig. 34.

Algae small filamentous tufts, up to 1 cm tall; axes and branches uniseriate near tips, each with a conspicuous apical cell; cells below multiseriate with 1–7 longitudinal walls per segment in side view; attached by rhizoidal filaments or discoid base. Axes sparsely, irregularly branched; axes and branches of similar diameter, (16–)25–45 μm in diameter; segments as long as or longer than wide. Secondary transverse cell walls occasional within longitudinal sections of segments. Phaeophycean hairs present.

Propagules Y-shaped; stalk basally narrowed, terminally with a slightly protruding central apical cell, and 2(–3) lateral, long, slender, cylindrical arms of more or less the same length (170–400 μm) and diameter (20–25 μm); each arm with a conspicuous apical cell. Unilocular sporangia on 1-cell pedicel, mostly spherical, 55–80 μm in diameter. Plurilocular sporangia on 1-cell pedicel,

elongate-ovoid, 55–63 μm long and 40–50 μm in diameter; two kinds, one with numerous small locules, another with fewer and larger locules (“male and female gametangia” of Setchell and Gardner, 1924a:pl. 19, fig. 58).

HABITAT. Partially endophytic within host cells and epiphytic above host surface; on various algae, notably on *Sargassum* and *Padina*, and epizoic on a parrotfish “beak” (Dawson, 1959a); mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Colorado to Ensenada de San Francisco (vicinity of Guaymas); La Paz to Punta Palmilla (vicinity of San José del Cabo). Pacific coast: Alaska to southern California; Isla Guadalupe; Punta de la Asunción, Baja California Sur to Oaxaca; Isla San Benedicto (Islas Revillagigedo); Clipperton Island; Costa Rica; Colombia; Chile; Hawaiian Islands; Korea; Japan.

TYPE LOCALITY. On *Cystoseira triquetra*, Nuweiba, Sinai, on the Gulf of Aqaba, Red Sea, Egypt.

REMARKS. *Sphacelaria rigidula* is a relatively common epiphyte during the spring in the Gulf. It has been widely reported in temperate to tropical waters as “*S. furcigera*” (Prud’homme van Reine, 1982). A Pacific coast species, *S. subfusca* Setchell et N. L. Gardner (1924b) from southern California, is morphologically close to *S. rigidula*. Although *S. subfusca* was considered to be a synonym of *S. rigidula* (Abbott and Hollenberg, 1976; Kitayama, 1994), it was kept as a separate species by Prud’homme van Reine (1982).

***Sphacelaria* subgen. *Propagulifera*
sect. *Tribuloides* Prud’homme van Reine**

Sphacelaria subgen. *Propagulifera* sect. *Tribuloides* Prud’homme van Reine, 1982:178.

Algae erect filaments, composed of axes that are more or less pinnately to irregularly branched, arising above a monostromatic or polystromatic discoid base, or stolons or rhizoids. Propagules are tribuliform (i.e., more or less triangular-shaped), broader at upper end, with 1 central and 2 lateral apical cells.

REMARKS. Keum et al. (1999) found two types of division sequences of the upper lateral apical cells of the propagule that produced their shape and number of cell segments below the propagule waist: (1) round, produced by oblique divisions to form round, conical protruding (horned) apical cells (i.e., Asian *S. californica*; see Keum et al., 1999: figs. 33–36; Figure 52A herein), and (2) rectangular, developed by an initial longitudinal and then a transverse division to form rectangular, nonprotruding

(flat) apical cells (for examples, see Keum et al., 1999: fig. 37 of Asian *S. californica* and also figs. 51–53 of Asian *S. novae-hollandica*; see also *S. hancockii* in Figure 52B herein). The number of segments under the waist of propagule (cf. Keum et al., 1999:fig. 33 versus Figure 52 herein) also affects the shape of the propagule.

Specimens of species recorded from the Gulf of California, along with type and type locality specimens of European *S. tribuloides*, southern California *S. californica*, and Gulf *S. hancockii*, need critical comparative morphological, molecular, and phylogenetic analyses to resolve their taxonomic status.

Three species are currently known in the northern Gulf of California.

***Sphacelaria californica* (Sauvageau)
Setchell et N. L. Gardner**

FIGURE 52A

Sphacelaria plumula var. *californica* Sauvageau, 1901:108, fig. 21.

Sphacelaria californica (Sauvageau) Setchell et N. L. Gardner, 1925:395, pl. 37: figs. 23–27; Abbott and Hollenberg, 1976:216, fig. 179; Boo and Chou, 1986:99, figs. 16–22; Sánchez-Rodríguez et al., 1989:41; Yoshida et al., 1990:281; Kitayama et al., 1991:189–193, figs. 1–22; Stewart, 1991:51; Prud’homme van Reine, 1993:150; Kitayama, 1994:52, figs. 7–11, 56G; González-González et al., 1996:164; Yoshida, 1998:197, fig. 2-3 G; Draisma et al., 1998:186–187, tbl. 2; Keum et al., 1999:24, figs. 1–41; Mendoza-González et al., 2000:25, figs. 12–15; L. Aguilar-Rosas et al., 2002:132; Riosmena-Rodríguez et al., 2005:101; Servière-Zaragoza et al., 2007:8; Pedroche et al. 2008 (in part; *S. californica* only):31.

Sphacelaria tribuloides sensu De A. Saunders, 1898:158, pl. 26: figs. 1–8 [non *Sphacelaria tribuloides* Meneghini, 1840:[2]].

Algae filamentous tufts, relatively stiff, up to 2.0 cm tall; main axes 25–50 μm in diameter in lower portion, widening to 60–95 μm in diameter in midportions; lower portion without laterals or only very few; attached by small polystromatic disc or, if epiphytic, by rhizoids. Upper portions of axes irregularly branched (sometimes more or less pinnate) with primary and secondary lateral branches; laterals narrowed at base. Apical cell prominent, 40–60 μm in diameter, 90–200 μm long; uppermost segments of uniseriate cells; segments below multiseriate, longitudinally divided by 1–5 walls; occasionally, longitudinal divided

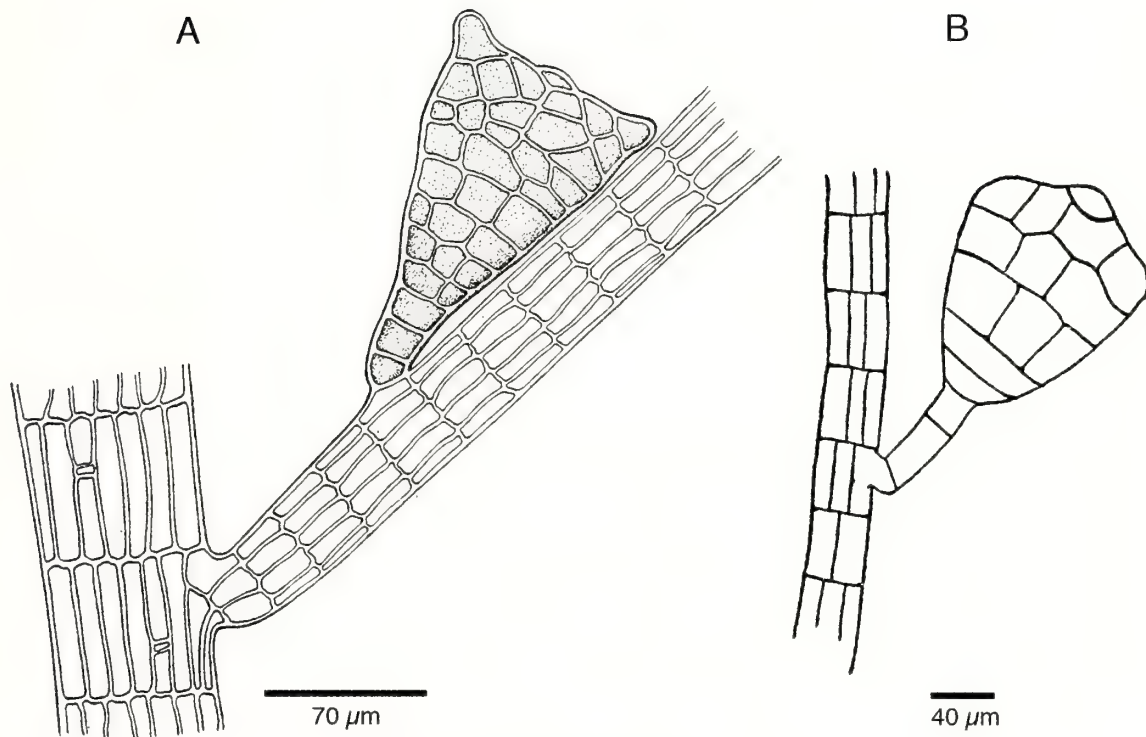


FIGURE 52. Two species of *Sphacelaria*. A. *Sphacelaria californica*: Propagule with lateral, rounded, slightly protruding apical cells and filament with both longitudinal divisions and two secondary transverse divisions in surface view (after Setchell and Gardner, 1925: pl. 37, fig. 7). B. *Sphacelaria hancockii*: Propagule with two lateral, rectangular, nonprotruding apical cells and filament without secondary transverse divisions (drawn from type specimen, EYD-[1940]-643, after Dawson, 1944: pl. 31, fig. 8).

cells with a few secondary transverse walls. Phaeophycean hairs may be absent or sparse to abundant.

Propagules ellipsoidal when young, tribuliform when mature, 140–170 μm long, 80–105 μm wide; with 1 central and 2 lateral, slightly protruding, round, conical apical cells (Figure 52A). Unilocular sporangia, spherical to oval, 40–50 μm long, 30–50 μm in diameter. Plurilocular sporangia obovate, borne on a 1-celled pedicel, 30–40 μm by 50–70 μm .

HABITAT. On rocks and in tide pools; high to mid intertidal.

DISTRIBUTION. Gulf of California: Puertecitos to San José del Cabo. Pacific coast: Isla Guadalupe; southern California to southernmost Baja California Sur; Islas Revillagigedo; Jalisco to Colima; China; Korea; Japan.

TYPE LOCALITY. San Diego, San Diego County, California.

REMARKS. Gulf records of *Sphacelaria californica* (L. Aguilar-Rosas et al., 2002; Riosmena-Rodríguez et al., 2005) were not seen by the author; the description is based on Setchell and Gardner (1925), and the sporangia

are based on Kitayama (1994). Although Kitayama et al. (1991) referred to this taxon as “*S. californica* Sauvageau ex Setchell et Gardner,” Sauvageau (1901:108) validly published this taxon as a variety, *S. plumula* var. *californica*. However, in the same publication, Sauvageau (1901:109), as “*Sphacelaria californica*?,” also suggested it was possibly a species by referring to it with a taxonomic query, but the first valid combination of the taxon as a species was made by Setchell and Gardner (1925).

***Sphacelaria hancockii* E. Y. Dawson**

FIGURE 52B

Sphacelaria hancockii E. Y. Dawson, 1944:225, pl. 31: fig. 8; Dawson, 1954e:325; Dawson, 1959a:8, 18; Dawson et al., 1960a:12; Dawson, 1961b:387; Huerta-Múzquiz and Tirado-Lizárraga, 1970:135; Huerta-Múzquiz and GarzaBarrientos, 1975:7; Stewart and Stewart, 1984:141; González-González et al., 1996:164; L. Aguilar-Rosas et al., 2000:132.

Sphacelaria mexicana W. R. Taylor, 1945:86, pl. 3: figs. 1–8; Dawson, 1954e:325; Servièrre-Zaragoza et al., 2007:8.

Sphacelaria californica sensu [in part, with reference Gulf of California *S. hancockii* specimens only] Abbott and Hollenberg, 1976:216; Mendoza-González et al., 2000:25; Pedroche et al., 2008:31 [non *Sphacelaria californica* (Sauvageau) Setchell et N. L. Gardner, 1925:395].

Small filamentous tufts, up to 12 mm tall, densely branched from base and sparsely, irregularly branched above; attached to rock by dense mat of entangled rhizoids. Erect filaments (30–)40–50(–60) μm in diameter; segments about as long as wide, with 1–3(–4) longitudinal divisions in side view, secondary transverse cell walls not seen. Phaeophyceal hairs abundant, up to 10 cells long; 0.5–1.0 mm long and to 15 μm in diameter.

Propagules bibuliform (as seen from below or the top) and tribuliform (triangular-shaped, as seen in side view), borne on pedicels of 2–3 cells, 100–110 μm long by 75–90 μm wide; upper end with 1 central and 2 lateral rectangular, flat apical cells, either not protruding (Figure 52B) or only barely protruding.

HABITAT. On rocks, sometimes entangled with other turf algae, such as *Cladophora*, *Ectocarpus*, or *Ceramium*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puertecitos to Isla Turners (off southern end of Isla Tiburón); Isla Carmen; San José del Cabo; Mazatlán, Sinaloa. Pacific coast: Isla Guadalupe; Bahía Sebastián Vizcaíno to Punta Abrejos, Baja California; Isla San Benedicto and Isla Socorro (Islas Revillagigedo); Colima to Oaxaca.

TYPE LOCALITY. San José del Cabo, Baja California Sur.

REMARKS. Dawson (1954e), in reporting *S. hancockii* from Baja California, noted that it and *S. mexicana* W. R. Taylor from Pacific Mexico both had bibuliform propagules (cf. Taylor, 1945:pl. 3: fig. 7) and considered the latter to be a synonym.

Sphacelaria hancockii may be related to *S. californica* and has been considered to be a synonym (Abbott and Hollenberg, 1976; Mendoza-González et al., 2000). However, the two differ morphologically: *S. hancockii* is densely branched basally and sparsely above; has narrower filaments, 30–60 μm in diameter; and has smaller propagules, 100–110 μm long by 75–90 μm wide. *S. californica* usually has no branches below and is densely branched above; has mostly larger diameter filaments, 40–95 μm ; and has longer propagules, 140–170 μm by 80–105 μm . Detailed studies of propagule development, along with vegetative

differences of Gulf *S. hancockii*, Gulf *S. californica*, and the type of *S. californica*, are required to determine if the characteristics differ consistently enough to be considered separate species (see Remarks under *Sphacelaria* subgen. *Propagulifera* sect. *Tribuloides*).

For now, it seems best to recognize them as different species, until more collections are made, especially of reproductive material, to facilitate detailed studies, including molecular and phylogenetic analyses to test the status of the Gulf taxon.

***Sphacelaria tribuloides* Meneghini**

FIGURE 53A–C

Sphacelaria tribuloides Meneghini, 1840:[2]; Dawson, 1959a:5, 18; Dawson, 1961b:387; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127, 130; Prud'homme van Reine, 1982:179, figs. 422–454; Huerta-Múzquiz and Mendoza-González, 1985:44; Mateo-Cid et al., 1993:50; Yoshida et al., 1990:28; Prud'homme van Reine, 1993:149; González-González, 1993:443; León-Tejera et al., 1993:204; León-Tejera and González-González, 1993:498; Servièrre-Zaragoza et al., 1993:482; Kitayama, 1994:59, figs. 12–15; González-González et al., 1996:300, 381; Yoshida, 1998:202, fig. 2-3 E; L. Aguilar-Rosas et al., 2000:132; Mendoza-González et al., 2000:28, figs. 38–41; Abbott and Huisman, 2004:190, fig. 72D,E; Mateo-Cid et al., 2006:49, 57; Pedroche et al., 2008:34.

Algae forming tufts of relatively stiff filaments; axes mostly unbranched or only sparsely, irregularly branched; axes and branches 25–50(–70) μm in diameter; attached below by discoid or stoloniferous base. Segments of axes and branches 25–60 μm in length; segments below uppermost uniseriate segments with 1–3(–5) longitudinal divisions in side view, each section 5–12 μm wide. Secondary transverse cell walls within longitudinal divided sections not present. Phaeophyceal hairs often present.

Propagules tribuliform, borne on pedicels of 1–3 cells, 90–130 μm long by 80–110 μm wide, upper end with 1 central apical cell and 2 large lateral apical cells, slightly protruding to somewhat apparent conical horns.

HABITAT. On rocks or epiphytic; intertidal.

DISTRIBUTION. Gulf of California: Playa Santa Teresa to Puerto Peñasco; Bahía Concepción to Isla San Diego. Pacific coast: Guerrero to Oaxaca; Isla Socorro (Islas Revillagigedo); Hawaiian Islands; Japan.

TYPE LOCALITY. La Spezia (Spèsa), on the Ligurian Sea, northern Italy.

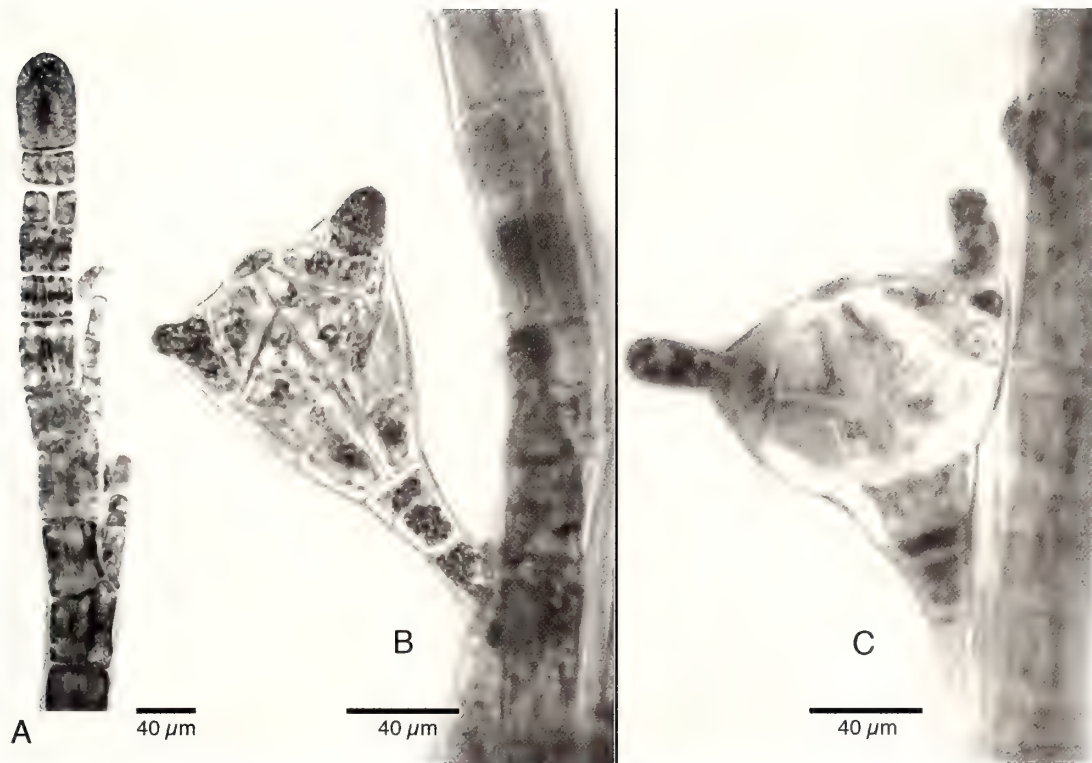


FIGURE 53. *Sphacelaria tribuloides*: A. Prominent apical cell of erect filament and secondary segments with longitudinal walls. B. Propagule with two lateral rounded protruding apical cells. C. Mature propagule with lateral apical cells elongated to conical horns. A–C. JN-4038.

REMARKS. The description of *Sphacelaria tribuloides* is based on specimens from Puerto Peñasco and on Prud'homme van Reine (1982) and Kitayama (1994).

DICTYOTALES

Dictyotales Bory de Saint-Vincent, 1828:142.

Dictyotales Kjellman, 1896:291.

Algae are erect, flattened and membranous, branched in one plane, and variously attached by a holdfast of rhizoidal filaments or by rhizoids along lower blade margin or, in a few species, by stoloniferous attachments. Growth is by an apical meristem, either a single cell, a group of apical cells, or an apical row of marginal cells. Sporophytes and gametophytes are parenchymatous in structure, with a medulla of one or more layers of large colorless cells and a single- to multiple-layer cortex of small cells with discoid plastids without pyrenoids. Phaeophycean hairs are either absent or present in bands or scattered tufts.

The life history phases, where known, are isomorphic. Sporophytes produce unilocular sporangia that are scattered or in rows or groups and with or without an

indusium or paraphyses. Each sporangium develops one, four, or eight nonmotile spores. Sexual reproduction is oogamous. Gametophytes are usually dioecious, with oogonia and antheridia usually in sori. There is one egg produced per oogonium. Antheridia are plurilocular, and each of the motile antherozoids have a single flagellum.

REMARKS. Members of this order are of widespread occurrence in tropical and subtropical seas. However, some are found in temperate seas and are particularly well developed in temperate South Australia (Womersley, 1987). On the basis of nrDNA sequences, the phylogeny of Rousseau et al. (2001) concluded the Dictyotales were the earliest lineage to diverge during the evolution of the Phaeophyceae.

The one family of the order is well represented throughout the Gulf of California.

DICTYOTACEAE

Dictyotaceae J. V. Lamouroux ex Dumortier, 1822:72, 101.

Algae are simple or branched in one plane. They can be straplike (e.g., *Dictyota*) or fanlike or bladelike (e.g.,

Padina). Structurally, they are composed of a medulla of large colorless cells in one or more layers and a cortical layer of one to several rows of small pigmented cells. Growth is by a single apical cell, group of apical cells, or marginal row of apical cells. Phaeophycecan hairs are present in tufts or zones and are simple, delicate, colorless, and mostly deciduous.

Reproductive structures are superficial on the thallus. Sporophytic reproduction is by nonmotile aplanospores, formed by sporangia that are isolated or in sori. Sporangia are mostly divided into a group of four (tetraspores) or eight (octospores) aplanospores. Oogonia are solitary or grouped in sori. Each oogonium forms a nonmotile single egg (ova). Plurilocular antheridia are grouped in sori and produce motile antherozoids.

REMARKS. Genera of the Dictyotaceae have traditionally been grouped into two taxonomic tribes, following, but not named by, Kjellman (1896): (1) the Dictyoteae Lamouroux (1809a) for genera characterized by growth from a single apical cell and (2) the Zonarieae Lamouroux (1809a) for genera with a group or marginal row of apical cells. However not all the species fit into these tribes. For example, some species of *Padina* exhibit both kinds of growth, with a “*Vaughaniella*-form” that has growth by a single apical cell and can undergo a morphogenetic change to growth by a marginal row of apical cells (Lewis et al., 1987). Sulfuric acid accumulation has been reported in some species of *Dictyopteris*, *Spatoglossum*, and *Zonaria* C. Agardh (1817) (Sasaki et al., 1999), and its presence or absence has been suggested to be an informative taxonomic character (Sasaki et al., 2004, 2005).

The genera *Dictyota*, *Dilophus* and *Rugulopteryx* are morphologically similar, separated primarily on the basis of their vegetative anatomy. *Dictyota* sensu stricto is distinguished by both a single-layered medulla and cortex throughout (Figure 54B). *Dilophus* sensu stricto has a medulla of two or more layers and a cortex of one cell layer. *Rugulopteryx* has a one cell layer medulla centrally and two or more layers in the margins, and a cortex of one-cell layer (Figure 54D).

More recent phylogenetic analysis has shown *Glossophora*, *Glossophorella* and *Pachydictyon* to be congeneric

with *Dictyota*, and revealed two genera, *Canistrocarpus* and *Rugulopteryx*, that could be distinguished from *Dictyota* (De Clerck et al., 2006; Hwang et al., 2009). However, the taxonomic status of *Dilophus* J. Agardh (1882) remains problematic. Setchell and Gardner (1925) and Hörnig et al. (1992a, 1992b, 1993) concluded that the medulla character alone was not enough to separate *Dilophus* and included it in *Dictyota*. Others have retained *Dilophus* (e.g., Dawson, 1950a; Womersley, 1987; Phillips, 1992; Huisman, 2000). Phillips (1992) recognized that the number of cells in the stalk that bears a sporangium (one or two-cells) in Australian *Dilophus* was of taxonomic importance, and some molecular phylogenies have supported their generic separation (e.g., Hoshina et al., 2004; Kraft et al., 2004). De Clerck et al. (2006) kept the two genera separate, noting this cannot be resolved until the generitype, *Dilophus gunnianus* J. Agardh (1882), has been studied.

Next to *Sargassum*, species of the Dictyotaceae, notably *Dictyota* and *Padina* are among the most abundant brown algae in the Gulf. In addition to the genera known in the northern Gulf, there are three others known in the southern Gulf: *Lobophora* J. Agardh (1894), with the report of *L. variegata* (J. V. Lamouroux) Womersley ex E. C. Oliveira (1977) by Dawson (1959a, as “*Pocockiella variegata*”) and Mateo-Cid et al. (2000b); *Taonia* J. Agardh (1848) with the record of *T. lennebackerae* Farlow ex J. Agardh (1894) by Mateo-Cid et al. (2002b); and *Dilophus* J. Agardh (1882) with the report *Dilophus pinnatus* E. Y. Dawson (1950a; = *Dictyota pinnata* (E. Y. Dawson) Hörnig, Schnetter et Prud’homme von Reine, 1993) (Espinoza-Ávalos, 1993; Mateo-Cid et al., 2000a, 2000b), and elsewhere in Pacific Mexico from Nayarit (León-Tejera et al., 1993; González-González, 1993), Jalisco (Pedroche and González-González, 1981; Servière-Zaragoza et al., 1993) and Michoacán (Stout and Dreckmann, 1993), and in South America from Pacific Colombia (Schnetter and Bula Meyer, 1982). In West Africa, material identified as *Dilophus pinnatus* was noted to be a growth form of *Padina durvillei* (Lawson and John, 1987).

There are five genera of Dictyotaceae represented in the northern Gulf of California.

KEY TO THE GENERA OF DICTYOTACEAE IN THE NORTHERN GULF OF CALIFORNIA

FIGURE 54A-I

- 1a. Thallus of flat, repeatedly branched straplike segments; growth from a single apical cell [Figure 54A] 2
- 1b. Thallus of flat, broad unbranched to branched fronds or blades; growth from a single clustered group of apical cells [Figure 54E] or separate groups of clustered apical cells [Figure 54G] or a continuous marginal row of apical cells [Figure 54I] 3

- 2a. Medulla usually a single cell layer with cortex of 1–2 cell layers [Figure 54B] or a medulla of 2–4 cell layers with cortex of 2–5 cell layers [Figure 54C] *Dictyota*
- 2b. Medulla 1 cell layer in central portion and 2–8 cell layers at the branch margins; cortex of 1 cell layer throughout [Figure 54D] *Rugulopteryx*
- 3a. Fronds with conspicuous midrib [Figure 54E]; internally of 1 or more cell layers at margins, increasing number of cell layers toward center of blade (midrib) [Figure 54F] *Dictyopteris*
- 3b. Fronds without midribs; internally, cell layers not increasing in number toward center of blade 4
- 4a. Fan-shaped or cup-shaped blades, sometimes lobed or torn; with distinctive inrolled margins [Figure 54I]; noncalcified or slightly to heavily calcified *Padina*
- 4b. Fronds irregularly divided or branched, narrow to broadly lanceolate; without inrolled margins [Figure 54G]; not calcified *Spatoglossum*

***Dictyopteris* J. V. Lamouroux**

FIGURE 54E,F

Dictyopteris J. V. Lamouroux, 1809d:332.

Algae are erect or prostrate and are generally clumped and composed of flat fronds in one plane or twisting and attached by a thickened, discoid to conical holdfast of compacted rhizoids. Branching pattern is subdichotomous to irregular. Fronds and branches are generally straplike, up to 25 mm wide, and have a pronounced midrib, up to 30 cells thick. Lateral veins are present in some but are lacking in the northern Gulf species. Growth is by an apical group of up to 15 cells. There is a single layer of small cortical cells, each with several chloroplasts, and a multi-layered medulla of larger cells. The midrib is conspicuous and much thicker, of 8–30 cells. The thallus wings (on each side of the midrib) are multilayered in most species (Figure 54F) and only 2 cell layers in a few of the species. Phaeophycean hairs are mostly scattered in groups over the surfaces.

Reproductive structures are solitary, in groups, or in sori and either embedded or projecting above both sides of the thallus surface. Sporophytes have subspherical to ovoid sporangia that are solitary or borne in sori that are scattered over the branches or near the midrib, are without a stalk or on one- to two-celled stalks, and produce a tetrad of spores. Gametophytes are dioecious. Oogonia are solitary or in small groups. Antheridia are composed of many tiered locules in large, whitish sori and are surrounded by one to three layers of sterile cells.

REMARKS. Among the Gulf's brown algae, *Dictyopteris* is most easily recognized by its straplike, subdichotomously branched fronds with conspicuous midribs. Sasaki et al. (1999) used presence or absence of sulfuric acid to separate morphologically similar species

of *Dictyopteris* and suggested it was a useful taxonomic character (Sasaki et al., 2004, 2005).

Two of the smaller, distromatic species have been reported in the southern Gulf: *Dictyopteris delicatula* J. V. Lamouroux (1809d), (Huerta-Múzquiz and Mendoza-González, 1985; Rocha-Ramírez and Siqueiros-Beltrones, 1991; Mateo-Cid et al., 2000b; Riosmena-Rodríguez et al., 2005; Mendoza-González and Mateo-Cid, 2005); and *D. repens* (Okamura) Børgesen (1924) by Dawson (1959b). Another, *D. polypodioides* (de Candolle) J. V. Lamouroux (1809b; see Silva et al. 1987), has been reported from Isla Guadeloupe and Pacific Baja California (Dawson, 1950d; Stewart and Stewart, 1984, both as *D. membranacea* (Stackhouse) Batters 1902).

One species is known in the northern Gulf of California.

***Dictyopteris undulata* Holmes**

FIGURE 55

Dictyopteris undulata Holmes, 1896:251, pl. 8: fig. 1; Abbott, 1972:260, fig. 1; Abbott and Hollenberg, 1976:212, fig. 176; Devlin, 1978:358; Huerta-Múzquiz, 1978:336; Lewbel et al., 1981:165; L. Aguilar-Rosas, 1982:31; Stewart and Stewart, 1984:141; Mendoza-González and Mateo-Cid, 1985:24; Benson, 1986:448; Sánchez-Rodríguez et al., 1989:40; R. Aguilar-Rosas et al., 1990:123; Stewart, 1991:48; Rocha-Ramírez and Siqueiros-Beltrones, 1991:32; Martínez-Lozano et al., 1991:23; Lluch-Cota et al., 1993:336; Mateo-Cid and Mendoza-González, 1994a:50; Kajimura, 1995:89; González-González et al., 1996:145; Pacheco-Ruiz and Zertuche-González, 1996b:171; Tanaka, 1998:75, figs. 1–15; Yoshida, 1998:211; Mateo-Cid et al., 2000b:196, figs. 13, 14, 64, 65, 94; Mendoza-González and Mateo-Cid, 2005:57, figs. 60–69; Mateo-Cid et al., 2006:49,

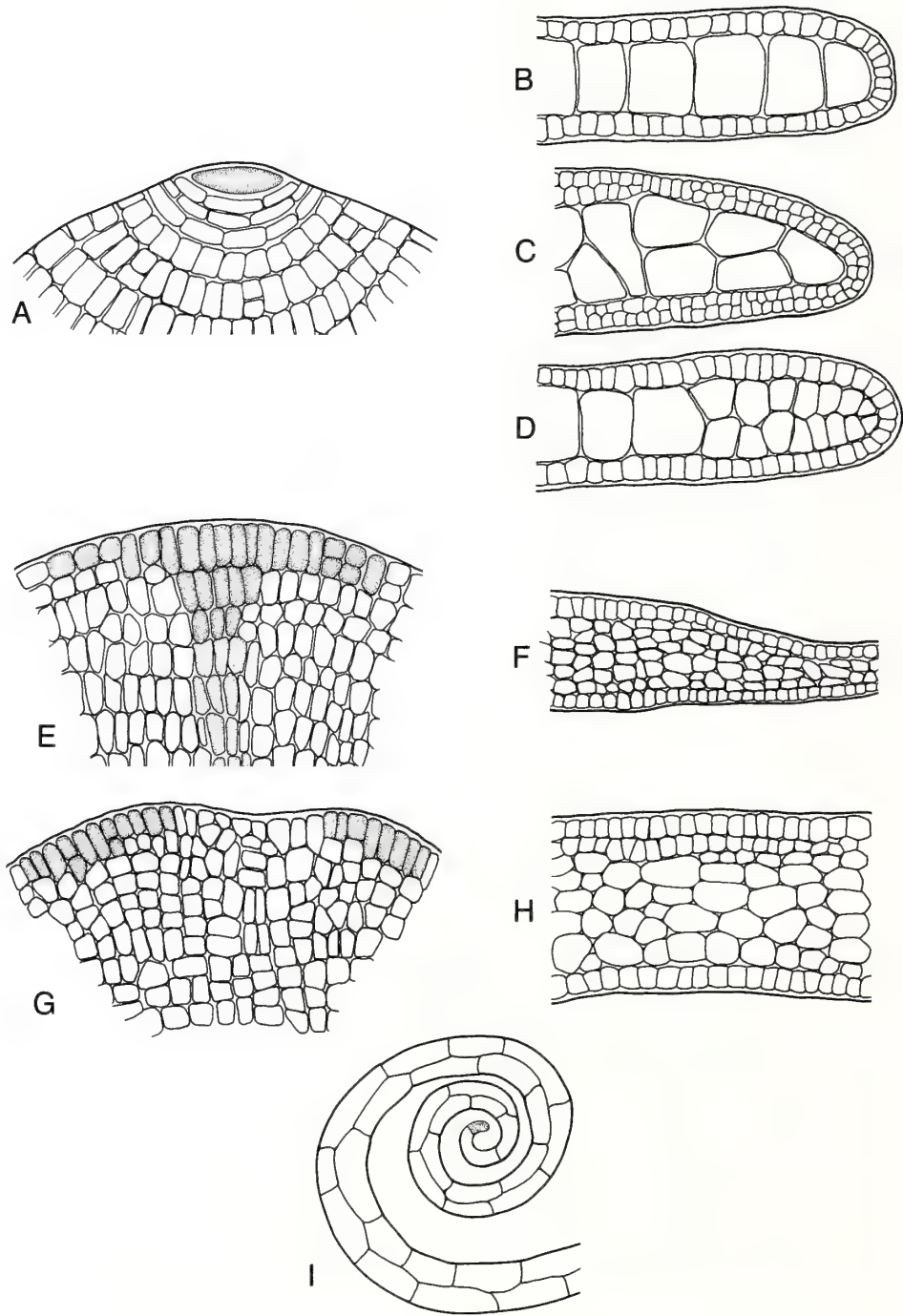


FIGURE 54. Northern Gulf of California genera of Dictyotaceae: Comparative diagrammatic illustrations of the apical growth region (meristematic cells stippled) and transections of internal anatomy. A. *Dictyota* and *Rugulopteryx*: Growth from single apical cell. B. *Dictyota* transection: Most species have single medullary layer surrounded by single layer of pigmented cortical cells. C. *Dictyota* transection: A few species (e.g., *D. coriacea*) may have more than one medullary cell layer at margins and more than one cortical cell layer. D. *Rugulopteryx* transection: One medullary cell layer centrally and more than one medullary cell layer at the margins, and a single cortical cell layer. E. *Dictyopteris*: Growth from a group of apical cells at center of distal blade margin. F. *Dictyopteris* transection: With thicker medulla at center midrib and progressively fewer cell layers outward toward the margins. G. *Spatoglossum*: Growth from separate groups of apical cells along distal margin of blade. H. *Spatoglossum* transection: Medullary layers of irregularly arranged cells and single cortical cell layer. I. *Padina*: Longitudinal section of inrolled margin: Growth from an apical row of meristematic cells along entire distal edge of blade, which is enclosed within the inrolled margin. Number of cell layers below single apical row is initially one and then becomes two (as shown); in Gulf species, the medullary cell layers increase in number toward the central portions and basal region of the blade (drawn by Alice R. Tangerini).

57; Pacheco-Ruiz et al., 2008:203; Pedroche et al., 2008:36.

Haliseris undulata (Holmes) Okamura, 1899b: Exsiccata No. 41; Okamura, 1902a:110; Okamura, 1907:51, pl. XI: figs. 1–10.

Neurocarpus undulata (Holmes) Okamura, 1928:190 [Corrigenda]; Okamura, 1936:172, fig. 88 (1–5).

Dictyopteris polypodioides sensu Hariot, 1891:217 [non *Dictyopteris polypodioides* (de Candolle) J. V. Lamouroux, 1809d:332].

Haliseris polypodioides sensu McClatchie, 1897:354 [non *Haliseris polypodioides* (de Candolle) C. Agardh, 1820:142; = *Dictyopteris polypodioides* (de Candolle) J. V. Lamouroux, 1809d:332].

Dictyopteris zonarioides Farlow, 1899:73; Dawson, 1951:52; Dawson, 1952:431; Dawson, 1959a:18; Dawson et al., 1960a:34, pl. 3: fig. 4, pl. 4: fig. 2; Dawson et al., 1960b:11; Dawson, 1961b:388; Dawson,

1966a:11; Guzmán del Prío et al., 1972:260; Norris, 1973:4; Fenical et al., 1973:2383; Espinoza-Ávalos, 1993:332; González-González et al., 1996:145.

Neurocarpus zonarioides (Farlow) M. Howe, 1914:69; Setchell and Gardner, 1924a:728; Setchell and Gardner, 1925:656, pl. 34: fig. 4, pl. 35: fig. 11, pl. 36: fig. 21, pl. 38: fig. 39, pl. 95; Dawson, 1944:229.

Algae erect, flat, irregularly dichotomously branched fronds, up to 35 cm tall, (3–)10–20 mm wide, with a prominent percurrent midrib and lacking any veins, often with undulate margins; ultimate branches shorter than lower segments; with rounded apices; arising from a more or less conical holdfast. In lower portions the wider blade may be worn away, leaving the midribs. Midribs may be tomentose. Thallus in transverse section up to 12 layers of cells and up to 400 μm thick. Growth from an apical group of meristematic cells.



FIGURE 55. *Dictyopteris undulata*: Habit; note the prominent midrib (JN-5801).

Sporangia grouped in sori, 750–1000 μm long, along both sides of the midrib. Oogonial and antheridial sori scattered over frond. Oogonium 95–150 μm tall by 95–125 μm wide.

HABITAT. On rocks, usually in shaded areas and tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to San José del Cabo. Pacific coast: southern California to Baja California Sur; Japan; China; Taiwan.

TYPE LOCALITY. Misaki, Kanagawa Prefecture, central Japan.

REMARKS. A seasonal species, *Dictyopteris undulata* occurs in the northern Gulf from February to August and appears to reach its peak in size as well as in numbers of individuals in late spring. Although previously collected during 1972–1975 at Punta la Gringa (vicinity of Bahía de los Ángeles), *D. undulata* was not encountered during the 1985–1986 surveys of Pacheco-Ruíz and Zertuche-González (1996b).

Some of the Gulf specimens with narrow fronds resemble *Dictyopteris johnstonei* N. L. Gardner (1940), a species described from Santa Cruz Island (California Channel Islands) and reported southward to Bahía de Todos Santos, Pacific Baja California (Silva, 1957; Mateo-Cid et al., 2000b; Mendoza-González and Mateo-Cid, 2005; Pedroche et al., 2008), and Isla San Benito (Dawson, 1961b; Abbott and Hollenberg, 1976). Silva (1957) has suggested the taxonomic status of California *D. johnstonei* Gardner (1940) needs to be resolved. Reinvestigations should include Gulf specimens morphologically similar to Pacific coast *D. johnstonei* (including its type locality) in comparative morphological studies and molecular analyses, to each other, and to the distinctive *D. undulata* of the Gulf, Japan (type locality), and Pacific coast (including type locality specimens of *Neurocarpus zonarioides*, considered a synonym of *D. undulata*).

***Dictyota* J. V. Lamouroux**

FIGURE 54A–C

Dictyota J. V. Lamouroux, 1809a:38.

Dictyota J. V. Lamouroux, 1809d:331.

Glossophora J. Agardh, 1882:108.

Glossophorella Nizamuddin et Campbell, 1995:258.

Pachydictyon J. Agardh, 1894:81.

Algae are erect or repent (prostrate), composed of flat ribbonlike fronds that are clumped or bushy in

appearance, and yellow- to dark brown, and some are iridescent. Branching may be regularly or irregularly dichotomous or alternate throughout; branches are up to 20 mm wide, with smooth, dentate, crenulate, or ciliate margins and usually obtuse apices. Most species are attached by a single, or several rhizoidal holdfasts, although a few species are attached by stoloniferous holdfasts. Secondary attachments may occur in some when thallus or its branches come in contact with the substratum. Phaeophycean hairs and surface proliferations may be present in tufts scattered over the thallus. Growth is by a single apical cell at the tip of each rounded or acute branch apex. The medulla of one or more layers of large colorless cuboidal cells is easily differentiated from the cortex of one or more layers of small pigmented cells, each with numerous discoid chloroplasts.

Reproductive structures are mostly in sori (some with solitary sporangia), scattered and protruding from both sides of the thallus surface. Sporangia, borne on a single stalk cell, are divided into four aplanospores and may be solitary, grouped in sori, or around hair tufts, over the upper portions of the frond. Gametangia are grouped in sori. Oogonia are in rows within sori, with each oogonium on a single stalk cell. Antheridia are produced in whitish, antheridial sori. Each antheridium, also on a single stalk cell, is composed of many tiers of locules and is surrounded by hyaline, elongated sterile cells.

REMARKS. Some members of *Dictyota* exhibit wide morphological variation, and this phenotypic plasticity and few taxonomic characters have resulted in confusion regarding discrete differences among many of the species. The taxonomic limits of Gulf species are poorly known, but “typical” forms of each can be recognized in the field. Detailed observations, temporal and spatial, on field populations will be helpful in understanding the morphological variation. Culture and life history studies and molecular analyses will aid in understanding species and phylogenetic relationships. Monographic studies of the genus in the Gulf and Pacific Mexico, such as those of De Clerck (1999, 2003) for the Indian Ocean and De Clerck et al. (2006), are critically needed.

Three species, all originally described from the western Atlantic, are recorded in the southern Gulf: *D. bartayresiana* J. V. Lamouroux (1809a) reported by Mateo-Cid et al. (2000b) and L. Aguilar-Rosas et al. (2000); “*D. cervicornis*” reported by Mateo-Cid et al. (1993, 2000b) and Cruz-Ayala et al. (2001) (note that *D. cervicornis* Kützing (1859) is now *Canistrocarpus crispatus* (J. V. Lamouroux) De Paula et De Clerck in De Clerck et al., 2006); and “*D.*

volubilis” reported by Huerta-Múzquiz and Mendoza-González (1985), Rocha-Ramírez and Siqueiros-Beltrones (1991), Cruz-Ayala et al. (2001), and Riosmena-Rodríguez et al. (2005) (note that *D. volubilis* Kützinger (1849)

is now *D. dichotoma* (Hudson) J. V. Lamouroux, 1809a; see De Clerck, 2003).

Currently seven species, including one variety, are recognized in the northern Gulf.

KEY TO THE SPECIES OF *DICTYOTA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Medulla of 2–4 (or more) cell layers; cortex of (1–)2–5 cell layers [Figure 54C] *D. coriacea*
 1b. Medulla usually 1 cell layer; cortex of only 1(–2) cell layer(s) [Figure 54B] 2
 2a. Thalli decumbent overlapping fronds; of short, relatively broad segments. *D. conrescens*
 2b. Thalli erect, fronds of strap-shaped segments 3
 3a. Frond margins with minute denticulations *D. crenulata*
 3b. Frond margins smooth or sometimes with marginal proliferations 4
 4a. Attached by spreading, simple to divided, terete, stoloniferous growths, up to 500 µm in diameter *D. stolonifera*
 4b. Attached by filamentous rhizoids, sometimes compacted into a holdfast 5
 5a. Fronds irregularly dichotomously branched (resulting from some branch segments growing longer than others)
 *D. flabellata*
 5b. Fronds dichotomously branched throughout (more or less even in lengths) 6
 6a. Fronds usually more than 5 mm wide; branched at angles usually less than 45°; margins entire or sometimes with marginal proliferations *D. vivesii*
 6b. Fronds narrower, less than 4 mm wide; branched at wide angles (mostly 90°–120°); margins entire
 *D. dichotoma* var. *intricata*

Dictyota conrescens W. R. Taylor

FIGURE 56A,B

Dictyota conrescens W. R. Taylor, 1945:89, pl. 10: fig. 2; Dawson, 1950a:92; Dawson, 1961b:388; Salcedo-Martínez et al., 1988:82; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Cruz-Ayala et al., 2001:190; Riosmena-Rodríguez et al., 2005:101; Pedroche et al., 2008:38.

Dictyota friabilis sensu Dawson, 1954d:401, fig. 16a,b; Dawson et al., 1960b:6, 14; Dawson, 1961b:388; Dawson, 1962b:190, fig. 50; Dawson, 1966a:12; Dawson, 1966b:56; Stout and Dreckmann, 1993:7; González-González et al., 1996:146; Silva et al., 1996b:234; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:203, figs. 31–34, 100; Mateo-Cid et al., 2006:49; Pedroche et al., 2008 (in part):43 [non *Dictyota friabilis* Setchell, 1926:91 (see De Clerck and Coppejans, 1999:tbl. 1; De Clerck, 2003:89)].

Algae decumbent, often forming low-growing mats of overlapping, delicate, short, and broad blades, up to 5 cm long and 6 mm wide; subdichotomously branched, with one segment of the dichotomy usually larger and

longer than the other; blades occasionally attached to each other by, usually marginal, rhizoids; base attached to substratum by masses of rhizoids. Transection 90–110 µm thick. Cortex a single layer of cortical cells, 5–18 µm tall by 10–14 µm in diameter. Medulla a single layer of large cells, 48–50 µm tall by 60–80 µm in diameter.

Sporangia globose, up to 160 µm in diameter, scattered over thallus. Oogonia scattered on surface in upper portions of branches; 90–110 µm tall by 80–85 µm in diameter.

HABITAT. Creeping, low growing, and loosely attached; often overgrowing other turf algae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de La Paz; Punta Arena to Cabo Pulmo. Pacific coast: Islas San Benito (off Baja California) to Bahía Magdalena (Baja California Sur); Rocas Alijos (west of Baja California Sur); Michoacán to Oaxaca.

TYPE LOCALITY. Punta Hughes (vicinity of Bahía Magdalena), about 5.6 km (3.5 miles) southeast of Cabo San Lázaro, Baja California Sur, Mexico.

REMARKS. Gulf specimens are in general agreement with Pacific Mexico *Dictyota conrescens* (Taylor, 1945); thus, for now, they are referred to this taxon. However, it has been noted that the type specimen of

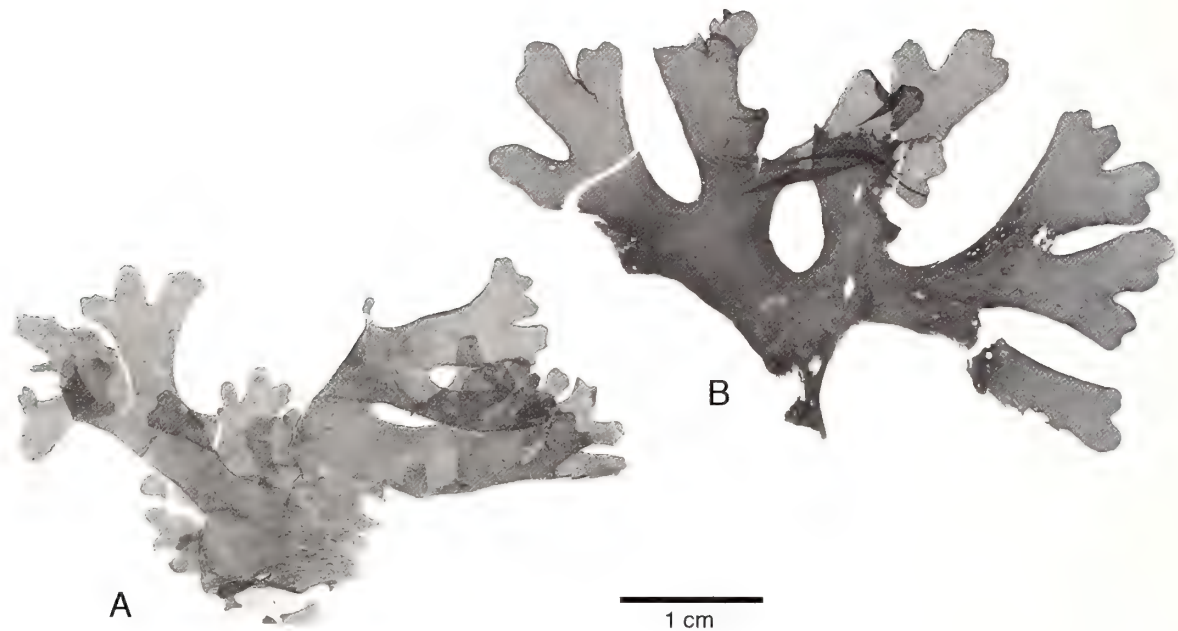


FIGURE 56. *Dictyota conrescens*: Low-growing, relatively broad, subdichotomously branched to subpalmate thalli. A. Isotype specimen (W. R. Taylor 34-598). B. Habit (JN-4695).

D. conrescens may be inadequate for clear interpretation (Dawson, 1950a). Although Cribb (1954) observed *D. conrescens* to be similar to another low-growing species, *D. friabilis* Setchell (1926), the northern Gulf *D. conrescens* differs in the field from *D. friabilis*, primarily in lacking its pale-bluish iridescent color (often with non-iridescent longitudinal stripes and/or noniridescent broad transverse bands; see De Clerck, 2003:89; De Clerck et al., 2005:104, fig. 75). Comparative morphological studies and molecular and phylogenetic analyses that include type locality *D. conrescens* and Gulf of California specimens are needed to clarify its taxonomic status.

***Dictyota coriacea* (Holmes)
Hwang, H. S. Kim et W. J. Lee**

FIGURE 57

Glossophora coriacea Holmes, 1896:251.

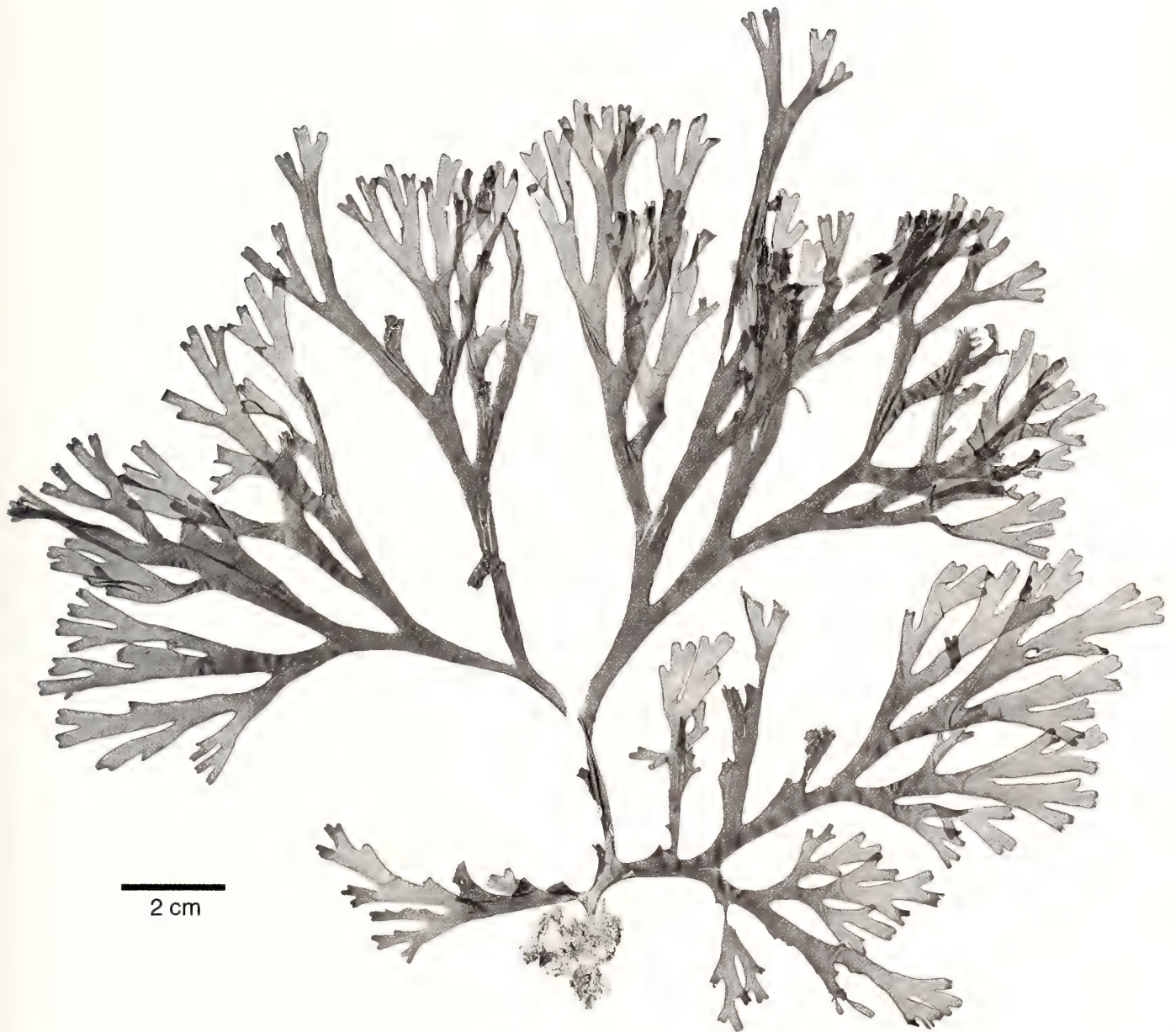
Dictyota coriacea (Holmes) Hwang, H. S. Kim et W. J. Lee, 2004:189; De Clerck et al., 2006:1285.

Pachydictyon coriaceum (Holmes) Okamura, 1899a:39, pl.1: figs. 31–34; Okamura, 1907:105, pl. 23: figs. 1–6, pl. 24: figs. 1–18; Okamura, 1936:165, fig. 84 (1–5);

Dawson, 1950a:85–86; Dawson, 1950b:67; Dawson, 1950e:268; Dawson, 1951:52; Dawson, 1959a:18; Dawson et al., 1960a:38, pl. 3: figs. 1–2; Dawson et al., 1960b:8–11; Kumagai, 1969:91, text figs. 1–4, pl. [1]: figs. 1–15; Norris, 1973:5; Abbott and Hollenberg, 1976:209, fig. 173; Norris and Bucher, 1976:4; Devinny, 1978:358; Littler and Littler, 1981:149, fig. 2; L. Aguilar-Rosas, 1982:31; Lewbel et al., 1981:162; Pacheco-Ruíz, 1982:70; Mendoza-González and Mateo-Cid, 1985:24; L. Aguilar-Rosas and Pacheco-Ruíz, 1989:81; Sánchez-Rodríguez et al., 1989:40; R. Aguilar-Rosas and Machado-Galindo, 1990:188; R. Aguilar-Rosas et al., 1990:123; Stewart, 1991:49; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:518; Mateo-Cid and Mendoza-González, 1994a:50; González-González et al., 1996:155; Pacheco-Ruíz and Zertuche-González, 1996b:171; Yoshida, 1998:223, pl. 2–4: fig. D, pl. 2–9: fig. C; Mendoza-González et al., 1999:59; Mateo-Cid et al., 2000b:205, figs. 41–44, 78, 101; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:46.

Glossophorella coriacea (Holmes) Nizamuddin in Nizamuddin and Campbell, 1995:259, fig. 3.

Dictyota johnstonii Setchell et N. L. Gardner, 1924a:730, pl. 18: figs. 54–56, pl. 39; Setchell and Gardner,



2 cm

FIGURE 57. *Dictyota coriacea*: Habit (JN-5522).

1925:653; Dawson, 1944:228 [in part]; Norris, 1973:5; Pacheco-Ruíz et al., 2008:203.

Pachydictyon binghamiae (J. Agardh) E. Y. Dawson, 1950a:84; León-Tejera and González-González, 1993:497; González-González et al., 1996:155 [non *Dictyota binghamiae* J. Agardh, 1894:72 (see Dawson, 1950e:267–268; Hollenberg and Abbott, 1966:19[629];

Abbott and Hollenberg, 1976:209, fig. 173; De Clerck, 2003:164, 182)].

Algae erect, olive-brown to dark brown, coriaceous, of flat, straplike, subdichotomously branched fronds, up to 25 cm tall and to 13 mm wide; multilayered medulla and cortex, 400–500 μm thick (in transection); attached

by a fibrous holdfast of rhizoidal cells developed from lower portion of the main axes. Branches mostly with one of the branch segments longer than the other above the dichotomous division (occasionally of more or less uniform length); margins smooth; branch apices rounded, with a conspicuous single large apical cell. Cortical cells 15–24 μm tall by 30–45 μm wide; 1–2 cortical cell layers toward the center of blade; 2–4 (or more) cell layers in blade margins of mid to upper portions of the thallus, often with more cortical cell layers in blade margins of the lower portion. Medulla of large cells, 75–145 μm tall by 140–195 μm wide; 1–2(–3) cell layers toward the center and 2–4 (or more) cell layers near blade margins.

Reproductive structures scattered on both surfaces of the upper branches. Sporangia solitary or in groups; 62–70 μm tall by 45–60 μm in diameter. Dioecious (where known). Oogonia aggregated in elliptical to elongate, dark-brown to “blackish” sori; 85–117 μm tall by 77–94 μm in diameter. Antheridia unknown in Gulf material (as reported in Japan: in numerous oval, whitish sori).

HABITAT. On rocks; mid intertidal to 10 m depths.

DISTRIBUTION. Gulf of California: Bahía de Los Ángeles to Isla San Ildefonso; Cabo San Lucas. Pacific coast: Oregon; central California to Bahía Magdalena, Baja California Sur; Oaxaca; Panama; China; Taiwan; Korea; Japan.

TYPE LOCALITY. Enoura, “neighborhood of Tokio [Tokyo]” (Holmes, 1896:149), Kanagawa, Honshū, Japan.

REMARKS. Gulf *Dictyota coriacea* may be separated in the field from other Gulf *Dictyota* species by its larger size, thicker fronds, darker color, and relatively coarser texture. Its Gulf distribution appears to be restricted to the central Gulf, Las Islas de la Cintura (Midriff Islands), and a few of the southern islands.

There has been some taxonomic confusion regarding the name of the Gulf specimens. Initially Dawson (1950a) concluded that the Japanese *Pachydictyon coriaceum* (Holmes) Okamura was a synonym of Californian *P. binghamiae* (J. Agardh) Dawson, but he later (Dawson, 1950e) discovered that the type of *Dictyota binghamiae* J. Agardh was a different taxon and those he previously identified as “*P. binghamiae*,” including Gulf material, were *P. coriaceum*. Since then, this interpretation has been followed (e.g., Hollenberg and Abbott, 1966; Abbott and Hollenberg, 1976).

De Clerck (2003) noted that additional research on taxa of Dictyotaceae with a multilayered cortex, such as *Pachydictyon* J. Agardh (1894), was needed to clarify their relationship with *Dictyota*. Hwang et al. (2004) studied

both Japanese and Korean *P. coriaceum* and, on the basis of molecular analyses, concluded them to be a species of *Dictyota* and restricted the distribution of *D. coriacea* to the western Pacific. Therefore the Gulf of California *D. coriacea* and the eastern Pacific *D. coriacea* (southern California; Pacific Mexico) need to be comparatively tested with the western Pacific (eastern Asia) *D. coriacea* (type locality: Japan) to see if they are the same species as currently understood. These studies should include type material of *Dictyota johnstonii* Setchell et N. L. Gardner (1924a), currently considered a synonym of *D. coriacea*. If Gulf specimens are found to be a species separate from the Japanese type locality *D. coriacea*, *D. johnstonii* would be the earliest valid name for the Gulf taxon.

Dictyota crenulata J. Agardh

FIGURE 58A,B

Dictyota crenulata J. Agardh, 1847:7; Setchell and Gardner, 1924a:730, pl. 18: figs. 50, 51; Setchell and Gardner, 1925:655; Taylor, 1939:8; Dawson, 1944:228; Taylor, 1945:90, pl. 10: fig. 1; Dawson, 1950a:88; Dawson, 1954a:3; Dawson, 1959a:5, 18; Dawson, 1961b:388; Brusca and Thomson, 1975:42; McEnroe et al., 1977:184; Huerta-Múzquiz and Mendoza-González, 1985:46; Salcedo-Martínez et al., 1988:82; Santelices, 1989:289, pl. GG: fig. 7; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Lluch-Cota et al., 1993:366; León-Tejera and González-González, 1993:497; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994b:43; González-González et al., 1996:294, fig. 16; Anaya-Reyna and Riosmena-Rodríguez, 1996:383; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:199, figs. 20, 21, 71, 96; Cruz-Ayala et al., 2001:190; De Clerck, 2003:145, 166; Riosmena-Rodríguez et al., 2005:101; Altamirano-Cerecedo and Riosmena-Rodríguez, 2007:575, figs. 1–6; Servièrre-Zaragoza et al., 2007:8; Pedroche et al., 2008:39.

Dilophus crenulatus (J. Agardh) Nizamuddin et Gerloff, 1979:867, pl. 1: figs. 1, 2, pl. 2: figs. 1, 2, pl. 7: figs. 1, 2 [note: lectotype (LD, Herb. Agardh-49042A) is illustrated in pls. 1, 2, 7].

Algae up to 15(–25) cm tall, of flat, dichotomously branched straplike fronds, (1–)2–4(–5.5) mm wide; margins with characteristic, conspicuous minute dentation; attached by multicellular rhizoids. Branching usually at wide angles; sometimes becoming subdichotomous;

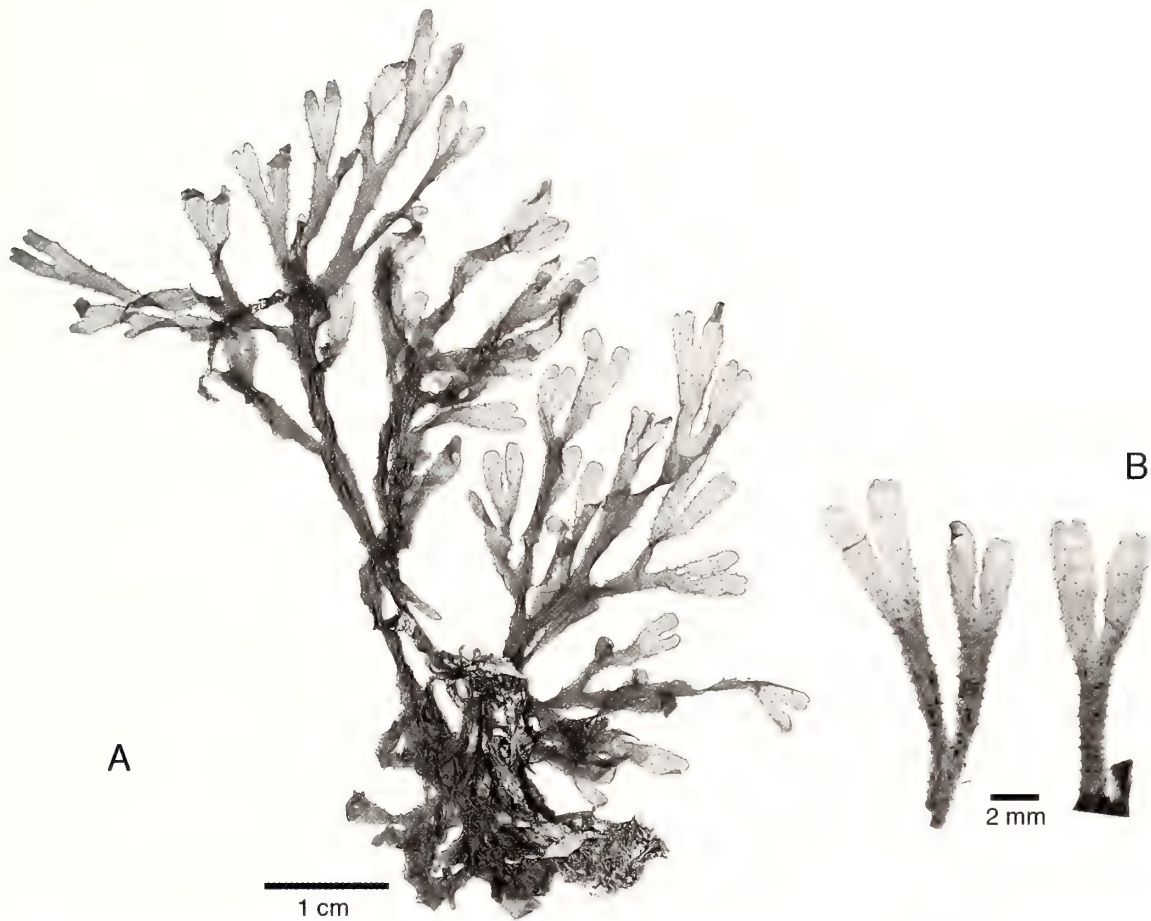


FIGURE 58. *Dictyota crenulata*: A. Habit (JN-4091a). B. Close-up of blades with characteristic dentate margins (JN-4114).

branches narrower below and widening upward; surface sometimes with numerous proliferations. Transection of 3–6 cell layers (1–4 medulla: 2 cortical), 90–150 μm thick, up to 500 μm thick near base. Cortex a single layer; cortical cells rounded, 20–50 μm in diameter. Medulla single layer to multilayered (latter evident in basal portion); medullary cells 55–100 μm tall by 35–50 μm wide.

Reproductive structures mostly in sori, scattered over branch surface, mostly in upper portions. Sporangia may be singular or a few in sorus, rounded, 75–90 μm in diameter. Oogonia in groups of 30–45 (in surface view), 4–6 (in transection view) in sori; 75–80 μm tall by 66–70 μm in diameter.

HABITAT. On rocks; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía Concepción to Cabo San Lucas. Pacific coast: Bahía Vizcaíno

to Todos Santos, Baja California Sur; Islas Revillagigedo; Jalisco to Oaxaca; Costa Rica; Chile.

TYPE LOCALITY. San Agustín, Oaxaca, Mexico (Agardh, 1847, “St. Augustin, Stilla Oceanen [Pacific Ocean]”).

REMARKS. Described from southern Pacific Mexico, *Dictyota crenulata* may reach its northern distribution limit in the central Gulf of California (Dawson, 1950a, 1961b). Altamirano-Cerecedo and Riosmena-Rodríguez (2007) found that thalli of Gulf *D. crenulata* near its northern limit (central Gulf) were shorter and wider than those of the southern Gulf, which were longer and narrower. Setchell and Gardner (1924a:730, pl. 18: fig. 50) and Dawson (1944) observed numerous small surface proliferations on specimens of Gulf *D. crenulata* that were developing in situ sporelings, apparently from germination of their spores. More recently, Altamirano-Cerecedo

and Riosmena-Rodríguez (2007) quantified surface and marginal proliferations.

***Dictyota dichotoma* var. *intricata*
(C. Agardh) Greville**

FIGURE 59A–C

Zonaria dichotoma var. *intricata* C. Agardh, 1820:134.

Dictyota dichotoma var. *intricata* (C. Agardh) Greville, 1830:58; Schnetter et al., 1987:193, figs. 2, 3; De Clerck, 1999:176, figs. 23A–C, 24A–E, ApI-12; De Clerck, 2003:76, figs. 23A–C [23B, holotype of *D. divaricata*], 24A–E; Servièrre-Zaragoza et al., 2007:8.

Dictyota divaricata J. V. Lamouroux, 1809b:43; Taylor, 1945:90 (as “*D. divaricata*, *prox.*”); Dawson, 1950a:91; Dawson, 1959a:18; Dawson, 1961b:388; Dawson, 1961c:407, pl. 11: fig. 2; Dawson, 1966a:12; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Chávez B., 1972:268; Pedroche and González-González, 1981:67; Schnetter and Bula Meyer, 1982:65, pl. 9: figs. E–G; Stewart and Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:40; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Mateo-Cid et al., 1993:50; González-González, 1993:443; León-Tejera and González-González, 1993:497; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994b:34; González-González et al., 1996:294; Pacheco-Ruíz and Zertuche-González, 1996b:171; León-Tejera and González-González, 2000:328; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:201, figs. 25–27, 98; Cruz-Ayala et al., 2001:190; L. Aguilar-Rosas et al., 2002:235; Hernández-Herrera et al., 2005:146; Dreckmann et al., 2006:154; Mateo-Cid et al., 2006:49; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:41.

Algae of erect, flat, dichotomously branched fronds, up to 4(–8) cm tall and 1.5–3(–4) mm wide; attached by rhizoids. Fronds branched with long and narrow dichotomies, often at wide angles; more or less uniform width throughout or narrower at each dichotomy upward and narrowest at apices. Transection 90–100 μm thick. Medulla and cortex, each a single layer of cells. Cortical cells 15–18 μm tall by 12–16 μm wide; medullary cells 60–75 μm tall by 54–56 μm wide.

Sporangia single on a stalk cell, scattered on both surfaces of frond. Oogonia 90–95 μm tall by 82–86 μm in

diameter; in sori without an indusium, scattered on upper portions of both surfaces. Antheridia unknown in Gulf specimens.

HABITAT. On rocks or occasionally entangled with other algae; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo San Lucas. Pacific coast: Isla Guadalupe; Punta Pequeña, Baja California Sur to Islas Revillagigedo; Jalisco to Chipas; Colombia.

TYPE LOCALITY. Cádiz, Spain.

REMARKS. Northern Gulf specimens previously called “*Dictyota divaricata*” are for now referred to *D. dichotoma* var. *intricata* on the basis of their morphological similarity, until needed comparative culture and molecular studies can be done to elucidate their taxonomic status. There still is much taxonomic and nomenclatural confusion regarding the “*Dictyota dichotoma* complex,” including *D. divaricata*. Hörnig and Schnetter (1988) concluded western Atlantic “*D. divaricata*” differed from those of the European Atlantic *Dictyota dichotoma*-complex and described them as a separate species, *D. pulchella* Hörnig et Schnetter. Further, there is some evidence that *D. dichotoma* (Hudson) J. V. Lamouroux (1809a) is restricted to warm-temperate and cold-temperate waters of the eastern Atlantic Ocean and Mediterranean Sea (Schnetter et al., 1987; De Clerck, 2003) and subtropical waters of the Canary Islands (Tronholm et al., 2008), and *D. dichotoma* var. *intricata* could be restricted to warm-temperate and subtropical regions of the Indian Ocean (De Clerck, 2003: 81).

Although some Gulf of California specimens are somewhat morphologically similar to *D. ceylanica* Kützling (1859), that species is apparently restricted to the tropical to subtropical Pacific and Indian oceans (De Clerck, 2003). Further, De Clerck (2003) has shown *D. dichotoma* var. *intricata* can be separated from *D. ceylanica* by its surface proliferations, size of thallus, and size of medullary and cortical cells; this separation is confirmed by molecular studies of De Clerck et al. (2001).

***Dictyota flabellata* (Collins)
Setchell et N. L. Gardner**

FIGURE 60

Dilophus flabellatus Collins in Collins, Holden and Setchell, 1901a:No. 834.

Dictyota flabellata (Collins) Setchell et N. L. Gardner, 1924b:12 [in part, excluding Monterey, California,

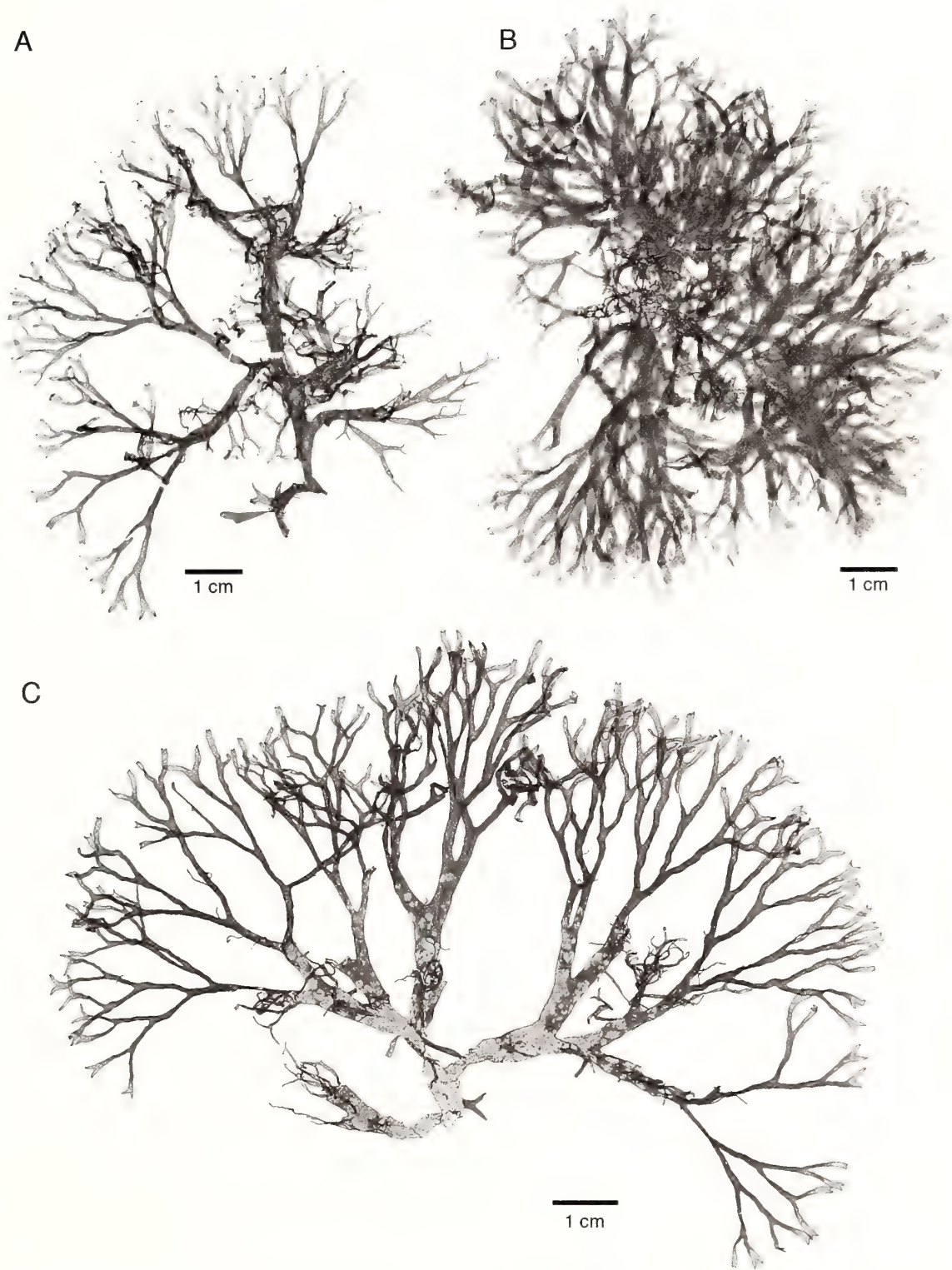


FIGURE 59. *Dictyota dichotoma* var. *intricata*: Specimens representing variation in morphology. A, C. Blade width distinctly narrows at dichotomies upward toward apices (A, JN-4087; C, JN-4094). B. Blade width with more gradual narrowing toward apices (JN-5630).

specimens]; Setchell and Gardner, 1925:652 [in part, excluding Monterey, California, specimens], pl. 34: fig. 3, pl. 35: fig. 7, pl. 36: figs. 13–17; Dawson, 1950a:89; Dawson, 1952:431; Dawson, 1959a:10, 18; Dawson et al., 1960a:34, pl. 3: fig. 3; Dawson, 1961b:388; Dawson, 1966a:12; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Earle, 1972:85; Norris, 1973:5; Brusca and Thomson, 1975:42; Abbott and Hollenberg, 1976:207, fig. 172; Robertson and Fenical, 1977:1071; McEnroe et al., 1977:182; Devinny, 1978:385; Littler and Littler, 1981:151, tbl. 3; figs. 4, 7; Lewbel et al., 1981:165; L. Aguilar-Rosas, 1982:31; L. Aguilar-Rosas et al., 1982:54; R. Aguilar-Rosas, 1982:84; Littler and Arnold, 1982:309; Pacheco-Ruiz, 1982:70; Stewart and Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:24; Mendoza-González and Mateo-Cid, 1986:421; Sánchez-Rodríguez et al., 1989:40; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Stewart, 1991:48; Martínez-Lozano et al., 1991:23; León-Tejera and González-González, 1993:497; Mateo-Cid et al., 1993:50; Lluch-Cota et al., 1993:366; Mateo-Cid and Mendoza-González, 1994a:50; González-González et al., 1996:146; Pacheco-Ruiz and Zertuche-González, 1996b:171; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Riosmena-Rodríguez et al., 1998:25; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000b:202, figs. 28–30, 74, 75; L. Aguilar-Rosas et al., 2002:235; De Clerck, 2003:150; Abbott and Huisman, 2003b:182, figs. 21, 22; Abbott and Huisman, 2004:204, fig. 77D; Riosmena-Rodríguez et al., 2005:101; Mateo-Cid et al., 2006:49, 57; Pacheco-Ruiz et al., 2008:203; Pedroche et al., 2008:42.

Dictyota hesperia Setchell et N. L. Gardner, 1924a:731, pl. 18: figs. 52, 53; Dawson, 1944:228; Dawson, 1950a:85, 89.

Dictyota johnstonii sensu Dawson, 1944:228 [in part]; Dawson, 1950e:268 [non *Dictyota johnstonii* Setchell et N. L. Gardner, 1924a:730, which is *Dictyota coriacea* (Holmes) Hwang, H. S. Kim et W. J. Lee, 2004].

Algae of one to several erect, straplike fronds, dichotomously branched up to 7 orders; up to 15 cm tall and 4–10(–15) mm wide; 120–135 μm thick; with smooth surfaces, entire margins, and rounded branch apices; attached by discoid holdfast of densely compacted rhizoids. Cortex and medulla each a single cell layer. Cortical cells 12–15 μm tall by 18–20 μm in diameter; medulla cells 60–90 μm tall by 75–76 μm wide.

Reproductive structures in sori, scattered on both surfaces of mid to upper portions of fronds. Dioecious.

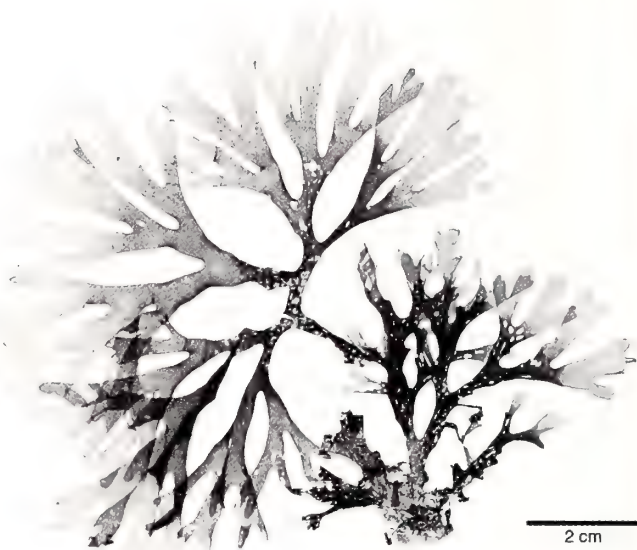


FIGURE 60. *Dictyota flabellata*: Habit (JN-3474).

Oogonia 90–96 μm tall by 85–90 μm in diameter; in groups of up to 30 in sori with indusium. Antheridial sori, 63–65 μm tall by 250–360 μm wide; antheridia 57–60 μm tall by 18–20 μm wide.

HABITAT. On rocks or rarely epiphytic on other algae; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: El Tornillal to Cabo Pulmo. Pacific coast: central California to southern Baja California Sur; Jalisco; Oaxaca; Panama; Hawaiian Islands.

TYPE LOCALITY. La Jolla, San Diego County, California.

REMARKS. The most common species of *Dictyota* in the northern Gulf of California, *D. flabellata* has been found growing from January to August. Individual fronds apparently do not persist throughout the entire season, but rather, successive generations continue to replace one another. Dawson (1950a) noted Taylor's (1945) specimens of "*D. flabellata*" from Costa Rica were probably "*D. dichotoma*" and "*D. flabellata*" from Pacific Panama were *D. coriacea*.

Dictyota stolonifera E. Y. Dawson

FIGURE 61A–C

Dictyota stolonifera E. Y. Dawson, 1962d:392, pl. 5: fig. A; González-González et al., 1996:147; De Clerck,

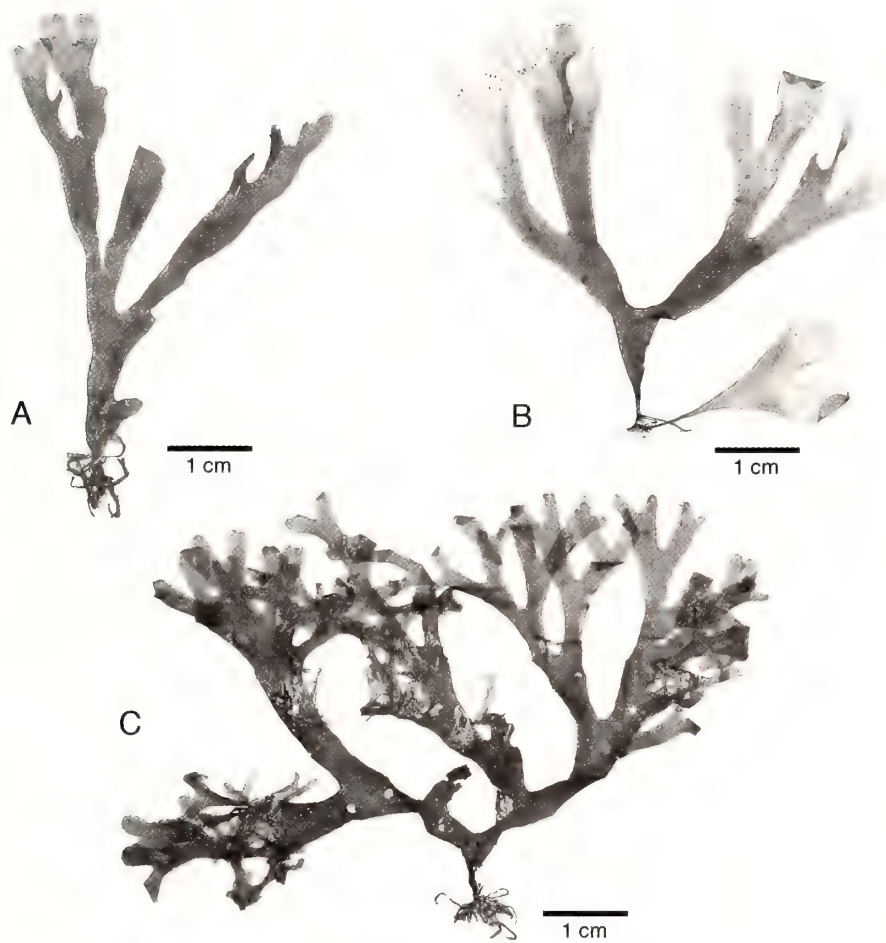


FIGURE 61. *Dictyota stolonifera*: Several thalli, each with basal stolons. A. JN-3865a. B. JN-4113a. C. EYD-27409.

2003:136, figs. 51A–E, 52A–E; Abbott and Huisman, 2003b:182; Abbott and Huisman, 2004:206, fig. 78C.

Dilophus stoloniferus (E. Y. Dawson) Schnetter et Bula Meyer, 1982:62, pl. 9: figs. H–O.

Algae of 1 to several, subdichotomously branched, flat straplike fronds, up to 6 cm tall and 3–4 mm wide, above a short compressed stipe, and attached to substratum by distinctive multilayered, stoloniferous growths, up to 500 μm in diameter. Branches lack proliferations, with smooth surface and hair tufts; margins entire; terminal portions of similar width as rest of frond (not reduced); rounded apices with concentric growth bands (not always evident), 600–1200 μm wide. Medulla a single cell layer, and 2 or more cell layers at margins; some medullary cell walls with secondary thickenings. Cortex a single cell layer of small pigmented cells.

Reproductive structures apparently scattered. Sporangia 70–100 μm in diameter, solitary or in small groups; each borne on a single stalk cell. Oogonia in scattered sori, up to 200 μm in diameter. Antheridia not seen.

HABITAT. On rocks and tidal platforms and in tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco. Pacific coast: Costa Rica; Nicaragua; Isla Gorgona Parque Nacional, Colombia; Hawaiian Islands.

TYPE LOCALITY. Intertidal; volcanic reef, Masachapa, Pacific Nicaragua.

REMARKS. *Dictyota stolonifera* can be distinguished in the field from other species of Gulf *Dictyota*, primarily by its simple to divided stoloniferous attachment growths. An eastern Pacific species, it has also been reported in the Indian Ocean (Copejans et al., 2000; De Clerck, 2003). Species limits of *D. stolonifera* need to

be tested, as it may include more than one taxon. Also, the generic status of *D. stolonifera* needs to be reinvestigated as the species had also been placed in *Dilophus*. Although it is very similar to *Rugulopteryx*, its sporangia are on two-celled stalks, whereas those of *D. stolonifera* are reported to be on one-celled stalks.

***Dictyota vivesii* M. Howe**

FIGURE 62

Dictyota vivesii M. Howe, 1911:497, pl. 27; Setchell and Gardner, 1925:654; Dawson, 1944:229; Taylor, 1945:89; Salcedo-Martínez et al., 1988:82; Stout and Dreckmann, 1993:7; González-González et al., 1996:147.

Dictyota dichotoma sensu Dawson, 1950a:90; Dawson, 1954d:401, fig. 15; Dawson, 1959a:18; Dawson,

1961b:388 [in part]; Martínez-Lozano et al., 1991:23; Mateo-Cid et al., 2000b:200, figs. 22–24, 72; Mateo-Cid et al., 2006:49; Pedroche et al., 2008 (in part):39 [non *Dictyota dichotoma* (Hudson) J. V. Lamouroux, 1809d:331; basionym: *Ulva dichotoma* Hudson, 1762:476].

Algae of 1 or more erect, straplike to oblong fronds, up to 15 cm tall and 5–8 mm wide; branching up to 10 orders, mostly dichotomously branched in lower portions, becoming subdichotomous upward; attached by a fibrous holdfast. Branches in mid to upper portions 135–160 μm thick; basal portion up to 240 μm thick; mostly with entire margins; apices mostly 1–2 mm wide. Medulla cells thin walled, 95–250 μm tall by 55–115 μm wide. Cortical cells elongated, 19–65 μm tall by 10–30 μm wide.

Sporangia in sori, scattered over frond surfaces. Gametangial structures not described by Howe (1911)



FIGURE 62. *Dictyota vivesii*. Habit (EYD-10938).

(Oogonia without indusium, in small groups on surface among hairs; oogonium pyriform, 80–93 µm tall and 60–75 µm in diameter. Antheridial sori 340–360 µm wide, antheridia 36–55 µm tall and 18–25 µm in diameter [after Mateo-Cid et al., 2000b, as “*D. dichotoma*”]).

HABITAT. On rocks and occasionally in tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de La Paz; San José del Cabo. Pacific coast: Baja California; Islas Revillagigedo; Michoacán.

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California.

REMARKS. Described from the southern Gulf, *Dictyota vivesii* has been confused with “*D. dichotoma*” (e.g., Dawson, 1944, 1950a). Although *D. dichotoma* has been extensively reported worldwide in tropical and subtropical areas, *D. dichotoma* sensu stricto is probably restricted to the northeast Atlantic and Mediterranean Sea (De Clerck, 1999, 2003).

While large specimens of *Dictyota vivesii* are readily recognized, smaller forms can be difficult to separate from some specimens of *D. flabellata* (Dawson, 1950a, as “*D. dichotoma*”). In the northern Gulf, *D. vivesii* is less frequent in occurrence than *D. flabellata*, and as with other *Dictyota* taxa of the Gulf, it is in need of critical study, including molecular and phylogenetic analyses, to elucidate its taxonomic status. Some “*Dictyota dichotoma*” specimens of Rocha-Ramírez and Siqueiros-Beltrones (1991), Servièrre-Zaragoza et al. (1993), Pacheco-Ruíz and Zertuche-González (1996b), L. Aguilar-Rosas et al. (2000), and Pacheco-Ruíz et al. (2008) may also belong here.

Padina Adanson

FIGURE 54I

Padina Adanson, 1763:13, 586; Silva, 1952:298–299; Papenfuss, 1977:275.

Algae are composed of one to several flat, fanlike or cup-shaped blades that sometimes are clumped together, basally attached by branched rhizoids compacted into a conical holdfast or rhizoids along lower blade margins. Blades may be entire, split, or eroded, with conspicuous (rarely faint) concentric lines or bands of phaeophyceal

hairs on one or both sides of the blade. Growth is by a continuous row of apical cells within an inrolled margin along the terminal edge of blade (herein the upper [dorsal] side of the blade is defined as the side that the inrolled margin is curled toward, and the back of the roll [opposite side] is referred to as the lower [ventral] side). Depending on the species, blades are two to many cell layers thick, and some vary from few near the inrolled margin to more numerous cell layers toward their base. Species may be uncalcified or lightly to moderately calcified on one or both sides of the blade. Internally, there is a medulla of one to several layers of large colorless cells and a cortex of a single cortical layer of pigmented cells on each side of the blade.

Sporangia are scattered in patches or in sori in concentric zones between the concentric bands of hairs. Gametophytes are usually dioecious. Oogonia are in sori between the hair lines. Antheridia are in sori, across from the oogonial sori in monoecious species, and in between the concentric zones of hairs in dioecious species.

REMARKS. Lewis et al. (1987) found two distinct morphologies in a species of *Padina*. In experimental field studies, small, turf-forming, narrow *Vaughaniella* Børgesen (1950; see Cribb, 1951) (= *Dictyerpa* Collins, 1901; = “*Dilophus*-like”) thalli were found in the presence of fish herbivory. However, in the absence of herbivory the *Vaughaniella*-form of the same individual thallus, through a morphogenetic change, rapidly developed directly into the fan-shaped *Padina*. Allender and Kraft (1983) noted creeping “*Vaughaniella* stages” in some of the Australian species of *Padina*. Culture studies of vegetative propagation in a Japanese *Padina* similarly showed a growth form that initially developed from a single apical cell and then developed meristems along its margin (Kajimura, 1993). Thus, some species of *Padina*, but apparently not all, have a morphologically different “*Vaughaniella*” form in their development, and the presence or absence of this morphogenetic growth form may prove helpful in the taxonomy of *Padina*.

Three species are recorded in the southern Gulf (Cruz-Ayala et al., 2001; Riosmena-Rodríguez et al., 2005; Ortuño-Aguirre and Riosmena-Rodríguez, 2007); *Padina concrescens* Thivy (in Taylor, 1945), *P. sanctae-crucis* Børgesen (1914), and *P. ramonribae* Ávila-Ortiz et Pedrocche (2005).

Six taxa, five species and one variety, are known in the northern Gulf of California.

KEY TO THE SPECIES OF PADINA IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Blades forming low-growing clustered rosettes; calcified, often overlapping and attached to each other and to substratum by rhizoids (without a stipe or holdfast) *P. mexicana* var. *mexicana*
- 1b. Blades erect, calcified or noncalcified, with a stipe and holdfast 2

- 2a. Blades 4–8 cell layers thick in mid to lower portions (2–6 medullary; 2 cortical) 3
 2b. Blades 8 or more cell layers thick in lower portions (6–16 medullary; 2 cortical) 4
 3a. Blades up to 15 cm tall, usually as wide as or wider than tall; slightly calcified; lower portion of 6–8 cell layers (4–6 medullary; 2 cortical) *P. gymnospora*
 3b. Blades up to 5 cm tall, torn or with divisions narrower than tall; noncalcified to lightly calcified (mostly on upper side); mid to lower portion of 4–6 cell layers (2–4 medullary; 2 cortical); short stipe up to 5 mm long *P. mexicana* var. *erecta*
 4a. Blades thick (300–450 μm thick), noncalcified, dark-brown; somewhat leathery; lower portion of 8–18 cell layers (6–16 medullary; 2 cortical) *P. durvillei*
 4b. Blades thinner (130–250 μm thick), noncalcified to lightly calcified; light-brown to olive-green; lower portion of 7–12 cell layers (5–10 medullary; 2 cortical) 5
 5a. Blades calcified on lower side near margins (noncalcified on upper side); with a stipe up to 5 mm long; lower portion of blade of 8–10 cell layers (6–8 medullary; 2 cortical); 130–200 μm thick *P. crispata*
 5b. Blades noncalcified to lightly calcified on both sides; with a long, conspicuous stipe, up to 2 cm long; lower portion of blade 9–12 cell layers (7–10 medullary; 2 cortical); 220–250 μm thick *P. caulescens*

Padina caulescens Thivy

FIGURE 63A,B

Padina caulescens Thivy in W. R. Taylor, 1945:99; Dawson, 1957b:11, fig. 3 (type specimen); Dawson, 1959a:5, 18; Dawson, 1961b:389; Dawson, 1961c:407, pl. 7: fig. 2; Dawson, 1962b:200, fig. 82; Chávez B., 1980:48; Mendoza-González and Mateo-Cid, 1986:421; Mateo-Cid et al., 1993:50; León-Tejera et al., 1993:200; González-González, 1993:443; Servière-Zaragoza et al., 1993:482; Mendoza-González et al., 1994:110; González-González et al., 1996:155, fig. 18; L. Aguilar-Rosas et al., 2000:132; Ávila-Ortiz and Pedroche, 2005:143, figs. 1 (isotype), 2–5; Hernández-Herrera et al., 2005:146; Pedroche et al., 2008:48.

Padina durvillei sensu Mateo-Cid et al., 2000b:208 [in part] [non *Padina durvillei* Bory de Saint-Vincent, 1827a:591].

Algae of 1 to several, entire to much divided, noncalcified to lightly calcified flabellate blades; up to 20 cm tall and to 15 cm wide; arising from a conspicuous flattened stipe, up to 2 cm long and to 1.5 mm thick (at lowermost portion), above a stupose rhizoidal holdfast. Blades often divided by repeated splitting; subdivisions up to 8 cm long and 0.5–1.5 cm wide; with zones of hairs about 1 mm apart (when present) on lower surface and opposed to hair lines on upper surface. Near inrolled margins, blades of 2 cell layers, up to 45 μm thick; midportions of 6–8 cell layers; lower portion of blade (7–)9–12 cell layers; 220–250 μm thick at base. Cortical cells 20–25 μm tall by 20–40 μm wide. Medullary cells in midportion up to 20–30 μm tall by 40–64 μm wide; in lowermost portion (16–)20–30 μm tall by 50–75(–100) μm wide.

Gametophytes dioecious. Oogonia single or paired in sori, up to 250 μm wide; in more or less continuous or broken bands between hair lines on blade surface. Antheridia in sori; patchy, more or less scattered on blade surface.

HABITAT. Low intertidal to shallow subtidal, down to 7(–9) m depths.

DISTRIBUTION. Gulf of California: Playa El Coloradito to Bahía Agua Verde. Pacific coast: Isla María Magdalena (Islas Tres Marías), Nayarit; El Salvador; Costa Rica.

TYPE LOCALITY. Isla María Magdalena, Islas Tres Marías, Nayarit, Pacific Mexico.

REMARKS. Mateo-Cid et al. (2000b), without comment, listed *Padina caulescens* as a synonym of *P. durvillei*. Ávila-Ortiz and Pedroche (2005) recognized *P. caulescens* as a distinct species but restricted its distribution to Isla María Magdalena, noting other Pacific coast herbarium specimens, previously identified as “*P. caulescens*,” belonged to other species.

While in general agreement with tropical Pacific Mexico *P. caulescens* sensu stricto, the northern Gulf specimens herein referred to *P. caulescens* have shorter stipe-like regions, up to 2 cm in length versus 5–6 cm lengths reported by Ávila-Ortiz and Pedroche (2005). Gulf of California *P. caulescens* needs to be further studied and molecularly and phylogenetically compared to type locality *P. caulescens* to test their taxonomic status.

Padina crispata Thivy

FIGURE 64A–C

Padina crispata Thivy in W. R. Taylor, 1945:100; Dawson, 1957b:10, fig. 2 (type specimens); Dawson, 1959a:4–6; Dawson, 1961b:389; Dawson, 1962b:200, fig. 82;

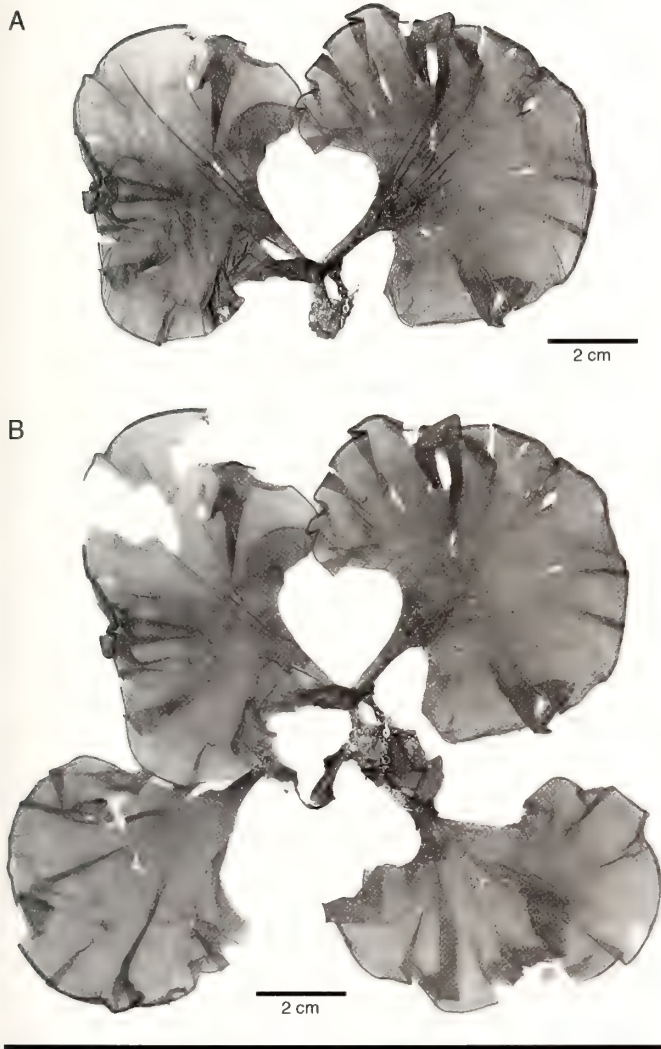


FIGURE 63. *Padina caulescens*: A. Habit (JN-4748). B. Clump of four blades; note the flattened, relatively long stipe of each blade (JN-4748).

Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Chávez B., 1972:268; Huerta-Múzquiz and Garza-Barrientos, 1975:7; Chávez B., 1980:47; Schnetter and Bula Meyer, 1982:64, pl. 10: fig. H; Huerta-Múzquiz and Mendoza-González, 1985:46; L. Aguilar-Rosas and R. Aguilar-Rosas, 1993:202; González-González, 1993:443; León-Tejera and González-González, 1993:497; Mateo-Cid et al., 1993:50; Stout and Dreckmann, 1993:7; Ávila-Ortiz and Pedroche, 1999:357, figs. 1–5; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000b:207, figs. 45, 46, 79, 103; López et al., 2004:10; Ávila-Ortiz and Pedroche, 2005:146, figs. 6 (isotype), 7–23; Servièrre-Zaragoza et al., 2007:8; Pedroche et al., 2008:48.

Padina tetrastromatica sensu Setchell and Gardner, 1930:149 [with a query], pl. 8: fig. 41; Chávez B., 1980:49; Dawson, 1961b:389 [with a query]; Servièrre-Zaragoza et al., 1993:482; González-González et al., 1996:156; Ávila-Ortiz and Pedroche, 1999:355 [non *Padina tetrastromatica* Hauck, 1887:43, which is *Padina antillarum* (Kützinger) Piccone, 1886:36 (see Wynne, 1998b:271; Wynne and De Clerck, 1999:286, figs. 1–10)].

Algae flat, erect flabellate blades, up to 6.0 cm tall and to 6 cm wide; uncalcified on upper side of blade, calcified on upper portion of lower side of blade; blade margins entire to divided or torn, into narrow crispate lobed blades, 1–4 cm wide; with a distinct stipe 0.5(–1.0) cm long and up to 1.0 mm thick; attached by stupose rhizoidal holdfast. Hair lines in zones 0.75 to 3.0 mm apart, either opposite on both sides of blade or only on upper surface. Outer margin near inrolled margins of 2 cell layers, 30–48 μ m thick, shortly becoming 2–4 cell layers, 65–120 μ m thick; midportion of 4–6 cell layers, 120–130 μ m thick; lower portion of 6–8(–9) layers, 160–220 μ m thick. Cortical cells: upper side 15–25 μ m tall by 10–20 μ m wide; lower side (12.5–)17–25 μ m tall by 20–30 μ m wide. Medullary cells 20–50(–65) μ m tall by 45–75(–105) μ m wide.

Sporangia 116–160 μ m tall by 63–75 in diameter; in sori without an indusium; on lower surface of blade; in irregular rows or scattered between hair zones. Oogonial sori, linear to round, up to 250 μ m in diameter, with a complete indusium when immature, later indusium only partially covering or absent; oogonia up to 69 μ m tall by 33–58 μ m in diameter. Antheridial sori up to 690 μ m, with an indusium; on lower surface in lines or patches; antheridia 50–67 μ m long by 19–30 μ m wide (after Ávila-Ortiz and Pedroche, 1999, 2005).

HABITAT. Intertidal.

DISTRIBUTION. Gulf of California: Playa El Coloradito; Bahía Concepción to Cabeza Ballena. Pacific coast: Punta Banda (Baja California) to Laguna San Ignacio (Baja California Sur); Isla Socorro (Islas Revillagigedo); Isla María Madre (Islas Tres Marias); Nayarit to Oaxaca; El Salvador; Costa Rica; Panama; Colombia.

TYPE LOCALITY. Gulfo Dulce, Pacific Costa Rica.

REMARKS. Ávila-Ortiz and Pedroche (1999) found Pacific Mexico specimens that had been identified as “*Padina tetrastromatica*” were actually *P. crispata*. Their Pacific Mexico specimens were calcified along the inner side of the inrolled margins, whereas Dawson (1957b) noted that the blades of Costa Rican *Padina crispata* had noncalcified upper surfaces and chalky, relatively

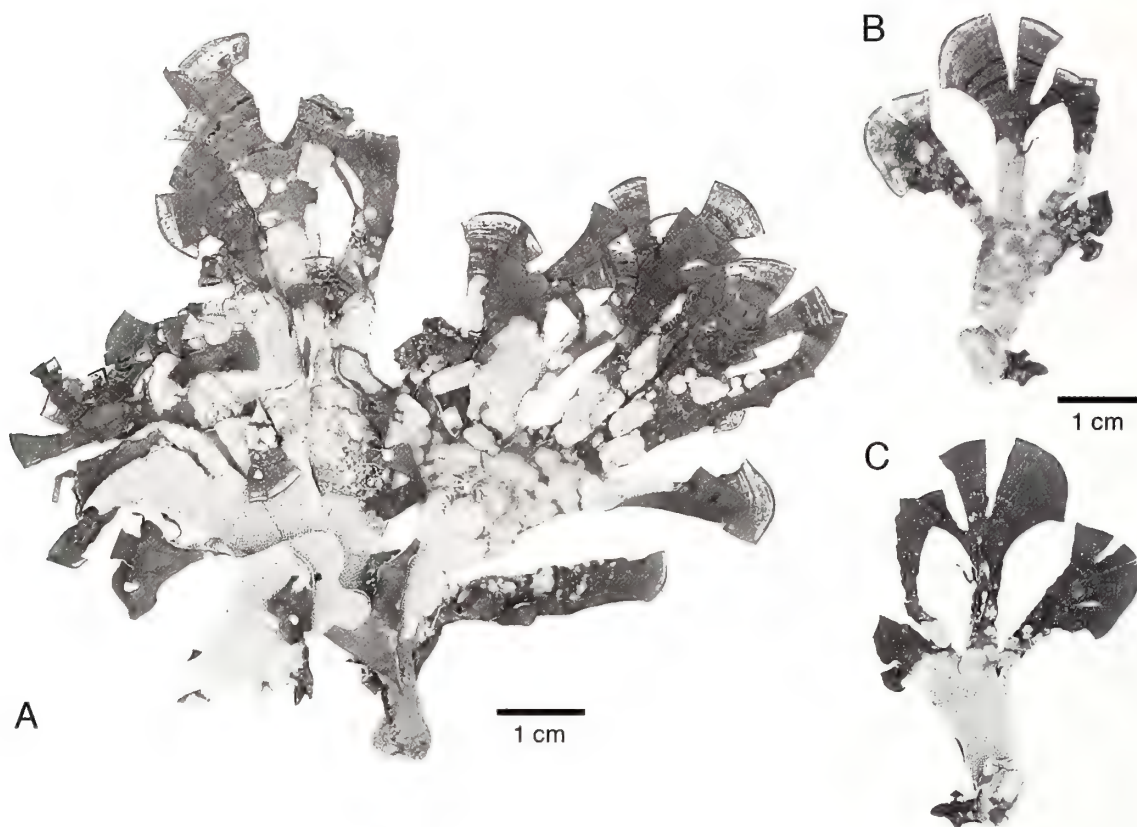


FIGURE 64. *Padina crispata* (EYD-20957): A. Habit, showing typically divided, narrow crispate lobes. B. Upper portion of blade calcified on the lower side. C. Noncalcified upper side of blade.

heavy calcified lower (inner side) surfaces. The taxonomic or ecological significance of this difference in calcification needs to be investigated. Although Thivy (in Taylor, 1945) originally described oogonia with an indusium, Mateo-Cid et al. (2000b) noted their specimens were without an indusium, and illustrations of Ávila-Ortiz and Pedroche (2005:figs. 20, 21) showed oogonial sori without and with partial and complete indusia. A Gulf specimen, noted as not being in good condition (Chávez B., 1980, as "*P. tetrastromatica*"), may also belong here.

***Padina durvillei* Bory de Saint-Vincent**

FIGURE 65

Padina durvillei Bory de Saint-Vincent, 1827a:591, as "*P. durvillaei*"; Bory de Saint-Vincent, 1827b: *Atlas*, pl. 21: fig. 1A–C; Bory de Saint-Vincent, 1828:147; Farrow, 1902:91; Howe, 1911:497; Setchell and Gardner, 1924a:729; Setchell and Gardner, 1925:661, pl. 93;

Setchell and Gardner, 1930:150; Dawson, 1944:230; Taylor, 1945:101; Dawson, 1951:52; Dawson, 1952:431; Dawson, 1957b:11; Dawson, 1959a:19; Dawson et al., 1960a:38, pl. 5: fig. 3; Dawson, 1961b:389; Dawson et al., 1964:22, pl. 18: fig. A; Dawson, 1966a:11; Chávez B., 1972:268; Hommersand, 1972:70; Norris, 1973:5; Brusca and Thomson, 1975:42; Huerta-Múzquiz, 1978:337; Chávez-B., 1980:47; Pedroche and González-González, 1981:65; Littler and Littler, 1981:151; Schnetter and Bula Meyer, 1982:65, pl. 10: fig. I; Stewart and Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:24; Norris, 1985:213, fig. 16.6; Mendoza-González and Mateo-Cid, 1986:421; Salcedo-Martínez et al., 1988:82; Sánchez-Rodríguez et al., 1989:41; Dreckmann et al., 1990:27; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Martínez-Lozano et al., 1991:23; Mateo-Cid and Mendoza-González, 1991:24; Mateo-Cid et al., 1993:50; León-Tejera et al., 1993:200; González-González, 1993:443; Stout

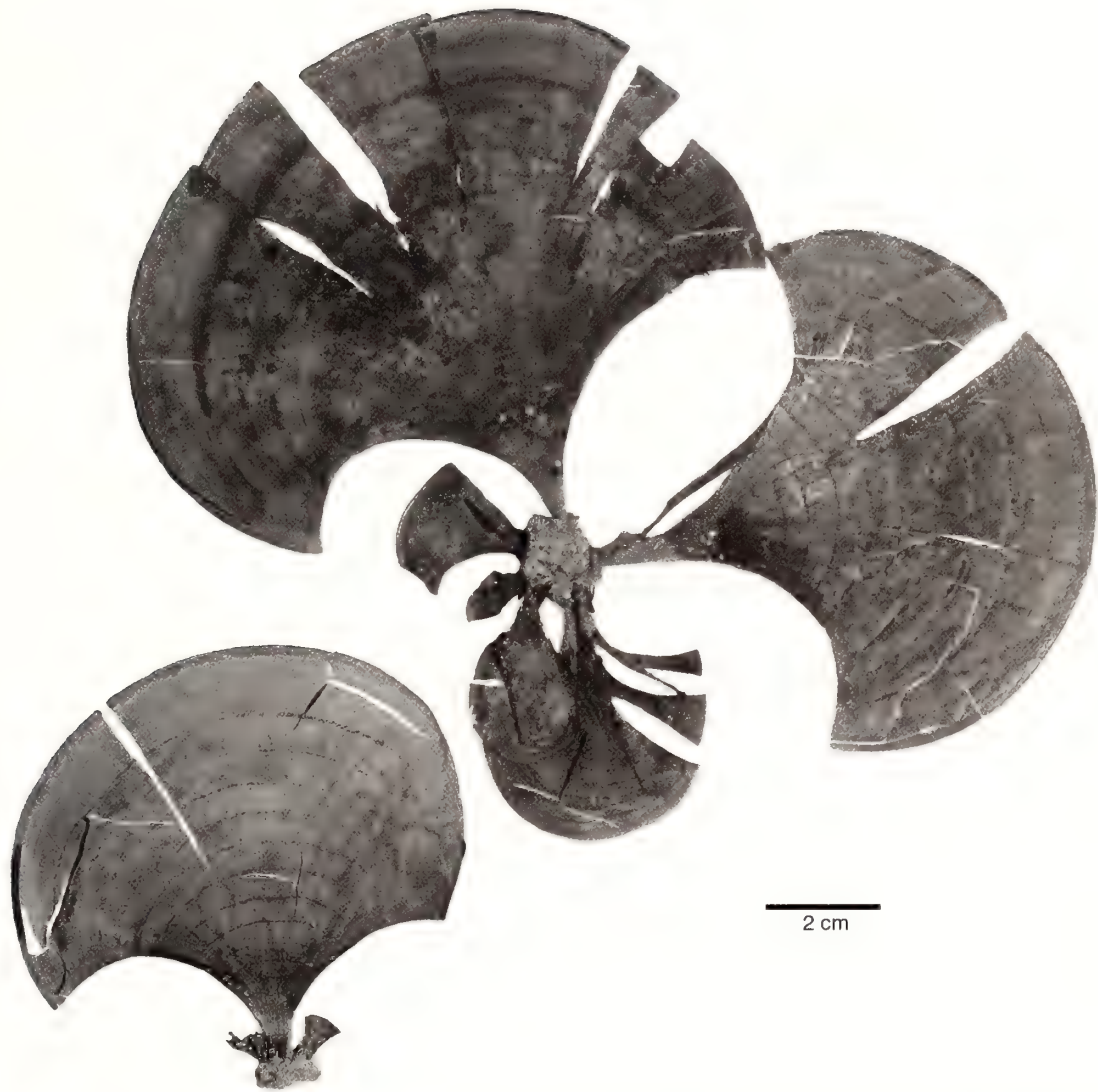


FIGURE 65. *Padina durvillei*: Leathery, flabellate blades with alternating concentric bands of hairs and reproductive structures (US Alg. Coll.-163415).

and Dreckmann, 1993:8; León-Tejera and González-González, 1993:497; Servièrè-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González, 1994a:50; Mendoza-González et al., 1994:110; González-González et al., 1996:156; Pacheco-Ruíz and Zertuche-González, 1996b:171; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Riosmena-Rodríguez et al., 1998:45; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:208 [in part, not including *P. caulescens*], figs. 48–50, 80, 81, 104; L. Aguilar-Rosas et al., 2002:235; López et al., 2004:10; Ávila-Ortiz and Pedroche, 2005:152, figs. 24

of type], 25–36; Hernández-Herrera et al., 2005:146; Riosmena-Rodríguez et al., 2005:102; Mateo-Cid et al., 2006:49, 58; Servièrè-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:50.

Algae of 1 to several, flabellate (fanlike) blades, up to 25(–40) cm tall and to 20 cm wide, dark-brown, coriaceous; above a short stipe, up to 1.0 cm long and 0.1–0.8 mm wide, arising from stupose rhizoidal holdfast. Blades not calcified; margins entire or divided, with divisions becoming lacinate, reniform, or flabellate; surface with conspicuous concentric hair zones. Inrolled margins of

blades of 2 cell layers, below becoming 6–7 cell layers and up to 100–180(–230) μm thick; midportion of 8(–10) cell layers, (160–)230–290 μm thick; lower portion of 10–18 layers, 300–450 μm thick. Cortical cells (12–)15–30 μm tall by 15–37 μm wide. Medullary cells 21–40 μm tall by 100–180 μm wide.

Sporangia ovoid, 100–135(–150) μm long and (45–)70–90 μm in diameter; sori with indusium (when immature) in irregular lines near margins, becoming scattered and in patches in mid to lower portions of blade on both sides. Oogonia 140 μm tall by 90 μm in diameter, with wall to 12 μm thick, in sori with or without indusium. Antheridia 50 μm tall by 17.5 μm in diameter; in sori in irregular lines and patches on both surfaces (Ávila-Ortiz and Pedroche, 2005).

HABITAT. On rocks; mid intertidal to shallow subtidal, to 7.5 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo San Lucas; Mazatlán, Sinaloa. Pacific coast: Isla Guadalupe; Isla Cedros; Isla Socorro (Islas Revillagigedo); Punta Rosalía, Baja California to Oaxaca; Costa Rica; Panama; Colombia; Galápagos Islands; Ecuador; Peru.

TYPE LOCALITY. Concepción, Chile (Bory de Saint-Vincent, 1827a) (note that Dawson et al. [1964:22] suspected this locality may be incorrect, stating that “from the present known distribution of the species it is questionable whether the alga was taken from such cool southern waters”).

REMARKS. *Padina durvillei* is generally considered a eastern Pacific species, but it has also been reported in Africa (Price et al., 1978; Lawson and John, 1987; Stegenga et al., 1997). Although the species name has been traditionally spelled “*durvillaei*,” the spelling was corrected to “*durvillei*” by Price et al. (1978:139) in accordance with the Botanical Code (see McNeill et al., 2006:Art. 60.11, Rec. 60C.1). Oogonial sori in *Padina durvillei* have been reported with an indusium (e.g., Mateo-Cid et al., 2000b) and without an indusium (Ávila-Ortiz and Pedroche, 2005).

In terms of algal biomass, *Padina durvillei* is second only to species of *Sargassum* as the most abundant brown alga in the northern Gulf. In winter, as observed in Puerto Peñasco, there is new settlement and rapid development of new recruits of *P. durvillei*. It also appears there is annual formation of new blades from a perennial base. Development of new blades begins in late fall and is most apparent in December, and maximum size is reached in January and February. During the spring and into the summer, the blades become split and divided, and epiphytes begin colonizing them. From July to October the blades show signs

of senescence, becoming deeply split, often eroded, and with the densest growth of epiphytes.

Padina gymnospora (Kützinger) Sonder

FIGURE 66

Zonaria gymnospora Kützinger, 1859:29, pl. 71: fig. 2 [see Allender and Kraft, 1983:86, fig. 7E (holotype picture)]. *Padina gymnospora* (Kützinger) Sonder, 1871:47; Allender and Kraft, 1983:89; Mendoza-González and Mateo-Cid, 1986:421; Mateo-Cid et al., 1993:50; González-González, 1993:443; León-Tejera and González-González, 1993:498; León-Tejera et al., 1993:200; Servière-Zaragoza et al., 1993:482; González-González et al., 1996:297, 340: fig. 19, 378; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:210, figs. 51–53, 82, 107; Abbott and Huisman, 2004:215, fig. 82A–D; Hernández-Herrera et al., 2005:146 [non *Padina gymnospora* sensu Vickers, 1905:58; Børgesen, 1914:46, fig. 155; Taylor, 1960:237; Earle, 1969:165; which is *Padina boergesenii* Allender et Kraft, 1983:87]. *Padina vickersiae* Hoyt in Howe, 1920:595; Taylor, 1960:236, pl. 34: fig. 1 [see Allender and Kraft, 1983:89].

Algae fanlike blades, up to 15 cm tall and 5–15 cm wide, usually as wide as or wider than long, yellowish-brown, simple with entire margins, ruffled; sometimes divided or torn into several lobes; calcified on both surfaces; above a short, stupose holdfast. Blades near inrolled margins of 2 cell layers, 30–50 μm thick; midportion of 4–6 cell layers, 75–80 μm thick; lower portion of 6–8 cell layers, 180–200 μm thick. Cortical cells 18–30 μm tall by 18–30 μm wide. Medullary cells 21–39 μm tall by (75–)100–180 μm wide. Hairs in concentric lines on both sides of blades.

Sporangia in sori with an indusium; sporangium up to 90 μm in diameter; solitary or grouped in noncontinuous bands between hair lines on both blade surfaces. Oogonia in sori; oogonium 80–100 μm tall by 65–90 μm in diameter. Antheridia in sori up to 240 μm wide.

HABITAT. Mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Playa El Coloradito to Estero Tastiota; Bahía Concepción to Cabo Pulmo. Pacific coast: Nayarit to Jalisco; Oaxaca; Hawaiian Islands; China; Japan.

TYPE LOCALITY. St. Thomas, West Indies (U.S. Virgin Islands).

REMARKS. The Gulf of California specimens are tentatively referred to *Padina gymnospora*.

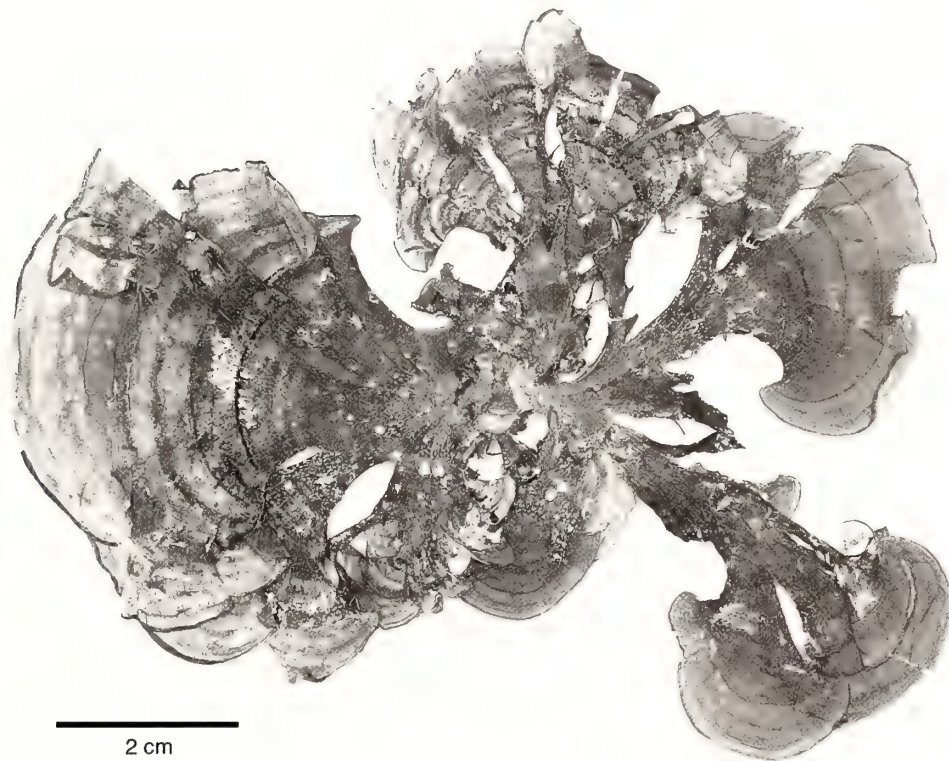


FIGURE 66. *Padina gymnospora*: Blades with ruffled margins and concentric bands of hairs between light calcification (JN-3425b).

Ávila-Ortiz and Pedroche (2005) found that herbarium specimens of tropical Pacific Mexico "*P. gymnospora*" they examined were either *P. crispata* or *P. mexicana* and noted that *P. gymnospora* should be applied to only material from the Atlantic. Thus, the Gulf of California "*P. gymnospora*" is in need of critical comparative studies, including molecular analyses with Caribbean *P. gymnospora* (type locality), to test their taxonomic and phylogenetic relationships.

Padina mexicana* E. Y. Dawson var. *mexicana

FIGURE 67

Padina mexicana E. Y. Dawson, 1944:231, pl. 52: fig. 2; Dawson, 1959a:19; Dawson, 1961b:389; Dawson, 1966a:11; Chávez B., 1980:48; Huerta-Múzquiz and Mendoza-González, 1985:46; Mateo-Cid and Mendoza-González, 1991:24; Rocha-Ramírez and Siqueiros-Beltrones, 1991:31; Mateo-Cid et al., 1993:50; Servièze-Zaragoza et al., 1993:482; Mendoza-González et al., 1994:110; Mateo-Cid and Mendoza-González, 1994b:43; González-González et al., 1996:156; Pa-

checo-Ruíz and Zertuche-González, 1996b:171; Anaya-Reyna and Riosmena-Rodríguez, 1996:862; Riosmena-Rodríguez et al., 1998:45; Ávila-Ortiz and Pedroche, 1999:357; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:68; Mateo-Cid et al., 2000b:211, figs. 54–56, 83–86, 106; Cruz-Ayala et al., 2001:190; Ávila-Ortiz, 2003:70, figs. 1–9; López et al., 2004:10; Ávila-Ortiz and Pedroche, 2005:158, figs. 37 (isotype), 38–41; Riosmena-Rodríguez et al., 2005:102; Mateo-Cid et al., 2006:49; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:54.

Algae low-growing, more or less prostrate, fan-shaped blades, light chalky whitish to grey-brown; blades often overlapping, forming clustered rosettes, attached to each other and to substratum by multicellular rhizoids along the lower portions of blades (without a stipe). Blades mostly entire, 1.5–3(–5) cm tall and 1.5–5.0 cm wide; moderately calcified (mostly on lower surface); concentric bands of hairs alternate with calcification. Blades near inrolled margin of 2 cell layers, 35–80(–100) μm thick; midportion of 4 cell layers, 90–170 μm thick; lower portions of 5–6 cell layers, 150–200(–280) μm thick. Cortical cells 17–33 μm



FIGURE 67. *Padina mexicana* var. *mexicana*: Blades adhering to each other to form rosettelike clusters (photo of living specimen viewed from above, Puerto Peñasco, Sonora, Mexico).

tall by 22–36 μm wide; medullary cells 19–37 μm by 24–48(–56) μm wide.

Sporangia in sori covered with a thin indusium; 90–120 μm long by 50–90 μm in diameter; patchy or discontinuous in irregular lines between the concentric bands of calcium carbonate only on the upper side. Oogonia 92–96 μm tall (Mateo-Cid et al., 2000b) by 73 μm in diameter; in sori with indusium (when immature), in concentric lines (Ávila-Ortiz and Pedroche, 2005). Antheridia not known.

HABITAT. On sand-covered rocks and tidal platforms; mid intertidal to shallow subtidal, to 3.3 m depth.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Cabo Pulmo. Pacific coast: Todos Santos, Baja California Sur; Sinaloa to Oaxaca.

TYPE LOCALITY. Isla Turners, off southeast Isla Tiburón, Las Islas de la Cintura, Gulf of California.

REMARKS. *Padina mexicana*, apparently an annual species, appears in spring (beginning of the warm-water season) and is found through summer, usually until

August. It is distinguished from other Gulf species of *Padina* by its smaller size, more or less prostrate, open-rosette clusters of chalky calcified fronds that are attached by rhizoids along the base of blade (i.e., lacks a stipe or holdfast). Although generally considered a Gulf of California to tropical Pacific Mexico species, it has also been reported from West Africa (Price et al., 1978; John et al., 2003, 2004).

***Padina mexicana* var. *erecta* Ávila-Ortiz**

Padina mexicana var. *erecta* Ávila-Ortiz, 2003:70, figs. 10–16; Ávila-Ortiz and Pedroche, 2005:161, figs. 42–45; Pedroche et al., 2008:55.

Algae erect, up 5 cm tall, with flat blades usually divided, uncalcified on both surfaces or calcified on lower surface; with a distinct stipe about 5 mm in length. Blade near inrolled margin of 2 cell layers, 40–80 μm thick; mid to low portions of blade of 4–6 cell layers, 80–120 μm thick in middle, and 130–220 μm thick in lower to basal

portions. Cortical cells 16–25 tall by 24–36 μm wide on upper surface and 24–30 μm tall by 24–36 μm wide on lower surface.

Sporangial sori with indusium; mostly on lower surface in continuous bands, occasionally on upper surface in irregular lines, alternating with zones of calcium carbonate, and occasionally in patches or discontinuous in irregular lines on lower surface; sporangia 80–130 μm tall by 50–80 μm in diameter. Gametangial thalli dioecious. Oogonial sori with an indusium; in regular, discontinuous, or irregular bands on both surfaces; oogonia 120 μm tall by 50 μm in diameter. Antheridial sori with indusium; on lower surface in discontinuous lines; antheridia 52 μm tall by 27 μm in diameter.

HABITAT. On rocks; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Bahía Concepción; Bahía de La Paz to Cabo San Lucas. Pacific coast: Todos Santos, Baja California Sur; Sinaloa to Oaxaca.

TYPE LOCALITY. Puerto Vicente Guerrero, Guerrero, Pacific Mexico.

REMARKS. In the field, *Padina mexicana* var. *erecta* is distinguished from *P. mexicana* var. *mexicana* by its erect habit, evident stipe, sporangia on both sides of blade, and blades that are with or without calcification (Ávila-Ortiz, 2003).

***Rugulopteryx* De Clerck et Coppejans**

FIGURE 54A, D

Rugulopteryx De Clerck et Coppejans in De Clerck, Leli-aert, Verbruggen, Lane, De Paula, Payo, and Coppejans 2006:1286.

Algae are erect, of strap-like flattened fronds that are dichotomously to irregularly branched, and attached by rhizoids restricted to basal portions of thallus, some with basal stoloniferous holdfasts. Fronds have entire margins and rounded apices, with surfaces that may be undulate or rugose, or flat and smooth; surface proliferations are found in some species. Medulla is composed of large cubical to rectangular, colorless cells. Central portions of the medulla are one cell layer thick, and two to eight cell layers at the branch margins and stoloniferous holdfasts. Cortex is composed of a single cell layer (occasionally two-cell layers in basal portion) of small cells. Each cortical cell with numerous discoid chloroplasts. Growth is by a single, protruding or emarginate, apical cell. Phaeophycean hairs are scattered in tufts.

Reproductive structures are scattered, and either within concavities of the frond surfaces, or protruding from the frond surface. Sporangia are ovoid to pyriform and may be solitary, in groups, or in sori. Borne on two-celled basal stalks, the sporangia are surrounded by an inconspicuous involucre, and produce four aplanospores (tetraspores). Oogonia are borne on a single stalk cell, in sori or small groups. Antheridia borne in many tiered locules that are in whitish sori, surrounded by 3–5 rows of pigmented multicellular paraphyses.

One species of *Rugulopteryx* is recognized in the northern Gulf of California.

***Rugulopteryx okamurai* (E. Y. Dawson) I.-K. Hwang, W. J. Lee et H.-S. Kim**

FIGURE 68

Dilophus okamurai E. Y. Dawson, 1950a:86, as “*D. okamurai*”; Dawson, 1961b:388; Hommersand, 1972:70; Tseng, 1983:196. pl. 99: fig. 1; Kajimura, 1992:95–97, figs. 1–17; González-González et al., 1996:147; Yoshida, 1998:220, pl. 2-8: fig. B, pl. 2-9: figs. A, B; De Clerck, 2003:180

Rugulopteryx okamurai (E. Y. Dawson) I.-K. Hwang, W. J. Lee et H.-S. Kim in Hwang, Lee, Kim and De Clerck 2009:5, figs. 1–49.

Dictyota okamurai (E. Y. Dawson) Hörnig, Schmetter et Prud’homme van Reine, 1992a:54; Hörnig et al., 1993:170; De Clerck, 2003:174; Pedroche et al., 2008:44.

Dictyota marginata Okamura, 1913:33, pl. 108: fig. 9, pl. 109: figs. 1–8, *nom. illeg.*, i.e., a later homonym of *Dictyota marginata* (C. Agardh) Greville, 1830:xliv, which = *Stoechospermum polypodioides* (J. V. Lamouroux) J. Agardh, 1848:100 (see De Clerck, 2003:173)].

Dilophus marginatus (Okamura) Okamura, 1915:154 [Corrigenda], *nom. illeg.*; Okamura, 1936:167, fig. 85 (1–3) [a later homonym of *Dilophus marginatus* J. Agardh, 1894:91, which is now *Rugulopteryx marginata* (J. Agardh) De Clerck et Coppejans in De Clerck et al., 2006:1286].

Algae of flattened, straplike fronds, up to 5 cm tall, and dichotomously to subdichotomously branched; attached below by rhizoids. Branches up to 5 mm wide, with segments of equal length, or with one segment of a pair frequently longer than the other; apices are rounded. Medulla of large colorless cells; one-cell layer thick toward center (seen in transection) and 2 or more cell

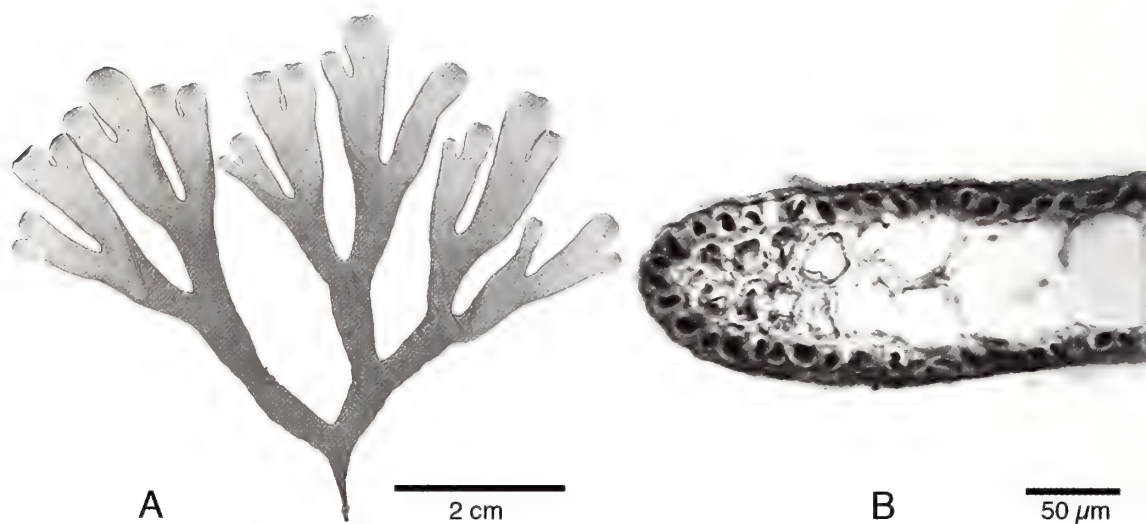


FIGURE 68. *Rugulopteryx okamurae*: A. Habit (JN-4086). B. Transection; note cortex of a single cell layer and medulla of more than one cell layer near margin (JN-3724).

layers in the margins. Cortex of small cells, of one-cell layer, throughout.

Reproduction not seen in Gulf material.

HABITAT. On rocks or occasionally entangled with other algae; low intertidal to shallow subtidal; also dredged from 19 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Cabeza Ballena to Bahía de San Lucas. Western Pacific coast: China (Tseng, 1983); Taiwan (Lewis and Norris, 1987); Japan (Yoshida, 1998); Korea (Lee and Kang, 2001).

TYPE LOCALITY. Enoshima, Kanagawa Prefecture (formerly Sagami Province), Honshū, Japan.

REMARKS. On the basis of their habit and morphological similarities, the northern Gulf specimens are referred to *Rugulopteryx okamurae*. The specific and generic status of the northern Gulf material of *R. okamurae* needs to be verified. Hwang et al. (2009) noted *R. okamurae* to be a subtropical to temperate western Pacific species, and did not include Gulf of California material, or the type (*Dictyota marginata* Okamura, 1913) or type locality material of *Dilophus okamurae* in their analyses. It would be interesting to study the life history of Gulf *R. okamurae* in culture and using molecular analyses to compare them to Japanese *R. okamurae* (type locality) and south Korean *R. okamurae* (Hwang et al., 2009) to test their phylogenetic relationships.

Although the species epithet has been spelled with different endings, the correct ending is *-e* (McNeill et al., 2006:Art. 60, Rec. 60C.1a), thus *R. okamurae*. A novel

form of vegetative propagation by the development of proliferous initials along the surface and margins of its fronds was shown in *R. okamurae* from Japan (Kajimura, 1992, as *Dilophus okamurae*).

Spatoglossum Kützing

FIGURE 54G,H

Spatoglossum Kützing, 1843:339.

Algae are erect, flattened fronds, up to 5 cm wide, that are subdichotomously to subpalmately divided and attached by a fibrous holdfast. The flat fronds are often expanded upward and are irregularly to more or less laterally branched up to four orders, with entire, undulate, or slightly dentate margins. A midrib is entirely lacking in most or only partly extended from the holdfast into the lower basal portion. Growth is from marginal meristems of small groups of apical cells. Thalli are multilayered, up to 10 cell layers in transection, with a medulla and cortex, not clearly demarcated. Medulla is composed of two to several rows of colorless large cells that become progressively smaller outward to a cortical layer of smaller pigmented cells. Hair tufts arise from depressions that are scattered on both surfaces.

Sporangia are scattered over both surfaces of the thallus; borne either completely above or partially embedded and partly protruding, or entirely embedded on the surface and, produce four aplanospores (tetraspores). Oogonia

are solitary or in groups and are usually raised and spread over the thallus surfaces. Antheridia are borne in small, partially or entirely embedded sori that are scattered over both surfaces.

REMARKS. Sasaki et al. (1999) used presence or absence of sulfuric acid to separate morphologically

similar species of *Spatoglossum* and suggested this was a useful taxonomic character (Sasaki et al., 2004, 2005).

One species, *Spatoglossum howellii* Setchell et N. L. Gardner (1937), has been reported in the southern Gulf of California (Hommersand, 1972). Two species are currently known in the northern Gulf of California.

KEY TO THE SPECIES OF *SPATOGLOSSUM* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Narrow lanceolate blades, up to 17 mm wide, with sparsely dentate margins; surface cells irregularly arranged; oogonia and antheridia embedded in cortical layer *S. lanceolatum*
 1b. Narrow blades expanding to 2(–3.5) cm wide, with entire margins; surface cells arranged in longitudinal rows; oogonia and antheridia projecting above surface *S. subflabellatum*

Spatoglossum lanceolatum E. Y. Dawson

FIGURE 69

Spatoglossum lanceolatum E. Y. Dawson, 1954e:328, pl. 1: figs. 1, 2, pl. 6; Dawson, 1961b:389; González-González et al., 1996:164; Pedroche et al., 2008:56.

Algae of few to several flat, 3–4 times irregularly, subdichotomously to subpalmately divided fronds, up to 28 cm tall, above a narrow slightly stupose stipe, up to 10 mm long and 1.0–2.0 mm wide; attached below by a discoid stupose cushion. Branches narrower near dichotomies, widening upward, becoming more or less lanceolate, to (3–)5–10(–17) mm broad; margins with irregularly spaced dentations; blades 200–250 μ m thick. Medulla of (3–)5–7 irregular layers of large cells, 40–65 μ m in diameter; sub-cortex of partial layers of similarly shaped smaller cells. Cortex of quadrangular cells, not projecting, outer walls forming a smooth surface; in surface view, cells of irregular shape and irregularly arranged (not in longitudinal rows).

Apparently monoecious. Oogonia ovate to hemispherical (or sometimes more or less angular), up to about 70 μ m in diameter; either solitary, in pairs, or in groups of 3–4; embedded within cortical layer (barely projecting above its surface). Antheridia in sori, 100–200 μ m in diameter, embedded in cortical layer and not projecting above surface; composed of densely packed cells, most 8–9 μ m in diameter; formed by periclinal cell divisions into irregular tiers within vertical columns, 30–40 μ m tall.

HABITAT. On rocks, in tide pools, and on tidal platforms; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Ensenada de San Francisco.

TYPE LOCALITY. North shore of Ensenada de San Francisco, near Punta de Las Cuevas, Sonora, Gulf of California.

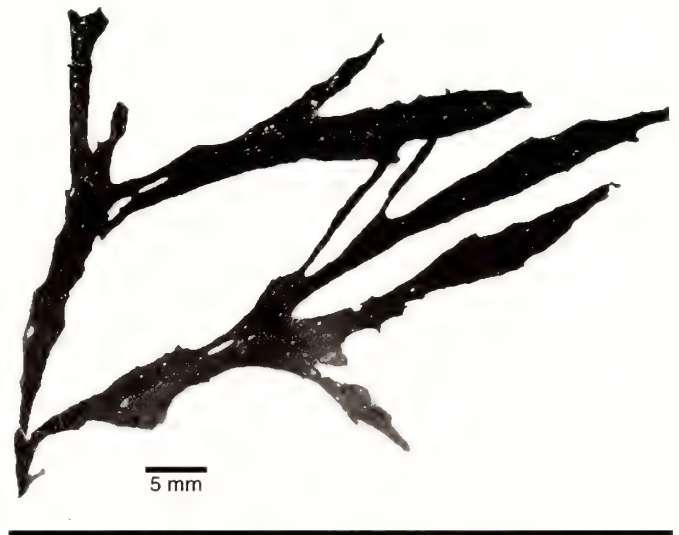


FIGURE 69. *Spatoglossum lanceolatum*: Part of the type specimen; note the irregularly and distantly spaced dentations (EYD-1966, after Dawson, 1954e: pl. 6).

REMARKS. *Spatoglossum lanceolatum*, a Gulf endemic species, is distinguished from other species of *Spatoglossum* by its narrower fronds with sparsely dentate margins, irregularly arranged surface cells, and the embedded (not projecting above blade surface) reproductive structures.

Spatoglossum subflabellatum E. Y. Dawson

FIGURE 70

Spatoglossum subflabellatum E. Y. Dawson, 1954e:326, pl. 1: figs. 3–5, pl. 5: fig. 2; Dawson, 1961b:389; Dawson, 1966a:11; Dawson, 1966b:56; Hommersand, 1972:70; Espinoza-Ávalos, 1993:333; González-González et al.,



FIGURE 70. *Spatoglossum subflabellatum*: Habit (JN-5902).

1996:164; Mateo-Cid et al., 2006:49; Pedroche et al., 2008:56.

Spatoglossum cf. *schroederi* sensu Dawson, 1959a:19, fig.1; Dawson, 1961b:389 [non *Spatoglossum schroederi* (C. Agardh) Kützing, 1859:21, pl. 51].

Algae of few to several flat, narrow, irregularly divided or deeply split subflabellate to subpalmate fronds, up to 25 cm tall, arising from a stupose basal cushion (up to 2 cm tall). Fronds cuneate and narrow at base, becoming wider distally to 2(–3.5) cm broad and up to 180 μm thick; with entire margins. Medulla of 2 irregular layers of large thin-walled cells, 40–70 μm in diameter; subcortex of partial layers of smaller, similarly shaped cells. Cortex a single layer of pigmented cells, 20–30 μm in diameter, with projecting rounded outer walls; in surface view, cells arranged in longitudinal rows and about twice as long as wide.

Sporangia unknown. Dioecious. Oogonia either solitary or in rows of 2–4 elevated on thallus surface; ovate, up to 70 μm long, borne on a modified cortical cell. Antheridia elevated in sori, 150–400 μm in diameter, scattered on thallus surface in groups; about 50 μm tall by 25 μm wide; each antheridium about 2.5 μm in diameter in vertical and horizontal rows.

HABITAT. On rocks and in crevices and tide pools; mid intertidal to shallow subtidal, down to 6 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Punta Los Frailes.

TYPE LOCALITY. Dredged 11–18 m depths, near Punta de Las Cuevas, Ensenada de San Francisco, Sonora, Gulf of California.

REMARKS. *Spatoglossum subflabellatum* is a Gulf endemic. The more recent collections of Dawson (1966a, 1966b) that he identified as *S. subflabellatum* included specimens that were much broader than those originally described (Dawson, 1954e). Thus, this broadly defined species concept is in need of critical study and may include more than one species. Further, Dawson (1966b:56) observed that the Isla San Pedro Nolasco specimens were intermediate morphologies between *S. subflabellatum* and *S. howellii* Setchell et N. L. Gardner (1937) and suggested that *S. subflabellatum* probably reflects “progressive speciation in the specialized environment of the northern Gulf of California.”

DESMARESTIALES

Desmarestiales Setchell et N. L. Gardner, 1925:554.

Algae are heteromorphic, with large sporophytes that are cylindrical, compressed, flattened, or bladelike, and may be entire or branched. Growth is trichothallic-like and initiated by individual filaments with bidirectional intercalary divisions. The resulting structure is pseudoparenchymatous, with a cortex developed from the descending rhizoidal filaments growing from the bases of lateral hairs. Cells have several discoid plastids and no pyrenoids.

Life histories, where known, are heteromorphic. The large sporophytes develop unilocular sporangia that produce zoospores. The gametophytes are microscopic filaments, and sexual reproduction is oogamous.

There is one family represented in the northern Gulf of California.

DESMARESTIACEAE

Desmarestiaceae (Thuret) Kjellman, 1880:10.

Sporophytes are erect cylindrical to flattened thalli, which are sparingly to abundantly branched or rarely entire and attached to the substratum by a discoid holdfast. Branching is opposite or alternate and generally pinnate. A pseudoparenchymatous cortex surrounds a single

filament, which initiates axial trichothallic-like growth of the bidirectional intercalary meristem. Some species have persistent or deciduous hairs on their margins that are irregularly scattered or in transverse whorls.

Unilocular sporangia are solitary or grouped in sori and produced by transformation of superficial cells of the thallus or of assimilatory filaments. Gametophytes are monoecious or dioecious, microscopic filamentous algae. Oogonia are usually produced on the filaments of a separate thallus, and each produces a single egg. Antheridia develop on filaments, and each antheridium produces a single biflagellate antherizoid.

One genus occurs in the northern Gulf of California, with its species apparently restricted to the Islas de la Cintura.

***Desmarestia* J. V. Lamouroux**

Desmarestia J. V. Lamouroux, 1813:43.

Sporophytic thalli are macroscopic, erect, with a single cylindrical or compressed main axis that is ligulate to broadly bladelike and usually pinnately or oppositely branched in most species or are simple and unbranched in a few, and attached below by a discoid holdfast. If the thallus is branched, the branches are cylindrical, compressed or flat, with opposite or alternate branchlets. Trichothallic growth occurs at the apices of the axis and branches. The main axial filament is surrounded by a thick medulla of large, colorless cells developed by downward growing hyphae. The cortical layer is composed of small cells that become progressively smaller toward the thallus surface. Cells have lenticulate plastids and vacuoles (in many species these contain sulfuric acid) and lack pyrenoids. Phaeophycean hairs are absent.

Unilocular sporangia are isolated and scattered over the surface cells, developing from the transformation of cortical cells, or on stalk cells in small sori along with one- to two-celled paraphyses. Gametophytic thalli, little known in nature, are microscopic, irregularly branched filaments, and endozoic or endophytic. Gametophytes may be monoecious or dioecious, and are dimorphic in cell size of the filaments. Elongated oogonia develop on the cells of filamentous thalli of larger diameter; each oogonium produces a single oocyte. Antheridia develop on cells of filamentous thalli of narrower diameter, are usually borne in clusters, and produce motile spermatozooids.

REMARKS. In collecting species of *Desmarestia*, care should be taken in placing it with other specimens. Many species of *Desmarestia* are known to contain sulfuric

acid in their cell vacuoles (Blinks, 1951; Eppley and Bovell, 1958; Sasaki et al., 2004), which is probably a herbivore deterrent (Anderson and Velimirov, 1982). The vacuolar sap, with a pH 0.44 to 2.0 (Schiff, 1962), will discolor or damage your other collections. McClintock et al. (1982) showed the acidic or nonacidic condition to be species specific, and the analyses of Peters et al. (1997) revealed that sulfuric acid vacuoles were strong phylogenetic characters.

Carbohydrates were elucidated in some species of *Desmarestia* (Carlberg et al., 1978). The sexual hormone desmarestene and its role in sperm release and sperm attraction in the sexual reproduction of *Desmarestia* has been described by Müller and Lüthe (1981) and Müller et al. (1982). Filamentous gametophytes of *Desmarestia*, although known from culture studies (e.g., Kornmann, 1962; Nakahara, 1984; Peters and Müller, 1986b), are apparently rare in nature and have not been found in the Gulf. Filamentous gametophytes have been found in the tissue of a Pacific Northwest sea pen, *Ptilosarcus gurneyi* (Anthozoa; Pennatulacea), and were cultured and grew to be sporophytes of *Desmarestia* (Dube and Ball, 1971). In the Antarctic, endophytic, monoecious filamentous gametophytes of *Desmarestia* were identified in the red alga *Curdiea racovitzae* Hariot (Moe and Silva, 1989).

Solely on the basis of vegetative morphology, the Gulf-endemic species *D. mexicana* and *D. filamentosa* were placed in synonymy with *D. ligulata* and *D. viridis*, respectively (Chapman, 1972b). Noting that vegetative characters may be of secondary importance and that reproductive structures are known for only a few of the species, Moe and Silva (1977) have questioned the conclusions of Chapman (1972a, 1972b).

Comparative morphological studies of vegetative characters and reproductive structures and life history culture studies, such as those of Peters and Müller (1986b) and Anderson and Bolton (1989), are needed for the northern Gulf taxa. These studies could test another morphological feature; e.g., Garbary (1978) suggested the surface characteristics of macroalgae may also be of taxonomic value, and Oates and Cole (1990b) found distinctive cell wall ornamentation on two species of *Desmarestia* from the northeast Pacific. Critical studies should also include DNA investigations to clarify the taxonomic status and phylogenetic relationships of the Gulf taxa.

Two taxa, apparently endemic, are known in the northern Gulf of California, and both contain sulfuric acid. While acknowledging the northern Gulf specimens are vegetatively similar to some species from the Pacific coast, they are ecologically and geographically isolated, with a restricted distribution to the cooler, subtidal waters

in the vicinity of Isla Ángel de la Guarda and adjacent areas and Isla San Esteban. Therefore, for now, two species are

recognized, one of these as a subspecies to reflect its possible relationship to a Pacific coast species.

KEY TO THE SPECIES OF *DESMARESTIA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli cylindrical to subcylindrical and narrow, less than 3 mm wide; oppositely branched to 3–5 orders *D. filamentosa*
- 1b. Thallus flat, of large, broad blades, greater than 10 mm wide; either unbranched or sparsely, oppositely branched to 1–2 orders *D. munda* subsp. *mexicana*

Desmarestia filamentosa E. Y. Dawson

FIGURES 71, 72

Desmarestia filamentosa E. Y. Dawson, 1944:236, pl. 76; Dawson, 1961b:392; González-González et al., 1996:144.

Desmarestia viridis sensu Chapman, 1972b:225, fig. 9 [in part, with reference to Gulf *Desmarestia filamentosa* only]; Abbott and Hollenberg, 1976:225, fig. 187; Norris and Bucher, 1976:6; González-González et al., 1996:145; Pacheco-Ruíz and Zertuche-González, 1996b:171; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:78 [non *Desmarestia viridis* (O. F. Müller) J. V. Lamouroux, 1813:45; basionym: *Fucus viridis* O. F. Müller, 1782:5].

Algae yellow-brown when fresh, pale green on drying, up to 92 cm tall; main axis cylindrical to subcylindrical, (1–)2–3 mm in diameter, percurrent and oppositely branched to 3–4(–5) orders; arising above a stipe, up to 5 cm long by 1–2 mm in diameter, and attached below by a small discoid holdfast. Branches mostly cylindrical and gradually reduced in size upward; ultimate branchlets 80–110 µm in diameter; apices with trichothallic filament with cortication below the meristematic zone (Figure 72A).

Reproduction not seen in Gulf of California specimens.

HABITAT. On rocks, sand/shell bottom; subtidal, (3–)10–23 m depths.

DISTRIBUTION. Gulf of California: Isla Mejía and Puerto Refugio, Isla Ángel de la Guarda to Bahía de Los Ángeles; Isla San Esteban.

TYPE LOCALITY. Puerto Refugio, Isla Ángel de la Guarda, Las Islas de la Cintura, Gulf of California.

REMARKS. Apparently a northern Gulf endemic, *Desmarestia filamentosa* is easily distinguished from the very large, flat, Gulf *D. munda* subsp. *mexicana* by its much smaller, narrower subcylindrical axes and

branches. Originally known only from the dredged type specimen (Dawson, 1944), numerous specimens of *D. filamentosa* were found in our diving off Roca Blanca, Puerto Refugio (Norris and Bucher, 1976, as “*D. viridis*”).

Dawson (1944) noted *D. filamentosa* was close to *D. media* (cf. Setchell and Gardner, 1925) and maybe to *D. pacifica* Setchell et N. L. Gardner (1924b, 1925). Chapman (1972b) considered *D. filamentosa* to be a synonym of *D. viridis*, a North Atlantic species that was subsequently reported on the Pacific coast from Alaska to Baja California (cf. Abbott and Hollenberg, 1976; Scagel et al., 1989). However, Abbott and Hollenberg (1976:222) suggested that most central California specimens identified as “*D. viridis*” were probably *D. kurilensis* Yamada (1935). Given the questionable taxonomic status of some species of *Desmarestia* in general (see “Remarks” under *Desmarestia*) and the ecological and geographical isolation of the Gulf taxon, it seems best to consider it a separate species, as *D. filamentosa*, until it can be further evaluated and its systematic status and phylogenetic relationships can be tested.

Desmarestia munda Setchell et N. L. Gardner subsp. *mexicana* (E. Y. Dawson) J. N. Norris, comb. nov.

FIGURE 73

Desmarestia mexicana E. Y. Dawson, 1944:236, pl. 77; Dawson, 1961b:393; González-González et al., 1996:145; Pedroche et al., 2008:78.

Desmarestia ligulata sensu Chapman, 1972a:2, 17 [in part, with reference to Gulf *Desmarestia mexicana* only]; Abbott and Hollenberg, 1976:222; Norris and Bucher, 1976:6; González-González et al., 1996:144; Pacheco-Ruíz et al., 2008:204 [non *Desmarestia ligulata* (Lightfoot) J. V. Lamouroux, 1813:25; *Fucus ligulatus* Lightfoot, 1777b:946].



FIGURE 71. *Desmarestia filamentosa*: Habit, specimen from the type locality (JN-5271).



FIGURE 72. *Desmarestia filamentosa*: A. Apex of a branch showing single trichothallic filament above the meristematic zone (arrow), below which the cortical envelope develops. B. Upper portion of a branch with opposite initials of lateral branches developing (JN-5271).

Algae large, up to 150 cm in length; of 1 or more thin, flat blades, up to 85 cm long and widening gradually upward from its basal stipitate region, to 8–20 cm in width. Thalli arising from a small, conical holdfast with a slender, compressed stipe, (2–)3–4 mm wide, that extends into main axis, 3–4 mm wide, bearing a terminal primary blade. Main axis may remain unbranched or with opposite lateral blades. Primary and lateral blades broadly lanceolate and unbranched or may become sparsely and oppositely branched with secondary blades formed on the margin of its lower portion. Blades with a slender, visible midrib and faint opposite lateral veins that gradually disappear or occasionally continue to become midrib of marginal blades. Blade margins coarsely serrate; spine-like outgrowth tapering gradually, with a terminal tooth pointed upward.

Reproduction not observed in Gulf of California specimens.

HABITAT. On rocks, sand/shell bottom; subtidal, 9–23 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda to Isla Estanque; Punta la Gringa, Bahía de Los Ángeles.

TYPE LOCALITY. Puerto Refugio, Isla Ángel de la Guarda, Las Islas de la Cintura, Gulf of California.

REMARKS. *Desmarestia munda* subsp. *mexicana* was originally known from a single dredged collection in the northern Gulf (Dawson, 1944, as “*D. mexicana*”). *Desmarestia munda* subsp. *mexicana* is easily recognized by its very large size and flat, long, and broad, thin blades; diving surveys at its type locality showed it to be rather abundant at 15–23 m depths (Norris and Bucher, 1976).

Although *Desmarestia mexicana* was considered by Chapman (1972a) to be one of the synonyms of a broadly redefined *D. ligulata*, Silva (1979:336) noted that taxonomic treatment is not convincing. The northern Gulf specimens show some similarities with larger specimens of the Pacific coast *D. munda* Setchell et N. L. Gardner (1924b; Dawson, 1945c), a species recorded from Alaska to central Baja California (Setchell and Gardner, 1925:567, pl. 89; Smith, 1944:121, pl. 17: fig. 1; Dawson, 1951:52; Dawson et al., 1960a:30, pl. 7: fig. 1). However, Gulf specimens of *D. munda* subsp. *mexicana* differ from *D. munda* subsp. *munda* in having much broader, longer blades (up to 20 cm wide and to 85 cm long) that either lack secondary blades or have secondary blades that are sparse and opposite off the margins of the primary blade (Figure 73) or lateral blades. Therefore, it seems best to recognize the Gulf taxon as a subspecies to reflect its possible relationship to the Pacific *D. munda*, until its systematic and phylogenetic status can be tested.

SPOROCHNALES

Sporochnales Sauvageau, 1926:364.

The sporophyte of these algae is a large erect macrophyte. Members usually have prominent, slender, terete or compressed main axes that are moderately to densely branched. The axes and branches are pseudoparenchymatous in structure and have characteristic terminal and/or lateral tufts of simple filaments. Growth occurs in the meristematic zone in apices of the axes and branches and in the intercalary meristem of each trichothallic filament of the terminal tufts. The cortical layer is composed of pigmented cells with discoid plastids and no pyrenoids. In contrast, the gametophytes, where known, are microscopic filamentous algae.



FIGURE 73. *Desmarestia munda* subsp. *mexicana*: Portion of thallus showing main axis with opposite lateral blades and primary blade with secondary blades developed oppositely along its margin (JN-5283).

Life histories are heteromorphic. Reproduction in the sporophytes is by meiospores produced in unilocular meiosporangia. The gametophytes are monoecious or dioecious, and reproduction is oogamous (Caram, 1965; Müller et al., 1985).

The order is represented by one family in the northern Gulf of California.

SPOROCHNACEAE

Sporochnaceae Greville, 1830:36.

Members of this family have a branched main axis that is usually very distinct. The axis and branches bear short, usually stalked, determinate branchlets that bear a conspicuous terminal tuft of filaments. Growth is trichothallic in the axis and branches from an apical meristem located below the tuft of filaments, and in each of these filaments, growth is from an intercalary meristem just above their base. Anatomical structure is initially uniaxial in the youngest growing portions, which soon become surrounded by developing cells to form a pseudoparenchymatous medulla of large colorless cells and an outer cortex of small pigmented cells.

Unilocular sporangia produced by the macroscopic sporophyte are superficial on the cortex or borne laterally off clustered paraphyses. These produce meiospores that when released, germinate and develop into gametophytes. Sexual reproduction is oogamous. Gametophytes are microscopic, branched uniseriate filaments that produce oogonia and antheridia.

One genus of the family is found in the northern Gulf of California.

Sporochnus C. Agardh

Sporochnus C. Agardh, 1817:xii.

Algae (sporophyte) have an erect cylindrical axis with few to many lateral branches, branched up to several orders and attached below by a fibrous holdfast. The main axis and branches are slender, threadlike to wiry, more or less indeterminate in growth, and terminate in a tuft of trichothallic filaments. Numerous determinate tufted branchlets, of more or less similar length, are borne on the axis and all orders of branches. These determinate branchlets in most species are stalked (pedicel) below a thicker fertile portion (sporangial receptacle) with a terminal tuft of trichothallic filaments, although in a few species they are without stalks (non-pedicellate).

The large sporophytes produce unilocular sporangia in a layer encircling the fertile portion of determinate branchlets below their terminal tuft (see, e.g., Womersley, 1987:fig. 103G). Unilocular sporangia are borne laterally on unbranched or branched paraphyses that have an enlarged spherical to subspherical terminal cell. Gametophytic thalli are microscopic branched filaments and are monoecious or dioecious. Sexual reproduction is oogamous.

REMARKS. Caribbean species of *Sporochnus* have been shown to produce some bioactive secondary metabolites, sporochnols A, B, and C (Shen et al., 1993). The natural products of the Gulf of California species should also be investigated.

Two species are found with a restricted distribution in the northern Gulf of California.

KEY TO THE SPECIES OF *SPOROCHNUS* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Ultimate tufted branchlets long, up to 9.0 mm long; sporangial receptacles with stalks 1.0–3.0(–4.0) mm in length *S. anomalus*
 1b. Ultimate tufted branchlets much shorter, mostly 0.5–1.0 mm long; sporangial receptacles mostly lacking stalks or, if present, minute, less than 240 µm in length *S. neushulii*

Sporochnus anomalus (Pallas) M. J. Wynne

FIGURES 74, 75A,B

Fucus anomalus Pallas, 1766:199, pl. 14: figs. 24, 24*[sic].

Sporochnus anomalus (Pallas) M. J. Wynne, 2003:78, fig. 1.

Sporochnus gaertnera C. Agardh, 1820:150; C. Agardh, 1824:259; Montagne, 1846:27.

Fucus gaertnera Gmelin, *nom. illeg.*, 1768:164, pl. XIX: figs. 1, 1a.

Sporochnus pedunculatus sensu Dawson, 1951:56 [non *Sporochnus pedunculatus* (Hudson) C. Agardh, 1820:149; basionym: *Fucus pedunculatus* Hudson, 1778: 587].

Sporochnus bolleanus sensu Dawson et al., 1960b:14; Dawson, 1961b:392; Norris and Bucher, 1976:4, figs. 3, 4; González-González et al., 1996:165; Pacheco-Ruiz



FIGURE 74. *Sporochmus anomalus*: Habit, branches with numerous stalked, tufted branchlets (JN-5264).

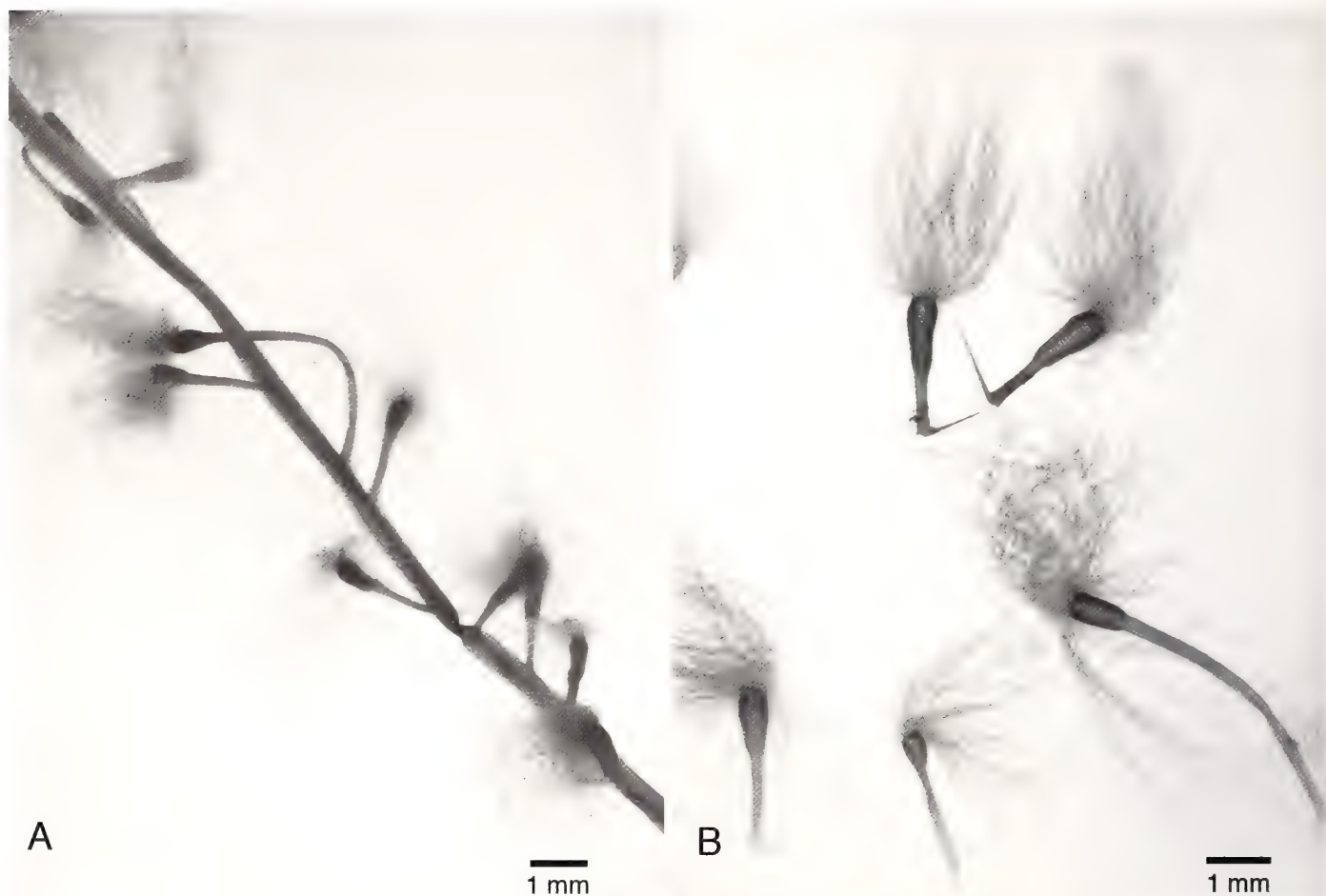


FIGURE 75. *Sporochmus anomalus*: A. Portion of a branch with determinate branchlets, each showing the sterile, long stalk, a wider fertile portion (receptacle), and an apical tuft of filaments (JN-5264). B. Overall length variations of determinate lateral branchlets, with stalk, receptacle (sporangial sori surrounding branch), and terminal tuft of assimilatory filaments (JN-5264).

and Zertuche-González, 1996b:171; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008(in part; Gulf of California records only):76 [non *Sporochmus bolleanus* Montagne, 1856:393].

Algae (sporophyte) erect, up to 44 cm tall, of terete branched axes; lateral branches up to 38 cm long. Determinate tufted branchlets on axes and branches usually numerous and up to 9.0 mm in length; composed of a long stalk, (1.0–)2.0–3.0(–5.0) mm long and up to 200 μ m in diameter, elongated cylindrical receptacle, 1.0–2.25 mm long, and a terminal cluster of filaments, 3.0–5.0(–6.0) mm long, extending from an apical pit.

HABITAT. On rocks and shells; subtidal, 20–30 m depths.

DISTRIBUTION. Gulf of California: Roca Blanca, Puerto Refugio (Isla Ángel de la Guarda) to Bahía de Los Ángeles. Pacific coast: Isla Guadalupe; Punta Abreojos to Punta Pequeña, Baja California Sur.

TYPE LOCALITY. Not given by Pallas (1766); Mediterranean was listed by Gmelin (1768).

REMARKS. The northern Gulf of California specimens of *Sporochmus anomalus* have measurements intermediate between two other species: larger than those of *S. pedunculatus* (Hudson) C. Agardh (1820) and smaller than those of *S. bolleanus* Montagne (1856) (cf. Taylor, 1960; Earle, 1969). Earle (1969) has noted that in the northeastern Gulf of Mexico certain forms of *S. bolleanus* have branchlets shorter than usual for this species, making it sometimes difficult to separate from *S. pedunculatus*

where the two occur together. The northern Gulf *Sporochnus* is tentatively referred to *S. anomalus*, until critical studies of northern Gulf specimens can be made to determine their taxonomic status and phylogenetic relationships.

***Sporochnus neushulii* J. N. Norris, sp. nov.**

FIGURE 76A-E

LATIN DESCRIPTION. Algae usque ad 31 cm longae, maiores teretes axes cum ramis plerumque alternis et lateralibus, usque ad 2.5 cm longis; ab imo affixae cum parvo discoidi hapterone. Axes et rami ferentes parvos et numerosos (plerumque denses) ramulos, radialiter dispositos, breves, determinatos, caespitosos, (0.25–)0.5–1.0(–2.0) mm longos, 200–600(–750) μ m in diametro, plerumque non-pedicellatos praecipue in altis partibus thalli, vel, quamvis rarum (ut videtur), si pedicelli adsunt, maxime minuti tantum usque ad 80(–240) μ m longi et usque ad 125 μ m in diametro. Sporangialia receptacula cylindricalia, magis vel minus ovoidea, cum terminalibus caespitibus pilorum. Uniloculares sporangiae, elongatae, latae lateraliter super paraphyses, quorum terminales cellululae largae et sphaericae usque sub-sphaericae sunt.

Algae (sporophyte) up to 31 cm tall, main terete axes with usually alternate, lateral branches, up to 12.5 cm long; attached below by a small discoid holdfast. Axes and branches bearing numerous (often dense), radially arranged, short, determinate, tufted branchlets, (0.25–)0.5–1.0(–2.0) mm in length, 200–600(–750) μ m in diameter; mostly without a stalk (pedicel), especially in upper portions of thallus, or, although apparently rare, with very minute stalks, only up to 80(–240) μ m long and up to 125 μ m in diameter.

Sporangial receptacles cylindrical, sometimes more or less ovoid, with terminal tuft of filaments from apical pit. Unilocular sporangia, clavate, 14–22 μ m in length and 3–4 μ m in diameter, borne laterally on paraphyses, with enlarged, spherical to subspherical terminal cell, 12–15 (–18) μ m in diameter.

Gametophytes unknown.

HABITAT. On rocks, subtidal; 20–30 m depths.

DISTRIBUTION. Gulf of California: Puerto Refugio, Isla Ángel de la Guarda.

HOLOTYPE. US Alg. Coll.-158492, 21 Apr 1974, coll. J. N. Norris & K. E. Bucher, JN-5262; isotypes: MICH; US Alg. Coll.

TYPE LOCALITY. Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Las Islas de la Cintura, Gulf of California.

ETYMOLOGY. The species is named in honor of the late Michael Neushul Jr. (University of California, Santa Barbara), professor, mentor, and friend, in recognition of his numerous contributions to marine botany (Lewis et al., 1994; Reed et al., 1994), for his teaching and encouragement to students, and particularly for his support of my Gulf of California research. He was inspired early on by E. Yale Dawson to study marine algae and become a scuba diver, and he also collected and published papers with Dawson on algae of southern California and Pacific Mexico.

REMARKS. *Sporochnus neushulii* is an endemic species, thus far only known from Puerto Refugio, Isla Ángel de la Guarda. The northern Gulf specimens somewhat resemble *S. apodus* Harvey (1859) in habit (cf. Womersley, 1967, 1987). The two differ in the nature of their sporangial receptacles. There is a complete absence of pedicels for the receptacles of *S. apodus* (Harvey, 1859: pl. XCII; Womersley, 1987: 278, fig. 101C–E; Brostoff, 1984, tbl. 1), whereas not all the receptacles of *S. neushulii* are nonpedicellate because some are on very minute pedicels. Their receptacles also differ in size and shape: in *S. apodus* they are 0.3–2.0(–4.0) mm in length and 200–300 μ m in diameter, broadest at their base, and slightly tapered upward; in contrast, they are mostly shorter in *S. neushulii*, 0.5–1.0(–2.0) mm in length and usually wider in diameter, 200–600(–750) μ m, and cylindrical (sometimes ovoid) and of similar diameter throughout. These two are also widely geographically separated from each other. *Sporochnus neushulii* is apparently restricted to the north end of Isla Ángel de la Guarda (29°32'N, 113°33'W), and *S. apodus* is known from Tasmania (type locality: George Town) and southern Australia (South Australia to Victoria; Womersley, 1987) (range approximately 33°–38.4°S, 134°–147°E). Thus, for now, they are recognized as different species.

Sporochnus neushulii also superficially resembles some *S. pedunculatus* (Hudson) C. Agardh (1820; type locality: England). However, *S. neushulii* differs from *S. pedunculatus* primarily by its sporangial receptacles, which usually lack stalks or have stalks, when present, that are very minute (less than 240 μ m long), and its sporangial receptacles are of similar or longer length, up to 2.0 mm. *Sporochnus pedunculatus*, from England (Fletcher, 1987) and the Mediterranean Sea, has sporangial receptacles that are slightly shorter in length, 0.5–1.0 mm, and borne on distinctive long stalks, up to 1 mm in length (Wynne, 2003).

Sporochnus pedunculatus has been reported on the Pacific coast from Santa Catalina Island, California Channel Islands (Mower and Widdowson, 1969, as “S.

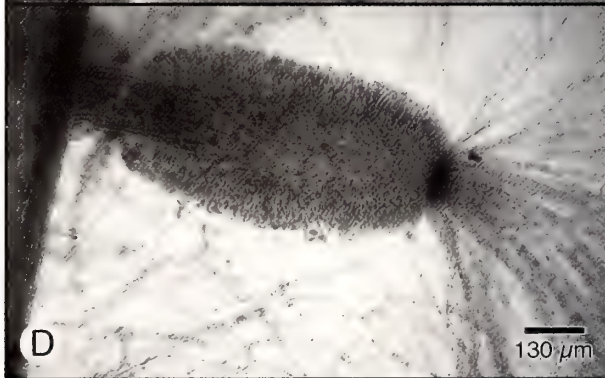
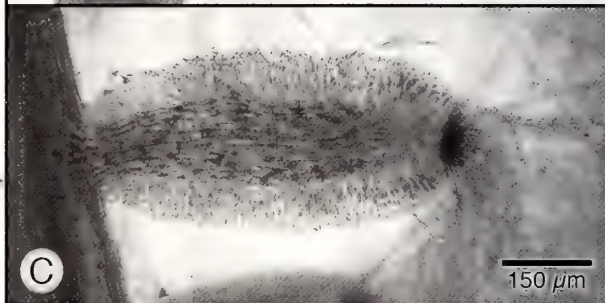
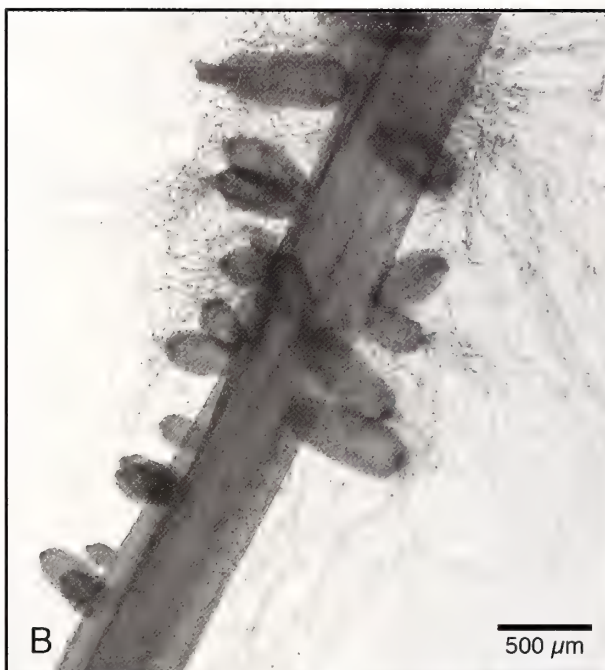


FIGURE 76. *Sporochmus neushulii* sp. nov., holotype (JN-5262; US Alg. Coll.-158492). A. Habit of holotype specimen. B. Portion of a branch with short, radially arranged, determinate, tufted branchlets. C. Example of a typical non-pedicellate determinate branchlet, completely covered by sporangial paraphyses from apical tuft to parent branch. D. Very minute, sterile stalk, as found on only a few of the determinate tufted branchlets. E. Portion of a receptacle showing a group of paraphyses, each with terminal subspherical cell (arrowhead), and developing laterally borne, unilocular sporangia (arrow).

apodus"), to Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur (Dawson et al., 1960b), and Isla Guadalupe (Setchell and Gardner, 1930; Stewart and Stewart, 1984). In contrast to *S. neushulii*, southern California *S. pedunculatus* (Abbott and Hollenberg, 1976) has much longer stalks (0.75–2.5 mm long) and longer (up to 2 mm long) and slightly narrower (up to 500 µm in diameter) sporangial receptacles. Finally, *S. pedunculatus* as reported in the western Atlantic (Taylor, 1960) and Gulf of Mexico (Earle, 1969) also has longer stalks (1–2 mm long) and generally smaller (0.75–1.25 mm; rarely to 2.0 mm long) and somewhat narrower (up to 500 µm in diameter) sporangial receptacles. Further studies and molecular analyses will be helpful in testing the taxonomic status and phylogenetics of the northern Gulf *S. neushulii* and California and Pacific Baja California *S. pedunculatus*.

RALFSIALES*

Ralfsiales Nakamura ex Lim et Kawai in Lim et al., 2007:464.

Ralfsiales Nakamura, 1972:152, *nom. invalid.*

Algae are crustose in at least one stage of their life history or have a crustose form only in the early stages of development (i.e., *Analipus* Kjellman, 1889; Wynne, 1971). The initial development of the thallus is disc-shaped in all members. Cells have one to several chloroplasts without pyrenoids.

Unilocular sporangia (zoidangia) are terminal or lateral and either with or without paraphyses. Plurilocular sporangia (zoidangia) are intercalary with terminal sterile cells. The Rubisco large subunit gene sequence is distinctive (Lim et al., 2007).

* Contributed by Daniel León-Álvarez and James N. Norris; D. León-Álvarez: Sección de algas del Herbario de la Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70–592, 04510 Mexico D.F., Mexico.

REMARKS. Although the Ralfsiales was first proposed by Nakamura (1972), the name lacked the required Latin description (see McNeill et al., 2006:Art. 36.2). Silva and de Reviere (2000) and León-Álvarez and Norris (2004) noted that since then, the name, although not validly published, had been used in the literature by many phycologists. The ordinal name was only recently validly published as Ralfsiales Nakamura ex Lim et Kawai (in Lim et al., 2007).

Originally, Nakamura (1972) proposed the order to include three families: Ralfsiaceae Farlow (1881), Lithodermataceae Hauck (1884), and Nemodermataceae J. Feldmann (1937). Subsequently, another family, the Mesosporaceae Tanaka and Chihara (1982), was added. Recently, the monotypic Nemodermataceae based on *Nemoderma* Kuckuck (1912), was removed from the Ralfsiales to a new order, the Nemodermatales Parente, R. A. Fletcher, F. Rousseau et N. Phillips (in Phillips et al., 2008).

There is one family represented in the northern Gulf of California.

RALFSIACEAE

Ralfsiaceae Farlow, 1881:17, 86.

Algae are discoid to spreading prostrate crusts or cushionlike, with smooth to convoluted surfaces. Crustose thalli growing on hard substrata are usually without rhizoids on their ventral surface and may be firmly attached or easily detached. Internally, crustose members are composed of a basal layer of horizontal radiating filaments, one to several cell layers thick, and middle to upper layers of assurgent to erect filaments produced by the basal cells. These layers may be loosely (e.g., *Hapalospongidion* De A. Saunders, 1899), moderately (e.g., *Petroderma* Kuckuck, 1897, and *Ralfsia confusa* Hollenberg, 1969), or closely packed (e.g., members of *Ralfsia* subgen. *Ralfsia* [= Batters, 1902:42, as "R. subgen. *Euralfsia*"]). Growth is from terminal cells of the horizontal and erect filaments or, in a few, intercalary from basal meristems of cortical

filaments. Cells have cup-shaped or plate-shaped chloroplasts without pyrenoids.

Reproductive structures are lateral, terminal, or intercalary on the reproductive filament and are usually associated with surrounding paraphyses or vegetative filaments (but lacking in a few) (León-Álvarez and Norris, 2004). Life histories, where known, are isomorphic, with unilocular or plurilocular sporangia (zoidangia) on separate individuals.

REMARKS. The Ralfsiaceae had been placed in the Ectocarpales (e.g., Wynne, 1981; Nelson, 1982; Scagel et al., 1989; Schneider and Searles, 1991; Silva et al., 1996a), or in the Myrionemataceae (e.g. Loiseaux, 1986), but on the basis of rDNA studies, Tan and Druehl (1994) concluded the family did not belong in the Ectocarpales,

and Draisma et al. (2003) stated molecular sequences of *Ralfsia* were needed to clarify their systematic and phylogenetic relationships. The ordinal taxonomic placement of the Ralfsiaceae was recently resolved in the molecular phylogeny of Lim et al. (2007), which supported the Ralfsiales. Taxonomic studies of members of the family include those of Tanaka and Chihara (1980a, 1980b, 1980c, 1981a, 1981b, 1982).

Riosmena-Rodríguez and Paul-Chávez (1997) have reported two genera in the southern Gulf from La Paz: *Endophlura* Hollenberg (1969) with *E. aurea* Hollenberg; and *Pseudolithoderma* Svedelius (in Kjellman and Svedelius 1910) with *P. nigrum* Hollenberg (1969).

Two genera, including one of uncertain taxonomic status, are known in the northern Gulf of California.

KEY TO THE GENERA OF RALFSIACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli low-growing clumps of overlapping linear, mostly horizontal, short branches *Hapterophycus*
 1b. Thalli crustose; flat, discoid to spreading, sometimes overlapping; of 2–3 layers: a basal layer of 1 or more horizontal filaments and 1–2 upper layers of assurgent or vertical filaments *Ralfsia*

***Hapterophycus* Setchell et N. L. Gardner in Setchell**

Hapterophycus Setchell et N. L. Gardner in Setchell, 1912:233.

Algae are low growing and spreading, but only slightly crustose, with linear, mostly horizontal, short branches. Medulla has a middle layer of horizontal filaments of elongated cells that have with downwardly directed filaments and assurgent filaments that end with adjoined erect filaments. Cryptostomata are present. Cells have a single parietal chloroplast. Unilocular sporangia are in broad sori; sessile at the base of multicellular paraphyses. Gametangia not confirmed.

REMARKS. The generic status of *Hapterophycus* is in need of investigation. In culture studies, Kogame (1996) has shown that Japanese specimens identified as "*H. canaliculatus*" were a sporophytic phase in the life history of a species of *Scytosiphon* C. Agardh (1820) and, on the basis of their morphological similarity to the generitype (*H. canaliculatus* Setchell et N. L. Gardner in Setchell, 1912), concluded them to be *Scytosiphon canaliculatus* (Setchell et N. L. Gardner) Kogame, thus reducing *Hapterophycus* to a synonym of *Scytosiphon* (Scytosiphonaceae). However, in culture studies of southern California *H. canaliculatus* (type locality: San Pedro,

California) neither Hollenberg (1941) nor Wynne (1969) observed erect thalli, and Wynne concluded there was a "direct type" of life history with a macroscopic alga with unilocular sporangia. Hollenberg (1941; see also Abbott and Hollenberg, 1976) concluded *Hapterophycus* should be in the Ralfsiaceae, close to *Ralfsia*. The question of its generic and familial placement and if the algae from California and Japan are the same species will need to be resolved by molecular and phylogenetic analyses.

There is one endemic species in the northern Gulf of California.

***Hapterophycus anastomosans* E. Y. Dawson**

FIGURE 77A,B

Hapterophycus anastomosans E. Y. Dawson, 1966b:56, figs. 2, 6A; Hollenberg, 1969:301; Wynne, 1969:7; González-González et al., 1996:152; Pacheco-Ruiz et al., 2008:204; Pedroche et al., 2008:26.

Algae form extensive, entangled mats, up to 40 cm or more in width; consisting of horizontal to partially erect, short, rigid (haptera-like) branches, subdichotomously to irregularly branched. Branches subcylindrical to compressed, up to 1.0 mm wide and to 15 mm long, simple to palmately divided terminally, with blunt, broadly rounded

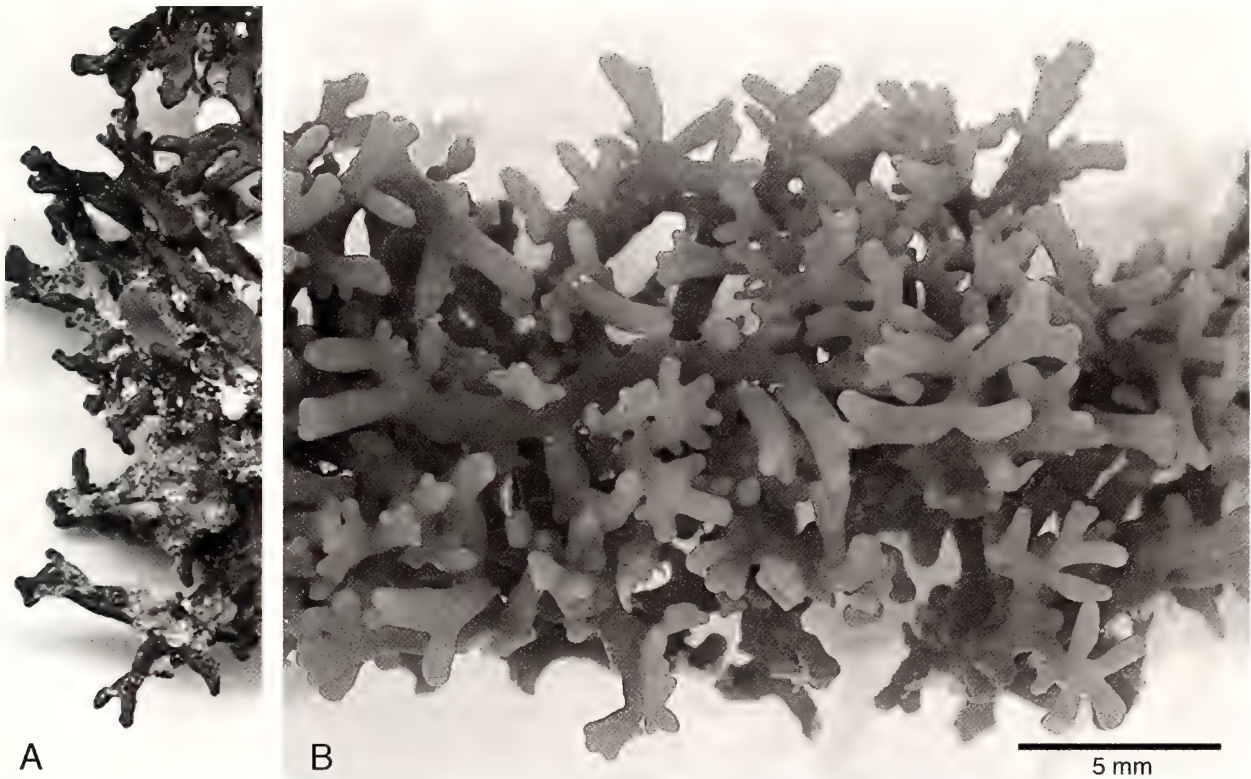


FIGURE 77. *Hapterophycus anastomosans*: Habit (holotype, EYD-26110; US Alg. Coll.-37228.). A. Portion of air-dried holotype specimen. B. Liquid-preserved portion of type specimen showing the entangled, fused, short branches that form the low-growing mat.

apices; entangled and fused at most lateral or terminal contacts by anastomosing growth, attachments give rigidity to thallus. Medulla in transection of compact, more or less isodiametric, angular cells of irregular size, 20–40 μm in diameter; in longitudinal section, central portion of irregularly oblong cells and outward cells in a “fountain pattern” toward the apices and cortical surfaces. Cortex of sparsely branched, anticlinal rows of 7–8 cells, 6–7 μm in diameter.

Reproduction not known.

HABITAT. On rocks, mid intertidal.

DISTRIBUTION. Gulf of California: Isla San Lorenzo; Isla Raza.

TYPE LOCALITY. Isla Raza, Islas de la Cintura, Gulf of California.

REMARKS. Apparently a Gulf endemic, the taxonomic status of *H. anastomosans* is in need of investigation (see also Remarks above under genus). Until the generic and specific status of Gulf *H.?* *anastomosans* can be tested by comparative morphological, life history, and molecular analyses with the generitype *H. canaliculatus*

Setchell et N. L. Gardner (in Setchell 1912) (type locality San Pedro), and those reported from southern California (Abbott and Hollenberg, 1976), Pacific Baja California (Dawson, 1951), and Isla Guadalupe (Stewart and Stewart, 1984), the Gulf of California taxon is referred to this genus with a query.

***Ralfsia* Berkeley in J. E. Smith et J. C. Sowerby**

Ralfsia Berkeley in J. E. Smith et J. C. Sowerby, 1843:pl. 2866.

Algae are crustose and loosely to firmly adherent (without rhizoids) to the substratum or attached by rhizoids. Initially, crusts are more or less disc shaped, but later spread and may become slightly lobed at the margins. Few to several crusts often grow close to each other, and each may become thicker by overgrowth of overlapping margins. Anatomically, there are two or three layers: a lower or basal layer of one to several horizontally radiating filaments, either with or without rhizoids from

its lowermost cells, and upper and/or middle layers developed from basal filaments that ascend to form more or less vertical, moderately to firmly adjoined, unbranched to sparingly branched filaments of similar length. Cells of the outer surface layer usually have one chloroplast per cell. Hairs are grouped in hair pits within the upper surface layers.

Reproductive structures are unilocular or plurilocular on separate algae. Unilocular structures are lateral or terminal and sessile or on one to few stalk cells (pedicel), usually associated with paraphyses, and grouped in superficial sori. Plurilocular structures are slender, of one to two rows of locules, with one to two sterile terminal cells, and grouped within the crust.

REMARKS. Life history studies of the species of *Ralfsia* thus far cultured are heteromorphic (with mostly asexual phases, but sexual phases have been reported for

some in culture studies), with an erect bladelike thallus (such as *Petalonia*) and a prostrate crustose *Ralfsia* or “*Ralfsia*-like” phase (e.g., Wynne, 1969, 1972; Nakamura and Tatewaki, 1975; Fletcher, 1978). Loiseaux (1968) found two species of *Ralfsia* to be apomeiotic with apparent isomorphic life histories. Culture and molecular studies of Gulf species should prove interesting and help elucidate their taxonomic status.

One species, *Ralfsia hesperia* Setchell et N.L. Gardner (1924b), has been reported in the southern Gulf (Carballo et al. 2002). In addition to those species known in the northern Gulf, there are at least two other species of “*Ralfsia*-like” crusts occurring on mid-intertidal rocks in the upper Gulf at Puerto Peñasco (Dawson, 1966a), but the lack of fertile material has left them undetermined.

Three species and one uncertain record are reported in the northern Gulf of California.

KEY TO THE SPECIES OF *RALFSIA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Crusts of 3 distinct layers: basal layer of 2–4 horizontal rows of basal filaments, upper medulla layer of assurgent rows of branching filaments, and multicellular cortical layer; unilocular sporangia on (3–)4–5(–6) celled pedicel . . . *R. hancockii*
- 1b. Crusts of 2 layers of filaments: a basal layer and an upper layer 2
- 2a. Upper layer of more or less assurgent filaments developed from basal layers; crusts usually more than 300 μm thick; mostly sessile sporangia *R. pacifica*
- 2b. Upper layer of erect, vertical rows of filaments above a thin basal layer of 1(–2) horizontal rows of basal filaments; crusts mostly less than 200 μm thick; unilocular sporangia on 1- to 6-celled pedicels *R. confusa*

Ralfsia confusa Hollenberg

FIGURE 78C

Ralfsia confusa Hollenberg, 1969:291, figs. 1–12; Abbott and Hollenberg, 1976:164, fig. 131; Stewart and Stewart, 1984:141; Dreckmann et al., 1990:26; Mateo-Cid and Mendoza-González 1992:23; León-Álvarez and González-González, 1993:461, 464; Mateo-Cid et al., 1993:49; González-González, 1993:443; León-Tejera et al., 1993:200; León-Tejera and González-González, 1993:497; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González 1994a:50; Mendoza-González et al., 1994:110; González-González et al., 1996:158; Rodríguez-Morales and Siqueiros-Beltrones 1999:22; Mateo-Cid et al., 2000a:67; Cruz-Ayala et al., 2001:190; Mateo-Cid and Mendoza-González 2003:21; Pedroche et al. 2008:28.

Ralfsia californica sensu Dawson, 1944:232 [in part; see Hollenberg, 1969:293] [non *Ralfsia californica* Setchell et N. L. Gardner, 1924b:2].

Algae, light to medium brown crusts, often coalescent, mostly 5–10 mm wide, and relatively thin, usually less than 200 μm thick and 150–250 μm thick in fertile portions. Basal layers of 1–2 horizontally elongate cells, 13.5–24.0 μm long and 9–12 μm in diameter. Upper layer of erect, vertical (not assurgent) filaments of 10–15 cells, 5–6 μm in diameter. Cells with a single chloroplast. Hair pits frequent.

Unilocular and plurilocular sporangia on separate thalli. Unilocular sporangia, 70–90 μm long by 20–25 μm in diameter, sessile or borne on pedicels of 1–2(–6) cells; associated with paraphyses of (3–)10–12 cells, 75–100 μm in length and 6–8 μm in diameter. Plurilocular sporangia mostly in uniseriate rows, 30–45(–60) μm in length and 5 μm in diameter, with a single sterile terminal cell, 7.5–10 μm long and mostly 5 μm in diameter.

HABITAT. On rocks; upper to low intertidal.

DISTRIBUTION. Gulf of California: Guaymas to Cabo Pulmo. Pacific coast: Washington; southern California to Baja California; Isla Guadalupe; Isla Socorro (Islas Revillagigedo); Sinaloa to Oaxaca.

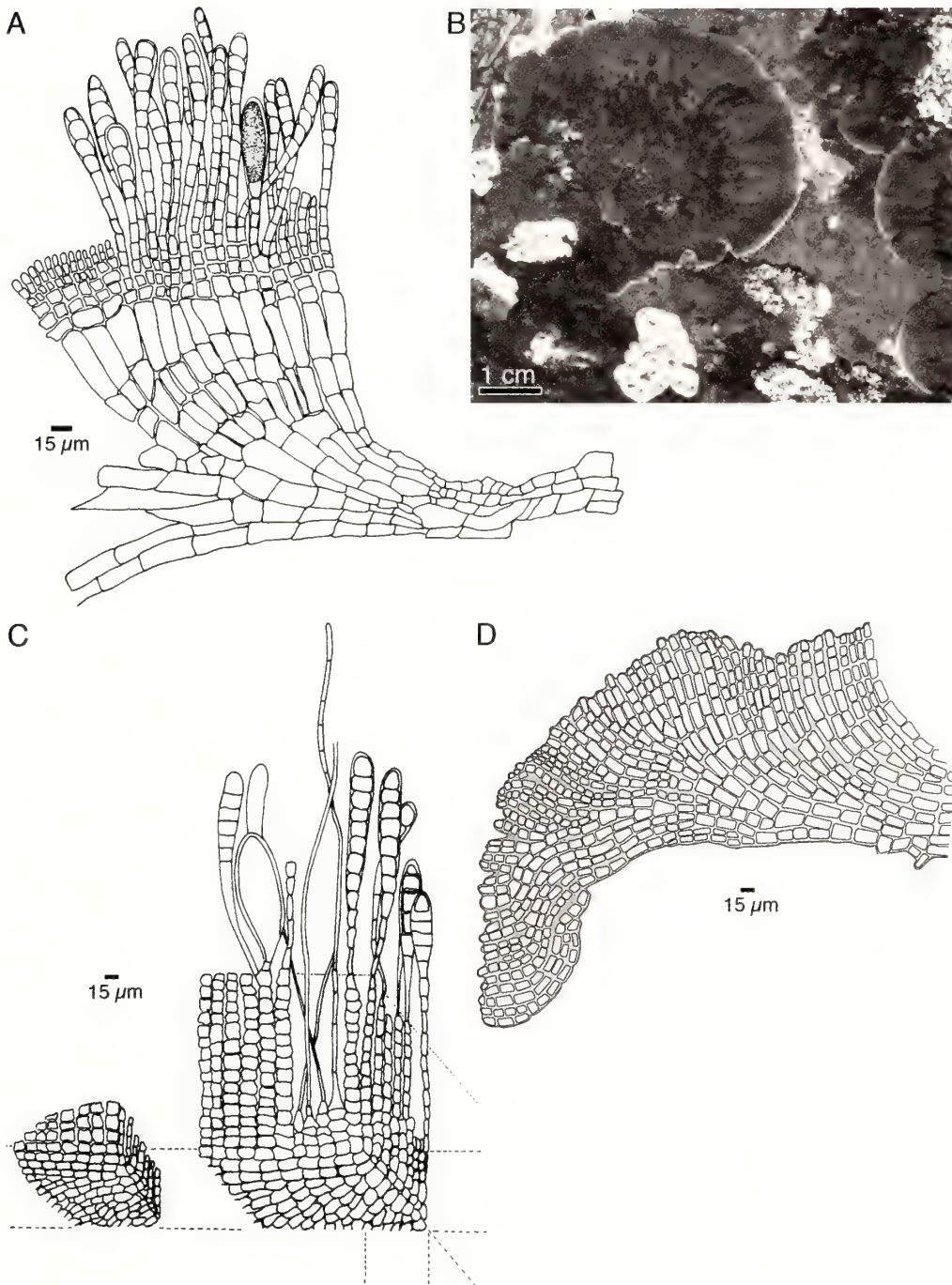


FIGURE 78. Species of *Ralfsia*. A, B. *Ralfsia hancockii*: A. Section of thallus showing assurgent branched rows of cells and unilocular sporangia on five-celled stalk and associated paraphyses. B. Habit, surface view of crust in the intertidal, showing the smooth surface and concentric lines of an orbicular crust. C. *Ralfsia confusa*: internal structure (three-dimensional depiction) showing vertical and horizontal growth of margin (left) and middle region showing vertical rows of cells, hairs in pits, and unilocular sporangia with associated paraphyses (right). D. *Ralfsia pacifica*: section through sterile crust showing filaments curving upward from basal layer. Illustrations A, C, and D drawn by Adrián Ramírez, UNAM; photo B taken by D. León-Álvarez.

TYPE LOCALITY. Corona del Mar, Orange County, California.

REMARKS. In describing *Ralfsia confusa* from southern California to Pacific Baja California, Hollenberg (1969:293) also suggested some of the Dawson collections (1944, as "*R. californica*") were probably this species; however, these thin Gulf specimens were not reproductive and thus are tentatively referred to *R. confusa*.

***Ralfsia hancockii* E. Y. Dawson**

FIGURE 78A,B

Ralfsia hancockii E. Y. Dawson, 1944:223, pl. 31: figs. 6, 7, pl. 54: fig. 2; Dawson, 1954a:3; Dawson, 1961b:387; León-Álvarez and González-González, 1993:461, 464; León-Álvarez and González-González, 1995:358, figs. 3, 4; González-González et al., 1996:158; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:67; León-Álvarez and González-González, 2003:614, figs. 2–12; López et al., 2004:10; Mateo-Cid et al., 2006:49, 57; Servièrre-Zaragoza et al., 2007:8; Pedroche et al., 2008:29.

Ralfsia expansa sensu Børgesen 1912a:123; Børgesen 1914:189 (see: León-Álvarez and González-González 2003:614); Chávez 1972:268; Tanaka and Chihara, 1980b:231, figs. 1B, 2C,D; González-González, 1993:443; León-Tejera et al., 1993:200 [non *Ralfsia expansa* (J. Agardh) J. Agardh, 1848:63].

Crusts light-brown to reddish brown, orbicular, up to 7 cm in diameter, upper surface smooth with radial and concentric growth lines or rugose to verrucose and with a conspicuous margin; vegetative portions 108–306 μm thick; reproductive portions 198–360 μm thick. Crusts firmly attached to substratum by rhizoids. Growth mainly unilateral; in thick portions, filaments may grow downward, tending toward bilateral symmetry. Base of 2–4 horizontal layers of thick-walled, elongate basal cells, 24–42 μm long and 10.5–15.0 μm in diameter; curving upward. Upper layer of assurgent, branching rows of cells; middle cells 22–31.5 μm long by 10.5–18 μm in diameter; outer cells of 4–7 layers of anticlinal cells, 6–10 μm long by 6–8.5 μm in diameter.

Unilocular sporangia, in sori sparsely scattered over thallus surface; ovoid, ellipsoid to clavate, 62.5–93 μm in length and 22–43 μm in diameter; terminal on a narrow stalk of 4–5 cells, 7.5–13 μm in diameter. Paraphyses slender of 10–18 cells, 100–150 μm long; basal cells 9–18 μm long by 3.8 μm in diameter; upper cells 6–12 μm long by

6–8 μm in diameter. Plurilocular sporangia not known for northern Gulf specimens.

HABITAT. Mid intertidal; on rocks and in tide pools; forming small continuous or isolated patches and often associated with crustose coralline algae.

DISTRIBUTION. Gulf of California: San Felipe to Puertecitos; Punta Arena to San José del Cabo. Pacific coast: Isla San Benedicto (Islas Revillagigedo); Nayarit to Oaxaca; Japan.

TYPE LOCALITY. Southern end of San José del Cabo, Baja California Sur.

REMARKS. Studies of León-Álvarez and González-González (1995, 2003) have clarified *Ralfsia hancockii*, and although some morphologically intergrading forms are found, two different morphological forms are recognized. One form is a light-yellowish-brown to dark-brown crust, 165–495 μm thick, with smooth upper surface without growth lines and sometimes greenish; strongly adhering to substratum by scattered rhizoids or without rhizoids (difficult to detach); anatomically tending toward unilateral symmetry. The other form is a light-brown to greenish crust, 108–750 μm thick; upper surface usually irregular, rough or sometimes verrucose, and with radial and/or concentric lines; partially attached to substratum (easily detached); anatomically of variable symmetry, usually tending toward irregular bilateral symmetry. Structures tentatively identified as "plurilocular sporangia" were found on Pacific Mexico *R. hancockii* (León-Álvarez and González-González, 2003), but thus far, no plurilocular reproductive structures have been reported in northern Gulf specimens.

***Ralfsia pacifica* Hollenberg**

FIGURE 78D

Ralfsia pacifica Hollenberg in G. M. Smith, 1944:95, pl. 12: figs. 4–6; Dawson, 1944:222; Dawson, 1961b:387; Smith, 1969:95, pl. 12: figs. 4–6; Hollenberg, 1969:296, figs. 17–18; Abbott and Hollenberg, 1976:167, fig. 135; Devinsky 1978:358; Pacheco-Ruíz, 1982:70; Dreckmann et al., 1990:26; González-González, 1993:443; León-Álvarez and González-González, 1993:461; Servièrre-Zaragoza et al. 1993:485; Mateo-Cid et al., 1993:49; González-González et al., 1996:158; Pacheco-Ruíz and Zertuche-González, 1996b:171; Riosmena-Rodríguez et al., 1998:45; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:68; López et al., 2004:10; Servièrre-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:30.

Ralfsia occidentalis Hollenberg in W. R. Taylor, 1945:81; Salcedo-Martínez et al., 1988:82.

Ralfsia verrucosa sensu Setchell and Gardner, 1925:497 [non *Ralfsia verrucosa* (Areschoug) Areschoug in E. Fries, 1845:124; basionym: *Cruoria verrucosa* Areschoug, 1843:264].

Crusts, irregularly circular, 2–10 cm broad, 0.4–1.0 mm thick, olive-brown to dark-brown, upper surface often with radial and concentric growth lines or ridges and firmly adhering to substratum without rhizoids. Basal layer filaments curving upward; of cells, 9–16 μm long by 11–32(–40) μm wide. Upper layer of forked filaments; of cells, mostly 6–8 μm in diameter and 12–24 μm long below, near the surface of similar diameter but shorter in length 6–15 μm ; hair pits frequent.

Unilocular sporangia oblong to clavate, up to 90 μm long and to 23 μm wide, usually sessile at base of paraphyses; borne in more or less circular sori, about 1 mm wide. Paraphyses of 9–12 cells, up to 150 μm long and up to 9 μm in diameter. Plurilocular sporangia in groups up to 1 mm in diameter within crust; uniseriate, up to 90 μm long, on cells shorter than broad (to 6 μm in diameter) of erect filaments, and with a single terminal sterile cell, 1.5–2.0 times long as wide.

HABITAT. On rocks; mid to low intertidal.

DISTRIBUTION. Gulf of California: Playa Santa Teresa; Bahía Tepoca to Isla San Esteban; Bahía Concepción to Cabo Pulmo; Matzatlán. Pacific coast: Alaska to Sinaloa; Isla Socorro (Islas Revillagigedo); Nayarit to Oaxaca.

TYPE LOCALITY. Corona del Mar, Orange County, California.

REMARKS. Although Womersley (1987) suggested that Pacific North America *Ralfsia pacifica* may not be distinct from the Australian *R. verrucosa*, most continue to recognize *R. pacifica* in Pacific Mexico (e.g., Abbott and Hollenberg, 1976; León-Álvarez and González-González, 1993; L. Aguilar-Rosas et al., 2000). The relationship of *R. pacifica* (type locality: southern California) and the Gulf of California *R. pacifica* to *R. verrucosa* (Areschoug) Areschoug in E. Fries (1845:124; type locality: Bohuslän, Sweden) requires further investigation (see also Tanaka and Chihara, 1980a, 1980b).

Uncertain Record:

Ralfsia californica Setchell et N. L. Gardner

Ralfsia californica Setchell et N. L. Gardner, 1924b:2; Setchell and Gardner, 1925:497, pl. 36: fig. 22; Daw-

son, 1944:223 [in part]; Dawson, 1961b:386 [in part]; González-González et al., 1996:158; Pedroche et al., 2008:27.

REMARKS. The report of *Ralfsia californica* from the northern Gulf is questionable since it was based on nonfertile specimens (Dawson, 1944). Culture studies of Pacific coast “*R. californica*” (as interpreted by Wynne, 1969, 1972) indicate that it is a sporophytic crustose phase in the heteromorphic life history of Pacific North American species of Scytosiphonaceae, including *Petalonia fascia* (O. F. Müller) O. Kuntze (1898) (see also Nakamura and Tatewaki, 1975; Dethier, 1981, 1987; Kogame, 1997a), which has been reported from Alaska to Baja California and Sinaloa (Scagel et al., 1989; Hansen, 1997; Perdoche et al., 2008). Other specimens similar to “*R. californica*” (Wynne, 1969, 1972) or *Ralfsia*-like crusts (Nakamura, 1965; Tatewaki, 1966) were found to be a phase in the life history of *Scytosiphon lomentaria* (Lyngbye) Link (1833).

Interestingly, southern California to Pacific Baja California specimens identified as “*R. californica*” were determined to be a new species, *R. confusa* Hollenberg (1969; Abbott and Hollenberg, 1976). Thus, “*R. californica*” from the Gulf clearly needs reinvestigation. Fertile specimens need to be found, and culture studies and DNA analyses are needed before its identification can be verified.

CUTLERIALES

Cutleriales Oltmanns, 1922:109.

Cutleriales Bessey, 1907:289.

Algae are erect or prostrate or partially prostrate and erect. Gametophytes may be cylindrical or narrow and slightly compressed and variously branched, with all branches having an apical tuft of unbranched filaments, or flat and fan shaped, with a fringed distal margin of monosiphonous unbranched filaments. Life histories are isomorphic or heteromorphic. Members of the latter group have gametophytes that are erect and a morphologically different macroscopic crustose sporophyte. Erect thalli have a trichothallic mode of growth, with intercalary cell division occurring near the base of each distal unbranched pigmented filament. Both gametophytes and sporophytes are parenchymatous in structure, with cortical layers of small pigmented cells and a medulla of irregularly arranged larger, colorless, rounded cells. Cortical cells have numerous discoid plastids and apparently lack pyrenoids; however, Hori and Ueda (1975) reported that although inconspicuous, small pyrenoids may also

be present. Single or small clusters of phaeophycean hairs arising from surface cells are scattered over the thallus surface.

Sporophytes (asexual phase) develop unilocular sporangia in sori scattered on the blade surface. Each sporangium produces 8, 16, or 32 motile meiospores. Gametophytes are either monoecious or dioecious, with gametangia borne in clusters on lower portions of simple or branched fertile filaments (which, in some, may extend into hairlike filaments). Sexual reproduction is anisogamous. Female gametangia have 8–16 large locules, while male gametangia have numerous smaller locules.

REMARKS. Recent study of the phylogenetic relationships of brown algae by Phillips et al. (2008:figs. 3, 4) have revealed the Cutleriaceae and Tilopteridaceae to diverge within the same group. Further, they considered these two families to be a single order Tilopteridales Kylin (1917; = Tilopteridales Bessey, 1907) and suggested that ordinal name be used. However, herein the more widely used Cutleriales Oltmanns sensu stricto is recognized for the order.

There is one family represented in the Gulf of California.

CUTLERIACEAE

Cutleriaceae Hauck, 1883:318; Hauck, 1884:403 [see Silva, 1980:71].

Cutleriaceae J. W. Griffith et Henfrey, 1856:179.

The family has the characteristics of the order and includes three genera: *Cutleria* Greville (1830), *Microzonia* J. Agardh (1894), and *Zanardinia* Nardo ex P. Crouan et H. Crouan (1857).

One genus, *Cutleria*, is represented in the Gulf of California.

Cutleria Greville

Cutleria Greville, 1830:xliv, 59.

Most species of *Cutleria* have an alternation of heteromorphic generations with an erect gametophyte and a prostrate crustose sporophyte. The latter was once considered to be a separate genus, *Aglaozonia* Zanardini (1843), until it was recognized as an alternate phase in the life history of *Cutleria* (Falkenberg, 1879; Yamanouchi, 1912; Drew, 1955). Gametophytic thalli of *Cutleria* are mostly compressed to flat and are either fan shaped or straplike (however, at least one species is cylindrical) and

may be entire or dichotomously to irregularly branched, with lacinated apices, and attached to the substratum by rhizoidal outgrowths or discoid holdfasts. Growth is by trichothallic meristems near the base of unbranched pigmented filaments that are either along the distal margin of flabellate blades or, in other species, terminal on the branch apices. These filaments coalesce with each other behind the apical tufts, and longitudinal divisions take place to form a parenchymatous thallus that develops a one- to two-celled cortical layer and a medulla of several layers of larger, colorless, rounded cells. Cortical cells contain many discoid chloroplasts without conspicuous pyrenoids. Phaeophycean hairs are usually grouped together in small clusters and are scattered over the surface.

Sporophytes of *Cutleria* (“*Aglaozonia*-phase”) are prostrate and flabellate to irregularly shaped and lobed thalli, from 3 to up to 10 cells thick, with tufts of phaeophycean hairs on their upper surface. Crusts are loosely attached to the substratum by rhizoidal filaments produced from their lower surface. Growth is by a row of meristematic cells along the thallus margin. The medulla is composed of irregularly placed large inner cells, and cortex is composed of smaller cells.

The life history, where known, is an alternation of heteromorphic generations. Unilocular sporangia of the encrusting sporophyte (“*Aglaozonia*-phase”) are sessile, cylindrical, and grouped in clusters on the crust surface. Plurilocular sporangia on sporophytic thalli that develop neutral plurispores have been reported in one species, *C. cylindrica* from Japan (Kitayama et al., 1992). Gametophytes of *Cutleria* are dioecious or monoecious. Plurilocular gametangia are typically grouped in superficial tufts on erect blade surfaces. Female gametangia are ovoid, with large locules, and produce gametes more than twice as long and wide as male gametes. Female gametes attract male gametes by the secretion of a sexual pheromone (Müller, 1974). Antheridial gametangia are elongated, with numerous smaller locules. Parthenogenesis of unfused female gametes and androgenesis of unfused male gametes have both been reported (Kitayama et al., 1992).

REMARKS. Gametophytes of *Cutleria* are typically reported to be annual or ephemeral, and sporophytes are usually reported to be perennial. The reported dominance in field populations of female gametophytic thalli has been partly explained by parthenogenetic females (Fletcher, 1987; Womersley, 1987; Kitayama et al., 1992). Unfused female gametes may either develop into female gametophytes or develop directly into the sporophyte (Kitayama et al., 1992; Nagasato et al., 1998).

There is one species, *Cutleria cylindrica* Okamura (1902b), reported on the Pacific coast from southern California (Hollenberg, 1978; Stewart, 1991) to northern Baja California (R. Aguilar-Rosas, 1994).

One endemic species occurs in the Gulf of California.

***Cutleria hancockii* E. Y. Dawson**

FIGURE 79A-F

Cutleria hancockii E. Y. Dawson, 1944:226, pl. 54: fig. 1; Dawson, 1953b:3; Dawson, 1961b:387; Dawson, 1966a:9–10; Hommersand, 1972:70; Norris, 1973:4; La Claire and West, 1978:93, figs. 1–31; La Claire and West, 1979:247, figs. 1–30; Littler and Littler, 1981:153, tbl. 4; Mendoza-González and Mateo-Cid, 1986:420; Espinoza-Ávalos, 1993:333; Mendoza-González et al., 1994:110; González-González et al., 1996:143; Pacheco-Ruíz and Zertuche-González, 1996b:171; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2000a:68; Riosmena-Rodríguez et al., 2001:461, fig. 1; Mateo-Cid et al., 2006:49, 58; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:58.

Zanardina prototypus sensu Dawson 1941:119 [non *Zanardinia prototypus* (Nardo) Nardo 1841:189, *nom. illeg.*; which is now *Zanardinia typus* (Nardo) P.C. Silva in Greuter 2000:2].

Gametophytic algae (Figure 79A–D) erect, light-brown to golden-yellow-brown, flat, fan-shaped blades with fringe of monosiphonous pigmented filaments along distal margin, blades often becoming lacinate; 1 to several blades per clump, up to 15(–22) cm high by (2.5–)10–21 cm wide; arising from a flattened, prostrate basal portion attached by rhizoids from its undersurface. Trichothallic growth occurs at the basal meristem of each monosiphonous unbranched filament near the transition from free filaments to consolidated blade. Blades parenchymatous below the fringed margin, with 1(–2) layer(s) of small pigmented cortical cells. Fronds 100–140(–180) μm thick. Cortical cells: in transection, brick-shaped, 6–9(–12) μm long by 5–9 μm wide; in surface view, quadrate with rounded corners. Medulla cells in transection, irregularly arranged, (45–)60–100(–125) μm long by (17–)35–53 μm wide.

Gametophytes dioecious, gametangial sori in tufts on thallus surface, coalescing to form concentric bands on mature thalli, on both surfaces of blade. One to a number of plurilocular gametangia develop on a fertile filament, a greater number of male gametangia in a series than female gametangia. Female gametangia develop laterally on fertile

filaments; initially, a protuberance forms a 2- and then 4-celled filament that divides twice longitudinally to form a gametangium of 4 tiers with 4 locules per tier (16 locules) and matures acropetally. Mature female gametangia are ovoid, usually biseriolate in lateral view, 40–55 μm long by 18–20 μm wide. Antheridial gametangia borne laterally (rarely terminal) on fertile filaments; mature antheridial gametangia often multiseriolate in lateral view, of 16 tiers with 4–6 locules per tier (64–96 locules). Antheridial gametangia cylindrical, 40–60 μm long by 7–9 μm wide. The uniseriate fertile filament continues on above both types of gametangia with a sterile portion that has shorter and wider cells (9.5–12 μm in diameter) and more pigmented cells than filament cells below it.

Aglaozonia*-phase of *Cutleria hancockii

Sporophytic thalli (“*Aglaozonia*-phase”; Figure 79 E,F) encrusting, brown to olive-brown, loosely attached, thin, prostrate blades, multilobed, small, up to 2 cm wide; loosely attached by branched, multicellular rhizoids. Lobes 2–5 mm wide, rounded; 70–85(–105) μm and often 6–7 cell layers thick. Thallus parenchymatous, arising from slightly larger, darker row of meristematic apical cells along the crust’s margin. Crust dorsiventral, cortical surface cells quadrate, 6–8 μm in diameter, lower cortex flanking substrate of larger cells, medulla of several slightly uneven layers of larger colorless cells.

HABITAT. On rocks or loosely attached to various fleshy algae and corallines; epizoic on mollusk shells and carapace of black sea turtle (*Chelonia mydas agassizii*); mid to low intertidal, occasionally in shallow subtidal, to 5 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla San Pedro Nolasco; Múlege to Bahía Concepción; Bahía de La Paz to Punta Arena (Baja California Sur); Mazatlán, Sinaloa.

TYPE LOCALITY. Gametophyte: low intertidal, rocky reef, Isla Turners (off Isla Tiburón), Las Islas de la Cintura, Gulf of California. Sporophyte: southwest shore of Isla Tiburón (opposite Isla Turners), Las Islas de la Cintura, Gulf of California.

REMARKS. Apparently a Gulf of California endemic, gametophytes of *Cutleria hancockii* in the northern Gulf occur seasonally from midwinter to midspring, only rarely extending into late spring (during cooler years). On the reef platform at Playa Estación, Puerto Peñasco, gametophytes are found in the mid to low intertidal from January to June, sometimes with the darker-brown, lobed crustose “*Aglaozonia*-phase.” *Cutleria hancockii* is easily

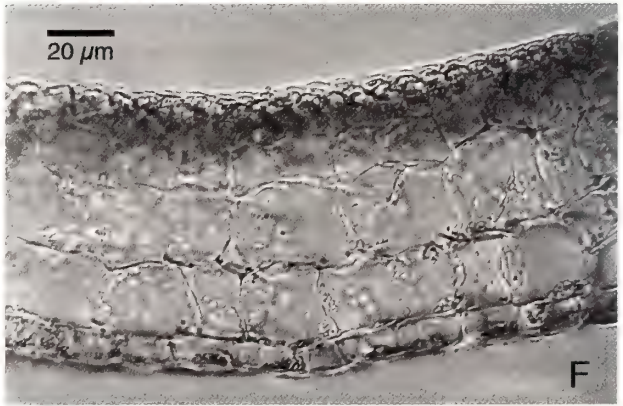
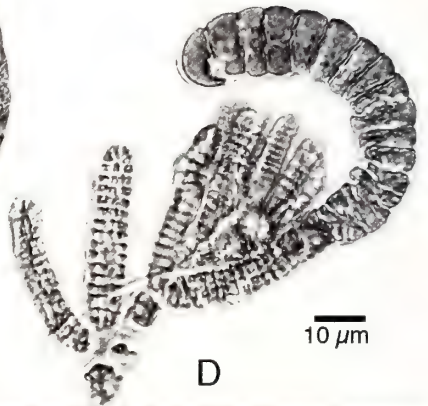
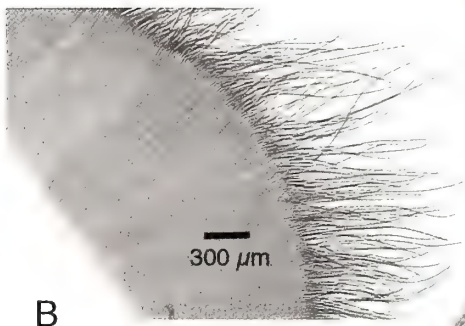


FIGURE 79. *Cutleria hancockii*: A–D. Gametophytes: A. Frond with concentric bands of dense reproductive filaments bearing male gametangia (JN-4953). B. Trichothallic growth occurs at meristems near the base of monosiphonous filaments fringing the frond margin (JN-4786). C. Fertile filament bearing female gametangia with large locules (JN-6040). D. Fertile filament bearing a row of male gametangia with numerous smaller locules (JN-7065). E, F. Sporophytes (*Aglaozonia*-phase of *Cutleria hancockii*): E. Surface view of a portion of the crust; note larger, darker apical cells lining margin (EYD-27365). F. Transection through dorsiventral crust (JN-3691b).

separated from somewhat similar looking Gulf *Padina*: *Cutleria* is more delicate, yellowish brown to golden light brown, with a fringed margin of monosiphonous filaments, whereas *Padina* is more rigid and darker brown, with an inrolled margin.

ECTOCARPALES

- Ectocarpales Setchell et N. L. Gardner, 1922c:403.
- Mesogloiales Nägeli, 1847:141, 252.
- Ectocarpales Bessey, 1907:288.
- Chordariales Setchell et N. L. Gardner, 1925:570.
- Dictyosiphonales Setchell et N. L. Gardner, 1925:586.
- Scytosiphonales Feldmann, 1949:112.

Gametophytic and sporophytic thalli exhibit a great diversity of size and shape. Some are erect tufts of unbranched or branched uniseriate filaments that are attached by basal rhizoids, and some are filaments that are entirely or partly endophytic. Others are cylindrical to compressed, foliose, saccate, or subglobose and may be simple and entire or branched, membranous or gelatinous in texture, with surfaces that are smooth, irregular or folded, or that may be perforated with holes of various sizes. Internally, the latter group are centrally solid or hollow, with a medulla either of colorless filaments surrounding a core of uniaxial or multiaxial filaments or of large, colorless parenchymatous cells. The cortex of pigmented filaments or small pigmented cells bears the reproductive structures and is with or without phaeophycean hairs. Growth is apical, intercalary, diffuse, or trichothallic in cortical filaments. Cells have a single or few to many ribbon-shaped or discoid chloroplasts, with one to several pyrenoids. Ultrastructural studies have shown a pedunculate pyrenoid with a cap layer

in the plastids (Evans, 1966; Hori 1971; Hori and Udea, 1975), a character unique to the Ectocarpales, and vesicle-like globules (physodes) that may be present or lacking.

Life histories, where known, may be any of four basic types: (1) isomorphic generations of sporophytes and gametophytes; (2) heteromorphic, with a large sporophyte and microscopic gametophytes; (3) heteromorphic, with either gametophytic or sporophytic macrothalli that have either a sporophytic or gametophytic crustose phase, respectively; or (4) some macrothalli that have direct development to the next phase.

Reproductive structures are terminal, lateral, or intercalary and may be either solitary or in series or in sori scattered over the thallus surface. Sporangia may be unilocular or plurilocular; both produce zoospores. Also, some have been found to have unilocular sporangia that produce meiospores, and a few with neutral plurilocular sporangia are known. Sexual reproduction is isogamous or anisogamous. Gametophytes develop plurilocular or unilocular gametangia that produce isogametes or anisogametes. Gametes in some have been shown to be capable of parthenogenetic development.

REMARKS. The taxonomy of the Ectocarpales is still in flux. There has been much debate about the distinctiveness of the orders Chordariales, Dictyosiphonales, Mesogloiales, and Scytosiphonales and if they should be included in the Ectocarpales. On the basis of molecular analyses, many now consider these orders to be part of the Ectocarpales (e.g., Rousseau and de Reviers, 1999a; Silva and de Reviers, 2000; Peters and Ramirez, 2001; Draisma et al., 2003; Cho et al., 2004; Adl et al., 2005; Phillips et al., 2008).

There are seven families represented in the northern Gulf of California.

KEY TO THE FAMILIES OF ECTOCARPALES IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae of uniseriate filaments throughout or basically filamentous (mostly uniseriate, but a few cells may divide longitudinally to become parenchymatous) 2
- 1b. Algae not filamentous; erect, terete to compressed or foliose and simple to branched or saccate or globose 4
- 2a. Filaments mostly uniseriate, becoming parenchymatous by a few longitudinal divisions; meristems random; reproductive structures developed within vegetative cells **Pylaiellaceae**
- 2b. Uniseriate filaments throughout; meristems intercalary; reproductive structures lateral or terminal 3

- 3a. Meristems localized or random on axes and branches; ribbonlike plastids with several pyrenoids **Ectocarpaceae**
 3b. Meristems mostly basal on axes and branches; discoid plastids usually with single pyrenoid **Acinetosporaceae**
 4a. More or less cylindrical, axes and branches, narrow diameter; internally solid parenchyma (not hollow); surface of irregularly arranged cells, and numerous shallow pits with conspicuous tufts of hairs; single plastid with 1 pyrenoid; growth by a subapical meristem **Chnoosporaceae**
 4b. Cylindrical to compressed and simple to branched or frondose, saccate, or globose; discoid plastids with pyrenoids; growth by diffuse intercalary meristems or single apical cell 5
 5a. Gametophytes erect, tubular to compressed, saccate, globose, or foliose, either open flat and entire or clathrate (with holes); internally, usually hollow; medulla parenchymatous, cortex of small cells; sporophytes crustose **Scytosiphonaceae**
 5b. Thalli variable: minute filaments or small to moderate size globose to lobed forms or cylindrical to compressed branched forms; internally, not hollow; medulla filamentous; cortex of filaments 6
 6a. Small, globose, subglobose, or lobed forms; without an evident basal layer **Leathesiaceae**
 6b. Minute filaments, epiphytic or endophytic, simple to branched with or without a distromatic basal layer or erect, cylindrical to compressed branched forms with a holdfast **Chordariaceae**

ACINETOSPORACEAE

Acinetosporaceae Hamel, 1931b:8 [as "Acinétosporacées"]; Hamel ex J. Feldmann, 1937:110.

Algae are uniseriate filaments that either are sparsely and irregularly branched or can be more densely branched and of variable branching patterns. Species grow as epiphytes or attached on hard substratum. Branches are often formed from the middle of an axial cell (appearing perpendicular to it) and have rounded or tapered and hairlike apices; some develop short, curved laterals (crampons) that attach to or become entangled with other algae. Intercalary meristematic growth regions are basal, usually near the base of laterals, or diffuse. Cells have numerous plastids, each with a pyrenoid.

Reproduction by fragmentation has been documented for some species (Amsler, 1984). Ovoid monosporangia, which are found in some, produce and release a single nonmotile spore. Unilocular and plurilocular sporangia are sessile, short-stalked, or intercalary (formed by direct transformation of vegetative cells). Plurilocular structures have been described with large locules (zoosporangia) in some species and with numerous small locules in others. Plurilocular gametangia, of different shapes and sizes, that produce isogametes or anisogametes are also known for many of the species.

REMARKS. Life histories for some members of the family are not completely understood. For example, there is no evidence that meiosis occurs in the unilocular sporangia, nor has sexual reproduction been observed in the type of the family (*Acinetospora pusilla* (Griffiths ex Harvey) De Toni, 1895b; = *A. crinita* (Carmichael) Kornmann, 1953). Müller (1986) reported apomeiotic unilocular sporangia and suggested that the loss of sexual reproduction could allow the establishment of geographically isolated populations and could account for the great variability within species of *Acinetospora*.

The report of *Asteronema breviarticulatum* (J. Agardh) Ouriques et Bouzon (2000; basionym: *Ectocarpus breviarticulatus* J. Agardh 1847) establishes the genus *Asteronema* Delépine et Asensi (1975) in the southern Gulf (Huerta-Múzquiz and Mendoza-González 1985, as "*E. breviarticulatus*"; Riosmena-Rodríguez and Paul-Chávez 1997; and Mateo-Cid et al. (2000a, as *Hincksia breviarticulata* (J. Agardh) P. C. Silva (in Silva et al., 1987). The familial placement of the genus is problematic, and it has been placed in the Ectocarpaceae, Scytothamnaeae Womersley (1987) or Acinetosporaceae.

Two genera are known in the northern Gulf of California.

KEY TO THE GENERA OF ACINETOSPORACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments relatively simple; with branches and reproductive structures below distinct intercalary meristems in lower portion of axes; above the meristematic zone filaments long and unbranched, with distal portion often appearing hairlike. **Feldmannia**
 1b. Filaments repeatedly branched, 2–4 orders; with intercalary meristematic zones and reproductive structures distributed throughout main axes and branches **Hincksia**

Feldmannia Hamel

Feldmannia Hamel, 1939b:xli.

Algae are small, usually epiphytic, erect tufts of uniseriate filaments; each of the axes, and branches, has a distinct localized intercalary meristematic zone near its base; and are attached below by rhizoids or sometimes by prostrate filaments. Branches are restricted to below the meristematic zone. Above the meristematic zone, the filaments are unbranched and become long, with hair-like ends. Cells contain several to many discoid chloroplasts with one to many pyrenoids.

Life histories, where known, are isomorphic. Reproductive structures are below the meristematic zones. Unilocular sporangia are ovoid to spherical. Plurilocular sporangia and plurilocular gametangia are multiseriate, similar in appearance, and apparently borne on separate thalli. Gametes are isogamous.

REMARKS. The taxonomic status of *Feldmannia* has been questioned by some phycologists. For example, Knoepffler-Péguy (1974) found some species of *Acinetospora* Bornet (1891) were involved in the life history of some species of *Feldmannia* and *Hincksia* and later concluded that these genera could not be convincingly separated on morphology and may represent a single variable genus (Knoepffler-Péguy, 1977). Later, Kim and Lee (1994), recognizing *Feldmannia*, proposed that the genus be based solely on the characteristics seen in the illustration of *Ectocarpus irregularis* Kützing (1855:pl. 62: fig. 1). Several others have also continued to recognize *Feldmannia* (e.g., Womersley, 1987; Silva et al., 1987; Silva et al., 1996a; Abbott and Huisman, 2004). Pedersen and Kristiansen (2001) elucidated generic characters and concluded that *Acinetospora*, *Feldmannia*, and *Hincksia* could be reliably distinguished. Life history culture studies and molecular analyses on the generitype, *Feldmannia lebelii* (Areschoug ex P. Crouan et H. Crouan) G. Hamel (1939a; basionym: *Ectocarpus lebelii* Areschoug ex P. Crouan et H. Crouan, 1867), will help clarify its generic status.

One species, *Feldmannia hemispherica* (De A. Saunders) Hollenberg (1971), has been reported in the southern Gulf (Mateo-Cid and Mendoza-González 1994a).

There is one species known in the northern Gulf of California.

***Feldmannia irregularis* (Kützing) Hamel**

FIGURE 80

Ectocarpus irregularis Kützing, 1845:234; Kützing, 1855:19, pl. 62: fig. 1 [note: illustration redrawn by

Kim and Lee, 1994: fig. 4A]; Dawson 1954a:3; Dawson, 1961b:385; González-González et al., 1996:149; Yoshida, 1998:168.

Feldmannia irregularis (Kützing) Hamel, 1939b:xvii, fig. 61f; Cardinal, 1964:54, fig. 29A–K; Hollenberg, 1970:61, fig. 1; Hollenberg, 1971:285; Abbott and Hollenberg, 1976:136, fig. 99; Stewart, 1991:39; Kim and Lee, 1994:154, figs. 1A,B, 2A–C, 3A–K, 4A,B; González-González et al., 1996:296; Abbott and Huisman, 2004:159, fig. 58A; Mateo-Cid et al., 2006:49; Servière-Zaragoza et al., 2007:8; Pedroche et al., 2008:20.

Giffordia irregularis (Kützing) Joly, 1965:72, pl. VIII: figs. 111–119.

Hincksia irregularis (Kützing) Amsler in Schneider et Searles, 1991:120, figs. 129–131.

Ectocarpus mucronatus De A. Saunders, 1898:152, pl. 19; Setchell and Gardner, 1925:429; Dawson, 1944:220; Dawson, 1961b:385; Dawson, 1966a:9; González-González et al., 1996:149.

Algae small, slender tufted thalli, up to 3 mm tall, of erect, loosely intertwined filaments that become elongated

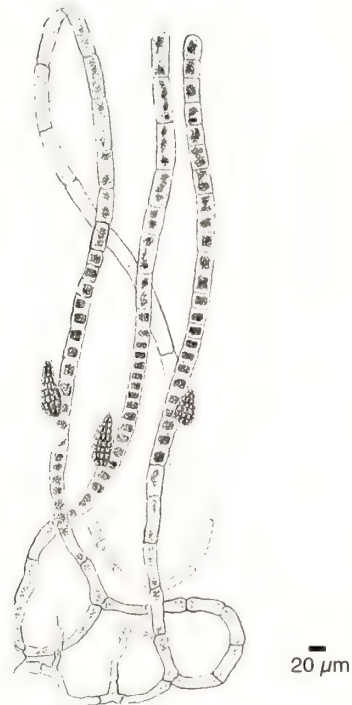


FIGURE 80. *Feldmannia irregularis*: Drawing of type specimen (from Kützing, 1855: pl. 62, fig. 1).

and taper slightly toward apices (terminal hairlike appearance due to elongated cells with fewer chloroplasts); attached below by a prostrate system of entangled rhizoidal filaments. Axes often sparse and irregularly branched several times below the intercalary meristematic zone (meristem shifts upward toward the lower-middle portion of the filament as it grows, obscuring its original basal position). Cells 18–20 µm in diameter; 0.5–1.0 times as long as wide in meristematic zone; 1–3 times as long as wide in lower portions and 2–5 times as long as wide in upper portions.

Unilocular sporangia unknown in Gulf material. Plurilocular sporangia sessile on branches below meristematic zone; elongate-conical, 90–150 µm long and 20–35 µm in diameter, often with attenuated apices.

HABITAT. Epizoic on the black sea turtle (*Chelonia mydas agassizii*; see Parham and Zug, 1996), epiphytic on *Sargassum* and probably other algae, and growing on rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Canal de Infernillo (between coast of Sonora and Isla Tiburón). Pacific coast: British Columbia to Oregon; southern California to Baja California; Isla San Benedicto (Islas Revillagigedo); Hawaiian Islands; Japan; China.

TYPE LOCALITY. On *Laurencia obtusa*, Adriatic Sea.

REMARKS. *Feldmannia irregularis* has a wide distribution (Guiry and Guiry, 2008), but its generic placement has been somewhat uncertain, in part because the type specimen of *Ectocarpus irregularis* Kützinger (1845) was not preserved and the original description was vague (Clayton, 1974). This uncertainty has resulted in the species being variously interpreted as belonging to other genera; e.g., Womersley (1987) noted that Australian *F. irregularis* exhibited intermediate characteristics of both *Feldmannia* and *Hincksia*, and Amsler (in Schneider and Searles, 1991) considered it to be *Hincksia irregularis*. However, studies of Kim and Lee (1994) support recognition of *Feldmannia irregularis*.

Life history culture studies and comparative molecular analyses on Gulf of California specimens referred to *F. irregularis* are needed to elucidate their taxonomic status and phylogenetic relationships.

Hincksia J. E. Gray

Hincksia J. E. Gray, 1864:12.

Giffordia Batters, 1893:86; Hamel, 1939b:X, as “*Giffordia* (Batters) Hamel.”

Algae are erect, tufts of uniseriate filaments with variable branching patterns, and attached below by rhizoids. Branching is to 2–3(–4) orders and unilaterally secund or tending to spiral or irregular, alternate, or opposite. Growth is diffuse by intercalary cell divisions. Meristems are scattered throughout the axes and near the base of most branches, with additional meristems distally. Meristematic zones are not always obvious but in some species are very distinct. Cells are more or less isodiametric to barrel-shaped and have numerous discoid chloroplasts, each with a single pyrenoid. True phaeophycean hairs are unknown.

Life histories are mostly of isomorphic alternating generations; however, some have repeating generations via spores or parthenogenic gametes. Reproductive structures are usually sessile and singular or in a series on the branches. Unilocular sporangia are apparently rare. Plurilocular sporangia are formed on the adaxial side of the supporting lateral branch and may also occur on the main axis. Plurilocular gametangia (where known) are of different sizes and shapes and produce anisogametes.

REMARKS. One species is reported in the southern Gulf, *Hincksia rallsiae* (Vickers) P. C. Silva (in Silva et al., 1987), by Mateo-Cid et al. (2000a).

Three species are known in the northern Gulf of California.

KEY TO THE SPECIES OF HINCKSIA IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments occasionally to frequently oppositely branched; plurilocular sporangia sessile, asymmetrically ovoid *H. granulosa*
- 1b. Filaments not oppositely branched, mostly dichotomous, alternate, unilaterally secund, or spiral; plurilocular sporangia sessile or pedicellate and fusiform or ellipsoidal to cylindrical 2
- 2a. Branching sparse, dichotomous below (nearly at algal host’s surface cells); apical cells blunt; plurilocular sporangia sessile or pedicellate, fusiform *H. bryantii*
- 2b. Branching alternate or unilaterally secund or spiral; apices attenuated; plurilocular sporangia sessile and ellipsoidal to cylindrical with rounded apices *H. mitchelliae*

***Hincksia bryantii* (Setchell et N. L. Gardner)
J. N. Norris, comb. nov.**

FIGURE 81C

Ectocarpus bryantii Setchell et N. L. Gardner, 1924a:720, pl. 17: fig. 45; Setchell and Gardner, 1925:440; Dawson, 1944:220; Dawson, 1961b:384; Dawson, 1966a:9; Dawson, 1966b:55; Huerta-Múzquiz and Mendoza-González, 1985:44; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Espinoza-Ávalos, 1993:333; González-González et al., 1996:147; Paul-Chávez and Riosmena-Rodríguez 2000:146; Mateo-Cid et al., 2006:49; Pedroche et al. 2008:16.

Algae tufted epiphytes, up to 2.5 mm high, of intertwined, uncorticated filaments, attached below by penetrating rhizoidal filaments. Branching below dichotomous (nearly at surface of algal host cells); above sparse with very few short, slightly tapering branchlets terminating in a blunt cell and lacking terminal hairs. Cells 28–64 μm long by 28–32 μm in diameter. Chloroplasts discoid.

Unilocular sporangia unknown. Plurilocular sporangia scattered along filaments; sessile or pedicellate on 1 cell; narrow to broadly fusiform, 70–100(–140) μm long by 25–35 μm wide.

HABITAT. Epiphytic on *Codium brandegeei* and *C. simulans*; mid to low intertidal.

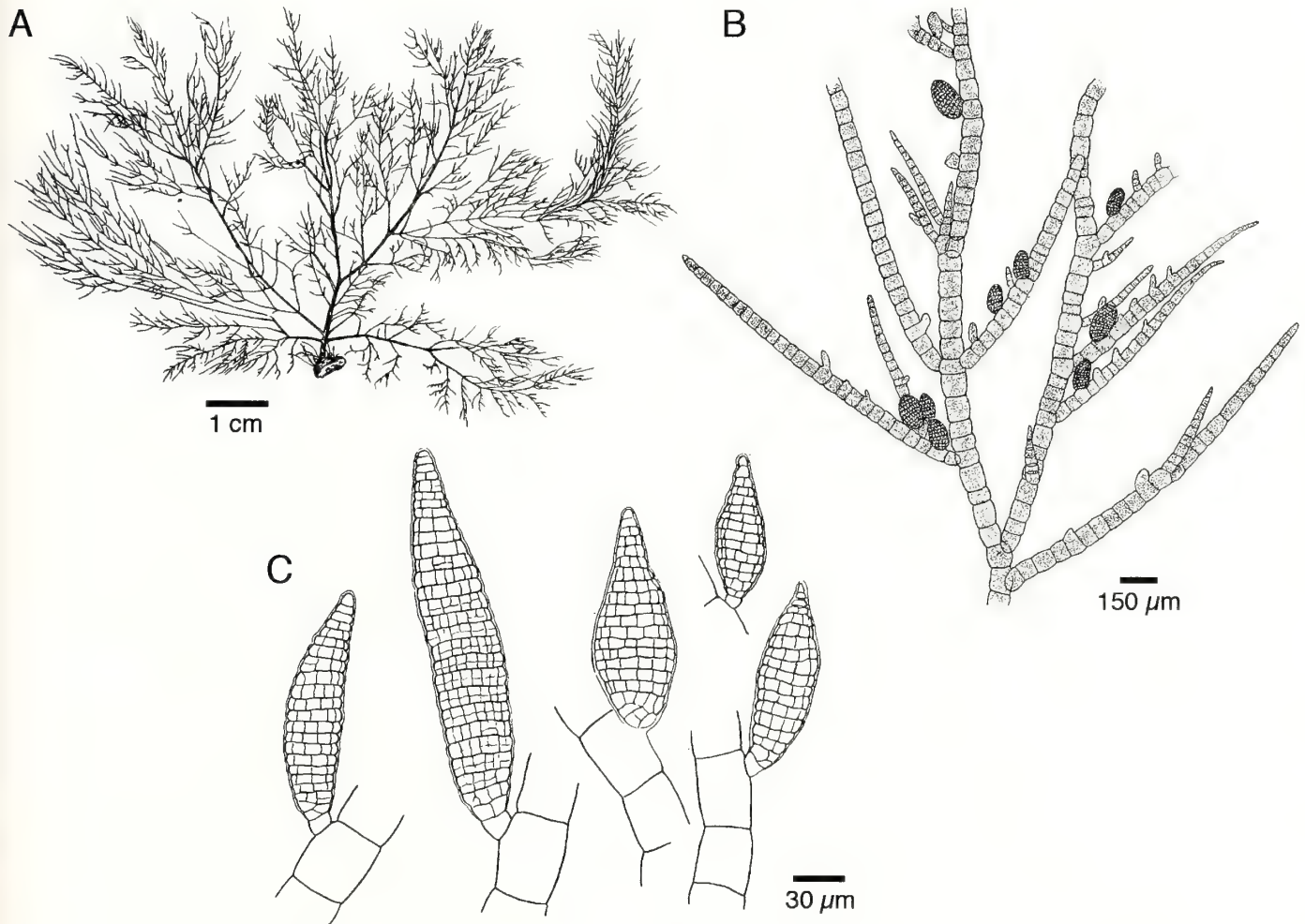


FIGURE 81. Two species of *Hincksia*. A, B. *Hincksia granulosa*: A. Habit, with lateral branches predominately opposite (from Saunders, 1898: pl. 24, fig. 3). B. Plurilocular sporangia sessile, asymmetrically ovoid, borne on lateral branches (from Saunders, 1898: pl. 24, fig. 4). C. *Hincksia bryantii*: Plurilocular reproductive structures; varying from narrow to broadly fusiform and either sessile or borne on one-celled pedicel (after Setchell and Gardner, 1924a: pl. 17, fig. 45).

DISTRIBUTION. Gulf of California: Puerto Peñasco; Isla Espíritu Santo to Bahía de La Paz.

TYPE LOCALITY. Epiphytic on *Codium brandegeei*, La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. The discoid chloroplasts and branching pattern of *Ectocarpus bryantii* Setchell et N. L. Gardner (1924a) suggest that it more properly belongs to *Hincksia*, and a new combination is proposed. Setchell and Gardner (1924a, as *E. bryantii*) noted that *Hincksia bryantii* could be related to the Gulf *Ectocarpus gonodoides* but it differed in its mode of branching. Further collections are needed to elucidate the generic placement and the phylogenetic relationship of *H. bryantii* to other species.

Hincksia granulosa (J. E. Smith) P. C. Silva

FIGURE 81A,B

Conferva granulosa J. E. Smith, 1811:pl. 2351.

Hincksia granulosa (J. E. Smith) P. C. Silva in Silva, Meñez et Moe, 1987:130; Stewart, 1991:39; Kim and Lee, 1992:252, figs. 7A–D, 8E–H; Hoffmann and Santelices, 1997:116, fig. 27; Yoshida, 1998:171; R. Aguilar-Rosas et al., 2005b:34; Pedroche et al., 2008:21.

Ectocarpus granulosa (J. E. Smith) C. Agardh, 1824:163; C. Agardh, 1828:45; De A. Saunders, 1898:156, pl. 24: figs. 3–5; Setchell and Gardner, 1925:426; Smith, 1944:81, pl. 11: figs. 1, 2; Dawson, 1945b:64; Dawson, 1960a:36; Dawson, 1961b:385; Dawson, 1962c:278; Devinsky, 1978:358; Mendoza-González and Mateo-Cid, 1986:420; González-González et al., 1996:149.

Giffordia granulosa (J. E. Smith) G. Hamel 1939b:xv, fig. 61E; Cardinal, 1964:39, figs. 19A–J, 20A–J; Abbott and Hollenberg, 1976:140, fig. 103; Fletcher, 1981:211; Pacheco-Ruiz, 1982:70; Mendoza-González and Mateo-Cid, 1986:420; Santelices, 1989:267, pl. DD: figs. 9–11; González-González et al., 1996:151.

Algae tufted, up to 2.5 cm high, intertwined filaments; lower axes of filaments corticated, upper portions uncorticated; attached below by penetrating rhizoidal filaments. Lateral branches predominately opposite, with short ultimate branchlets; branches and branchlets taper distally and terminate in a blunt apical cell and lack terminal hairs. Cells mostly shorter than wide, 35–80 μm long, 50–80(–100) μm in diameter; with numerous discoid chloroplasts.

Unilocular sporangia unknown in Gulf material (reported elsewhere to be globose). Plurilocular sporangia adaxial along branches and branchlets; sessile, broadly

ovate, asymmetrical, 45–60(–100) μm long by 40–60 μm in diameter.

HABITAT. Epiphytic on *Codium*, also probably on other algae and on rocks; intertidal.

DISTRIBUTION. Gulf of California: Isla Pelicano, Bahía Kino. Pacific coast: Alaska to Baja California; Chile; Japan.

TYPE LOCALITY. Brighthelmston (Brighton) and Shoreham, Sussex, England.

REMARKS. Description of *Hincksia granulosa* is based primarily on Abbott and Hollenberg (1976) since I have not seen the Sonoran specimens reported by Mendoza-González and Mateo-Cid (1986).

Hincksia mitchelliae (Harvey) P. C. Silva

FIGURE 82

Ectocarpus mitchelliae Harvey, 1852:142, pl. 12G: figs. 1–3; D. A. Saunders, 1898:153, pl. 21: figs. 1, 2; Setchell and Gardner, 1925:428; Setchell and Gardner, 1930:140; Dawson, 1944:220; Dawson, 1954:5; Dawson, 1961b:385; Dawson, 1966a:9.

Hincksia mitchelliae (Harvey) P. C. Silva in Silva, Meñez et Moe, 1987:73; R. Aguilar-Rosas and Machado-Galindo, 1990:188; Stewart, 1991:39; Kim and Lee, 1992:246, figs. 3A–D, 5A–D; González-González, 1993:443; León-Tejera and González-González, 1993:497; Stout and Dreckmann, 1993:6; Mendoza-González et al., 1994:110; González-González et al., 1996:153; Mendoza-González and Mateo-Cid, 1996:70, 85, pl. 18: figs. 75–77; Hoffman and Santelices, 1997:119, fig. 28; Yoshida, 1998:171; L. Aguilar-Rosas et al., 2000:132; León-Tejera and González-González, 2000:328; Mateo-Cid and Mendoza-González, 2003:21; Abbott and Huisman, 2004:162, fig. 59C; R. Aguilar-Rosas et al., 2005b:34; Mateo-Cid et al., 2006:49; Dreckmann et al., 2006:154; Servière-Zaragoza et al., 2007:8; Pedroche et al., 2008:22.

Giffordia mitchelliae (Harvey) Hamel, 1939a:66; Hamel, 1939b:XIV, fig. 61c,d; Cardinal, 1964:45, fig. 23A–H; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Abbott and Hollenberg, 1976:143, fig. 105; L. Aguilar-Rosas, 1982:84; Schnetter and Bula Meyer, 1982:55, pl. 8: figs. C, D; Stewart and Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:44; Mendoza-González and Mateo-Cid, 1985:24; Mendoza-González and Mateo-Cid, 1986:420; Sánchez-Rodríguez et al., 1989:40; Mateo-Cid et al., 1993:49; González-González et al., 1996:296.

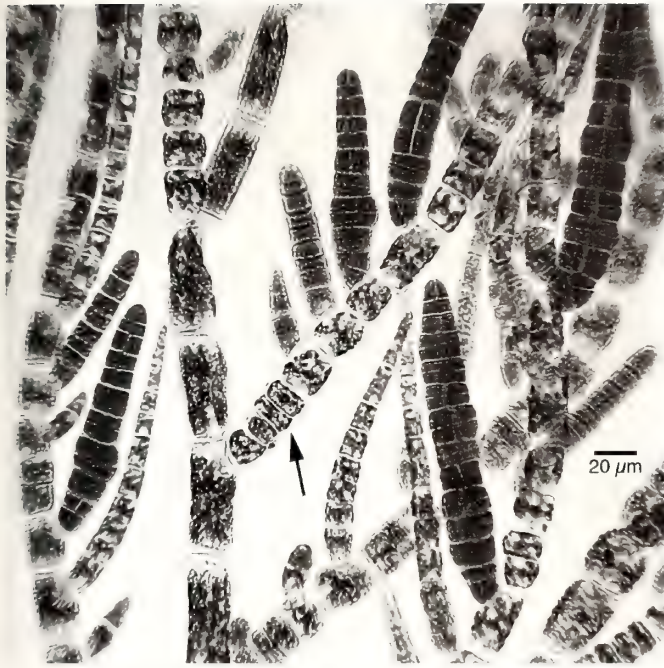


FIGURE 82. *Hincksia mitchelliae*: Filaments with intercalary meristem (arrow) at base of branch and several sessile, ellipsoid to cylindrical plurilocular sporangia with rounded apices, borne on adaxial side of branches, often arranged in short series (JN-4774).

Algae tufted, 1–4 cm tall, often densely branched in mid to upper portions; attached to host by creeping rhizoidal filaments. Filaments of main axis up to 50 μm in diameter; branching alternate or unilaterally secund or spiral; apices often attenuated. Intercalary meristematic zones scattered along axes and near base of branches. Cells 1–3 times longer than wide; 20–120 μm long by 20–40 μm in diameter; with numerous discoid plastids.

Unilocular sporangia not seen in Gulf material (reported elsewhere as sessile, ovoid to elliptical, 40–45 μm long by 15–20 μm in diameter). Plurilocular sporangia sessile on main axes and adaxial on lateral branches, often in short series (2–5); more or less cylindrical, tapering slightly with rounded apices, (40–)60–150 μm long by 30–45 μm in diameter; with 1–3(–4) locules in each horizontal row (seen in lateral view).

HABITAT. Epiphytic on *Sargassum* and *Ralfsia*, occasionally on other algae, and epizoid on the black sea turtle, *Chelonia mydas agassizii* (see Parham and Zug, 1996); mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Canal de Infernillo (between Isla Tiburón and Campo Ona, Sonora); Bahía Concepción to San José del

Cabo. Pacific coast: central California to Sinaloa; Isla San Benedicto (Islas Revillagigedo); Michoacán to Chiapas; Colombia; Chile; Hawaiian Islands; Taiwan; Korea; Japan.

TYPE LOCALITY. Nantucket, Nantucket County, Massachusetts.

REMARKS. The northern Gulf collection of *Hincksia mitchelliae* (US Alg. Coll.-158145), growing on the carapace of a black sea turtle in the Canal de Infernillo (between Campo Ona, Sonora, and Isla Tiburón), extends its known distribution south from Puerto Peñasco (Dawson, 1966a). Southern Gulf collections of Dawson (1959a, as “*E. sp. aff. E. mitchelliae*”) were also referred to this species, but with doubt.

CHNOOSPORACEAE

Chnoosporaceae Setchell et N. L. Gardner, 1925:400, 552.

Algae are composed of terete to compressed axes and usually subdichotomously divided branches above a crustose or discoid holdfast. Internally they have a solid, pseudoparenchymatous structure of elongate, colorless cells in the medulla that is developed from a subapical meristem below the outer cortical layer. The cortex is composed of one to two layers of small, pigmented, irregularly arranged cells and numerous shallow pits with conspicuous tufts of colorless hairs (cryptoblasts). Each cortical cell has a single chloroplast with one pyrenoid.

Life histories are apparently heteromorphic but are not fully known for most of the species. An independent crustose phase that repeated itself was described by Fotos (1981), and a heteromorphic life history was reported in culture studies of *C. implexa* J. Agardh (1848) from Japan (Kogame, 2001). Unilocular and plurilocular reproductive structures, both sporangia (zoidangia), are known in the sporophytic crustose phase of one species. Plurilocular structures are found in the erect phase and either develop in association with the colorless hairs or sometimes may be separate from these hairs.

REMARKS. Although some consider the Chnoosporaceae to be a synonym of the Scytosiphonaceae (e.g., Kogame, 2001), others continue to recognize it as a distinct family (e.g., Silva et al., 1996a; Yoshida, 1998; Abbott and Huisman, 2004), primarily on the basis of its members having vegetative cells that contain a single chloroplast with one pyrenoid. Molecular analysis of *C. pacifica* J. Agardh (lectotype of the genus) will help elucidate the taxonomic status and phylogenetic relationships of this monotypic family.

The family's single genus, *Chnoospora*, occurs in the northern Gulf of California.

Chnoospora J. Agardh

Chnoospora J. Agardh, 1847:7.

Gametophytes are erect tufts, clumps, or partly decumbent mats, and composed of one to several, more or less terete to compressed axes arising from a crustose holdfast. Axes are dichotomously, subdichotomously, or irregularly branched. Growth is in the subapical meristematic row of cells. Anatomically, the medulla is solid, and pseudoparenchymatous, composed of large and small colorless medullary cells, and the cortex is of one to two layers of smaller pigmented cells. The surface layer is of irregularly arranged cortical cells and numerous shallow pits from which groups of colorless hairs extend. Each cortical cell has a single chloroplast and a pyrenoid.

Unilocular and plurilocular structures (zoidangia) are developed on discoid sporophytes for at least one species (Kogame, 2001) and have been reported as "densely packed around groups of hairs" to form "more or less continuous sori" (Lawson and John, 1982:134). Plurilocular gametangia that produce isogametes are developed on the erect thalli in superficial sori or may be associated with colorless hairs on the outer surfaces.

REMARKS. The generitype of *Chnoospora* was not specifically designated by Agardh (1847), and Setchell and Gardner (1925) were apparently the first to choose a lectotype, *C. pacifica* J. Agardh, for the genus.

Reproductive structures in *Chnoospora* were first described by Barton (1898) and Børgesen (1924) and later more completely described by Fotos (1981) and Kogame (2001), who also found a repeating crustose phase in culture studies. In the most complete life history study, erect dioecious gametophytes of Japanese *C. implexa* produced isogametes in plurilocular gametangia that formed zygotes, which grew into crustose sporophytes. Under long-day photoperiod conditions the latter developed plurilocular zoidangia that produced sporophytic crusts repeatedly, whereas under short-day regimes the crusts developed unilocular zoidangia that grew into the dioecious, erect gametophytes (Kogame, 2001). Some strains of cultured *C. implexa* exhibited a direct life history with gametophytic thalli produced without sporophytes (Kogame, 2001).

Three other species are reported in the southern Gulf and Pacific Mexico: *C. implexa* J. Agardh (1848) by Dawson (1959a, 1959b, 1960c, 1961b); *C. minima* (K. Hering) Papenfuss (1956) by Chávez B. (1972), Pedroche

and González-González (1981), Huerta-Múzquiz and Mendoza-González (1985), León-Tejera and González-González (1993), Stout and Dreckmann (1993), Mateo-Cid et al. (1993), and Servière-Zaragoza et al. (1993); and *C. pannosa* J. Agardh (1848) from Isla Guadalupe (Setchell and Gardner, 1930; Stewart and Stewart, 1984).

One species is reported in the northern Gulf of California.

Chnoospora pacifica J. Agardh

FIGURE 83A-C

Chnoospora pacifica J. Agardh, 1847:7; Kützing, 1859:36, pl. 86: fig. 1; Setchell and Gardner, 1924a:728; Setchell and Gardner, 1925:553; Okamura, 1936:236; Dawson, 1944:234; Taylor, 1945:82; Dawson, 1954a:4, pl. 3: fig. 1; Huerta-Múzquiz and Tirado-Lizárraga, 1970:127; Huerta-Múzquiz, 1978:339; Mendoza-González and Mateo-Cid, 1986:421; Salcedo-Martínez et al., 1988:82; León-Tejera and González-González, 1993:497; Servière-Zaragoza et al., 1993:482; González-González et al., 1996:141; Hernández-Herrera et al., 2005:146.

Chnoospora fastigiata a [var.] *pacifica* (J. Agardh) J. Agardh, 1848:171-172; Børgesen, 1924:263, figs. 11, 12.

Chnoospora minima sensu Dawson 1959b:8; Mateo-Cid et al. 1993:49; Pedroche et al. 2008:63 [non *Chnoospora minima* (K. Hering) Papenfuss 1956:69].

Algae erect, up to 6 cm tall, of few to many more or less cylindrical to compressed branched axes, up to 2 mm in diameter, arising from a basal crustose holdfast. Branched dichotomously to subdichotomously; branches of more or less the same diameter throughout, tapering to slightly smaller apices. Surface with irregularly arranged cortical cells and scattered, noticeable groups of colorless hairs, up to 3 mm long, extending from shallow pits. Medulla of thick-walled, small to large, colorless cells; cortex of 1-2 layers of smaller pigmented cells.

Plurilocular uniseriate and biseriate structures, up to 80 µm long, develop in long sori on branch surfaces.

HABITAT. Intertidal.

DISTRIBUTION. Gulf of California: Bahía San Pedro (north of San Carlos); Bahía Concepción to Bahía de La Paz. Pacific coast: Isla San Benedicto (Islas Revillagigedo); Isla María Magdalena (Las Islas Tres Marías); Nayarit to Oaxaca; Hawaiian Islands; Rapa Nui (Easter Island).

TYPE LOCALITY. San Agustín, Oaxaca, Mexico (Agardh, 1847, "St. Augustin, Stilla Oceanen [Pacific Ocean]").

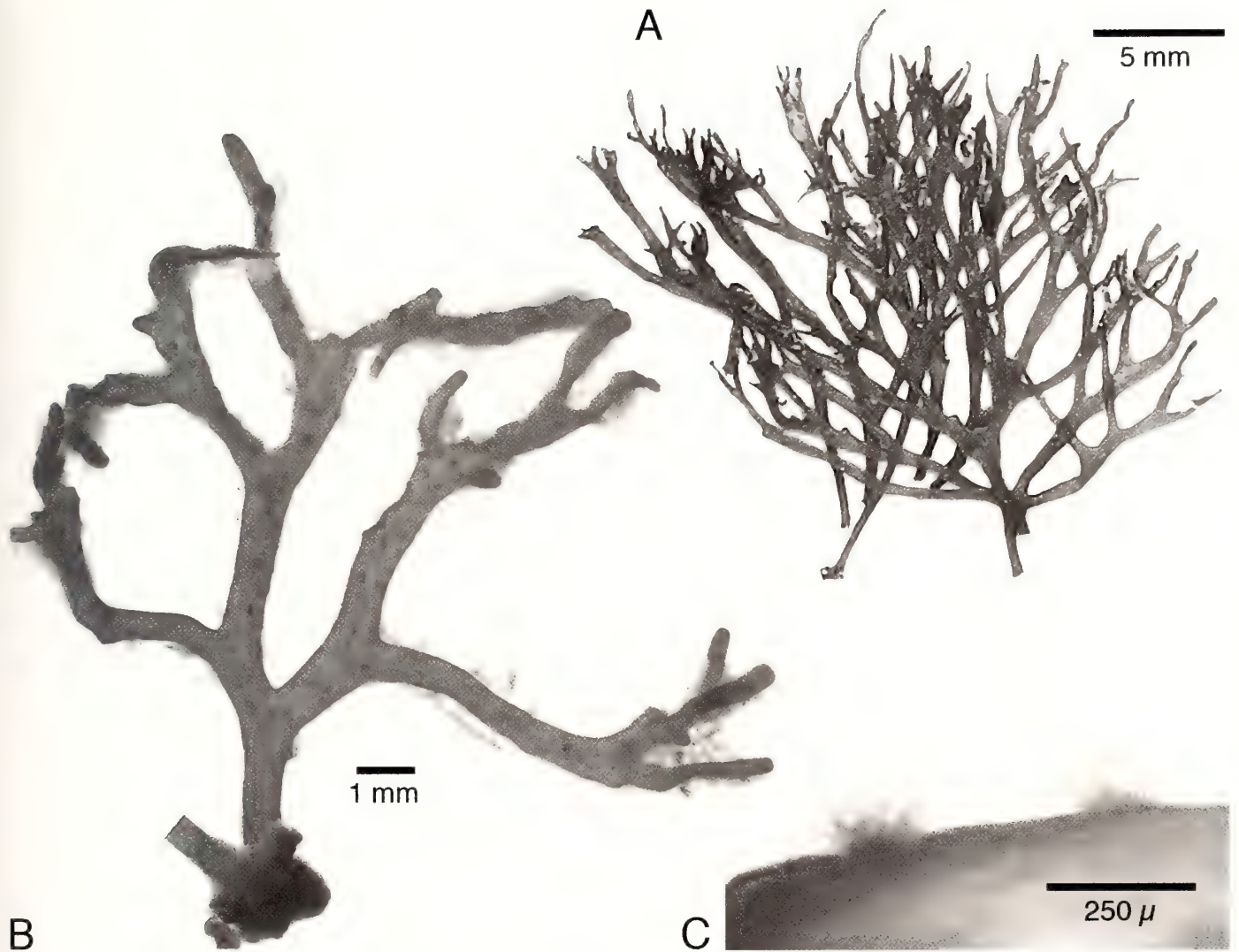


FIGURE 83. *Chnoospora pacifica*, EYD-12121: A. Habit, air-dried herbarium specimen. B. Liquid-preserved specimen showing scattered groups of hairs from shallow pits. C. Close-up of clumps of hairs extending from superficial pits.

REMARKS. Described from southern Oaxaca, Pacific Mexico (Agardh, 1847), *Chnoospora pacifica* was first reported in the southern Gulf by Setchell and Gardner (1924a). Subsequently, Dawson (1944) noted its absence from further Gulf collections and suggested it may be a strictly tropical species, limited to the southernmost Gulf (Dawson, 1961b). More recently, *C. pacifica* was reported from Sonora in the northern Gulf by Mendoza-González and Mateo-Cid (1986); although I have not seen their specimens, *Chnoospora* is very distinctive, with characteristic scattered pits in the thallus surface from which tufts of colorless hairs extend (Figure 83B,C).

Some have considered the Pacific Mexico *C. pacifica* to be a synonym of the South African *C. minima* (K. Hering) Papenfuss (1956; cf. Levring, 1938:22, fig. 10, pl. 4: fig. 12, as "*C. pacifica*"; basionym: *Fucus minimus* K. Hering, 1841). Others have continued to recognize them as separate species; e.g., Servièrre-Zaragoza et al. (1993) reported both occurring in Jalisco and Nayarit, Pacific Mexico. Until the types and type locality materials of *C. pacifica* (generitype) and *C. minima* have been reexamined and tested using molecular and phylogenetic analyses and compared to the Gulf of California *C. pacifica*, it seems best to recognize them as separate species.

CHORDARIACEAE

Chordariaceae Greville, 1830:44.

Dictyosiphonaceae Kützinger, 1849:484 as "Dictyosiphonaceae."

Elachistaceae Kjellman, 1890:41.

Myrionemataceae Nägeli, 1847:145, 252 as "Myrionemeae."

Myriotrichiaceae Kjellman, 1890:46.

Punctariaceae (Thuret) Kjellman, 1880:9; Punctarieae Thuret in Le Jolis, 1863:14, 21.

Spermatochneaceae Kjellman, 1890:32.

Algae are microscopic or macroscopic, erect or partly erect, and variable in size and shape, ranging from (1) simple to branched filaments or tufts, (2) cushion-shaped to irregularly lobed forms, or (3) cylindrical to compressed, simple, entire, or branching forms, attached by basal filaments. Some are membranous or gelatinous in texture. Some of the species are filamentous or have a filamentous form in their life history. Other species are structurally differentiated, with a medulla composed of filaments that surround a central axis (core) of one or more colorless filaments, each of which grows from an apical cell; internally, they may be either solid or hollow when mature. Cells divide radially from the central medullary filaments and

give rise to whorls of outer assimilatory filaments. These assimilatory filaments bear reproductive structures, and hairs or paraphyses may also be present or absent. Growth may be apical, marginal, diffuse, or intercalary in cortical filaments. Cells have one to several discoid, elongate, or irregular chloroplasts and usually one pyrenoid.

Life histories, where known, are mostly heteromorphic, usually with a macroscopic pseudoparenchymatous sporophyte of uniaxial or multiaxial structure and a usually smaller or microscopic filamentous gametophytic phase. Sporophytes produce unilocular sporangia, which are borne at the base of paraphyses. Plurilocular structures are uniseriate or multiseriate and may be sessile or pedicellate or borne at the base of paraphyses or on special branches growing from the outer cortical cells. Gametophytes are filamentous and produced unilocular or plurilocular gametangia. Gametes are usually of unequal size.

REMARKS. On the basis of molecular phylogenies, Peters and Ramírez (2001) considered the Chordariaceae to include several families (see those listed above as synonyms). In addition to the genera known in the northern Gulf, another, *Haplogloia* Levring (1939), has been reported in the southern Gulf by Mateo-Cid et al. (1993, as *H. andersonii* (Farlow) Levring).

There are three genera represented in the northern Gulf of California.

KEY TO THE GENERA OF CHORDARIACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Erect, terete, narrow axis and branches (up to 1.0 mm in diameter), up to 20 cm or more in length; more or less alternately to irregularly branched *Nemacystus*
 1b. Much smaller, microscopic to minute uniseriate filaments, less than 3 mm tall and 5–15 µm in diameter 2
 2a. Sparingly branched filaments, up to 0.5 mm tall, above a discoid base of laterally adjoined prostrate filaments which become mostly distromatic *Hecatonema*
 2b. Uniseriate filaments entirely to partly endophytic, up to 3 mm in length; without a discoid base *Streblonema*

***Hecatonema* Sauvageau**

Hecatonema Sauvageau, 1897:248.

Algae are minute, discoid to irregularly shaped or cushion-shaped filamentous, crustose thalli. Structurally, they are composed of a mostly distromatic basal layer of laterally adjoined, radiating filaments. Most cells of these basal filaments grow parallel to the substratum or, if epiphytic, on the surface of the host. Longitudinal divisions of the basal filament cells occur inconsistently, thus forming a partly distromatic disc; other cells of the filaments may divide in an intercalary manner or marginally. Some

of the lower filament cells may produce rhizoids that penetrate the cells of the host alga; the upper cells develop an erect, simple, unbranched or branched filament or an endogenous hair or a hyaline paraphysis-like structure (ascocyst) or a reproductive structure. Cells contain one to several discoid chloroplasts and one pyrenoid.

Unilocular sporangia, where known, are usually sessile or sometimes pedicellate on the basal layer. Plurilocular sporangia are multiseriate, variable in shape, sessile, and terminal or lateral.

REMARKS. The taxonomic status and placement of the genus *Hecatonema* needs further investigation. Culture studies have shown some *Hecatonema*-like

microthalli to produce macrothalli that are other genera, e.g., *Asperococcus* Lamouroux (1813), *Desmotrichum* Kützing (1845), *Myriotrichia* Harvey (1835), or *Punctaria* Greville (1830) (see Loiseaux, 1967, 1969; Clayton, 1974; Lockhart, 1982; Fletcher, 1984; Pedersen, 1984); therefore, some phycologists have placed *Hecatonema* in the Punctariaceae (Thuret) Kjellman (1880; e.g., Christensen, 1980; Fletcher, 1987; Womersley, 1987; Wynne, 1998a). However, other species of *Hecatonema* have been shown to have an isomorphic life history and do not develop macrothalli in culture (e.g., Clayton, 1974; Pedersen, 1984). These species have been placed in the Myrionemataceae (e.g., Abbott and Hollenberg, 1976; Schneider and Searles, 1991; Silva et al., 1996a). Most recent investigations consider both the Myrionemataceae and Punctariaceae as

members of a more broadly defined Chordariaceae (e.g., Peters and Ramírez, 2001; Wynne, 2005).

Easily overlooked, future studies of these microscopic to minute filamentous brown algae will probably reveal more species in the Gulf of California.

Currently there is one species known in the northern Gulf of California.

***Hecatonema streblonematoides*
(Setchell et N. L. Gardner) Loiseaux**

FIGURE 84A,B

Compsonema streblonematoides Setchell et N. L. Gardner, 1922a:353, pl. 35: fig. 4; Setchell and Gardner, 1925:481; Dawson, 1961b:391.

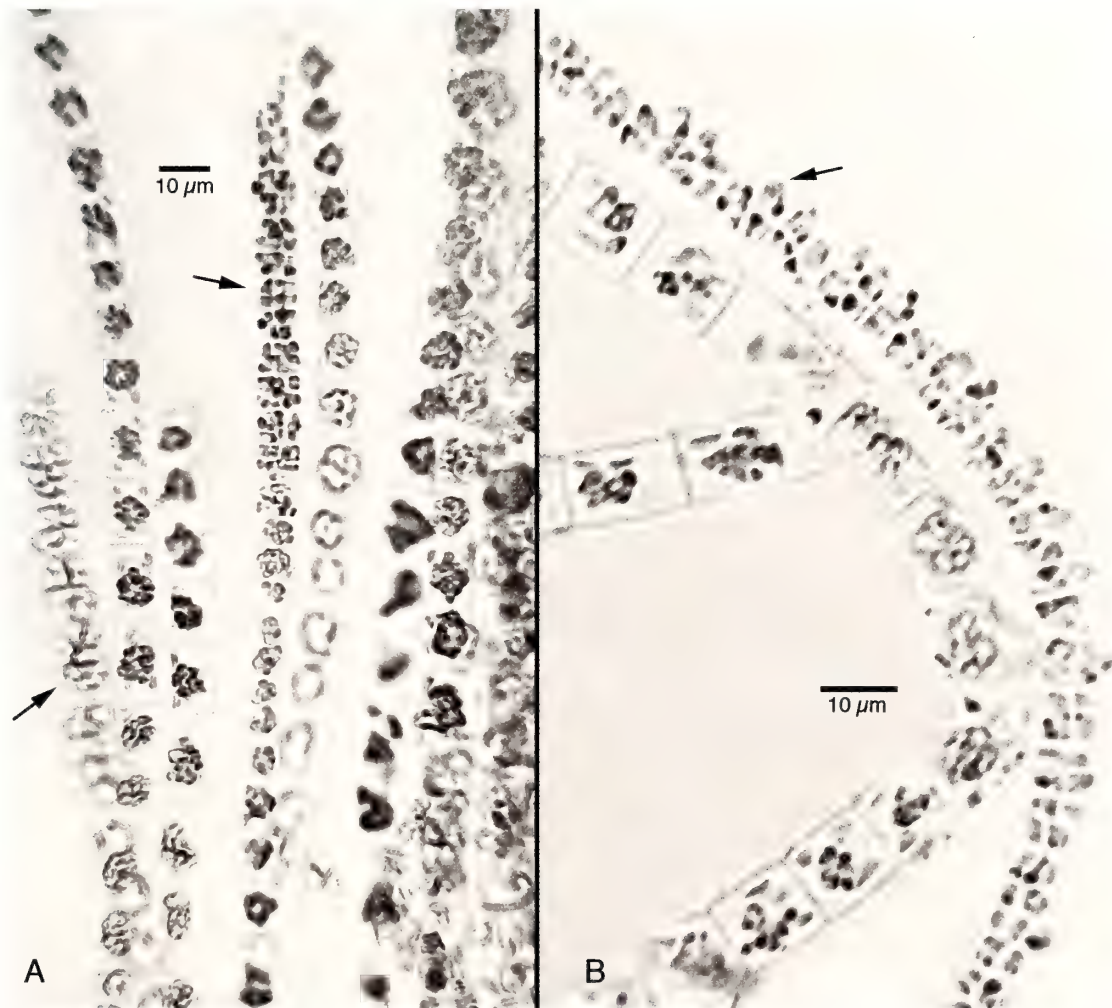


FIGURE 84. *Hecatonema streblonematoides*: Upper portions of filaments from a dense tuft (JN-4033). A. Two filaments with terminal plurilocular gametangia (arrows). B. Plurilocular gametangium with short lateral protuberances (arrow).

Hecatonema streblonematoides (Setchell et N. L. Gardner) Loiseaux, 1970b:253, figs. 2, 3; Abbott and Hollenberg, 1976:162, fig. 130; Stewart, 1991:40; González-González et al., 1996:153; Pedroche et al., 2008:62.

Compsonema myrionematoides Setchell et N. L. Gardner, 1922a:361, pl. 36: fig. 1; Setchell and Gardner, 1925:483; Smith, 1944:109; Dawson, 1961b:390.

Compsonema nummuloides Setchell et N. L. Gardner, 1922a:359, pl. 35: figs. 5, 6; Setchell and Gardner, 1925:475; Dawson, 1961b:391.

Compsonema pusillum Setchell et N. L. Gardner, 1922a:356, pl. 37: fig. 3; Setchell and Gardner, 1925:477, pl. 54: fig. 3; Smith, 1944:108; Dawson, 1961b:391.

Compsonema ramulosum Setchell et N. L. Gardner, 1922a:362, pl. 39: figs. 1–5; Setchell and Gardner, 1925:486; Smith, 1944:111; Dawson, 1961b:391.

Compsonema secundum Setchell et N. L. Gardner, 1922a:361, pl. 37: figs. 1, 2; Setchell and Gardner, 1925:483, pl. 54: figs. 1, 2; Smith, 1944:109, pl. 15: fig. 4; Dawson, 1961b:391; Servièrre-Zaragoza et al., 1993:482; González-González et al., 1996:374; Pedroche et al., 2008:69.

Compsonema secundum f. *terminale* Setchell et N. L. Gardner, 1922a:366, pl. 37: figs. 4, 5; Setchell and Gardner, 1925:484, pl. 54: figs. 4, 5; Mendoza-González and Mateo-Cid, 1986:420; Servièrre-Zaragoza et al., 1993:482; González-González et al., 1996:143, 374; Yoshida, 1998:269; Mateo-Cid et al., 2006:58; Pedroche et al., 2008:69.

Compsonema speciosum f. *piliferum* Setchell et N. L. Gardner, 1922a:356, pl. 38: figs. 1, 2; Setchell and Gardner, 1925:485; Dawson, 1961b:391.

Hecatonema clavatum Setchell et N. L. Gardner, 1922a:378, pl. 40: figs. 1–4; Setchell and Gardner, 1925:491; Dawson, 1961b:391.

Hecatonema variabile Setchell et N. L. Gardner, 1922a:377, pl. 41: figs. 1–12; Setchell and Gardner, 1925:490; Smith, 1944:113; Dawson, 1961b:391.

Algae minute tufts form a discoid to irregular cushion, 2–10 mm in diameter; basal layer mostly distromatic, and 1 cell layer at margins; attached below by rhizoids; erect filaments unbranched, mostly 100–500 μm tall (older specimens reported up to 1000 μm tall and with secund branching). Filaments of cylindrical cells, 5–7 μm in diameter basally and 10–12(–15) μm above. Cells with (1–)2–4(–5) chloroplasts. Endogenous hairs, up to 7 μm in diameter; rare in juveniles, abundant in mature specimens. Ascocysts rare, sessile or lateral on erect filaments, 20–50 μm long by 10–15 μm in diameter.

Unilocular sporangia erect on basal filaments, sessile, lateral or pedicellate; 40–80 μm long by 15–30 μm in diameter. Plurilocular structures very variable in shape and position; sessile, 40 μm long and 12 μm in diameter, or pedicellate, 40–180 μm long by 12–17 μm in diameter, or lateral or in long terminal rows on erect filaments, up to 400 μm in length (sometimes resembling a cockscomb; see Setchell and Gardner, 1925:pl. 54: fig. 1).

HABITAT. Epiphytic on *Padina durvillei* and *P. caulescens*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Kino. Pacific coast: Alaska to central California; Baja California; Jalisco to Nayarit; Japan.

TYPE LOCALITY. On pneumatocyst of *Nereocystis luetkeana*, Tomales Bay, Marin County, California.

REMARKS. *Hecatonema streblonematoides* has been recorded from the Sonora coast at Puerto Peñasco (Loiseaux, 1970b) and in the vicinity of Bahía Kino at Isla Pelicano and Segundo Cerro Prieto (Mendoza-González and Mateo-Cid, 1986, as “*Compsonema secundum* f. *terminale*”). The form of *H. streblonematoides* we have collected (Playa Hermosa, vicinity of Puerto Peñasco, JN-4033; US Alg. Coll. slide 5350) closely resembles those originally described as *Compsonema secundum* (see Setchell and Gardner, 1925:pl. 54: fig. 2).

Smith (1944, as “*C. secundum*”) noted its sporangia were so variable that it was impossible to distinguish the type species of *C. secundum* from the forma, *C. secundum* f. *terminale*. On the basis of culture and morphological studies, Loiseaux (1970b) concluded *H. streblonematoides* was a single species that included *C. secundum* and several other northeastern Pacific taxa previously placed in *Compsonema* or *Hecatonema*. The species encompassed within the broadly taxonomically defined *H. streblonematoides* (Loiseaux, 1970b) need to be molecular phylogenetically and morphologically tested.

***Nemacystus* Derbès et Solier**

Nemacystus Derbès et Solier, 1850:269.

Algae are erect, lax, with cylindrical narrow axes, 400–1000 μm in diameter, usually irregularly branched, and attached by a small discoid holdfast. The single axial filament of the medulla (usually evident in the upper portions) grows by divisions of a dome-shaped apical cell. Surrounding the axial filament are large pseudoparenchymatous cells that develop from filaments growing downward from the base of the assimilatory filaments. The outermost pseudoparenchymatous cells bear pigmented assimilatory filaments that are simple or branched at their

bases, straight or curved, and up to 20 cells in length. Colorless phaeophycean hairs develop from basal cells of the assimilatory filaments, and together with the assimilatory filaments, they cover the surface, giving it a hairy or furry appearance under low magnification.

Life histories, where known (e.g., Migita and Yotsui, 1972; Yotsui, 1980), are either direct from spores of plurilocular sporangia or heteromorphic, with macroscopic sporophytes and microscopic gametophytes. Sporophytes produce two kinds of sporangia: unilocular, ovoid to pyriform sporangia that are borne at base of assimilatory filaments and plurilocular sporangia that are uniseriate and borne on simple or sometimes branched pedicels at the base of assimilatory filaments (Yotsui, 1976, 1980). Microscopic "streblonematoid" gametophytes, known in some species (e.g., *N. decipiens* (Suringar) Kuckuck, 1929), bear few-celled, uniseriate gametangia that produce isogametes (Peters and Müller, 1986a; Peters, 1987).

There is one species, originally described from the southern Gulf, and known to occur throughout the Gulf of California.

***Nemacystus brandegeei* (Setchell et N. L. Gardner) Kylin**

FIGURE 85A-C

Meneghiniella brandegeei Setchell et N. L. Gardner, 1924b:5; Setchell and Gardner, 1925:549, pl. 47: fig.11, pl. 49: fig.16.

Nemacystus brandegeei (Setchell et N. L. Gardner) Kylin, 1940:49; Dawson, 1944:232; Dawson, 1949:230; Dawson, 1959a:19, fig. 2; Dawson, 1961b:392; Hommersand, 1972:70; Norris, 1973:6; Huerta-Múzquiz and Mendoza-González, 1985:46; González-González et al., 1996:155; de Jong and Prud'homme van Reine, 1997:6; de Jong, 1999:88; L. Aguilar-Rosas et al., 2000:132; Mateo-Cid et al., 2006:58; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:62.

Haplogloia andersonii sensu Norris, 1973:6; Pacheco-Ruíz et al., 2008:204 [non *Haplogloia andersonii* (Farlow) Levring, 1939:50; basionym: *Mesogloia andersonii* Farlow, 1889:6].

Algae soft, dark-brown, slender cylindrical main axes, irregularly and alternately branched, mostly up to 20 cm (to 1.0 m) long and up to 500–600(–1000) μm in diameter. Main axis and branches develop from a single apical cell; initial axial filament more evident in upper portions. Internally of large, thin-walled, colorless, pseudoparenchymatous cells; innermost up to 100 μm wide by up to 400 μm long; outward mostly 45 μm by 125 μm ; outermost cells

36 μm by 65 μm . Assimilatory filaments up to 140(–160) μm in length, composed of 6–12 cells with discoid plastids; basal cells smaller, 5–7 μm in diameter, distal cells relatively larger and moniliform, 7–10(–13) μm in diameter. Phaeophycean hairs with a basal meristem; 3–8 μm in diameter.

Unilocular sporangia ovoid, 41 μm long by 32 μm in diameter. Plurilocular sporangia on single or branched pedicels; mostly uniseriate, up to 50 μm long, and up to 10 μm in diameter.

HABITAT. Epiphytic or entangled with various algae, notably *Sargassum*; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to La Paz. Pacific coast: west side of Laguna Ojo de Liebre (Scammon's Lagoon), opposite Isla La Concha (Baja California Sur).

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California, Mexico.

REMARKS. In the field, *Nemacystus brandegeei* is recognized by its thin cylindrical axes, which are mostly irregularly branched (usually less than 600 μm in diameter), and slippery texture.

***Streblonema* Derbès et Solier**

Streblonema Derbès et Solier, 1851:100.

Algae are minute, uniseriate, branched filaments, up to 3 mm in height. They may be entirely endophytic, growing between cells of the host, or partly endophytic, with both creeping and erect portions above the host's surface. Growth is mostly diffuse. Cells have one to several band-shaped or discoid plastids and are without pyrenoids. Colorless hairs are usually present.

Reproductive structures are terminal or lateral on erect or creeping filaments, mostly extending above surface cells of its host. Unilocular structures are only known in a few species. Plurilocular sporangia are cylindrical or ovoid and uniseriate or multiseriate and occur either on the same thallus or on separate thalli. Gametophytes are apparently unknown.

REMARKS. Many species of *Streblonema* are problematic or poorly known, and studies have revealed the genus to be paraphyletic. Some, but apparently not all, may be distinct independent species (Pedersen 1984). These species of *Streblonema* may have evolved by complete suppression of the macrothallus, or their sexual reproduction has been lost.

Streblonema microthalli have been found physically connected to a macrothallus. Pedersen (1978), studying the

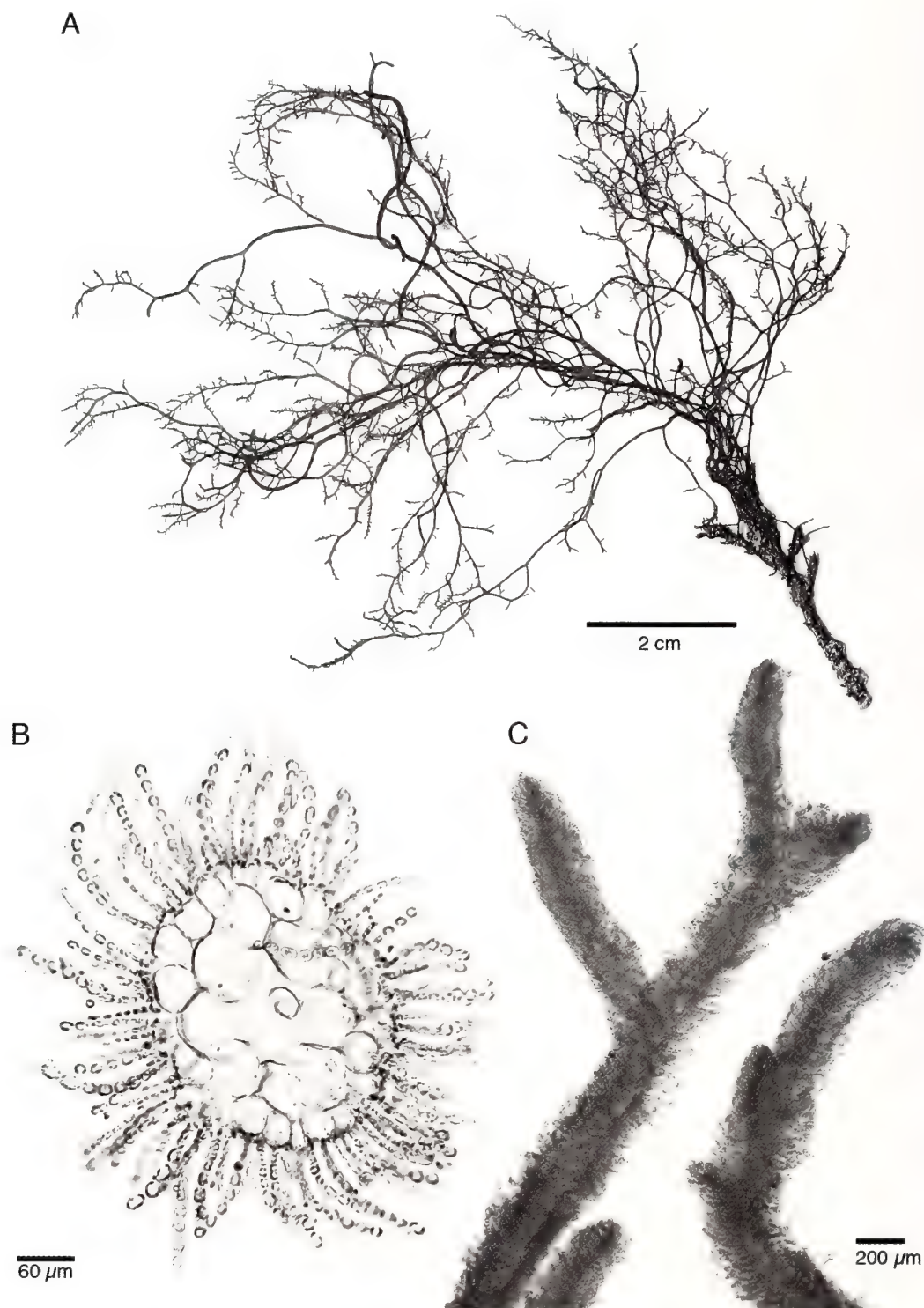


FIGURE 85. *Nemacystus brandegeei*: A. Habit (JN-3985), epiphytic on *Sargassum*. B. Transection of a liquid-preserved specimen showing single axial filament cell and pseudoparenchymatous cortex, grading from larger inner cells to smaller outer cells that bear the assimilatory filaments. C. Furry external appearance of axes and branches derived from well-developed outer layer of free assimilatory filaments and phaeophycean hairs. B, C. EYD-25847.

life history of *Myriotrichia clavaeformis* Harvey (1834), found its prostrate system was probably *S. sphaericum* (Derbès et Solier) Thuret in Le Jolis (1863), the possible generic type of *Streblonema*. Culture studies have shown other *Streblonema* to be a microthallus phase in the heteromorphic life history of other species of brown macroalgae. For example, *Streblonema*-like microthalli were found to be life history phases of *Litosiphon laminariae* (Lyngbye) Harvey (1849) (Pedersen, 1981, as *Litosiphon pusillus*), *Sphaerotrichia divaricata* (J. Agardh) Kylin (1940) (Ajisaka and Umezaki, 1978), and *Stilophora tenella* (Esper) P. Silva (in Silva et al., 1996a; = *S. rhizodes* (C. Agardh) J. Agardh, 1841) (Peters and Müller, 1986a; Peters, 1987).

One species of *Streblonema* may be responsible for an algal disease. The endophytic infestations that result in loss of quality of *Undaria* (human food, known as wakame) in Japan are caused by *S. aecidioides* (Rosenvinge) Fosile in DeToni (1895b) (Yoshida and Akiyama, 1979) (note that molecular evidence places *S. aecidioides* in a group of kelp endophytes, *Laminariocolax* Kylin, 1947a; Burkhardt and Peters, 1998).

Three species of *Streblonema* are reported from Pacific Baja California (see L. Aguilar-Rosas, 1985; R. Aguilar-Rosas and M. Aguilar-Rosas, 1986) and Isla Guadalupe (Dawson, 1961b; Stewart and Stewart, 1984).

One species and one undetermined species are recorded from the northern Gulf of California.

***Streblonema transfixum* Setchell et N. L. Gardner**

FIGURE 86

Streblonema transfixum Setchell et N. L. Gardner, 1922b:391; Setchell and Gardner, 1925:446; Dawson, 1945c:28; Abbott and Hollenberg, 1976:156, fig. 121; R. Aguilar-Rosas and M. Aguilar-Rosas, 1986:18; Scagel et al., 1989:139; González-González et al., 1996:165; Pedroche et al., 2008:24.

Algae minute filaments; lower portion, partly endophytic of irregularly branched filaments, 4–5 μm diameter, and upper portion of erect, unbranched filaments. Upper filaments short, of squarish to slightly rectangular cells, (5–)7–15 μm long and 7–10 μm diameter. Cells with band-shaped chloroplast.

Unilocular sporangia unknown. Plurilocular sporangia terminal on filaments; cylindroconical, 40–60 μm long and up to 15 μm wide; with locules in both longitudinal and transverse rows.

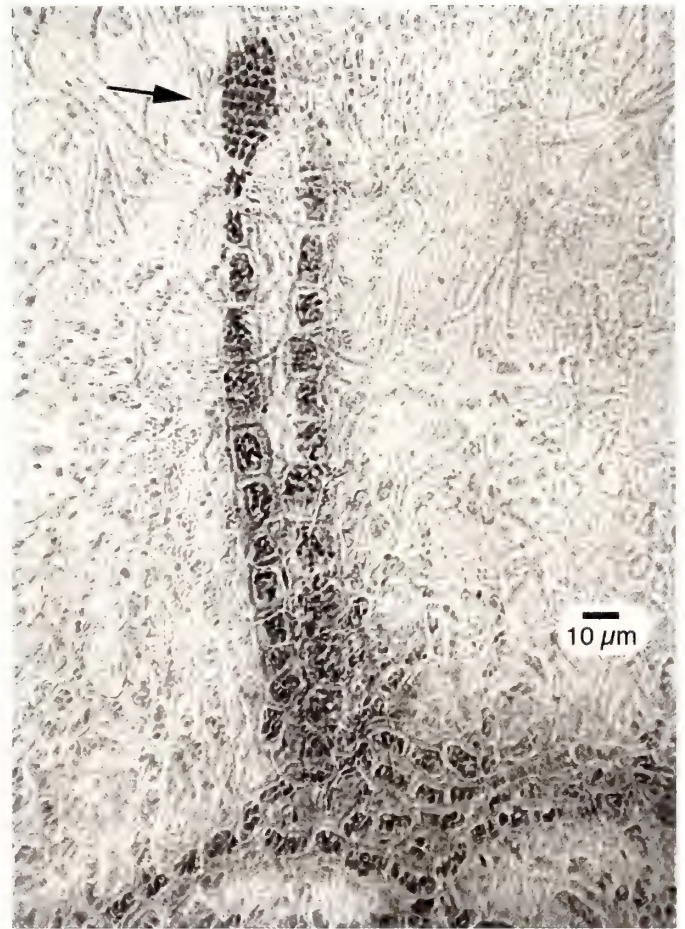


FIGURE 86. *Streblonema transfixum*: Habit, uniseriate unbranched filaments; one filament bearing a terminal plurilocular structure (arrow) with locules in longitudinal and transverse rows; epiphytic on *Gracilaria textorii* (JN-4411c).

HABITAT. Partly endophytic-epiphytic on *Gracilaria textorii*; shallow subtidal, 10 m depths.

DISTRIBUTION. Gulf of California: Isla Coronado (Isla Smith), Bahía de Los Ángeles. Pacific coast: British Columbia to Oregon; central California to northern Baja California.

TYPE LOCALITY. On *Desmarestia herbacea*, San Pedro, Los Angeles County, California.

REMARKS. Gulf specimens from Isla Coronado (JN-4411c; US Alg. Coll. slide 4257) are tentatively referred to *Streblonema transfixum* and represent a new record for the Gulf of California. Previously, *S. transfixum* has been known on *Desmarestia* (Smith, 1944; R. Aguilar-Rosas and M. Aguilar-Rosas, 1986), and *Gracilaria* would be an unusual host for this species. Life history and

molecular studies are needed to confirm the identification of this species in the northern Gulf of California.

***Streblonema* sp. A**

Streblonema sp. of La Claire II and West, 1977:127, figs. 1–4.

Microscopic, endophytic, and partly emerged irregularly branched filaments above surface cells of host, *Cutleria hancockii*. Reproduction not observed.

HABITAT. Endophytic or epiphytic on gametophytes of *Cutleria hancockii*; mid to low intertidal.

DISTRIBUTION. Gulf of California: Punta Pelicano (vicinity of Puerto Peñasco), Sonora.

REMARKS. Filaments of a *Streblonema* sp. A were collected on gametophytes of *Cutleria hancockii* in the upper Gulf (La Claire II and West, 1977). Spores of the *Streblonema* were isolated and grown in culture studies, and ultrastructural study revealed viruslike particles (previously unknown in brown algal vegetative cells) within their cytoplasm (La Claire II and West, 1977). Studies of future collections, as well as life history culture and molecular analyses, are needed to identify the species.

ECTOCARPACEAE

Ectocarpaceae C. Agardh, 1828:9.

Members of this family are generally small or occasionally microscopic, branched, uniseriate filaments. The erect filaments can be corticated or uncorticated throughout and are usually attached by a disc-shaped base or a creeping rhizoidal holdfast, but some may penetrate the host or substrata. The branches are most often uniseriate, but in a few they are biseriate. Cells have a few to many parietal or axially elongated, band-shaped plastids and one to several pyrenoids.

Reproductive structures, unilocular or plurilocular sporangia and plurilocular gametangia, are borne laterally on branches or are intercalary in some and are formed by transformation of vegetative cells. Plurilocular and unilocular structures sometimes occur on the same thallus.

Sporangia produce meiospores (zoospores). Gametangia produce isogametes or anisogametes.

One genus is represented in the northern Gulf of California.

***Ectocarpus* Lyngbye**

Ectocarpus Lyngbye, 1819:130.

Algae are erect, uniseriate filaments that are sparsely to densely irregularly branched and basally attached by rhizoids and/or prostrate filaments. The main axis may be uncorticated or, in some, corticated by descending rhizoidal filaments. Growth is diffuse by intercalary meristems (among the vegetative cells). Axis and branches often terminate in elongated terminal cells or colorless "pseudohairs." Cells have one to several parietal, band-shaped or ribbon-like chloroplasts and usually several pyrenoids per plastid.

Life histories are isomorphic or heteromorphic with only slightly different generations; however, a few species are known to be only asexual. Reproductive structures are similar in appearance and sessile or pedicellate. Unilocular and plurilocular sporangia can be borne on the same alga or on separate thalli. Unilocular sporangia are globose or ellipsoidal, usually sessile, or terminal on short laterals. Plurilocular sporangia are usually terminal but, in some, may develop from vegetative cells below a pseudohair. Plurilocular gametangia are borne on separate thalli, and the gametes are isogamous.

REMARKS. *Ectocarpus* is worldwide in distribution, with species that often exhibit wide phenotypic plasticity. The relationship of the species of *Ectocarpus* recorded in the Gulf to other known species is in need of critical study, including comparative morphological and life history studies and DNA analyses. Further field exploration will probably yield additional species in the Gulf of California.

Three species are reported in the southern Gulf (Huerta-Múzquiz and Mendoza-González 1985; Mateo-Cid et al., 2000a; Cruz-Ayala et al., 2001): *Ectocarpus corticulatus* De A. Saunders (1898), *E. chantrasoides* Setchell et N. L. Gardner (1922c) and *E. simulans* Setchell et N. L. Gardner (1922c).

Seven species are recorded in the northern Gulf of California.

KEY TO THE SPECIES OF *ECTOCARPUS* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Filaments corticated basally; distally narrowing in diameter; cells more or less barrel-shaped; plurilocular sporangia more or less cylindrical with a conical upper portion *E. acutus*
 1b. Filaments not corticated basally; cells not barrel-shaped; plurilocular sporangia not cylindrical 2

- 2a. Upper branches usually in secund pattern; plurilocular sporangia up to 500 μm (or more) in length, with a sterile apex or long extension *E. siliculosus*
- 2b. Upper branches usually not in secund series; plurilocular sporangia shorter and without sterile apices 3
- 3a. Two distinct kinds of reproductive structures on same thallus; plurilocular structures: one of multiseriate rows of locules and the other of a uniseriate row of large locules *E. commensalis*
- 3b. Different kinds of reproductive structures on separate thalli: unilocular and plurilocular sporangia and plurilocular gametangia 4
- 4a. Reproductive structures borne on both prostrate and erect filaments *E. parvus*
- 4b. Reproductive structures restricted to erect filaments 5
- 5a. Epiphytic on *Codium* *E. gonodioides*
- 5b. Growing on rocks or crustose coralline algae 6
- 6a. Thalli small, filaments infrequently branched, about 20 μm in diameter, apices usually blunt; plurilocular sporangia sessile, to 175 μm long, without apical extensions *E. hancockii*
- 6b. Thalli larger, filaments abundantly branched, up to 50 μm in diameter; plurilocular sporangia pedicellate, to 400 μm long, with apical extension of cells *E. sonorensis*

Ectocarpus acutus Setchell et N. L. Gardner

FIGURE 87A,B

Ectocarpus acutus Setchell et N. L. Gardner, 1922c:404, pl. 48: figs. 36–39, pl. 49: figs. 40, 41; Setchell and Gardner, 1925:415; Smith, 1944:80, pl. 10: fig. 1; Dawson, 1961b:383; Abbott and Hollenberg, 1976:123, fig. 83; Pacheco-Ruíz, 1982:70; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Mateo-Cid and Mendoza-González, 1991:23; Mateo-Cid and Mendoza-González, 1994b:42; González-González et al., 1996:147; Hoffmann and Santelices, 1997:110, fig. 25; Rodríguez-Morales and Siqueiros-Beltrones, 1999:17, 22; Paul-Chávez and Riosmena-Rodríguez, 2000:146; Mateo-Cid et al., 2006:57; Servièrre-Zaragoza et al., 2007:3, 8; Pedroche et al., 2008:15.

Algae filamentous, up to 5 cm tall; usually densely branched; attached by prostrate, entangled filaments (not penetrating deeply into host). Main filaments corticated below by rhizoidal filaments growing into holdfast and not corticated above; branching mostly alternate below and secund above; with branches gradually narrowing and becoming attenuated distally. Cells of filaments more or less barrel-shaped; in lower to middle portions (16–)24–120 μm long and 40–60 μm in diameter; with few irregular band-shaped chloroplasts, each with several pyrenoids.

Unilocular sporangia unknown. Plurilocular sporangia on 1–2 celled pedicels; more or less cylindrical with a conical upper portion, 100–150(–230) μm long and 20–35 μm in diameter.

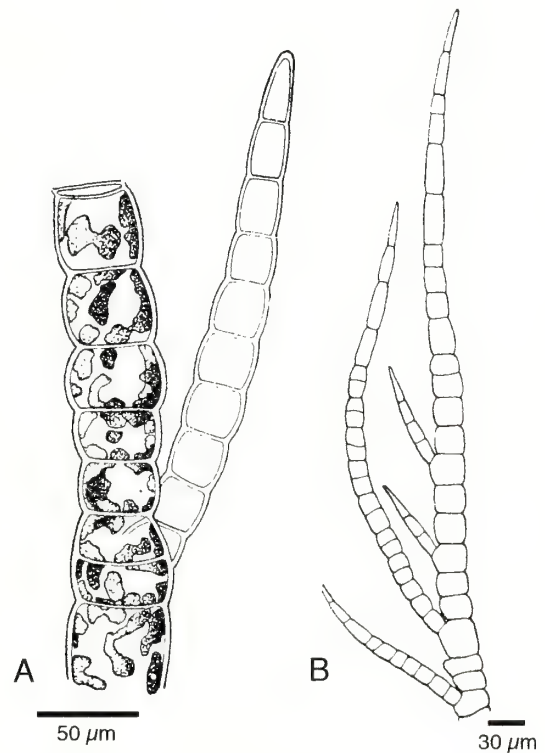


FIGURE 87. *Ectocarpus acutus*: A. Portion of a filament showing the barrel shape of the cells with irregular band-shaped chloroplasts (from Setchell and Gardner, 1922b: pl. 48, fig. 38). B. Upper portion of filament showing branches attenuated toward acute apices (from Setchell and Gardner, 1922b: pl. 48, fig. 39).

HABITAT. Epiphytic, usually on brown algae; intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Isla Espíritu Santo to Bahía de La Paz. Pacific coast: British Columbia to Baja California Sur; Colima; Chile.

TYPE LOCALITY. Carmel, Monterey County, California.

***Ectocarpus commensalis*
Setchell et N. L. Gardner**

FIGURE 88A

Ectocarpus commensalis Setchell et N.L. Gardner, 1922c:407, pl. 48: figs. 32–35; Setchell and Gardner, 1925:424; Smith, 1944:86; Dawson, 1961b:384; González-González et al., 1996:147; Mateo-Cid et al., 2006:57; Pedroche et al., 2008:16.

Ectocarpus dimorphus P. C. Silva *nom. nov.*, 1957:42; Dawson, 1961b:384; Silva, 1979:332.

Ectocarpus variabilis (De A. Saunders) G. M. Smith, *nom. illeg.*, 1942:647, figs. 1–4 [note *Ectocarpus variabilis* Vickers, 1905:59 is an earlier homonym]; Smith, 1944:85, pl. 10: figs. 2–4; Dawson, 1945b:64; Dawson, 1951:52; Dawson, 1954b:111; González-González et al., 1996:149.

Ectocarpus confervoides f. *variabilis* De A. Saunders, 1898:155, pl. 23: figs. 1–10; Setchell and Gardner, 1925:414, pl. 46: fig. 7; Dawson, 1944:220.

Algae epiphytic, forming tufts up to 1.0 cm tall. Erect filaments uncorticated, sparingly and predominately alternate branched; upper ends attenuated, with round apices; prostrate filaments irregularly branched, attached to but not penetrating host cells. Cells of erect filaments 10–75(–90) μm long by (10–)15–30 μm in diameter, with band-shaped chloroplasts.

Plurilocular structures of two kinds, both pedicellate (1–3 celled stalk), and usually borne on separate branches of same individual: (1) multiseriate, 10–15 locules wide, fusiform to ovoid, 75–180 μm long by 15–35 μm in diameter; each locule about 0.2 μm in diameter; and (2) a uniseriate row, 70–200 μm in length; of 2–15 barrel-shaped large locules, each 15–35 μm in diameter.

HABITAT. Epiphytic on *Sargassum* and probably other algae; low intertidal.

DISTRIBUTION. Gulf of California: Isla Turners (off south end of Isla Tiburón). Pacific coast: British Columbia to Baja California Sur; Nayarit.

TYPE LOCALITY. Not stated by Saunders (1898); Point Pinos, Pacific Grove, Monterey County, California, given by Smith (1944).

REMARKS. Description of *Ectocarpus commensalis* is based primarily on Dawson (1944, as “*E. confervoides* f. *variabilis*”) and Smith (1944, as “*E. variabilis*”). Although considered to be conspecific with *E. parvus* by Abbott and Hollenberg (1976), Silva (1979, as “*E. dimorphus*”) noted that the epiphytic *E. commensalis* should probably be separated from the epilithic *E. parvus*.

***Ectocarpus gonodioides*
Setchell et N. L. Gardner**

FIGURE 88B

Ectocarpus gonodioides Setchell et N. L. Gardner, 1924a:721, pl. 17: fig. 44; Setchell and Gardner, 1925:439; Dawson, 1944:221; Smith, 1944:86; Dawson, 1961b:384; Dawson, 1966a:9; Dawson, 1966b:55; Abbott and Hollenberg, 1976:126, fig. 87; González-González et al., 1996:148; Pacheco-Ruíz and Zertuche-González, 1996b:171; Mateo-Cid et al., 2006:49; Pacheco-Ruíz et al., 2008:203; Pedroche et al., 2008:16.

Algae minute tufts, up to 550 μm high, epiphytic, attached by rhizoidal filaments deeply penetrating into the host. Erect filaments near base, almost colorless, sparsely branched at host’s surface; upper filaments simple, mostly becoming attenuated toward apices. Cells 1–2 times as long as wide; lower cells 18–24 μm in diameter; upper cells 10–14 μm in diameter. Chloroplasts not adequately described in Gulf specimens.

Unilocular sporangia unknown. Plurilocular gametangia pedicellate, on 1–2 celled stalk, borne near base of filaments; narrowly fusiform, up to 125 μm long by 20–28 μm wide.

HABITAT. Epiphytic on *Codium macdougalii* (= *C. brandegeei*) and *C. cuneatum* (= *C. simulans*); mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de Los Ángeles; Bahía Agua Verde to Cabo Pulmo. Pacific coast: central California.

TYPE LOCALITY. Isla Coronado (Isla Smith), Las Islas de la Cintura, Gulf of California.

REMARKS. Setchell and Gardner (1924a:722), in describing the Gulf *E. gonodioides*, stated “the chromatophores are too much disorganized for characterization.” Recording this species from Carmel, central California, Smith (1944:86) noted it differed somewhat

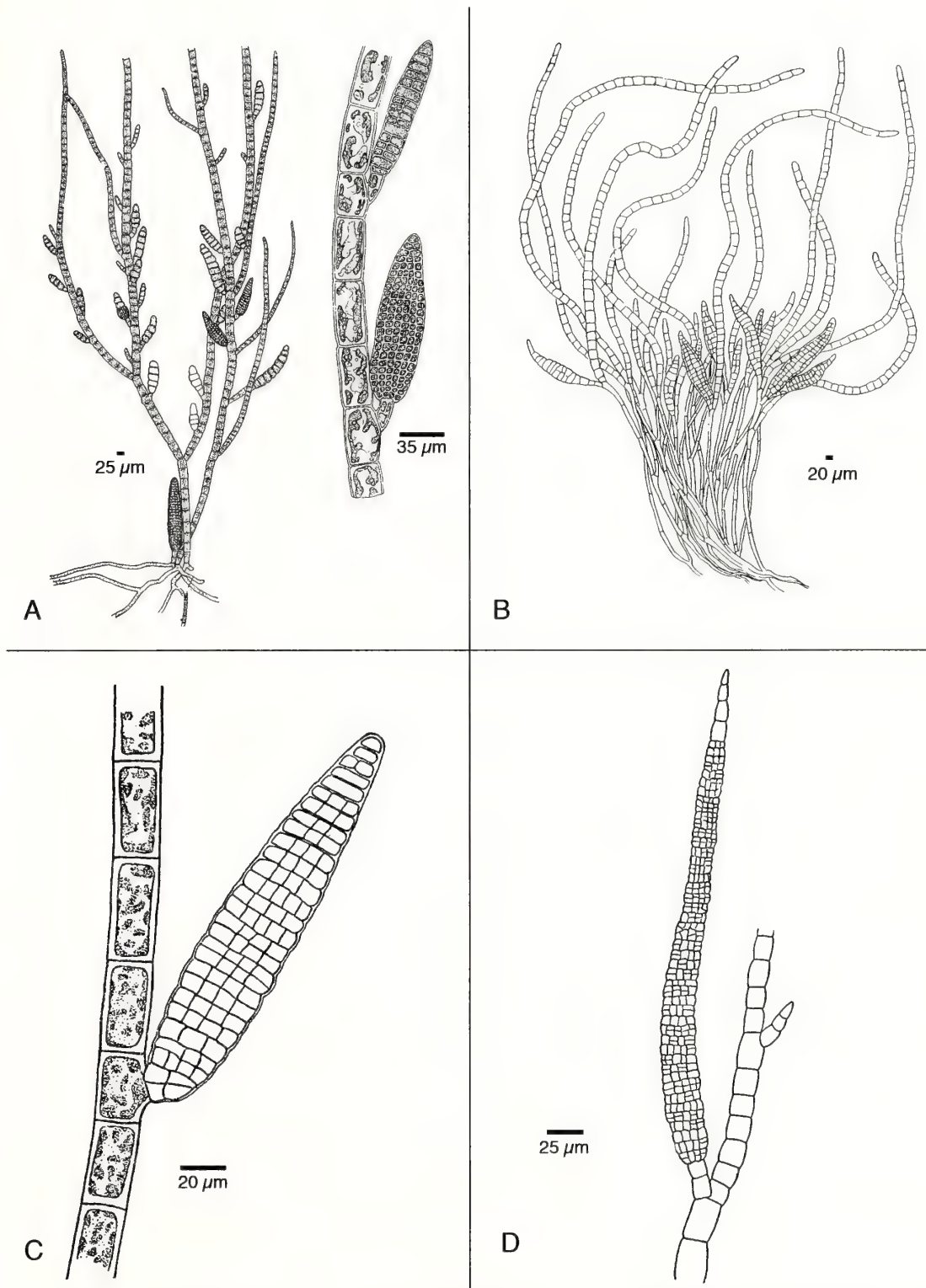


FIGURE 88. Four species of *Ectocarpus*. A. *Ectocarpus commensalis*: Filaments bearing both multiseriate and uniseriate plurilocular sporangia (from Saunders, 1898: pl. 23, figs. 1, 9). B. *Ectocarpus gonodioides*: Tuft of filaments showing plurilocular reproductive structures borne right above the rhizoidal portion that penetrates the host (drawn from type specimen, *I. M. Johnston-47e*; Setchell and Gardner, 1924a: pl. 17, fig. 44). C. *Ectocarpus hancockii*: Portion of a filament bearing a sessile, plurilocular sporangium (drawn from type specimen, *EYD-[1940]133*, Dawson, 1944: pl. 31, fig. 4). D. *Ectocarpus sonorensis*: Portion of a filament bearing a narrow, elongate plurilocular sporangium with sterile apical cells (drawn from type specimen, *Drouet & Richards-3281*, Dawson, 1944: pl. 31, fig. 5).

from those of the Gulf of California type locality and described its plastids as band-shaped, and later, Abbott and Hollenberg (1976:126) noted there were few per cell. Until further collections of Gulf type locality material are made and its plastids and mode of growth are described and tested with molecular analyses, it is best to retain the species here (see also "Remarks" under *E. hancockii*).

***Ectocarpus hancockii* E. Y. Dawson**

FIGURE 88C

Ectocarpus hancockii E. Y. Dawson, 1944:222, pl. 31: fig. 4; Dawson, 1961b:385; Espinoza-Ávalos, 1993:333; González-González et al., 1996:149; L. Aguilar-Rosas et al., 2000:132, 134; Pedroche et al., 2008:18.

Algae tufted, 4–5 mm high, saxicolous or epiphytic on crustose coralline algae, attached by a mat of cells and basal filaments. Erect filaments infrequently branched, about 20 µm in diameter, apices usually blunt. Cells 30–60 µm in length and up to 20 µm in diameter. Plastids probably band-shaped.

Unilocular sporangia unknown. Plurilocular sporangia, abundant, lateral, sessile, 125–175 µm long by 28–32 µm in diameter.

HABITAT. On rocks and on crustose coralline algae; mid intertidal.

DISTRIBUTION. Gulf of California: El Faro de San Felipe (lighthouse of San Felipe); Isla Turners.

TYPE LOCALITY. Reef off Isla Turners (off southeast end of Isla Tiburón), Las Islas de la Cintura, Gulf of California.

REMARKS. The generic placement of the Gulf-endemic *Ectocarpus hancockii* remains uncertain, as characters necessary for generic separation, such as the plastids or type of growth, were not given in the original description (Dawson, 1944). However, in Dawson's illustration (1944, pl. 31: fig. 4) the plastids appear to be mostly band-shaped, and thus, for now, this species is retained in *Ectocarpus*. Further study, including DNA analyses, on future collections from the type locality should lead to a better understanding of this species.

***Ectocarpus parvus* (De A. Saunders) Hollenberg**

FIGURE 89

Ectocarpus siliculosus var. *parvus* De A. Saunders, 1898:153, pl. 22: figs. 1–9.

Ectocarpus parvus (De A. Saunders) Hollenberg, 1971:283; Abbott and Hollenberg, 1976:126, fig. 89 [in part]; L. Aguilar-Rosas, 1982:31; Pacheco-Ruiz, 1982:70; Mendoza-González and Mateo-Cid, 1985:24; Mendoza-González and Mateo-Cid, 1986:420; Stewart, 1991:38; Servièrre-Zaragoza et al., 1993:482; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:517; Mendoza-González et al., 1994:109; González-González et al., 1996:149; Mendoza-González and Mateo-Cid, 1996:69, 85, pl. 17: figs. 69–72; Cruz-Ayala et al., 2001:190; Dreckmann et al., 2006:154.

Ectocarpus confervoides f. *parvus* (DeA. Saunders) Setchell et N. L. Gardner, 1922c:414; Setchell and Gardner, 1925:413; Dawson, 1961b:384.

Ectocarpus confervoides f. *pygmaeus* sensu Setchell and Gardner, 1925:415 [non *E. confervoides* f. *pygmaeus* (Areschoug) Kjellman, 1890:77; basionym: *Ectocarpus pygmaeus* Areschoug in Kjellman, 1872:85].

Ectocarpus confervoides var. *pygmaeus* sensu Hollenberg and Abbott, 1968:1237 [non *E. confervoides* var. *pygmaeus* (Areschoug) Rosenvinge, 1893:883; the basionym, *E. pygmaeus* Areschoug in Kjellman, 1872:85, is a synonym of *Ectocarpus fasciculatus* Harvey, 1841:40 (see Russell, 1966:270)].

Algae erect, forming short, filamentous tufts, 5–10 mm high. Filaments uncorticated, 20–30 µm in diameter; simple or sparingly, more or less alternately branched; attenuated at branch apices. Cells of filaments 25–75 µm in length, 20–30 µm in diameter; upper cells shorter than lower cells. Chloroplasts irregularly band-shaped.

Unilocular and plurilocular sporangia not reported in northern Gulf material.

HABITAT. Growing on rocks; low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla Pelicano, Bahía Kino; Bahía de La Paz. Pacific coast: Alaska to Baja California Sur; Sinaloa to Chiapas.

TYPE LOCALITY. On "sand-colored rocks," San Pedro, Los Angeles County, California (Saunders, 1898).

REMARKS. The relationship of *Ectocarpus parvus* with *E. commensalis* is problematic. While recognizing *E. parvus* as a separate taxon (including those misidentified as "*E. confervoides* var. *pygmaeus*"), Scagel et al. (1989) noted its taxonomic status, as well as that of other morphologically similar taxa, is uncertain. Future collections will be helpful in understanding the degree of variation and the status of this taxon within the Gulf of California. Specimens of "*E. confervoides* f. *pygmaeus*"

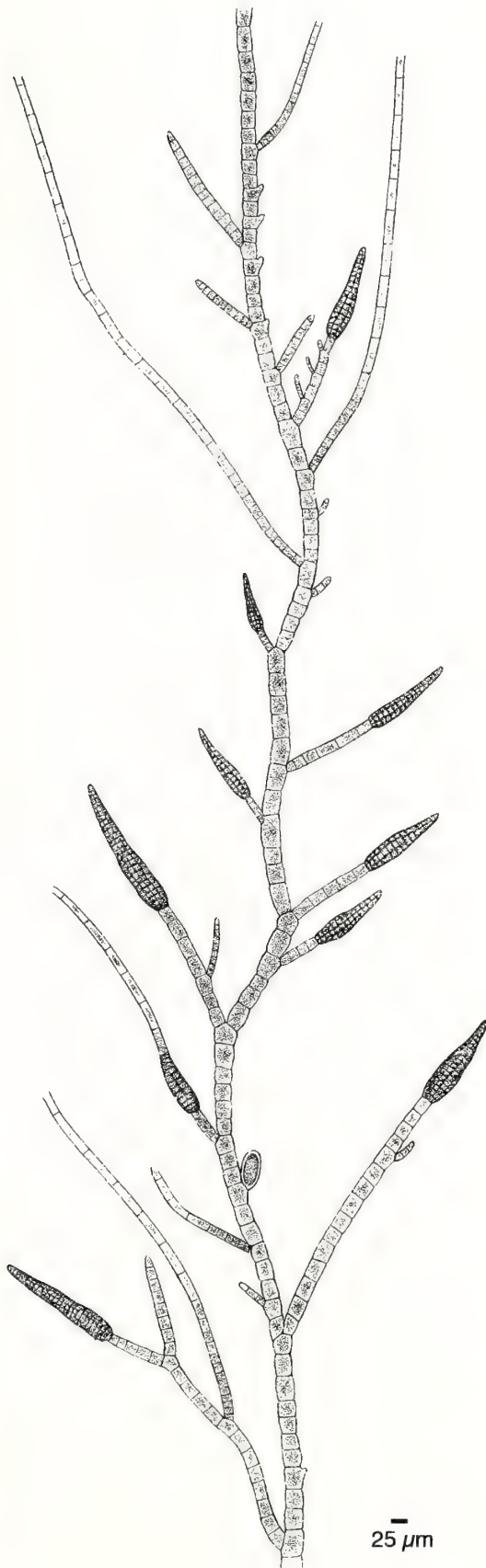


FIGURE 89. *Ectocarpus parvus*: Habit, portion of a filament showing terminal and lateral plurilocular sporangia (drawn from type specimen, W.A. Setchell-1213, Saunders, 1898: pl. 22, fig. 1).

as reported from Sonora (Mendoza-González and Mateo-Cid, 1986) and Nayarit (León-Tejera et al., 1993) may also be this species.

***Ectocarpus siliculosus* (Dillwyn) Lyngbye**

Conferva siliculosa Dillwyn, 1809: 69, Suppl. pl. E.

Ectocarpus siliculosus (Dillwyn) Lyngbye, 1819:131, pl. 43B,C; Setchell and Gardner, 1925:410; Doty, 1947:31; Dawson, 1961b:385; Abbott and Hollenberg, 1976:128, fig. 90; Silva, 1979:332; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid and Mendoza-González 1991:23; Mateo-Cid and Mendoza-González 1992:23; Mateo-Cid and Mendoza-González 1994b:42; González-González et al., 1996:376; Kitayama, 1996:224, figs. 2, 3; Yoshida, 1998:166; L. Aguilar-Rosas et al., 2000:132, L. Aguilar-Rosas et al., 2002:235; Pedroche et al., 2008:18.

Algae forming tufts, up to 2.0 cm tall, composed of uniseriate, uncorticated filaments; branching subdichotomous in lower portion and alternately secund above; larger branches 45–60 μm in diameter, ultimate branchlets 10–25 μm in diameter. Cells (0.6–)1–2 times as long as wide; with ribbon-shaped chloroplasts and several pyrenoids.

Plurilocular sporangia conical, usually on short pedicels (also reported sessile), 90–500(–600) μm long, 15–25(–40) μm in diameter; with sterile tip or sometimes with hairlike multicellular extension.

HABITAT. On rocks, limestone, and clay, in tide pools, or epiphytic on *Codium*; often becomes free-floating; high to mid intertidal.

DISTRIBUTION. Gulf of California: El Tornilal to Puertecitos. Pacific coast: Alaska to Baja California Sur; Nayarit to Colima, Peru; Chile; China; Japan.

SYNTYPE LOCALITIES. Cromer in Norfolk and Hastings in East Sussex, England (Silva et al., 1996a).

REMARKS. *Ectocarpus siliculosus* has been recorded in the northern Gulf by L. Aguilar-Rosas et al. (2000, 2002); description is based on Abbott and Hollenberg (1976).

***Ectocarpus sonorensis* E. Y. Dawson**

FIGURE 88D

Ectocarpus sonorensis E. Y. Dawson, 1944:221, pl. 31: fig.5; Dawson, 1961b:385; Espinoza-Ávalos, 1993:333; González-González et al., 1996:149; Pedroche et al., 2008:20.

Algae filamentous, light green-brown, up to 10 cm tall, abundantly branched, with main filaments up to 50 µm in diameter, and branches attenuating distally from 40 µm to 12 µm in diameter; secondary and other order branches, slender, somewhat cylindrical, and tapering upwards to a sharp point; branches bearing numerous short, spine-like secondary branchlets near apices. Cells thin-walled, 1.25–1.50 times as long as wide; with pale chloroplasts apparently lining the wall.

Unilocular sporangia unknown. Plurilocular sporangia borne on 2-celled pedicels, slender, up to 400 µm long by 20–25 µm in diameter, with an apical, pointed extension of vegetative cells, 30–120 µm long.

HABITAT. On rocks; intertidal.

DISTRIBUTION. Gulf of California: Guaymas.

TYPE LOCALITY. “On rocks in tidal stream,” 3 km east of Guaymas, Sonora, Gulf of California (Dawson, 1944).

REMARKS. Apparently a Gulf of California endemic, *Ectocarpus sonorensis* is known only from the type collection.

PYLAIELLACEAE

Pylaiellaceae P. M. Pedersen, 1984:50, as “Pilayellaceae.”

Algae are filamentous, with erect and sometimes low-growing portions, attached by rhizoids. Filaments are mostly uniseriate, becoming parenchymatous by longitudinal divisions of the cells.

Sporangia are formed by the transformation of vegetative cells.

REMARKS. Pedersen (1984) considered the Pylaiellaceae to be close to some families of the orders Dictyosiphonales and Tilopteridales, noting that the more or less frequent formation of longitudinal walls in *Pylaiella* justifies its position among the parenchymatous brown algae. However, Wynne (1986) questioned the taxonomic significance of this character and placed *Pylaiella* in the Ectocarpaceae and, later (Wynne, 2005), within the Acinetosporaceae (both Ectocarpales). Herein the Pylaiellaceae is recognized as a family within the Ectocarpales (Silva et al., 1996a).

***Pylaiella* Bory de Saint-Vincent**

Pylaiella Bory de Saint-Vincent, 1823:393.

Algae are filamentous, composed of creeping and erect portions, which may be simple or more or less opposite, alternate, or irregularly branched, and attached by rhizoids. Filaments are initially uniseriate and without a terminal hair; later, these filaments may be frequently divided by longitudinal walls (some interpret this as becoming parenchymatous) and taper upward into pseudohairs (note that true phaeophycean hairs are absent). Growth is by intercalary divisions, which are generally diffuse throughout the thallus or sometimes localized. Cells have numerous discoid plastids and a single pyrenoid.

Thalli are isomorphic, sometimes with both unilocular and plurilocular structures on the same individual. Plurilocular and unilocular sporangia are barrel-shaped or subspherical, are intercalary in catenate series with lateral openings, and are formed by direct transformation of vegetative cells. Plurilocular gametangia are oblong to more or less cylindrical.

REMARKS. The original spelling, *Pylaiella* Bory de Saint-Vincent (1823) has been conserved over “*Pilayella*” (Silva et al., 1999; Compère, 2003). Species of *Pylaiella* exhibit a wide range of phenotypic plasticity; thus, the species concepts are in need of testing and clarification.

Although species of *Pylaiella* are not well known in the Gulf, large loose-lying mats of another species, *P. littoralis* (Linnaeus) Kjellman (1872), have created environmental problems on the northeastern coast of the United States (Wilce et al., 1982).

One undetermined species is now recorded from the northern Gulf of California.

***Pylaiella* sp. A**

Alga minute and filamentous. Main axes branched irregularly alternate.

Sporangia not seen.

HABITAT. In a tide pool, entangled with *Antithamnionella spirographidis*; low intertidal.

DISTRIBUTION. Gulf of California: Punta Pelicano, Puerto Peñasco.

REMARKS. A minute specimen of *Pylaiella* (JN-3979) establishes the genus as occurring in the northern Gulf. Unfortunately, the material is not fertile; thus, the species cannot be determined. It is noted herein to call its presence to the attention of future collectors.

LEATHESIACEAE*

Leathesiaceae Farlow, 1881:16, 79.

Corynophlaeaceae Oltmanns, 1922:23 [see Silva, 1980: 71, 73].

Sporophytic algae are cushionlike, globose, or hemispherical, some becoming irregularly globular, with smooth to convoluted surfaces and without a distinct basal layer. Assimilatory filaments are anticlinally arranged, with intercalary growth. Cells of assimilatory filaments contain several chloroplasts, each with a pyrenoid.

Life histories, where known, are heteromorphic with a sporophytic macrothallus and a haploid filamentous microthallus. Sporophytes may have unilocular and/or plurilocular sporangia on the same or separate thalli. Presumed gametophytes are filamentous, microscopic thalli, with uniseriate gametangia.

REMARKS. Some taxonomists consider the Leathesiaceae to be synonymous with the family Chordariaceae on the basis of morphological and life history similarities. Molecular phylogenetic analyses of the generitype *Leathesia tuberiformis* S. F. Gray (1821; which is now *Leathesia marina* (Lyngbye) Decaisne, 1842, basionym *Chaetophora marina* Lyngbye 1819; *L. difformis* (Linnaeus) J. E. Areschoug, 1847; see Pedroche et al., 2008) will help resolve the familial status.

One of the genera, *Myriactula* Kuntze (1898), is represented by two poorly known endemic species in the southern Gulf: *Myriactula johnstonii* (Setchell et N. L. Gardner) Feldmann (1945; basionym: *Gonodia johnstonii* Setchell et N. L. Gardner 1924a); and *M. marchantiae* (Setchell et N. L. Gardner) Feldmann (1945; basionym: *Gonodia marchantiae* Setchell et N.L. Gardner 1924a).

There is one genus recorded in the northern Gulf of California.

***Leathesia* S. F. Gray**

Leathesia S. F. Gray, 1821: 279, 301.

Algae are globular to hemispherical or irregularly convoluted and internally solid or initially solid and later

becoming hollow. Species are epiphytic or growing on solid substratum. Growth is by intercalary cell divisions. Internal structure is of two kinds of filaments: inner medullary filaments that are loosely arranged, dichotomously to trichotomously branched, and composed of large, elongated, colorless cells; and outer multicelled assimilatory filaments that are composed of cylindrical pigmented cells that terminate with a large globular cell. Cells of assimilatory filaments contain several chloroplasts with pyrenoids. Phaeophycean hairs, often common, are among the assimilatory filaments and project above the surface layer.

The life history is heteromorphic, with plurispores of sporophytic macrothalli producing filamentous microthalli and unfused gametes of the latter developing gametophytes (e.g., Kylin, 1933; Dangeard, 1969). Unilocular and plurilocular sporangia develop on the basal cells of the assimilatory filaments, sometimes on the same individual. Unilocular sporangia are ovoid to ellipsoid and are usually separated from each other. Plurilocular sporangia with locules in uniseriate rows are usually grouped together.

REMARKS. Two taxonomic sections of the genus were recognized by Inagaki (1958). *Leathesia* sect. *Leathesia* includes members that are hollow, with a reticulated medullary layer, and *Leathesia* sect. *Primariae* includes those that are solid, with densely packed medullary filaments. Species of the latter section resemble the genus *Corynophlaea* Kützinger (1843) in their inner anatomy; however, they are different genera. Ajsaka (1984) cultured one member, *L. japonica* Inagaki (1958), and reported the occurrence of filamentous thalli that resembled *Polytretus reinboldii* (Reinke) Sauvageau (1900; = *Botrytella reinboldii* (Reinke) Kornmann et Sahling, 1988) and formed plurilocular sporangia with several lateral release pores in its life history.

One species has been reported in the northern Gulf of California.

***Leathesia nana* Setchell et N. L. Gardner**

FIGURE 90A-C

Leathesia nana Setchell et N. L. Gardner, 1924b:3; Setchell and Gardner, 1925:511, pl. 43: fig. 67; Smith, 1944:115, pl. 15: fig. 1; Dawson, 1958:65; Dawson, 1961b:391; Hollenberg, 1971:285, fig. 3; Abbott and Hollenberg, 1976:177, fig. 143; Pacheco-Ruiz, 1982:70; Tseng, 1983:174, pl. 88: fig. 1; R. Aguilar-Rosas et al., 1984a:152; R. Aguilar-Rosas et al., 1984b:161; R. Aguilar-Rosas et al., 1990:123; González-González

* Contributed by Luis E. Aguilar-Rosas, Raúl Aguilar-Rosas, and James N. Norris; L. Aguilar-Rosas: Instituto de Investigaciones Oceanológicas, Universidad Autónoma de Baja California, Km 107 carretera Tijuana-Ensenada, 22830 Ensenada, Baja California, Mexico; R. Aguilar-Rosas: Facultad de Ciencias Marinas, Universidad Autónoma de Baja California.

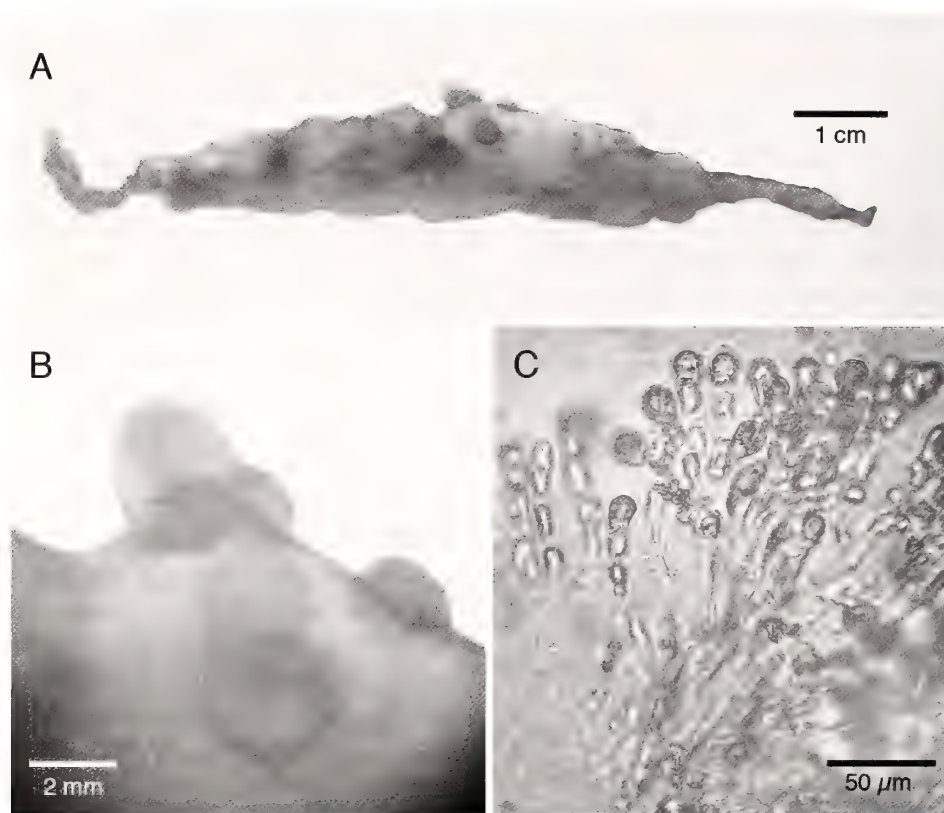


FIGURE 90. *Leathesia nana*: A. Several thalli epiphytic on a leaflike blade of *Sargassum sinicola*. B. Habit of several small globose thalli. C. Transection of thallus showing three- to five-celled assimilatory filaments with a larger, subspherical, terminal cell (CMMEX-6447).

et al., 1996:154; L. Aguilar-Rosas et al., 2000:127, 136; Mateo-Cid et al., 2006:58; Pedroche et al., 2008:60.

Algae small, more or less globose or hemispherical, 1.0–3.0(–5.0) mm in diameter; mostly with a smooth surface and usually not hollow; epiphytic on *Sargassum*. Assimilatory (cortical) filaments of 3–4(–5) elongate cells, (6–)7–8 μm in diameter, with a larger, subspherical terminal cell, 10 μm in diameter. Medullary filaments of larger colorless cells. Hairs not observed in Gulf specimens (reported as present or absent for the species).

Reproductive structure not observed in upper Gulf of California specimens.

HABITAT. Epiphytic on *Sargassum sinicola* and *S. herporhizum*; intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco; Playa El Coloradito. Pacific coast: northern Washington to Cabo Colnett, Baja California; China.

TYPE LOCALITY. Monterey, Monterey County, California.

REMARKS. The northern Gulf *Leathesia nana* were found on brown algae, species of *Sargassum* (L. Aguilar-Rosas et al., 2000; Mateo-Cid et al., 2006). This is a new host, as central California *L. nana* are known as epiphytes on the sea grass *Phyllospadix* (Setchell and Gardner, 1924b, 1925; Smith, 1944) and on the red algae *Neorhodomela larix* (Turner) Masuda (1982; = *Rhodomela larix* (Turner) C. Agardh, 1822) and *Odonthalia floccosa* (Esper) Falkenberg (1901), both Rhodomelaceae (Sparling, 1971; Abbott and Hollenberg, 1976).

Although reproductive structures were not seen in upper Gulf specimens, two kinds of sporangia are reported in California *L. nana* (Hollenberg, 1971; Abbott and Hollenberg, 1976): plurilocular sporangia, uniseriate, of 4–6 locules, 20–30 μm long and 3.5–5.0 μm in diameter, borne at base of 3- to 4-celled paraphyses, with a globular terminal cell only slightly larger than lower cells (Setchell and Gardner, 1925); and unilocular sporangia 25–40(–50) μm long and 10–20 μm in diameter, borne at base of 4- to 6-celled assimilatory filaments with a large

globular terminal cell (larger than those that bear plurilocular sporangia; Hollenberg, 1971:fig. 3). Specimens of *L. nana* with plurilocular sporangia are known only on *Phyllospadix*, whereas those with unilocular sporangia are almost exclusively on *Neorhodomela* and *Odonthalia* (Abbott and Hollenberg, 1976).

Webber (1981, as "*L. difformis*") suggested *L. nana* was a growth-form of *L. marina* (Lyngbye) Decaisne, and Scagel et al. (1989, as "*L. difformis*"), considering the study of Novacek (1987), reduced *L. nana* to a synonym of *L. marina*. Comparative molecular and morphological studies of *L. marina* (type locality: Båstad, Sweden), central California "*L. difformis* sensu Smith (1944) and Abbott and Hollenberg (1976)," *L. nana* (type locality: Monterey), and the northern Gulf *L. nana* are needed to elucidate the taxonomic status and phylogenetic relationships of these four.

SCYTOSIPHONACEAE

Scytosiphonaceae Farlow, 1881:15, 62.

Algae of this family exhibit a wide variety of forms and can be tubular, compressed, or flattened and elongated,

cylindrical, foliose, spherical, or saccate. The habit of these algae can be entire, irregularly shaped, or branched. Structurally, they are multiaxial and pseudoparenchymatous, with a medulla of large colorless cells and a cortical layer of small pigmented cells, and can be either solid or hollow centrally. Growth in most of the members is intercalary or from subapical cells. Cells have a large plastid with a pyrenoid, and vesicle-like globules (physodes) may be present or lacking. Phaeophycean hairs are present and either isolated or grouped in superficial pits.

Life histories, where known, are heteromorphic. Reproductive structures are in sori. Sporophytes produce unilocular and plurilocular sporangia. Sexual reproduction is by unilocular gametangia and uniseriate or multiseriate plurilocular gametangia that produce isogametes or anisogametes.

REMARKS. The report of two members of the family in the northern Gulf (Mendoza-González and Mateo-Cid, 1986), *Petalonia binghamiae* (J. Agardh) Vinogradova (1973; = *Endarachne binghamiae* J. Agardh 1896) and *Petalonia fascia* (O. F. Müller) Kuntze (1898), needs to be confirmed.

Four genera of the Scytosiphonaceae are known in the northern Gulf of California.

KEY TO THE GENERA OF SCYTOSIPHONACEAE IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Minute to small epiphytes or endophytes; a disclike basal layer of monostromatic filaments, with erect, short, simple to laterally branched filaments *Compsomena*
- 1b. Large, erect, and centrally hollow (not filamentous) and may be cylindrical and tubular or compressed, or globose or saccate, or open and sheetlike with or without holes (netlike) 2
- 2a. Thalli either long, narrow cylindrical axes and branches, up to 3 mm in diameter, or low-growing clumps of more or less cylindrical to compressed entangled branches, up to 6 mm in diameter *Rosenvingea*
- 2b. Thalli globose or saccate or open sheetlike or netlike 3
- 3a. Thalli may be spherical to irregularly globose or saccate or more or less tubular irregularly lobed branches or open sheetlike without holes *Colpomenia*
- 3b. Thallus three-dimensional "net" of small to large holes, usually torn open and forming netlike sheets *Hydroclathrus*

Colpomenia (Endlicher) Derbès et Solier

Colpomenia (Endlicher) Derbès et Solier, 1851:95.
Asperococcus β. *Colpomenia* Endlicher, 1843:26.

Algae are more or less globose or saccate and hollow, occasionally forming prostrate expanses or open expanded sheets. The surface may be smooth, lobed, or constricted, or may be heavily convoluted and with prominent protuberances. Some may become torn or open and flattened with age. The medulla is composed of large

colorless cells, the innermost medullary layer facing the open hollow cavity. The cortex is generally one layer of small pigmented cells and has scattered tufts of hairs with basal meristems.

Plurilocular gametangia are borne in superficial sori associated with paraphyses, scattered over the thallus surface.

Four species of *Colpomenia* are recognized in the northern Gulf of California. Another, *C. peregrina* Sauvageau (1927), has been reported in the southern Gulf (Cruz-Ayala et al., 2001).

KEY TO THE SPECIES OF *COLPOMENIA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Thalli consisting of erect, clustered, fingerlike sacs arising from a common prostrate holdfast; wall of sacs thin, delicate, usually less than 100 μm thick *C. phaeodactyla*
- 1b. Thalli not fingerlike sacs, but range from spherical, balloonlike to irregularly shaped, low-growing or sessile expanses or clumps of branched thalli; thicker and firmer, >200 μm in thickness 2
- 2a. Thalli forming a spreading clump of adherent, irregular lobed branches; smooth surface *C. ramosa*
- 2b. Thalli globose or expanded sacs (occasionally open and flat sheets); lacking definite branches; smooth, convoluted, or tuberculate surface 3
- 3a. Thalli with tuberculate, warty surface; of a crisp, rigid texture; thickness exceeding 500 μm (often up to 1.0 mm); plurilocular structures up to 25 μm long *C. tuberculata*
- 3b. Thalli with smooth or convoluted surface; flaccid, never tuberculate or rigid; thinner in transection, 300–500 μm thick; plurilocular structures 40 or more μm long 4
- 4a. Thallus hollow, vesicle-like or globose *C. sinuosa*
- 4b. Thallus open, broad or expanded thin sheets *C. sp. A*

Colpomenia phaeodactyla
M. J. Wynne et J. N. Norris

FIGURE 91A

Colpomenia phaeodactyla M. J. Wynne et J. N. Norris, 1976:5, figs. 4, 5a,b, 9a, 11c; Littler and Littler, 1981:151, tbl. 3, figs. 4, 5, 7; Norris, 1985:209, fig. 16.3 (bottom); Santelices, 1989:289, pl. GG: fig. 7; Yoshida et al., 1995:280; González-González et al., 1996:142; Pacheco-Ruíz and Zertuche-González, 1996b:171; Hoffmann and Santelices, 1997:159, fig. 40; Yoshida, 1998:305, fig. 2-21G; Mateo-Cid et al., 2006:49, 58; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:64.

Colpomenia sinuosa f. *deformans* sensu Setchell and Gardner, 1924a:726, pl. 19: figs. 61, 62; Setchell and Gardner, 1925:542; Dawson, 1949:239 [in part; Gulf of California specimens only]; Dawson, 1944:233; Dawson, 1966a:11; Wynne, 1972:137, figs. 1, 17, 18; Wynne, 1973:141 [non *Colpomenia sinuosa* f. *deformans* Setchell et N. L. Gardner, 1903:242; which is *Colpomenia bullosa* (De A. Saunders) Yamada, 1948:6].

Colpomenia bullosa sensu Norris, 1973:6; Pacheco-Ruíz et al., 2008:204 [non *Colpomenia bullosa* (De A. Saunders) Yamada, 1948:6; basionym: *Scytosiphon bullosus* De A. Saunders, 1898:163].

Algae usually forming clusters of long, hollow sacs, golden brown (darker when fertile), 8–15(–25) cm long, 0.8–1.5(–5.5) cm wide, arising from a compressed base attached to the substrate. Sacs flaccid and delicate, elongated and tapering toward base; hollow throughout; thin,

70–88(–110) μm thick. Medulla 2–3 cells thick, of large colorless cells. Outer cortex a single layer of small cuboidal cells, each with 1 chloroplast; tufts of colorless hairs rare. Subcortex also a single layer of slightly larger cells.

Unilocular sporangia unknown. Plurilocular structures, uniseriate and biseriate, 28–38 μm long; forming dense, extensive sori over surface of erect sacs; paraphyses rare (if present, more or less same height as plurilocular structures).

HABITAT. On tops of rocks and tidal platforms; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas. Pacific coast: Bahía San Bartolomé to Bahía Asunción (Baja California Sur); Costa Rica; central Chile; Japan.

TYPE LOCALITY. Playa Estación, Puerto Peñasco, Sonora, Gulf of California.

REMARKS. Named for the brown finger-like appearance of its elongated sacs, *Colpomenia phaeodactyla* is an ephemeral species and can be relatively common at some locales in the upper Gulf from December to May. It is quite flaccid, lying on the substratum when exposed during low tides, and during high tides it is submerged and vertical, with the hollow portions appearing to be at least partly filled with air.

Ramírez and Rojas V. (1991) considered Chilean records identified as "*C. phaeodactyla*" (Santelices et al., 1989; Ramírez and Santelices, 1991) to be *C. durvillei* (Bory de Saint-Vincent) Ramírez (see Wynne, 1999, for clarification of status of this taxon). However, Hoffmann and Santelices (1997) recognized *C. phaeodactyla* from central Chile.

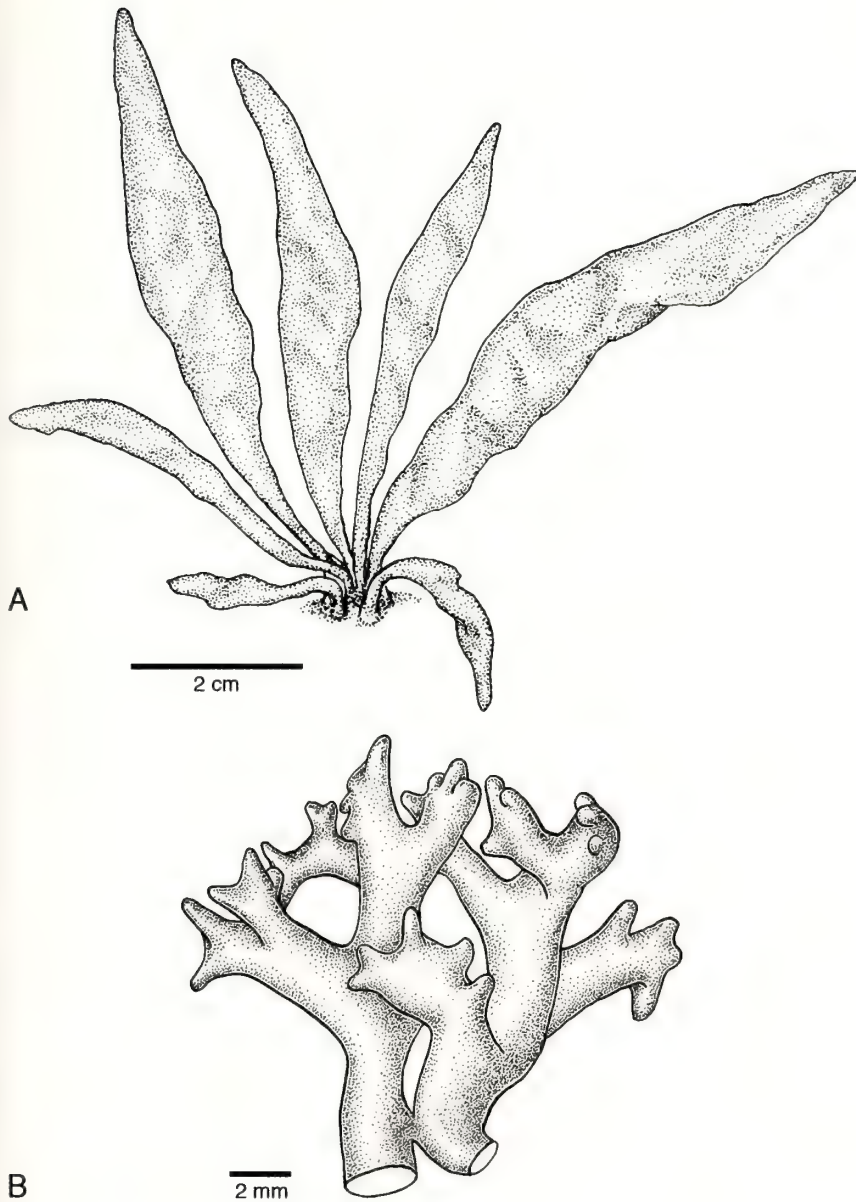


FIGURE 91. Two species of *Colpomenia*. A. *Colpomenia phaeodactyla*: Habit of several fingerlike hollow sacs (JN-4759). B. *Colpomenia ramosa*: Upper portion of thallus showing branching pattern (JN-4697).

***Colpomenia ramosa* W. R. Taylor**

FIGURE 91B

Colpomenia ramosa W. R. Taylor, 1945:84, pl. 6, fig. 2; Dawson, 1949:228, 250; Dawson, 1951:52; Dawson, 1952:431; Dawson, 1961b:394; Wynne and Norris, 1976:11, fig. 8a,b; Mendoza-González and Mateo-Cid, 1985:24; Ramírez and Rojas V., 1991:16, figs. 4, 8; Martínez-Lozano et al., 1991:23; Mendoza-González et al., 1994:110; González-González et al., 1996:142; Pacheco-Ruíz and Zertuche-González, 1996b:171;

Mateo-Cid and Mendoza-González, 1997:59, pl. 7: figs. 28, 29, pl. 9: fig. 39; Mateo-Cid and Mendoza-González, 2003:22; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:65.

Rosenvingea intricata sensu Dawson, 1944:233 [in part], pl. 52: fig. 1 [non *Rosenvingea intricata* (J. Agardh) Børgesen, 1914:26].

Algae forming adherent clumps, up to 4 cm broad and to 2 cm tall, with several areas of attachment. Thallus of congested, hollow, more or less cylindrical to compressed axes, irregularly subdichotomously to polychotomously

branched; broader basally, becoming narrower distally; terminal branch divisions cylindrical, short, 1–2 mm in diameter by 2–3 mm long, with rounded ends. In transection, outer wall 200–500 μm thick, of 6–8 cell layers; cells larger inward toward hollow cavity, becoming smaller outward to small-celled cortex.

Plurilocular sporangia in sori, uniseriate, with 10–12 locules, 35–40 μm long.

HABITAT. Often entangled with other algae; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Isla Wil-lard, Bahía San Luis Gonzaga to Bahía Tepoca; Isla Espiritu Santo to Bahía de La Paz. Pacific coast: Baja California to Sinaloa; Guerrero to Oaxaca; Costa Rica; Galápagos Islands; Chile.

TYPE LOCALITY. Bahía Sur, Isla Cedros, Baja California, Pacific Mexico.

***Colpomenia sinuosa* (Mertens ex Roth)
Derbès et Solier**

FIGURES 5A, 92A

Ulva sinuosa Mertens ex Roth, 1806:327, pl. 12: figs. a–c. *Colpomenia sinuosa* (Mertens ex Roth) Derbès et Solier, 1851:95; Derbès and Solier, 1856:11, pl. 22: figs. 18–20; Saunders, 1898:164, pl. 32: figs. 7, 8; Setchell and Gardner, 1925:539, 541, pl. 45: figs. 82–86; Dawson, 1944:232; Dawson, 1951:52; Dawson, 1959a:19; Dawson et al., 1960a:30, pl. 9: fig. 1, 2; Dawson,

1962b:199, fig. 77; Dawson, 1966a:10; Earle, 1972:85; Clayton, 1975: 187, tbl. 1, figs. 5–7, 12, 13; Abbott and Hollenberg, 1976:204, fig. 168; Wynne and Norris, 1976:2, figs. 1, 2a,b, 11a; L. Aguilar-Rosas, 1982:31; Parsons, 1982:291, figs. 2, 3, 11, 12; Schnetter and Bula Meyer, 1982:65, pl. 10: fig. N; Stewart and Stewart, 1984:141; L. Aguilar-Rosas et al., 1985:125; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:24; Sánchez-Rodríguez et al., 1989:40; Santelices, 1989:280, pl. FF: fig. 3; R. Aguilar-Rosas et al., 1990:123; Martínez-Lozano et al., 1991:23; Ramírez and Rojas V., 1991:16, figs. 2, 6; Rocha-Ramírez and Siqueiros-Beltrones, 1991:24; Stewart, 1991:44; Mateo-Cid et al., 1993:50; R. Aguilar-Rosas and M. Aguilar-Rosas, 1994:518; Mendoza-González et al., 1994:110; González-González et al., 1996:143; Pacheco-Ruíz and Zertuche-González, 1996b:171; Hoffmann and Santelices, 1997:156, fig. 39; Yoshida, 1998:305, fig. 2-21 H; Mateo-Cid et al., 2000a:68; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:179, fig. 67A,B; R. Aguilar-Rosas et al., 2005b:34; Hernández-Herrera et al., 2005:146; Mateo-Cid et al., 2006:49, 58; Servière-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:66.

Algae globose or vesicle-like, hollow, golden- to medium-brown, flaccid and slippery, up to 14 cm in diameter; 200–500 μm thick; becoming compressed, irregularly convoluted and expanded; attached by rhizoids on lower surface. Medulla and subcortex of 4–6 layers of

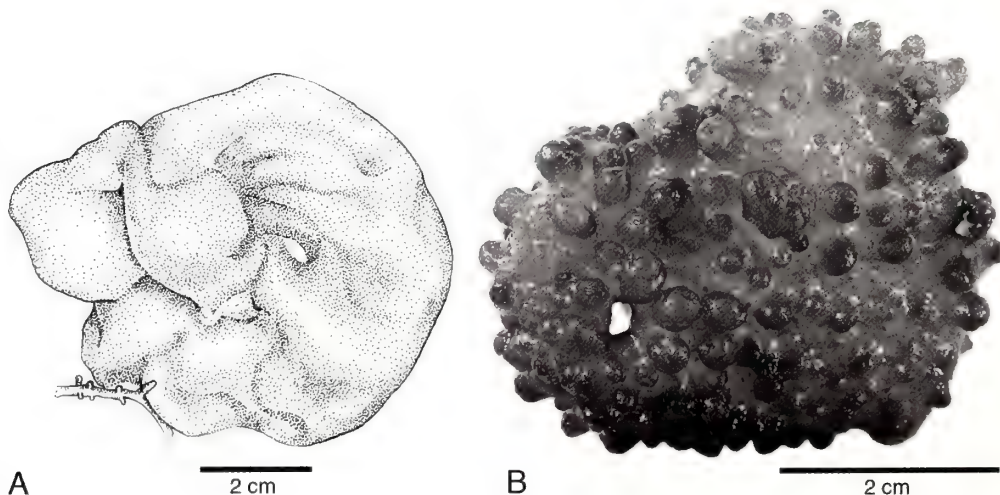


FIGURE 92. Two species of *Colpomenia*. A. *Colpomenia sinuosa*: Habit, showing smooth, slightly convoluted surface (JN-4580). B. *Colpomenia tuberculata*: Habit, photo of live specimen showing protuberances (from Puerto Peñasco, Sonora, Mexico).

large, irregularly shaped cells; gradually becoming smaller toward outer surface layer of small cuboidal cells.

Unilocular sporangia unknown. Plurilocular sporangia uniseriate (to partially biseriate), up to 40 µm long, in sori covered with a cuticle, clustered often around an invaginated tuft of hairs. Paraphyses usually longer than plurilocular sporangia, to 55 µm long.

HABITAT. On rocks and tidal platforms or epiphytic on various algae; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía Agua Verde; Bahía de La Paz to Cabo San Lucas. Pacific coast: southern California to Baja California Sur; Sinaloa to Jalisco; Isla Clarión (Islas Revillagigedo); Hawaiian Islands; Panama; Colombia; Chile.

TYPE LOCALITY. "Location uncertain" (Parsons, 1982); given as near Cádiz, Spain (Silva et al., 1996a).

REMARKS. In the northern Gulf of California, specimens of *Colpomenia sinuosa* were found only with plurilocular sporangia (Wynne and Norris, 1976). Interestingly, the life history of *C. sinuosa* in the Azores was found to be highly variable (Toste et al., 2003b) with three different kinds of life histories: (1) asexual plurisporous from gametophytes that developed directly into new gametophytes; (2) heteromorphic (involving an alternation of a macrothallus and a filamentous prostrate thalli), and either diplohaplontic or monophasic life history; and (3) isomorphic, monophasic life histories.

***Colpomenia* sp. A**

Colpomenia sinuosa? of Wynne and Norris, 1976: 5, fig. 3 ["open expanded sheet form"].

Colpomenia sinuosa f. *expansa* sensu Norris 1973:6; Pedroche et al. 2008:67 [non *Colpomenia sinuosa* f. *expansa* De A. Saunders 1898:164; which is now *Colpomenia expansa* (De A. Saunders) Y.-P. Lee 2008:116].

Algae thin, broadly expanded open sheets, up to 25 cm wide, with smooth surfaces and margins.

Reproductive structures not seen.

HABITAT. On rocks; shallow subtidal, 4–16 m depths.

DISTRIBUTION. Gulf of California: Puerto Calamajue (Bahía de Calamajue) to Bahía San Francisco; Isla San Esteban; Puerto Escondido to Isla Carmen.

REMARKS. Relatively large specimens of open expanded sheets of *Colpomenia* sp. A, were collected in the

Gulf (Norris, 1973:6; Wynne and Norris, 1976:5, as *C. cf. sinuosa*). These may possibly be undescribed or another taxon or form of *Colpomenia*. Although somewhat similar to the Gulf of California *C. sinuosa* f. *expansissima* Setchell et N. L. Gardner (1924a:726; Dawson, 1944, as "*C. sinuosa* f. *tuberculata*"), these Gulf specimens have smooth surfaces and lack the minute, spinelike projections of *C. sinuosa* f. *expansissima*. Further collections are needed for study to clarify the taxonomic status of these Gulf open-sheet specimens.

***Colpomenia tuberculata* De A. Saunders**

FIGURE 92B

Colpomenia tuberculata De A. Saunders, 1898:164, pl. 32: figs. 1–3; Wynne, 1972:137, fig. 2; Wynne and Norris, 1976:8, figs. 6, 7a,b, 11b; Abbott and Hollenberg, 1976:204, fig. 169; Littler and Littler, 1981:150, tpls. 2–4, figs. 3–7; Stewart, 1982:54; Huerta-Múzquiz and Mendoza-González, 1985:46; Norris, 1985:209, fig. 16.3 (top); Santelices, 1989:281, pl. FF: fig. 2; Sánchez-Rodríguez et al., 1989:40; R. Aguilar-Rosas et al., 1990:123; Ramírez and Rojas V., 1991:16, figs. 3, 7; Stewart, 1991:44; Rocha-Ramírez and Siqueiros-Beltrones, 1991:32; Martínez-Lozano et al., 1991:23; Mateo-Cid et al., 1993:50; González-González et al., 1996:143; Pacheco-Ruíz and Zertuche-González, 1996b:171; Hoffmann and Santelices, 1997:162, fig. 41; Riosmena-Rodríguez et al., 1998:45; Mateo-Cid et al., 2000a:68; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:180, fig. 67C,D; Mateo-Cid et al., 2006:49, 58; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:67.

Colpomenia sinuosa f. *tuberculata* (De A. Saunders) Setchell et N. L. Gardner, 1903:242; Setchell and Gardner, 1924a:725; Setchell and Gardner, 1925:541; Dawson, 1944:233; Dawson, 1959a:19; Dawson, 1966a:11; Norris, 1973:6; González-González et al., 1996:143.

Algae olive- to dark-brown globose or hemispherical, up to 15 cm in diameter, to irregularly shaped, compressed expanses, up to 24 cm wide; rigid and crisp, 0.6–1.5 mm thick; surface coriaceous, deeply convoluted and sometimes folded, covered with blunt tubercles (protuberances), 1.0–10 mm high and 1.0–10 mm wide. Cortex of 4–5 small cuboidal cells; hairs arising in tufts from deep invaginations; subcortex and medulla of 4–8 large colorless cells, becoming increasingly smaller outward.

Unilocular sporangia unknown. Plurilocular sporangia, uniseriate (occasionally with biseriate portions), with 5–7

locules, 16–23 μm long; in extensive sori over entire thallus. Paraphyses slightly shorter than plurilocular sporangia.

HABITAT. On rocks and tidal platforms; occasionally epiphytic on other algae; mid to low intertidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to San José del Cabo. Pacific coast: southern California to Baja California Sur; Sinaloa; Hawaiian Islands; Ecuador; Chile.

TYPE LOCALITY. Near San Pedro, Los Angeles County, California.

Compsonema Kuckuck

Compsonema Kuckuck, 1899:58.

Algae discoid, composed of a monostromatic basal layer of irregular contorted filaments and upper erect filaments that are simple and unbranched or branched laterally.

Plurilocular sporangia multiseriate, borne on erect filaments.

REMARKS. *Compsonema* has been placed in the Ectocarpaceae or the Myrionemataceae (now = Chordariaceae) (e.g. Abbott and Hollenberg, 1976). The generic status of *Compsonema* has been questioned. For example, Loiseaux (1970a) concluded one species of *Compsonema* was a phase in the life history of a *Scytosiphon*, and on the basis of studies of the generitype, *Compsonema gracile* Kuckuck (1899), Pedersen and Sokhi (1990) placed the genus in the Scytosiphonaceae. Further studies may reveal some species of *Compsonema* in the Gulf of California to be microthallus phases in the life history of other brown algae.

One species, *Compsonema intricatum* Setchell et N. L. Gardner (1922a), is reported in the southern Gulf (Mendoza-González et al. 1994).

Two species are currently known in the northern Gulf of California.

KEY TO THE SPECIES OF *COMPSONEMA* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Plurilocular sporangia long and narrow, 24–30 μm long and 6–8 μm in diameter *C. immixtum*
 1b. Plurilocular sporangia longer and much wider, 60–130 μm long and 18–28 μm in diameter. *C. serpens*

***Compsonema immixtum* Setchell et N. L. Gardner**

Compsonema immixtum Setchell et N. L. Gardner, 1924a:724, pl. 17: fig. 49; Setchell and Gardner, 1925:487; Dawson, 1944:222; Dawson, 1961b:390; González-González et al., 1996:143; Pacheco-Ruiz et al., 2008:204; Pedroche et al., 2008:69.

Algae minute, epiphytic; lower portion of prostrate basal filaments, creeping among the plurilocular reproductive structures of the host alga; upper portion with numerous erect, short unbranched filaments, most bearing plurilocular structures.

Unilocular sporangia not known. Plurilocular sporangia (?), narrow, ellipsoid, 24–30 μm long, and 6–8 μm in diameter; terminal on erect, short filaments (extending above the plurilocular structures of the host alga).

HABITAT. Epiphytic on *Colpomenia phaeodactyla*; intertidal.

DISTRIBUTION. Gulf of California: Isla Partida.

TYPE LOCALITY. Isla Partida, Islas de la Cintura, Gulf of California.

REMARKS. A poorly known species, Setchell and Gardner (1924a) commented that *Compsonema immixtum* was close to both *Myrionema* Greville (1827) and *Compsonema* and placed it in the latter genus on the basis of its plurilocular structures. Abbott and Hollenberg (1976:160) stated that in their opinion, several of the Setchell and Gardner (1922) species of *Compsonema*, including the Gulf of California *C. immixtum*, did not merit recognition. However, it is included herein in hopes that when it is once again collected, its taxonomic status, life history, and phylogenetic relationships will be investigated and its unique habit and association with *Colpomenia phaeodactyla* will be elucidated.

***Compsonema serpens* Setchell et N. L. Gardner**

FIGURE 93

Compsonema serpens Setchell et N. L. Gardner, 1922a:363, pl. 39: fig. 7; Setchell and Gardner, 1925:480; Smith, 1944:110, pl. 15: fig. 3; Dawson, 1960b:391; Norris and Abbott, 1972:89; Abbott and Hollenberg, 1976:160, fig. 128; Mendoza-González and Mateo-Cid, 1992:21; Servièrre-Zaragoza et al., 1993:482; González-González

et al., 1996:374; L. Aguilar-Rosas et al., 2000:133; Pedroche et al., 2008:70.

Algae minute, epiphytic, lower portion of irregularly branched prostrate filaments with a few endophytic rhizoids attached to host; above erect, unbranched (rarely subulate) filaments, up to 550 μm tall. Erect filaments narrower in diameter at base and near the apices. Cells of basal filaments 5–9 μm in diameter; wider in midportions, 10–12(–17) μm in diameter.

Unilocular sporangia not known. Plurilocular sporangia, conical, 60–130 μm long, 18–28 μm in diameter; terminal on erect pedicel of several cells above basal filaments.

HABITAT. Epiphytic and endophytic on *Padina durvillei*; intertidal.

DISTRIBUTION. Gulf of California: Playa El Coloradito to Puertecitos. Pacific coast: British Columbia; northern to central California; Jalisco.

TYPE LOCALITY. Cypress Point, Monterey County, California.

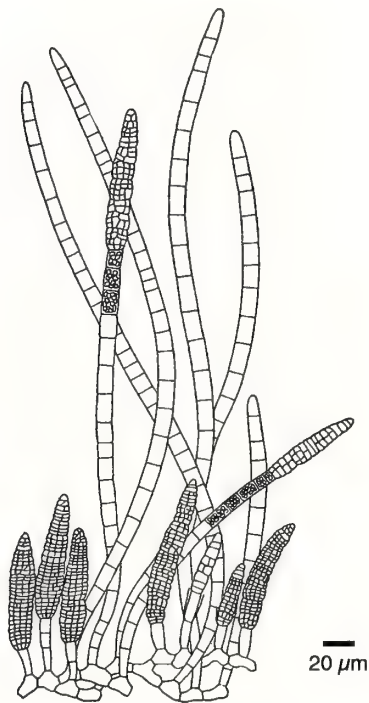


FIGURE 93. *Compsonea serpens*: Erect filaments, with terminal plurilocular reproductive structures, arising from prostrate filaments (drawn from type specimen, N. L. Gardner-4684, Setchell and Gardner, 1922a: pl. 39, fig.7).

REMARKS. *Compsonea serpens* was reported in the northern Gulf by L. Aguilar-Rosas et al. (2000); description of the species is based on Abbott and Hollenberg (1976).

Hydroclathrus Bory de Saint-Vincent

Hydroclathrus Bory de Saint-Vincent, 1825:419.

Algae are a three-dimensional net, often becoming torn, perhaps from grazing or physical stress, to form small- to large-holed, netlike sheets. Initially saccate, the thalli become irregularly shaped and convoluted with perforations of varying sizes that sometimes may join together to form larger holes. Outer cortical cells are small and pigmented, and large colorless medullary cells of up to several layers thick are above a usually hollow center. Hairs are borne in shallow depressions scattered over the thallus surface.

Life history is a heteromorphic alternation of the perforated thallus that produces plurilocular structures and a filamentous phase with both plurilocular and unilocular structures; the latter are known only in culture (Toste et al., 2003a).

One species is reported in the northern Gulf of California.

Hydroclathrus clathratus (C. Agardh) M. Howe

FIGURE 94

Encoelium clathratum C. Agardh, 1823:412.

Hydroclathrus clathratus (C. Agardh) M. Howe, 1920:590; Setchell and Gardner, 1924a:727; Setchell and Gardner, 1925:543; Dawson, 1944:324; Dawson, 1959a:19; Dawson, 1961b:395; Dawson, 1962b:197–198, figs. 74, 229; Abbott and Hollenberg, 1976:206, fig.170; L. Aguilar-Rosas, 1982:30, 31; Stewart and Stewart, 1984:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:24; Mendoza-González and Mateo-Cid, 1986:421; Sánchez-Rodríguez et al., 1989:40; R. Aguilar-Rosas et al., 1990:123; Oates and Cole, 1990a:12–16; Stewart, 1991:46; Rocha-Ramírez and Siqueiros-Beltrones, 1991:32; Martínez-Lozano et al., 1991:23; Mateo-Cid et al., 1993:50; González-González et al., 1996:297; Pacheco-Ruíz and Zertuche-González, 1996b:171; Kogame, 1997b:228, figs. 7–14; Yoshida, 1998:306; Cruz-Ayala et al., 2001:190; Kraft and Abbott, 2003:246, figs. 2–11; Abbott and Huisman, 2004:183, fig. 68C,D;

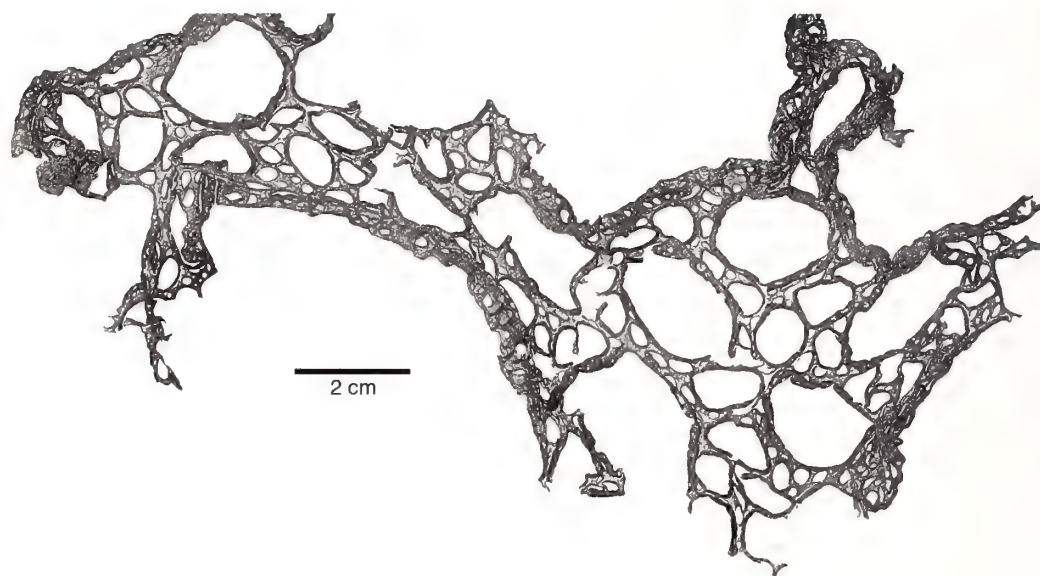


FIGURE 94. *Hydroclathrus clathratus*: Habit, of a sheetlike thallus with numerous small to large holes (US Alg. Coll.-36619).

R. Aguilar-Rosas et al., 2005b:34; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:70.

Hydroclathrus cancellatus Bory de Saint-Vincent, 1825:419; Setchell and Gardner, 1924a:727.

Algae netlike, initially more or less globose, then becoming irregularly shaped and convoluted with numerous irregularly shaped, variously sized holes; often torn into sheets; somewhat coarse and slippery; attached by groups of rhizoids along the lower surface. Surface perforations from less than 1 mm in diameter to holes over 3 cm in width; larger holes often with inrolled margins; surface distance between the perforations usually less than 2 mm. Colorless hairs in clusters of 3–15 within shallow pits, scattered over and extended above thallus surface. Thallus thickness from less than 200 μm to over 900 μm . Medulla of up to 6 layers of thin-walled, subspherical to ovoid colorless medullary cells, 60–320 μm , around hollow center. Cortex of 1–2 layers of pigmented cells, 6–7.5 μm by 7–17 μm ; surface layer in transection papillate, of domed cells, 10–15(–20) μm tall.

Plurilocular sporangia 5–7 μm by 10–12(–25) μm , in 2–3 rows of 3–4 locules; in irregularly shaped sori, usually near hair tufts. Sori scattered and grow separately, spread and coalesce, sometimes covering much of the surface.

HABITAT. On rocks or occasionally epiphytic or entangled on other algae; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Perla, northeast end of Isla Tiburón to Bahía de Los

Ángeles; Bahía Concepción to Bahía de La Paz. Pacific coast: southern California to Laguna Ojo de Liebre (Scammon's Lagoon), Baja California Sur; Ecuador; Chile; Hawaiian Islands; China; Japan; Vietnam.

TYPE LOCALITY. "Uncertain" (see Silva et al., 1996a:631). Lectotype with locality of Belle-Île, Brittany, France, was selected by Howe (1920); however, neither *Hydroclathrus clathratus* or mollusk shells found with the lectotype collection are known from this locality (Hamel, 1937; Silva et al., 1996a; Kraft and Abbott, 2003). Other syntype locales of the basionym, *Encoelium clathratum* C. Agardh (1823), were Rauki, Waigeo Island, Moluccas, Indonesia; and Shark Bay, Western Australia.

REMARKS. Generally considered a warm-water species, *Hydroclathrus clathratus* was reported in the northern Gulf by Mendoza-González and Mateo-Cid (1986) and Pacheco-Ruíz and Zertuche-González (1996b). This description of *H. clathratus* is after Kraft and Abbott (2003).

Rosenvingea Børgesen

Rosenvingea Børgesen, 1914:22.

Algae are terete to compressed, erect but mostly lax. They are branched alternately, oppositely, subdichotomously, or irregularly. Internally, they are hollow, except near the base, where they are filled with rhizoidal filaments. Growth is intercalary and apical. A few layers of pseudoparenchymatous cells face the hollow center and

outwardly join the surface layer of small pigmented cells. Phaeophyceae hairs are distributed over the thallus.

Plurilocular gametangia are borne in sori with groups of hairs. Sori are scattered over the thallus surface.

REMARKS. The erect, cylindrical species of *Rosenvingea* are problematic, with species largely separated by branching pattern. Characters of vegetative anatomy and reproductive structures need to be clari-

fied for type species, and comparative morphological and DNA analyses are needed to define species limits. Further studies of Gulf of California specimens, including fertile material and DNA analyses, are needed to assess their taxonomic status in comparison to the western Atlantic taxa.

Three species are known in the northern Gulf of California.

KEY TO THE SPECIES OF ROSENVIINGEA IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Algae clumps of low-growing mats of entangled branches; branches more or less cylindrical to compressed, 2–6 mm in diameter; attached by rhizoids from branches *R. intricata*
 1b. Algae erect; of narrow, terete axes and branches, less than 2 mm in diameter; attached by single holdfast 2
 2a. Thalli sparsely and irregularly branched; up to 1 mm in diameter; thin in transection (3–4 cell layers) *R. antillarum*
 2b. Thalli mostly oppositely or occasionally irregularly branched; mostly 1.5 to 2.5 mm in diameter; thicker in transection (4–6 cell layers) *R. floridana*

Rosenvingea antillarum

(P. Crouan et H. Crouan) M. J. Wynne

Stilophora antillarum P. Crouan et H. Crouan in Schramm et Mazé, 1865:2; Schramm and Mazé, 1866:3; Mazé and Schramm, 1878:116.

Rosenvingea antillarum (P. Crouan et H. Crouan) M. J. Wynne, 1997:334, fig. 1; L. Aguilar-Rosas et al., 2002:235; Pedroche et al., 2008 (in part; excluding records of *R. floridana*):72.

Algae erect, composed of terete, internally hollow, axes and branches, up to 25 cm long, and 0.5–1.0 mm in diameter. Branching sparse and irregular, 2–3 orders.

Plurilocular reproductive structures uni- to biserial, of 6–7 locules; 32–36 µm long and 4–6 µm in diameter; with enlarged cells (“apparently paraphyses”).

HABITAT. Intertidal.

DISTRIBUTION. Gulf of California: El Tornillal to Punta Gorda, Sonora.

TYPE LOCALITY. Le Moule, Grande-Terre, Guadeloupe, French West Indies.

REMARKS. *Rosenvingea antillarum* was reported in the upper Gulf by L. Aguilar-Rosas et al. (2000); since I have not seen their specimens, the description is based on Wynne (1997).

Rosenvingea floridana (W. R. Taylor) W. R. Taylor

FIGURE 95A,B

Cladosiphonia? floridana W. R. Taylor, 1928:113, pl. 15: figs 10–14.

Rosenvingea floridana (W. R. Taylor) W. R. Taylor, 1955:72, pl. IV; Taylor, 1960:262, pl. 29: figs. 7, 8; Abbott and Hollenberg, 1976:202, fig. 165; Mateo-Cid and Mendoza-González, 1997:59, pl. 8: figs. 34, 35, pl. 9: fig. 38.

Rosenvingea antillarum sensu Pedroche et al., 2008 (in part; only records of *R. floridana*):72 [non *Rosenvingea antillarum* (P. Crouan et H. Crouan) M. J. Wynne, 1997:334].

Rosenvingea aff. *sanctae-crucis* sensu Norris and Bucher, 1976:7, fig. 5a,b; Pacheco-Ruiz et al., 2008:204; Pedroche et al., 2008:72 [non *Rosenvingea sanctae-crucis* Børgesen, 1914:22, figs. 14–17].

Algae composed of terete, internally hollow axes and branches, up to 55 cm long and (0.5–)1.5–2.5 mm in diameter. Branching often predominately opposite, sometimes irregular, 2–3(–4) orders; branches narrowed at their base. Transection with internal hollow cavity; outer wall composed of 4–5(–6) cell layers, 90–120 µm thick.

Reproductive structures not observed in Gulf material.

HABITAT. On rocks or occasionally entangled with other algae; low intertidal to shallow subtidal, 3–9 m depths.

DISTRIBUTION. Gulf of California: El Tornillal to Punta Gorda; Puerto Refugio, Isla Ángel de la Guarda; Punta la Gringa, Bahía de Los Ángeles. Pacific coast: Santa Catalina Island (California Channel Islands); Oaxaca.

TYPE LOCALITY. East Cay, Dry Tortugas Islands (Dry Tortugas National Park), Florida.

REMARKS. The northern Gulf specimens are tentatively referred to *Rosenvingea floridana*. Wynne (1997) considered *R. floridana* to be a synonym of



FIGURE 95. *Rosenvingea floridana* (JN-5471): A. Habit. B. Portion of tubular thallus showing opposite branching (arrow heads).

R. antillarum. Although both are terete species, *R. antillarum* has narrower axes (up to 1.0 mm in diameter), is thinner (up to 60 μm thick), has 3–4 cell layers, and is sparsely and irregularly branched (Wynne, 1997:334, fig. 1). Our Gulf specimens (Norris and Bucher, 1976) have wider axes (1.5–2.5 mm in diameter), are thicker (90–120 μm), have 4–6 cell layers, and are mostly oppositely branched (a character that can be seen in Taylor, 1955:pl. IV) to occasionally irregularly branched; and thus, Gulf specimens are closer to the characteristics of *R. floridana* sensu stricto (see Taylor, 1955:72). A terete specimen of

Dawson (1944, as “*R. intricata*”) from Isla Estanque may also belong here.

***Rosenvingea intricata* (J. Agardh) Børghesen**

FIGURE 96

Asperococcus intricatus J. Agardh, 1847:7.
Rosenvingea intricata (J. Agardh) Børghesen, 1914:26; Taylor, 1928:111, pl. 15: figs. 15–17; Dawson, 1944:233 [in part]; Taylor, 1945:83 [as “*R. intricata prox.*”]; Daw-

son, 1959a:19; Taylor, 1960:262, pl. 36, fig. 2; Dawson, 1961b:395; Wynne and Norris, 1976:12; Huerta-Múzquiz and Mendoza-González, 1985:46; Rocha-Ramírez and Siqueiros-Beltrones, 1991:32; Servièrre-Zaragoza et al., 1993:482; Mateo-Cid et al., 1993:50; González-González et al., 1996:298, 380; Mateo-Cid et al., 2000a:68; Cruz-Ayala et al., 2001:190; Abbott and Huisman, 2004:185, fig. 69A–C; Servièrre-Zaragoza et al., 2007:8; Pacheco-Ruíz et al., 2008:204; Pedroche et al. 2008:72.

Algae forming low-growing clumps of more or less cylindrical to compressed, crisp, hollow branches, up to 30 cm long, and subdichotomously to irregularly branched; attached by groups of rhizoids at several places along the lower branches or sometimes unattached and free-floating. Branches (2–)4–6 mm in diameter, becoming narrower distally to ultimate branches; apices mostly rounded. Transection of 3–4 cell layers, less than 100 µm thick. Cells in surface view in more or less longitudinal series or irregularly arranged. Phaeophycean hairs in groups scattered over thallus surface.

Plurilocular structures, biseriate, in small, discrete sori scattered over thallus surface.

HABITAT. On rocks or shells, in tide pools, or free-floating; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Punta Bufeo to Isla Ángel de la Guarda; Bahía Concepción to Punta Arena. Pacific coast: Isla Clarión and Isla Socorro (Islas Revillagigedo); Guerrero to Oaxaca; China; Japan; Hawaiian Islands; Ecuador.

TYPE LOCALITY. Veracruz, Veracruz (estado), Gulf of Mexico, Mexico.

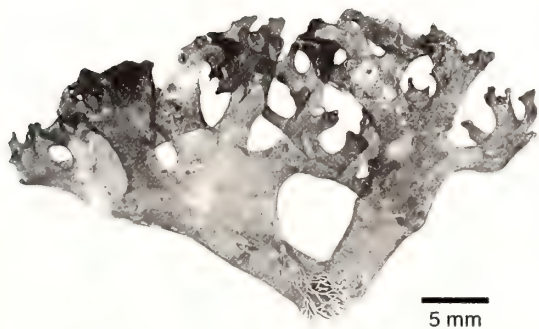


FIGURE 96. *Rosewingea intricata*: Upper portion of clump showing compressed tubular branches that narrow in diameter toward tips (US Alg. Coll.-163441).

REMARKS. In the Gulf, *Rosewingea intricata* seems to prefer calmer protected habitats, bays, and lagoons, often living in large depressions or holes in sand bottoms. Large, broad specimens, similar to those illustrated by Dawson (1944:pl. 52, fig. 1, as “*R. intricata*”) from Isla Willard, Bahía Tepoca and Isla Espiritu Santo, were recognized to be *Colpomenia ramosa* W. R. Taylor by Wynne and Norris (1976).

FUCALES

Fucales Bory de Saint-Vincent, 1827c:62.

Fucales Kylin, 1917:309.

Algae of this order are all macroscopic, often very large and rather sturdy in structure, flattened to cylindrical, and branched. Branching in flattened forms is dichotomous (e.g., *Fucus*, common in temperate regions). Others, such as *Sargassum* (abundantly represented in the Gulf and widespread in tropical to temperate areas worldwide), are variously branched but mostly radial about a central cylindrical axis. Growth in most is initiated by a single apical cell, usually sunken within an apical pit, and diffuse in a few members. Divisions from the apical cell result in a parenchymatous structure in many species; only a few have a filamentous structure. Cells have several discoid plastids and no pyrenoids.

Asexual reproduction is generally absent in the Fucales. The majority have only a parenchymatous sporophyte. Sexual reproduction is mostly oogamous, but at least one species is anisogamous. Members are monoecious or dioecious, with reproductive structures developed within conceptacles. In some monoecious species the reproductive structures of both sexes are produced within the same conceptacle. Vegetative division of the initial cell produces a layer of cells which line the conceptacle. The upper lining produces hairs which project through the opening of the cavity (ostiole), and the basal layer develops paraphyses. The oogonia are borne on the conceptacle wall, usually on a stalk cell, and the antheridia are on branched filaments. Antheridia normally produce 64–128 biflagellated, pyriform-shaped antherizoids. The number of eggs produced by the oogonia is variable. The primary nucleus in the oogonium undergoes meiotic divisions followed by a single mitotic division of each of the four nuclei produced. This results in eight haploid eggs (e.g., as in *Fucus*), but in others, four, six, or seven of them degenerate.

REMARKS. On the basis of DNA sequence data, Rousseau and de Reviers (1999b) proposed a phylogeny of the Fucales that included additional families, merged

the Cystoseiraceae with the Sargassaceae, and expanded the ordinal characters.

One family is represented in the northern Gulf of California.

SARGASSACEAE

Sargassaceae Kützing, 1843:349, 359.

Cystoseiraceae Kützing, 1843:349, 353, as "Cystosireae."

Members of this family are among the most highly morphologically differentiated algae. They have a basal attachment that is distinct from the erect axis or stemlike parts. The stipe and primary axes are cylindrical, are usually branched, and bear leaflike blades with a basal pedicel. Blades are with or without a midrib or cryptostomata (sterile pits) and have smooth, dentate, or serrate margins. Vesicles (flotation structures) are usually present and are borne laterally, terminally, or within short branchlets.

Reproductive structures, oogonia and antheridia, are contained within monoecious or dioecious receptacles in regular branches or in specialized receptacle branchlets. Each oogonium develops a single egg, and the antheridia produce numerous antherizoids.

There is one genus, *Sargassum*, well represented in northern Gulf and widely distributed throughout the Gulf of California.

Sargassum C. Agardh

Sargassum C. Agardh, 1820:1.

Algae are light to dark brown and morphologically differentiated into holdfasts, stipes, terete to compressed axes and branches, leaflike blades, buoyant vesicles, and reproductive branchlets (receptacles). Primary axes have few to numerous, radially or distichously arranged lateral branches of determinate or indeterminate growth and are usually above a stipe that is attached below to the substratum by a holdfast that is discoid, crustose, conical, or lobed or with protuberances or rhizoidal to rhizomatous. Ultimate branchlets are leaflike blades that may be simple or divided, subcylindrical, filiform, or compressed to flattened and broad, with entire, dentate, or serrate margins and with or without a midrib or cryptostomata (sterile pits). Vesicles (usually present) are subspherical to ovoid above a pedicel and with or without terminal extensions. Growth is from a three-sided cell in an apical depression. Internally, the stipe and branch axes are composed of a

central medulla of elongate cells, surrounded by a core of isodiametric cells outward to the meristoderm (surface tissue that acts as meristem with cells often dividing).

Reproductive receptacles (specialized branchlets) develop in axils of lateral branches, ultimate branchlets, and leaflike blades and are single or grouped in clusters. Receptacles are simple or branched and can be terete, angular, or compressed, with a smooth, verrucose, or spinous surface. Receptacles within the receptacles are ostiolate and contain either oogonia or antheridia or both.

REMARKS. Species of *Sargassum* are worldwide in tropical to temperate seas and are often quite large, 10–100 cm in length (some may be up to 3 m or more tall). In the Gulf of California, species of *Sargassum* comprise the bulk of the biomass of fleshy macroalgae, providing habitat for diverse communities of epiphytic algae and a canopy for understory algae, invertebrates (Brusca, 1980), and fishes (Thomson and Lehner, 1976; Thomson et al., 2000). Gulf species of *Sargassum*, such as *S. sinicola*, could be important sources for alginates, and it has been suggested they could be harvested in spring, the season of maximum biomass and high yield (Rodríguez-Montesinos et al., 2008).

In addition to those of the northern Gulf, there are six other species reported in the southern Gulf (Dawson 1959a; Huerta-Múzquiz and Mendoza-González 1985; Rocha-Ramírez and Siqueiros-Beltones 1990, 1991; Martínez-Lozano et al. 1991; Riosmena-Rodríguez et al. 2005): *Sargassum cylindrocarpum* Setchell et N. L. Gardner (1924a), *S. horridum* Setchell et N. L. Gardner (1924a); *S. howelli* Setchell (1937b); *S. liebmanni* J. Agardh (1847); *S. pacificum* Bory de Saint-Vincent (1828), and *S. palmeri* Grunow (1915).

A Japanese species, *S. muticum* (Yendo) Fensholt (1955), introduced in British Columbia in the 1940s (Scagel, 1956, 1957) now ranges on the Pacific coast from southeast Alaska to Baja California Sur (Abbott and Hollenberg, 1976; Silva, 1979; Norton, 1981; L. Aguilar-Rosas et al., 1982; Deysher and Norton, 1982; R. Aguilar-Rosas et al., 1984a, 1984b; R. Aguilar-Rosas and L. Aguilar-Rosas, 1985, 1993; Scagel et al., 1989; R. Aguilar-Rosas and Machado-Galindo, 1990; Espinoza, 1990b; Rocha-Ramírez and Siqueiros-Beltrones, 1991; Stewart, 1991; R. Aguilar-Rosas et al., 2005b). Riosmena-Rodríguez et al. (1992) have suggested the invasive *S. muticum* in Pacific Baja California could continue its expansion southward and may colonize into the Gulf of California.

Eight species, two subspecies, and one form of *Sargassum* are found in the northern Gulf of California.

KEY TO THE SPECIES OF *SARGASSUM* IN THE NORTHERN GULF OF CALIFORNIA

- 1a. Leaf-like blades without a midrib; holdfast small, discoid, conical, or irregularly discoid to spreading crust 2
 1b. Leaf-like blades either with inconspicuous or distinct midribs; holdfast not crustose. 5
 2a. Leaf-like blades subcylindrical to slightly compressed, long and very narrow, 10–22 mm long by 1.0–1.5 mm wide; vesicles with long apiculate extensions; holdfast disc-shaped to spreading crust *S. johnstonii*
 2b. Leaf-like blades wider and mostly asymmetrical 3
 3a. Upper leaf-like blades, to 8 mm long by 4–7 mm wide; some almost as wide as long; discoid holdfast *S. macdougalii*
 3b. Upper leaf-like blades larger, mostly longer than 12 mm in length 4
 4a. Axes branched; leaf-like blades 12–16 mm long; vesicles subspherical to ellipsoidal, smooth, with short apiculate extensions; holdfast presumably discoid *S. acinacifolium*
 4b. Axes unbranched; upper leaf-like blades mostly 20–25 mm long; vesicles ellipsoidal with long, usually dentate, foliaceous extensions; holdfast knotty, of short protuberances. *S. sonorensis*
 5a. Leaf-like blades variable in shape and size, with an inconspicuous midrib; 5.0–12.5 mm long; smallest blades symmetrical and dentate; midsized blades asymmetrical, as wide as long, and partly dentate; and largest blades symmetrical, elongated, and dentate; holdfast discoid *S. lapazeanum*
 5b. Leaf-like blades symmetrical, longer than wide, with a conspicuous midrib; holdfast of long branching rhizomes or woody and conical or knotty with short protuberances 6
 6a. Several thalli arising from long, branched, narrow in diameter rhizomes that are attached below at various points by hap-
 tera; leaf-like blades usually without cryptostomata (or rarely with only a few cryptostomata) 7
 6b. Thallus arising from a single woody, discoid to conical holdfast or a coarse, knotty holdfast; leaf-like blades with conspicu-
 ous to inconspicuous cryptostomata 8
 7a. Leaf-like blades mostly smaller, 15–25 mm by 2–5 mm; with a midrib (often less distinct or not evident toward apices) and
 slightly and irregularly dentate or uneven margins; without or with inconspicuous cryptostomata *S. herporhizum*
 7b. Leaf-like blades mostly larger, 30–60(–110) mm by 4–10 mm; with a distinct midrib and serrate margins of regularly, evenly
 spaced, pronounced dentation; mostly without cryptostomata (or rarely a few cryptostomata on only a few blades)
 *S. brandegeei*
 8a. Thalli usually lax; axes smooth; holdfast coarse, knotty, with short, thick protuberances *S. sinicola* subsp. *sinicola*
 8b. Thalli usually not as lax; axes muricate; holdfast conical, woody *S. sinicola* subsp. *camouii*

Sargassum* subgen. *Sargassum

REMARKS. Dawson (1944, as “*S.* subgen. *Eusargassum*”) considered all the Gulf of California species of *Sargassum* to be in *S.* subgen. *Sargassum*. However, Phillips (1995:118, tbl. 1) noted their subgeneric placement to be “unknown.” Thus, as has been previously noted, there is still much work to be done.

The four morphological groups of Dawson (1944) for the Gulf of California species of *Sargassum* are herein described and designated by the name chosen by him for the principal or most representative species of each group. Recognizing that many of the Gulf species of *Sargassum* are problematic, poorly known, or inadequately defined, it is helpful in attempting to identify specimens to first associate them with the suite of characters of these morphological groups.

***Sargassum* sect. *johnstonii* E. Y. Dawson ex J. N. Norris, sect. nov.**

“The *Johnstonii* Group” of Dawson, 1944:239, pls. 32, 33.

LATIN DESCRIPTION. Sectio cum sequentibus characteribus: laminae folio similes, maxime angustae, sub-cylindratae usque ad compressae, sine costa, et cryptostomata frequenter praesentia; vesiculae ellipticae cum longis apiculatis extensionibus.

The section is characterized by leaf-like blades that are very narrow, subcylindrical to compressed, without a midrib, and with cryptostomata usually present; vesicles are elliptical and with long apiculate extensions.

TYPE SPECIES. *Sargassum johnstonii* Setchell et N. L. Gardner, 1924a:737, pl. 20: fig. 72, pl. 21: fig. 80.

There is one species, and one form in the northern Gulf of California.

***Sargassum johnstonii* Setchell et N. L. Gardner**

FIGURES 6, 97A,B

Sargassum johnstonii Setchell et N. L. Gardner, 1924a:737, pl. 20: fig. 72, pl. 21: fig. 80; Setchell and Gardner, 1925:719; Dawson, 1944:240, pl. 23: figs. 1–15, pl. 33: figs. 1, 2, 17–22; Dawson, 1961b:400; Dawson, 1966a:12; Norris, 1973:7, pl. 13; Huerta-Múzquiz, 1978:337; Littler and Littler, 1981:151, tbl. 3, figs. 4, 5, 7; McCourt, 1984a:142; McCourt, 1984b:141; Mendoza-González and Mateo-Cid, 1985:26; Mendoza-González and Mateo-Cid, 1986:421; Rocha-Ramírez and Siqueiros-Beltrones, 1990:19; Rocha-Ramírez and Siqueiros-Beltrones, 1991:26; Espinoza-Ávalos, 1993:333; Phillips, 1995:118; González-González et al., 1996:161; Pacheco-Ruíz and Zertuche-González, 1996b:171; L. Aguilar-Rosas et al., 2002:235; Mateo-Cid et al., 2006:50, 58; Pacheco-Ruíz et al., 2008:205; Pedroche et al., 2008:95.

Sargassum guardiense Setchell et N. L. Gardner, 1924a:723, pl. 19: fig. 64; Setchell and Gardner, 1925:713; González-González et al., 1996:160.

Algae with several erect axes, up to 1(–2) m long, arising from a perennial, parenchymatous, disc-shaped to spreading crustose holdfast. Axes and branches terete and smooth. Leaf-like blades narrow, lanceolate to linear, slightly compressed to flattened, up to 10 mm long and 0.5–1.5 mm wide; margins smooth to sparsely dentate; without a midrib and with few to many cryptostomata. Vesicles on short pedicels, subspherical to elliptical, up to 4 mm long and 1 mm wide; apiculate with foliaceous crests or extensions, up to 5 mm long.

Receptacle branchlets narrow in diameter, branching up to 4 orders, dentate in varying degrees. Antheridial receptacles smaller in diameter than oogonial receptacles.

HABITAT. On rocks; high to low intertidal; occasionally shallow subtidal.

DISTRIBUTION. Gulf of California: El Tornilal to Bahía de La Paz. Pacific coast: Baja California Sur.

TYPE LOCALITY. Isla Jorge (George's Island), off Sonora, Gulf of California.

REMARKS. The distinctive crustlike, spreading holdfast of *Sargassum johnstonii* and its narrow (up to 1.5 mm wide), lanceolate to linear leaflike blades make

it one of the Gulf species easiest to recognize in the field. Although generally considered a Gulf-endemic species, *S. johnstonii* has also been reported from India (Thivy and Chauhan, 1964; Silva et al., 1996).

***Sargassum johnstonii* f. *gracile*
Setchell et N. L. Gardner**

FIGURE 98

Sargassum johnstonii f. *gracile* Setchell et N. L. Gardner, 1924a:738, pl. 21: fig. 76; Setchell and Gardner, 1925:720; Dawson, 1944:241, pl. 33: figs. 3–16; Dawson, 1961b:400; Norris, 1973:7; González-González et al., 1996:161; Mateo-Cid et al., 2006:50; Pedroche et al. 2008:96.

Sargassum johnstonii f. *laxius* Setchell et N. L. Gardner, 1924a:737, pl. 21: figs. 75, 81; Setchell and Gardner, 1925:719; Norris, 1973:7; González-González et al., 1996:161.

Although very similar to *Sargassum johnstonii* f. *johnstonii*, this form, *S. johnstonii* f. *gracile*, differs in being more slender, lax, and longer, with fewer branches; having leaf-like blades less closely spaced and longer, up to 22.5 mm long, usually filiform and not as flattened, with abundant conspicuous cryptostomata; and having vesicles with long, terete apicula.

HABITAT. Often floating, in drift, or cast ashore; probably low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas.

TYPE LOCALITY. Cast ashore, Guaymas, Sonora, Gulf of California.

REMARKS. Setchell and Gardner (1924a) noted the type specimen lacked basal parts.

***Sargassum* sect. *lapazeanum*
E. Y. Dawson ex J. N. Norris, sect. nov.**

“The *Lapazeanum* Group” of Dawson, 1944:241, pls. 34–37.

LATIN DESCRIPTION. Sectio cum sequentibus caracteribus: laminae folio similes planae, expansae et assymetricae, cum costa absenti vel aliquando presenti sed inconspicua, afixae cum hapterone rhizomatozo.

The section is characterized by leaf-like blades that are flattened, expanded, and asymmetrical, without a midrib

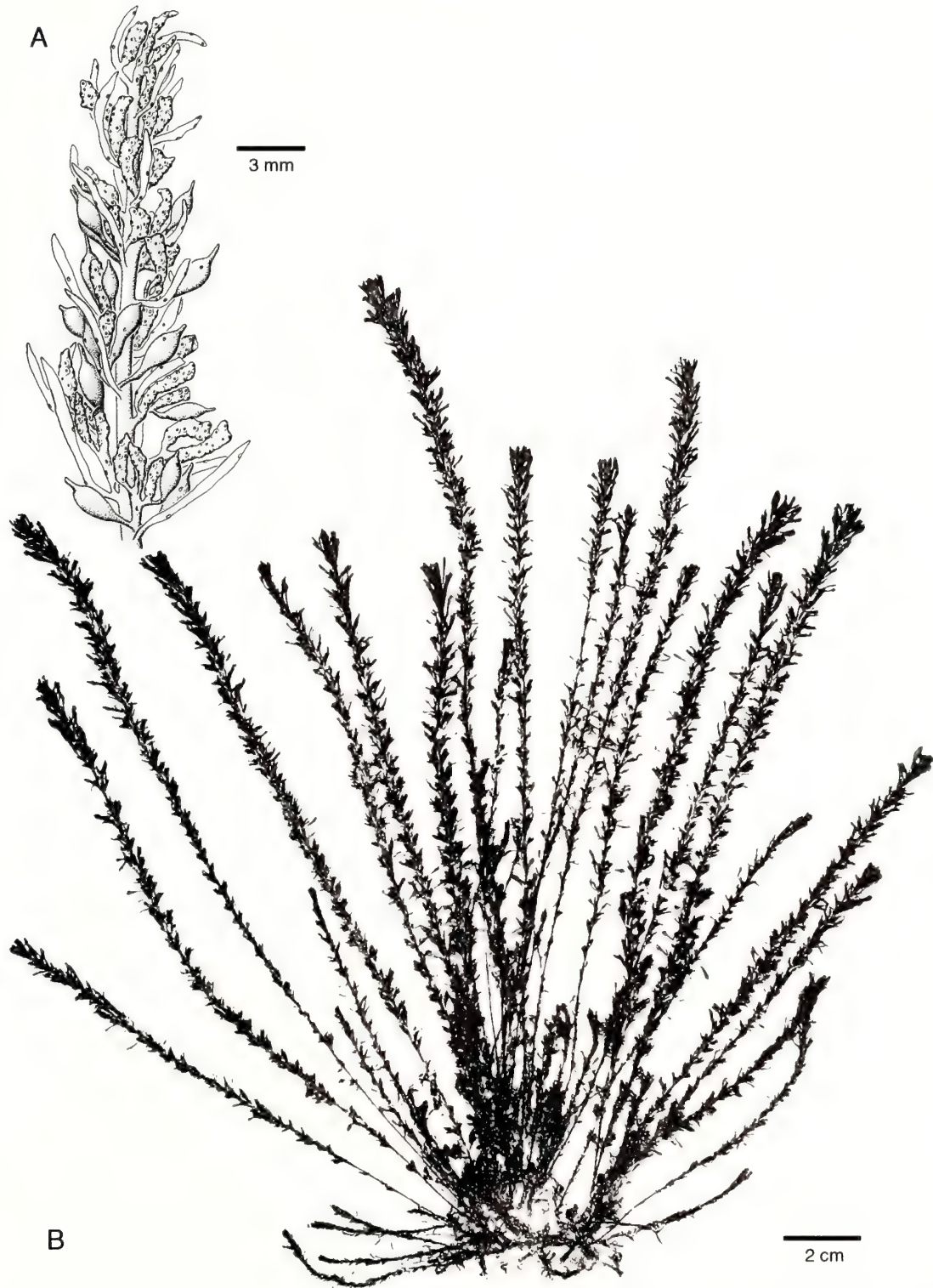


FIGURE 97. *Sargassum johnstonii*: A. Upper portion of a branch showing the narrow, elongate leaf-like blades, elliptical vesicles with apiculate extensions, and receptacle branchlets (EYD-27204). B. Habit, multiple axes arising from a crustose holdfast (JN-4559).



FIGURE 98. *Sargassum johnstonii* f. *gracile*: Habit, isotype specimen (D. R. Marchant-28a; US Alg. Coll.-56958).

or occasionally, if present, inconspicuous, and attached by rhizomatous holdfast.

TYPE SPECIES. *Sargassum lapazeanum* Setchell et N. L. Gardner, 1924a:733, pl. 20: fig. 74.

There are four species found in the northern Gulf of California.

***Sargassum lapazeanum*
Setchell et N. L. Gardner**

FIGURE 99A,B

Sargassum lapazeanum Setchell et N. L. Gardner, 1924a:734, pl. 20: fig.74; Setchell and Gardner,

1925:714; Dawson, 1944:243, pl. 34: figs. 1–34; Dawson, 1961b:400; Norris, 1973:7; Huerta Muzquiz, 1978:337; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1986:421; Rocha-Ramírez and Siqueiros-Beltrones, 1990:18; Rocha-Ramírez and Siqueiros-Beltrones, 1991:26; Martínez-Lozano et al., 1991:23; Mateo-Cid et al., 1993:50; Phillips, 1995:118; González-González et al., 1996:161; Núñez-López and Casas-Valdez, 1997:19; Paul-Chávez and Riosmena-Rodríguez, 2000:137; Cruz-Ayala et al., 2001:190; Rivera and Scrosati, 2006:178; Rivera and Scrosati, 2008:45–49; Pacheco-Ruíz et al., 2008:205; Pedroche et al., 2008:96.



FIGURE 99. *Sargassum lapazeanum*: A. Habit. B. Close-up showing smooth axes and small leaflike blades with dentate margins and prominent cryptostomata. A, B. Isotype specimen (D. R. Marchant-21; US Alg. Coll.-56961).

Sargassum bryantii Setchell et N. L. Gardner, 1924a:733, pl. 21: fig. 83.

Sargassum insulare Setchell et N. L. Gardner, 1924a:735, pl. 20: figs. 67, 68, pl. 21: fig. 78; Setchell and Gardner, 1925:717.

Erect axes, up to 1 m or more long, above a terete stipe, up to 2 cm long; with 5–7 terete, smooth primary branches from which several long, slender secondary branches arise; attached by a parenchymatous disc, formed by fusing of short haptera. Leaf-like blades, variable in shape, 5–20



FIGURE 100. *Sargassum acinacifolium*: A. Upper portion of a branch showing a leaf-like blade with coarsely dentate portion, several vesicles with apiculate extensions, and receptacle branchlets (drawn from type, Setchell and Gardner, 1924a: pl. 21, fig. 82). B, C. Isotype specimen (*T. S. Brandegee-2*; UC 221158).

mm long, with a short pedicel, without or sometimes with an inconspicuous midrib, and few to abundant conspicuous cryptostomata. Smallest blades more or less symmetrical with dentate margins; midsized blades asymmetrical, often as wide as long in midportions, with crenate to dentate lower margins and often smooth upper margins; upper blades symmetrical, larger, often widest toward apices, and with dentate margins. Vesicles among receptacles, spherical to subspherical, ellipsoidal, up to 2 mm long, usually with a short, small apical blade-like extension.

Receptacles intermixed with blades and vesicles; on short pedicel at base of a blade; spinulose, branched 2–3 times, up to 7 mm long.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Bahía San Francisquito to Cabo San Lucas.

TYPE LOCALITY. La Paz, Baja California Sur, Gulf of California.

***Sargassum acinacifolium*
Setchell et N. L. Gardner**

FIGURE 100A–C

Sargassum acinacifolium Setchell et N. L. Gardner, 1924a:732, pl. 21: fig. 82; Setchell and Gardner, 1925:713; Dawson, 1944:244, pl. 37: figs. 1–26; Dawson, 1961b:399; Dawson, 1966a:12; De Lara Isassi, 1992:22; González-González et al., 1996:159; Mateo-Cid et al., 2006:50; Pedroche et al., 2008:92.

Algae erect with terete, smooth axes and branches; leaf-like blades asymmetrical, mostly 12–16 mm long, without a midrib and originally described without cryptostomata (see Remarks below); upper side (adaxial) of blades with concave, smooth margins and lower side and apical margins coarsely dentate; holdfast unknown (“probably a parenchymatous disc;” see Dawson, 1944:244). Vesicles on a short pedicel among or at base of receptacles; subspherical to ellipsoidal, 1.5–2.5 mm in diameter, smooth, with short, simple apicula extending to about half of vesicle’s length.

Oogonial receptacles nearly cylindrical and branched 2–3 times, smooth or slightly dentate toward apices (Dawson, 1944:fig. 18). Antheridial receptacles branched 2–3 times and dentate (Dawson, 1944:figs. 17, 24).

HABITAT. On rocks and tidal platforms; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas.

TYPE LOCALITY. “Guaymas (?),” Sonora, Gulf of California (Setchell and Gardner, 1924a).

REMARKS. *Sargassum acinacifolium* is apparently a northern Gulf endemic. The basal parts of the type specimen are unknown (Setchell and Gardner, 1924a), although Dawson (1944) has suggested they are probably a parenchymatous disc. Although the leaf-like blades were described as being without cryptostomata (Setchell and Gardner, 1924a), illustrations of *S. acinacifolium* by Dawson (1944:pl. 37: figs. 2–3, 19–26; the latter figures were drawn from the type specimen) show some to have cryptostomata, thus sharing that character with *S. lapazeanum* and *S. sonorensis*. Until *S. acinacifolium* can be adequately described and molecularly and phylogenetically analyzed, it remains a poorly known species.

***Sargassum macdougallii* E. Y. Dawson**

FIGURE 101A,B

Sargassum macdougallii E. Y. Dawson, 1944:245, pl. 35: figs. 1–8, pl. 36: figs. 1–7, pl. 37: figs. 27–30; Dawson, 1959a:19; Dawson, 1961b:400; Dawson, 1966b:59; Huerta-Múzquiz and Mendoza-González, 1985:46; Espinoza-Ávalos, 1993:333; Phillips, 1995:118; González-González et al., 1996:161; Pacheco-Ruíz and Zertuche-González, 1996b:171; Pacheco-Ruíz et al., 2008:205; Pedroche et al., 2008:97.

Several erect terete, smooth axes, up to 50 cm long, arising from a slender stipe, to 1 cm long, attached below by a discoid holdfast. Leaf-like blades asymmetrical, without a midrib and lacking cryptostomata; mostly up to 8 mm long by (2.5–)4–6(–7) mm wide (sometimes almost as wide as long); upper blades usually larger, longer than wide, up to 15(–20) mm long. Blade margins sharply denticulate (usually more prominent at apices); lower portion of upper side of blade concave and smooth. Vesicles ellipsoidal, with foliar apical extensions (usually about as long as length of vesicle).

Receptacles unknown.

HABITAT. On rocks; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Libertad to Guaymas; Puerto Escondido to Bahía de La Paz.

TYPE LOCALITY. Puerto Libertad, Sonora, Gulf of California.

REMARKS. *Sargassum macdougallii* is said to differ from *S. lapazeanum* primarily by its longer vesicles with elongated foliaceous extensions and larger upper leaflike blades, up to 15(–20) mm long (Dawson, 1944).



FIGURE 101. *Sargassum macdougalii*: A. Habit (JN-5975). B. Upper portion of an axis showing characters of asymmetrical leaflike blades and some vesicles (JN-5944).



FIGURE 102. *Sargassum sonorensis*: Habit of young thallus showing asymmetrical leaflike blades and holdfast of short protuberances (arrow) (JN-5205).

Both *S. macdougalii* and *S. lapazeanum* are attached by parenchymatous discoid holdfasts. The nature of the holdfast helps separate them in the field from *S. sonorensis*, which has a knobby holdfast with short protuberances.

***Sargassum sonorensis* E. Y. Dawson**

FIGURE 102

Sargassum sonorensis E. Y. Dawson, 1960a:36; Dawson, 1961b:400; Phillips, 1995:118; González-González et

al., 1996:163; Mateo-Cid et al., 2006:50; Pedroche et al., 2008:102.

Sargassum asymmetricum E. Y. Dawson, nom. illeg., 1944:244, pl. 36: figs. 8–18; Dawson, 1966a:12; González-González et al., 1996:159 [non *Sargassum asymmetricum* Yamada, 1942:563, figs. 30, 31; Yamada, 1944:3 (which is now a synonym of *Sargassum alternato-pinnatum* Yamada, 1942; see Yoshida, 1988; Noro and Nanba, 1990; Ajisaka et al., 1994)].

Algae erect of terete, smooth primary axes, unbranched, up to 60 cm long, arising above a slender stipe, up to 1 cm long, attached below by a small, knotty holdfast of short protuberances, up to 1.5 cm wide. Leaf-like blades, mostly asymmetrical, resulting from a usually smooth, concave upper side; without a midrib; with small, inconspicuous cryptostomata; blade margins dentate. Upper blades 20–25 mm long, sometimes more or less lobed; lowermost blades usually smaller, 3–6 mm long, and variable in shape: from lanceolate with blunt apices to more or less triangular. Vesicles ellipsoid, usually with dentate foliaceous extensions, 1–3 times longer than vesicle.

Oogonial receptacles unknown. Antheridial receptacles, up to 1.0 cm long, branched 2–4 times, upper portions dentate.

HABITAT. On rocks; low intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas.

TYPE LOCALITY. On shore, southern end of Isla Tiburón (opposite Isla Turners), Las Islas de la Cintura, Gulf of California.

REMARKS. *Sargassum sonorensis* can be separated from other morphologically similar members of this section primarily by its holdfast, which is knotty, with short protuberances, in contrast to the parenchymatous discoid holdfast found in the other species of this group. In addition to its holdfast, *S. sonorensis* differs from similar *S. acinacifolium* by its larger blade sizes. These two are both problematic species, and their relationship needs further study.

Originally described as *Sargassum asymmetricum* E. Y. Dawson (July 1944), it was the second use of the name “*asymmetricum*” in *Sargassum*. The earliest use of the name was *S. asymmetricum* Yamada (1942; April 1944) from Japan. Therefore, since *S. asymmetricum* E. Y. Dawson is a later homonym, a replacement name, *S. sonorensis*, was given for the northern Gulf of California species by Dawson (1960a).

***Sargassum* sect. *sinicola* E. Y. Dawson ex J. N. Norris, sect. nov.**

“The *Sinicola* Group” of Dawson, 1944:245, pls. 38–39.

LATIN DESCRIPTION. Sectio cum sequentibus characteribus: laminae folio similes, longiores quam latae, symmetricae, cum costa, margines dentatae usque ad serratae, cryptostomata presentia, saepe abundantia; vesiculae

sub-sphaericae usque ad sphaericae; hapteron ligneum, conicum vel nodosum cum parvis protuberationibus.

The section is characterized by leaf-like blades that are longer than wide, symmetrical, with a midrib, dentate to serrate margins, and cryptostomata present, often abundant; vesicles are subspherical to spherical; holdfasts are woody, conical, or knotty, with short protuberances.

TYPE SPECIES. *Sargassum sinicola* Setchell et N. L. Gardner, 1924a:736, pl. 20: fig. 73.

REMARKS. There are two subspecies of *Sargassum sinicola* known in the northern Gulf of California. Another member of this section, *S. horridum* Setchell et N. L. Gardner (1924a), is known from the southern Gulf (Dawson, 1944, 1959.; Pedroche et al., 2008).

***Sargassum sinicola* Setchell et N. L. Gardner
subsp. *sinicola***

FIGURES 103, 104, 105A

Sargassum sinicola Setchell et N. L. Gardner, 1924a:736, pl. 20: fig. 73; Setchell and Gardner, 1925:718; Dawson, 1944:247, pl. 35: fig. 10, pl. 38: figs. 5–11, pl. 39: figs. 1–11; Dawson, 1959a:19; Dawson, 1961b:400; Dawson, 1966a:13; Norris, 1973:8; Huerta-Múzquiz, 1978:337; Stewart and Stewart, 1984:142; McCourt, 1984b:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1985:26; Mendoza-González and Mateo-Cid, 1986:421; Ortega et al., 1987:77; Espinoza-Ávalos and Rodríguez-Garza, 1985:115, fig. 1; Espinoza-Ávalos and Rodríguez-Garza, 1987:183; Sánchez-Rodríguez et al., 1989:41; Espinoza-Ávalos and Rodríguez-Garza, 1989:141; Espinoza, 1990a:1; Rocha-Ramírez and Siqueiros-Beltrones, 1990:20 [in part]; Rocha-Ramírez and Siqueiros-Beltrones, 1991:26; Martínez-Lozano et al., 1991:23; Mateo-Cid et al., 1993:51; Phillips, 1995:118; González-González et al., 1996:163; Pacheco-Ruiz and Zertuche-González, 1996b:171; Riosmena-Rodríguez et al., 1998:45; Mateo-Cid et al., 2000a:68; Cruz-Ayala et al., 2001:190; L. Aguilar-Rosas et al., 2002:235; Mateo-Cid et al., 2006:50, 58; Pacheco-Ruiz et al., 2008:205; Rodríguez-Montesinos et al., 2008:33; Pedroche et al., 2008:100.

Sargassum polyacanthum f. *americanum* Setchell et N. L. Gardner, 1924a:736; Setchell and Gardner, 1925:718; González-González et al., 1996:162.

Algae up to 60 cm long; of smooth axes and branches above a short stipe, attached below by a knotty, coarse



FIGURE 103. *Sargassum sinicola* subsp. *sinicola*: Habit; note holdfast of rhizomelike protuberances (arrow) (EYD-21568).

holdfast with short, thick protuberances. Leaf-like blades, long and narrow, very variable in size, 30–60(–90) mm long and (2–)3–5 mm wide; with a midrib, inconspicuous cryptostomata, and irregularly dentate margins. Vesicles smooth, mostly spherical, up to 6 mm

in diameter, with a pedicel, and sometimes with a small terminal apicula.

Receptacle branchlets forked up to 4 times, subcylindrical, smooth, with acuminate apices, and scattered among vesicles in upper portions of the thallus. Oogonial



FIGURE 104. *Sargassum sinicola* subsp. *sinicola*: Habit, smooth axes and long, leaflike blades with irregularly dentate margins and vesicles with a pedicel (JN-3119).

receptacles generally shorter and more robust than the antheridial receptacles.

HABITAT. On rocks and tidal platforms; usually low intertidal to shallow subtidal, occasional in mid intertidal tide pools.

DISTRIBUTION. Gulf of California: Piedras de La Salina to Cabo San Lucas. Pacific coast: Isla Guadalupe; Baja California Sur.

TYPE LOCALITY. Eureka, near La Paz, Baja California Sur, Gulf of California.

REMARKS. The most common of the species of *Sargassum* in the northern Gulf, *S. sinicola* usually reaches its largest size in spring. *Sargassum sinicola* subsp. *sinicola* is recognized by its characteristic coarse, knotty holdfast, smooth branch axes, leaf-like blades that are always longer than wide and with dentate margins, a percurrent midrib and cryptostomata, and its round, smooth vesicles. Unusual reproductive forms of *S. sinicola*, with both oogonial and antheridial conceptacles in the receptacle branchlets, were reported from Puerto Peñasco by Dawson (1944:pl. 39: figs. 6, 7).

Some specimens of *S. sinicola* can be confused with the southern Gulf *S. horridum*. Characters pointed out by Rocha-Ramírez and Siqueiros-Beltrones (1991) that distinguish *S. horridum* are spinose or terminally dentate receptacles of oogonial thalli, strongly muricate stipes and axes, leaf-like blades that are wavy or ruffled. Both *S. sinicola* subsp. *sinicola* and *S. horridum* primarily differ from *S. sinicola* subsp. *camouii* in having holdfasts of short, rhizome-like protuberances.

Another species, *Sargassum californicum* (Grunow) Setchell (1937b; basionym *S. fuliginosum* var.? *californica* Grunow, 1916), was listed as a synonym of *S. sinicola* by Dawson (1944). Since it was described from the Pacific coast (Grunow, 1916: 173, type locality: “*ad litora Californiae*”) and was subsequently reported in the Gulf of California (Setchell and Gardner, 1924a, as “*S. paniculatum*”), it has remained a poorly known and largely overlooked species (e.g., not mentioned by Abbott and Hollenberg, 1976, or Phillips, 1995). Specimens of “*S. paniculatum*” sensu Setchell and Gardner (1924a, 1925, 1930; non *S. paniculatum* J. Agardh, 1848) from the Gulf, along with those from Isla Guadalupe (Pacific Mexico), were also referred to *S. californicum* by Setchell (1937b) when he made the taxonomic combination. Shortly after this, Dawson (1944) considered *S. californicum* (Grunow) Setchell (1937b) to be a synonym of the Gulf *S. sinicola* and also included “*S. paniculatum*” sensu Setchell and Gardner (1924a, 1925, 1930). Since then, this taxonomic interpretation of *S. sinicola* has been followed (e.g., Dawson, 1961b; Stewart and Stewart, 1984; Rocha-Ramírez and Siqueiros-Beltrones, 1990; González-González et al., 1996). Although presumably somewhat similar to *S. sinicola*, the Pacific coast *S. californicum* appears to differ in having slightly muricate axes, leaf-like blades that lack a midrib, and subspherical to ovate vesicles, some slightly pointed, on relatively long pedicels (cf. Grunow, 1916; Setchell and Gardner, 1925:pl. 46: fig. 5). Thus, the morphology and relationship of the little-known California *S. californicum* to the Gulf *S. sinicola* needs to be

reinvestigated. Either these two are taxonomically the same species, as proposed by Dawson (1944), or *S. californicum* is a separate species.

***Sargassum sinicola* subsp. *camouii*
(E. Y. Dawson) J. N. Norris et Yensen, comb. nov.**

FIGURES 105B, 106

Sargassum camouii E. Y. Dawson, 1944:248, pl. 35: figs. 9, 11–13; Dawson, 1961b:399; Dawson, 1966a:13; Norris, 1973:12, 20; McCourt, 1984a:142; McCourt, 1984b:141; Huerta-Múzquiz and Mendoza-González, 1985:46; Mendoza-González and Mateo-Cid, 1986:421; Sánchez-Rodríguez et al., 1989:41; De Lara Isassi, 1992:22; Mateo-Cid et al., 1993:51; González-González et al., 1996:159; Mateo-Cid et al., 2006:50, 58.

Sargassum sinicola var. *camouii* (E.Y. Dawson) J. N. Norris et Yensen in Pedroche et al., 2008:101.

Algae erect and rigid, up to 60 cm tall, axes rough, usually muricate, and densely branched; attached by solid, woodlike holdfast, initially discoid, becoming conical. Leaf-like blades lanceolate, mostly 30–60 mm long and 3–6 mm wide; with a midrib, dentate margins, and numerous cryptostomata (not always as evident on dried specimens). Vesicles spherical, smooth, 3–4.5 mm in diameter.

Oogonial receptacles, more or less cylindrical, branched 1–3 orders, and somewhat spiny.

HABITAT. On rocks and tidal platforms and in tide pools; mid intertidal to shallow subtidal.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Isla San Esteban; Bahía Concepción to Bahía de La Paz. Pacific coast: Bahía Sebastián Vizcaíno to Bahía Magdalena, Baja California Sur.

TYPE LOCALITY. South end of Isla Tiburón, Las Islas de la Cintura, Gulf of California.

REMARKS. The new combination *Sargassum sinicola* subsp. *camouii* is proposed to reflect its possible relationship to *S. sinicola*. Although similar in most characteristics with *S. sinicola* subsp. *sinicola*, *S. sinicola* subsp. *camouii* is generally darker in color and is distinguished by its woody conical holdfast (see Dawson, 1944:pl. 35: fig. 9), rough to muricate primary axis, mostly muricate upper axes, and a more rigid habit. Critical studies, including DNA analyses, are needed to test its taxonomic and phylogenetic status.

Unfortunately, the type specimen lacked a holdfast (Dawson, 1944); it was the only specimen saved when all others were lost on a boat trip returning from Isla

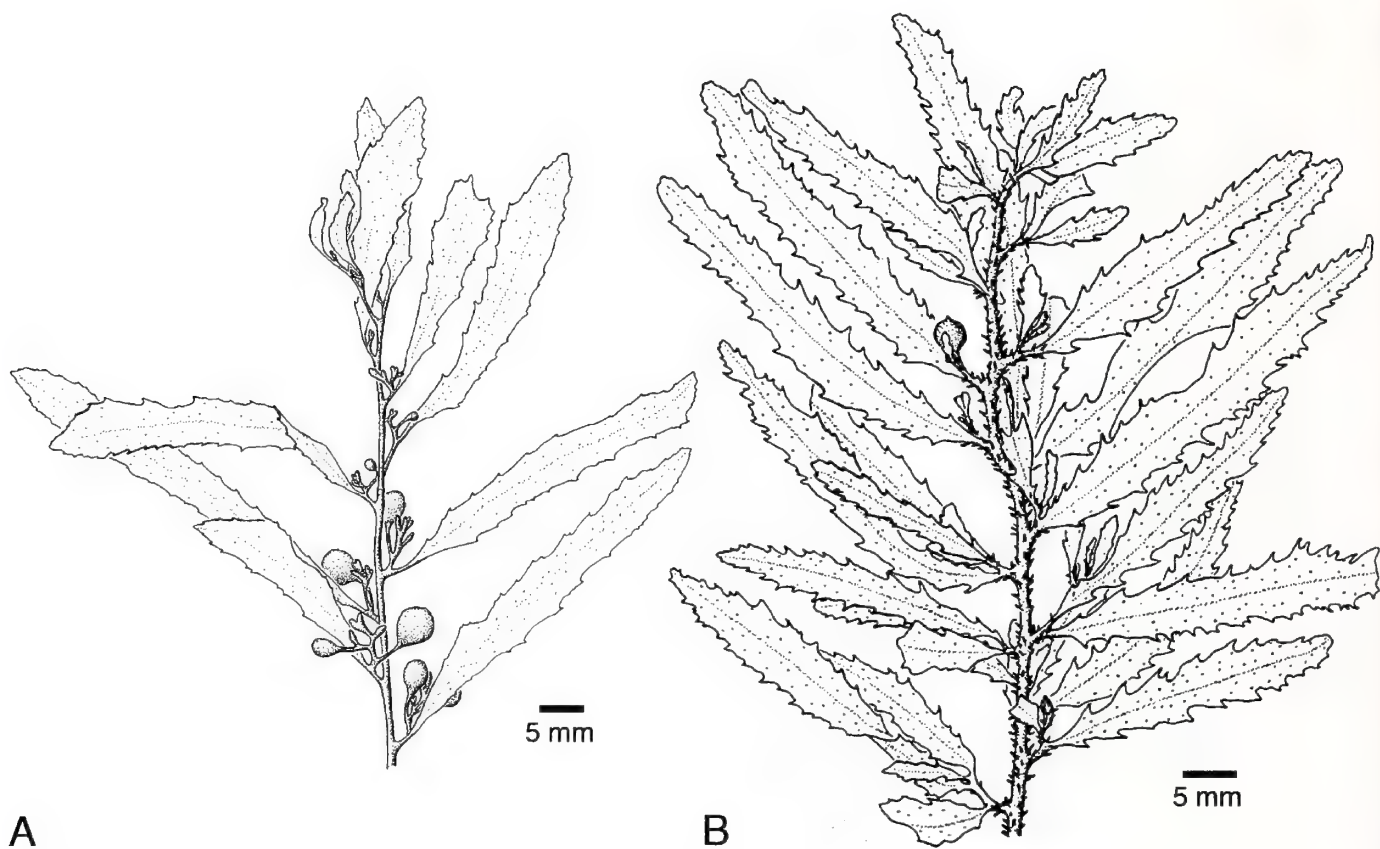


FIGURE 105. Comparison of *Sargassum sinicola*: A. *Sargassum sinicola* subsp. *sinicola*, showing smooth axes, irregular dentate margin of leaflike blades, vesicles, and developing receptacles (JN-3119). B. *Sargassum sinicola* subsp. *camouii*, showing muricate axes, regular dentate margins of leaflike blades, and vesicles (JN-3250).

Tiburón, and the description of the holdfast was based on field notes and another (paratype) specimen from another locality, "a bay, 10 miles northwest of Guaymas" (probably Bahía San Carlos).

Sargassum* sect. *herporhizum
E. Y. Dawson ex J. N. Norris, sect. nov.

"The *Herporhizum* Group" of Dawson, 1944:249, pl. 40: figs. 1–26.

LATIN DESCRIPTION. Sectio cum sequentibus characteribus: laminae folio similes cum costa, cum cryptostomatibus absentibus vel, si praesentibus, inconspicuis; vesiculae cum apiculata extensione; hapteron cum lungis, expansis, saepe intricatis rhizomatibus.

The section is characterized by leaf-like blades that have a midrib and are without cryptostomata or, if present, with inconspicuous cryptostomata; vesicles with an

apiculate extension; holdfast of long, spreading, often entangled rhizomes.

TYPE SPECIES. *Sargassum herporhizum* Setchell et N. L. Gardner, 1924a:739, pl. 20: figs. 69–71.

REMARKS. Currently there are two species from the northern Gulf of California and another, *Sargassum liebmannii* J. Agardh (1847, 1889), from Pacific Mexico (Baja California to Oaxaca; González-González et al., 1996) that belong to this section.

Sargassum herporhizum
Setchell et N. L. Gardner

FIGURES 107, 108A,B

Sargassum herporhizum Setchell et N. L. Gardner, 1924a:739, pl. 20: figs. 69–71; Setchell and Gardner, 1925:720; Dawson, 1944:249, pl. 40: figs. 1–12; Dawson, 1961b:400; Dawson, 1966a:13; Norris, 1973:7; Huerta-Múzquiz, 1978:337; McCourt, 1984b:141;



FIGURE 106. *Sargassum sinicola* subsp. *camouii*: Habit; note insert (lower right) showing conical holdfast attached to rock (JN-6064).

Rocha-Ramírez and Siqueiros-Beltrones, 1990:19; De Lara Isassi, 1992:22; Espinoza-Ávalos, 1993:333; Phillips, 1995:118; González-González et al., 1996:160; Pacheco-Ruíz and Zertuche-González, 1996b:171; Cruz-Ayala et al., 2001:190; Mateo-Cid et al., 2006:50,

58; Pacheco-Ruíz et al., 2008:205; Pedroche et al., 2008:93.

Algae up to 30 cm long, with several erect terete, smooth axes, alternately to irregularly branched, often



FIGURE 107. *Sargassum herporhizum*: Habit, showing basal attachment of entangled rhizomes (JN-4963).

whorled, above entangled rhizomes. Primary axis initially arising from a small discoid base that develops numerous, branching, narrow in diameter (less than 3 mm), repent cylindrical rhizomes that are attached at various points by small haptera; several erect secondary

axes arise along horizontal rhizomes as they lengthen. Leaf-like blades, long and narrow, 15–25 mm long and 2–5 mm wide, with a midrib (sometimes less distinct or faint on uppermost blades); cryptostomata absent or few and inconspicuous; margins vary, uneven or slightly to

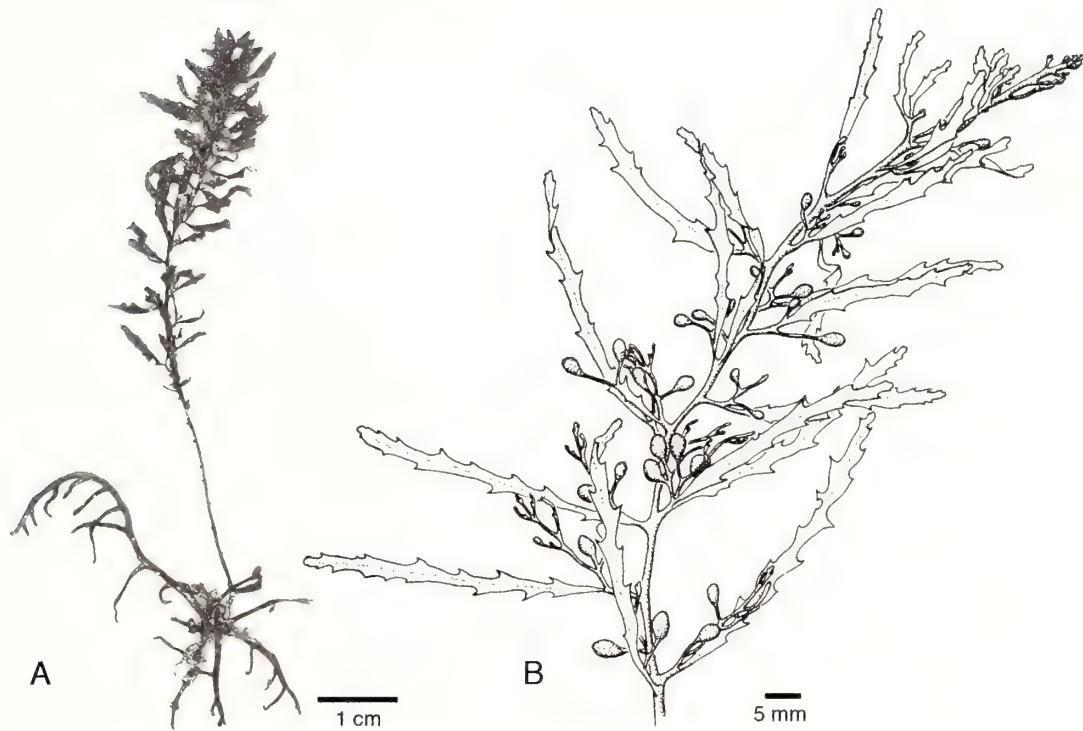


FIGURE 108. *Sargassum herporhizum*: A. Young thallus arising from basal rhizomes (JN-5870b). B. Upper portion of thallus showing long, thin leaflike blades, with faint midrib and serrate margins, pedicellate vesicles, and receptacles (JN-3117).

irregularly dentate. Vesicles spherical to ovoid, mostly smooth, up to 3 mm in diameter; on pedicels; occasionally apiculate.

Dioecious; receptacle branchlets scattered among vesicles, narrow, subcylindrical, up to 10 mm long, branched, on short pedicel, with conspicuous conceptacles.

HABITAT. On rocks and tidal platforms and in tide pools; mid intertidal to shallow subtidal, down to 6 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Bahía de La Paz. Pacific coast: Jalisco; Galápagos Islands.

TYPE LOCALITY. Isla San Jorge (George's Island), off Sonora, Gulf of California.

REMARKS. Seasonal observations of *Sargassum herporhizum* at Playa Estación, Puerto Peñasco, showed it to be one of the three dominant species of *Sargassum*, along with *S. johnstonii* and *S. sinicola* subsp. *camouii* (see also McCourt, 1984a, 1984b). Some intertidal specimens can be difficult to separate from *S. brandegeei*, but *S. herporhizum* has smaller, narrower leaf-like blades with less distinct midribs and margins that are only slightly

and irregularly dentate or sometimes uneven (see also "Remarks" for *S. brandegeei*).

***Sargassum brandegeei* Setchell et N. L. Gardner**

FIGURE 109A–C

Sargassum brandegeei Setchell et N. L. Gardner, 1924a:736, pl. 21: fig. 79; Setchell and Gardner, 1925:718; Dawson, 1944:249, pl. 40: figs. 13–26; Taylor, 1945:120 [with a query]; Dawson, 1959a:19; Dawson, 1961b:399; Dawson, 1966a:12; Norris, 1973:7; Huerta-Múzquiz, 1978:337, 338; Pedroche and González-González, 1981:67; Rocha-Ramírez and Siqueiros-Beltrones, 1990:18–19 [in part, only *S. brandegeei*]; Servièrre-Zaragoza et al., 1993:482; Phillips, 1995:118; González-González et al., 1996:159; Pacheco-Ruíz et al., 2008:204; Pedroche et al., 2008:93.

Algae up to 30 cm long, of 1 to several erect, terete, smooth axes, branching alternately to irregularly. Primary axis initially from a discoid base that develops numerous,



FIGURE 109. *Sargassum brandegeei*: A. Habit, showing developing basal rhizomes (JN-6034). B, C. Smooth axes, with long and comparatively wider leaflike blades, with midribs and moderate to deeply serrate margins (JN-4829).

irregularly branched, narrow in diameter, decumbent rhizomes that become entangled and attach by haptera at various points. Leaf-like blades, longer than wide, mostly 30–60(–110) mm long and 4–10 mm wide; with a midrib and without cryptostomata (note some observed with very few cryptostomata); margins regularly, moderately to deeply, serrate. Vesicles spherical to subspherical, (2–)3–5 mm in diameter, smooth, and usually apiculate or sometimes with a foliaceous extension; borne on pedicels (more or less equal to or longer than their diameter) at base of leaflike blades or scattered among receptacles.

Receptacle branchlets relatively short, up to 20 mm long, branched mostly to 2 orders, smooth, and with blunt, rounded apices.

HABITAT. On rocks and tidal platforms and in tide pools; low intertidal to shallow subtidal to 8 m depths.

DISTRIBUTION. Gulf of California: Puerto Peñasco to Guaymas. Pacific coast: Jalisco; Galápagos Islands (?).

TYPE LOCALITY. Cast ashore, probably Guaymas, Sonora, Gulf of California (Setchell and Gardner 1924a).

REMARKS. Northern Gulf specimens generally agree with *Sargassum brandegeei* as described, including that most have leaf-like blades that lack cryptostomata (Setchell and Gardner, 1924a; Dawson, 1944), but a few specimens were observed to also have a small number of scattered cryptostomata on some of their leaf-like blades.

Dawson (1966a) observed that some of the intertidal *S. brandegeei* were not always clearly distinct from *S. herporhizum*. However, the size of the leaf-like blades and the nature of their margins distinguish these two in the field. *Sargassum brandegeei* has larger, longer, and comparatively wider blades, with a distinct midrib, and margins of regularly, evenly spaced, pronounced serration; in contrast, *S. herporhizum* has smaller, narrower blades, with less distinct midribs (sometimes very faint or not apparent on blades of the upper thallus and not always evident on the upper portion of some individual blades; see Figure 108B), and margins that are uneven or slightly, irregularly dentate.

Uncertain Record:

***Sargassum agardhianum* Farlow ex J. Agardh**

Sargassum agardhianum Farlow ex J. Agardh, 1889:93; 38, pl. 16:fig. 1; Mendoza-González and Mateo-Cid,

1986:421; Martínez-Lozano et al., 1991:23; González-González et al., 1996:159; Pedroche et al., 2008(in part; Gulf of California records only):93.

REMARKS. Described from San Diego, California, *Sargassum agardhianum* (J. Agardh, 1889) is known on the Pacific coast from southern California to central Baja California (Dawson et al., 1960a; Abbott and Holtenberg, 1976; Pacheco-Ruíz, 1982; Stewart and Stewart, 1984; R. Aguilar-Rosas et al., 1990; Stewart, 1991; Phillips, 1995). The reported presence of this species in the northern Gulf of California needs to be verified by reexamining specimens identified as *S. agardhianum* (Mendoza-González and Mateo-Cid, 1986; Martínez-Lozano et al., 1991).

EXCLUDED RECORDS OF PHAEOPHYCEAE

LAMINARIALES

Laminariales Migula, 1908:173, 243.

Laminariales Kylin, 1917:308.

REMARKS. In 25 years of collecting in the Gulf of California, Dawson himself did not collect any members of the Laminariales. Since then, neither I nor others have encountered or reported any Laminariales in field collecting and diving surveys in the northern Gulf.

ALARIACEAE

Alariaceae Setchell et N. L. Gardner, 1925:591.

Egregia Areschoug

Egregia Areschoug, 1876:66.

***Egregia laevigata* Setchell**

Egregia laevigata Setchell, 1896:44; Dawson, 1946a:83; Dawson, 1946b:182; Dawson, 1947:43; Dawson, 1949:241; González-González et al., 1996:149; Pedroche et al., 2008:79.

REMARKS. Two beach drift specimens of *Egregia laevigata* reputed to be from Bahía de Los Ángeles were recorded in the northern Gulf (Dawson, 1946a). Later, Dawson (1949b) noted *E. laevigata* had been erroneously reported in the Gulf of California.

LESSONIACEAE

Lessoniaceae Setchell et N. L. Gardner, 1925: 621.

***Macrocystis* C. Agardh**

Macrocystis C. Agardh, 1820:46.

***Macrocystis pyrifera* (Linnaeus) C. Agardh**

Fucus pyriferus Linnaeus, 1771:311.

Macrocystis pyrifera (Linnaeus) C. Agardh, 1820:47;
Setchell and Gardner, 1924a:728; Dawson, 1944:237;

González-González et al., 1996:154; Pedroche et al., 2008 (in part; only Gulf of California record):85.

REMARKS. A single specimen, about 3 ft. long, apparently adrift, was caught on [the] log-line of [the] vessel between Isla Espiritu Santo and La Paz and "brought aboard the vessel, but no specimens were found growing attached within the Gulf" (Setchell and Gardner, 1924a:728; Dawson, 1944). Since then, there has never been any published reports of attached *Macrocystis*, nor any further reports of drift specimens in the Gulf of California.

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Appendix 1:

List of New Taxa and Combinations

I. CHLOROPHYTA

Ctenocladales: Ulvellaceae

Epicladia condensata (Setchell et N. L. Gardner) J. N. Norris, *comb. nov.*

Epicladia mexicana (Setchell et N. L. Gardner) J. N. Norris, *comb. nov.*

II. PHAEOPHYCEAE

Desmarestiales: Desmarestiaceae

Desmarestia munda Setchell et N. L. Gardner subsp. *mexicana* (E. Y. Dawson)
J. N. Norris, *comb. nov.*

Sporochnales: Sporochnaceae

Sporochmus neushulii J. N. Norris, *sp. nov.*

Ectocarpales: Acinetosporaceae

Hincksia bryantii (Setchell et N. L. Gardner) J. N. Norris, *comb. nov.*

Fucales: Sargassaceae

Sargassum sect. *johnstonii* E. Y. Dawson ex J. N. Norris, *sect. nov.*

Sargassum sect. *lapazeanum* E. Y. Dawson ex J. N. Norris, *sect. nov.*

Sargassum sect. *sinicola* E. Y. Dawson ex J. N. Norris, *sect. nov.*

Sargassum sect. *herporhizum* E. Y. Dawson ex J. N. Norris, *sect. nov.*

Sargassum sinicola Setchell et N. L. Gardner subsp. *camouii* (E. Y. Dawson)
J. N. Norris et Yensen, *comb. nov.*

Appendix 2: Endemic Taxa of the Gulf of California that Occur in the Northern Gulf

I. CHLOROPHYTA

Ctenocladales: Ulvellaceae

Entocladia marchantiae

Epicladia condensata

Epicladia mexicana

Cladophorales: Cladophoraceae

Cladophora macdougalii

Cladophora tiburonensis

Siphonocladales: Valoniaceae

Valoniopsis hancockii

Bryopsidales: Codiaceae

Codium brandegeei

II. PHAEOPHYCEAE

Ishigeales: Ishigeaceae

Ishige sinicola

Dictyotales: Dictyotaceae

Spatoglossum lanceolatum

Spatoglossum subflabellatum

Desmarestiales: Desmarestiaceae

Desmarestia filamentosa

Desmarestia munda subsp. *mexicana*

Sporochnales: Sporochnaceae

Sporochnus neushulii

Ralfsiales: Ralfsiaceae

Hapterophycus anastomosans

Cutleriales: Cutleriaceae

Cutleria hancockii

Ectocarpales: Acinetosporaceae

Hincksia bryantii

Ectocarpales: Chordariaceae

Nemacystus brandegeei

Ectocarpales: Ectocarpaceae

Ectocarpus hancockii

Ectocarpus sonorensis

Ectocarpales: Scytosiphonaceae

Compsonema immixtum

Fucales: Sargassaceae

Sargassum johnstonii f. *gracile*

Sargassum lapazeanum

Sargassum acinacifolium

Sargassum macdougalii

Sargassum sonorensis

Sargassum brandegeei

Appendix 3: Algal Specimens Illustrated: Species Locality Information and Herbarium

I. CHLOROPHYTA

Entocladia marchantiae (Figure 9A): Epiphytic on *Gracilaria textorii*, north end of Isla Coronado, Bahía de los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (JN-4411b; US Alg. Coll. slide 4257).

Entocladia polysiphoniae (Figure 9B): Endophytic on *Polysiphonia*, El Desemboque, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (JN-5190; US Alg. Coll.-157757 and slide 5344).

Entocladia sp. (Figure 9C): Epiphytic on *Cladophora*, Islas de los Gemelos, Bahía de los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (JN-4492b; US Alg. Coll. slide 4154).

Entocladia viridis (Figure 9D,E): Epiphytic on *Chaetomorpha aerea*, El Desemboque, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (JN-5180b; US Alg. Coll. slide 4144).

Stromatella monostromatica (Figure 11A,B): Epiphytic on *Polysiphonia*, Isla la Ventana, Bahía de los Ángeles, Baja California, Coll. J. N. Norris, M. Helvey, and H. Sleeper (JN-4442b; US Alg. Coll. slide 4160).

Ulvella lens (Figure 12A): Epiphytic on *Cladophora graminea*, channel between Isla Mejia and Isla Ángel de la Guarda, Puerto Refugio, Isla Ángel de la Guarda, Coll. E. Y. Dawson (EYD[1940]-271; US Alg. Coll. slide 4165).

Ulvella setchellii (Figure 12B): Epiphytic on *Cladophora* cf. *microcladioides*, Bahía Aqua Dulce, Isla Tiburón, Coll. E. Y. Dawson (EYD-46-980; US Alg. Coll. slide 892).

Ulva californica (Figure 14A): Vicinity of Punta Peñasco, Sonora, Coll. E. Y. Dawson (EYD-27407; US Alg. Coll.-55027).

Ulva californica (Figure 14B): Isla Willard, N end of island, Bahía de San Luis Gonzaga, Baja California, Coll. J. N. Norris and K. E. Bucher (JN-5425; US Alg. Coll.-157778).

- Ulva lactuca* (Figure 15): La Paz, Baja California Sur, Coll. O. Holguín Q. (*ChP-1606*; US Alg. Coll.-36624).
- Ulva lobata* (Figure 16): Punta la Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris (*JN-6103a*; US Alg. Coll.-157781).
- Ulva nematoidea* (Figure 17A): Ensenada, Bahía de Todos Santos, Baja California (Pacific Mexico), Coll. E. Y. Dawson (*EYD-10421*; US Alg. Coll.-41727).
- Ulva nematoidea* (Figure 17B): San Isidro, Baja California (Pacific México), Coll. Clair Etienne (US Alg. Coll.-8799).
- Ulva rigida* (Figure 18): Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (*JN-5742*; US Alg. Coll.-157779).
- Ulva acanthophora* (Figure 19A): Punta la Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5455*; US Alg. Coll.-157716).
- Ulva acanthophora* (Figure 19B): Estuary, Bahía de los Animas, Baja California, Coll. G. Bockus (*JN-383*; US Alg. Coll.-89466).
- Ulva clathrata* (Figure 20): Bahía Cholla, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4994*; US Alg. Coll.-157727).
- Ulva flexuosa* (Figure 21A,B): Epizoic on carapace of female black sea turtle (*Chelonia mydas agassizii*), vicinity of Campo Ona, Canal de Infiernillo, Sonora, Coll. R. S. Felger, E. Moser, and G. Mendez (*JN-4790*; US Alg. Coll.-157732 and slide 4172).
- Ulva intestinalis* (Figure 22): El Tornillal, Sonora, Coll. D. G. Lindquist (*JN-3327*; US Alg. Coll.-157741).
- Ulva linza* (Figure 23): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris (*JN-3694*; US Alg. Coll.-157743).
- Chaetomorpha antennina* (Figure 24A): Near Bahía San Carlos, Ensenada de San Francisco, Sonora, Coll. E. Y. Dawson (*EYD-11023*; US Alg. Coll.-39950).
- Chaetomorpha aerea* (Figure 24B): El Desemboque, Sonora, Coll. R. E. Schultes, R. S. Felger, and A. T. Weil (*JN-5180a*; US Alg. Coll. slide 4144).
- Cladophora graminea* (Figure 28A): West side of large rock, Rocas Consag, Coll. D. G. Lindquist (*JN-3118*; US Alg. Coll.-157544).
- Cladophora hesperia* (Figure 29A): Puerto Lobos on Bahía Tepoca, Sonora, Coll. E. Y. Dawson (*EYD-832*; US Alg. Coll.-30072 and slide 4170).
- Cladophora microcladioides* (Figure 30B): Bahía Kino, Sonora, Coll. E. Y. Dawson (*EYD-2928*; US Alg. Coll.-30073 and slide 4166).
- Phyllocladion pulcherrimum* (Figure 33): East side of Punta Concepción, Baja California Sur, Coll. J. Bleck (*EYD-25872*; US Alg. Coll.-36522).
- Phyllocladion robustum* (Figure 34A): Isla San Pedro Nolasco, Coll. E. Y. Dawson (*EYD-18555*; US Alg. Coll.-5603).
- Valoniopsis pachynema* (Figure 36C): Photo of living clump from Puerto Peñasco, Sonora.
- Bryopsis pennata* (Figure 37): South of rocky shore fronting Laboratorio de Biología Marina, vicinity of Punta Peñasco, Sonora, Coll. A. E. Dennis (*EYD-27451*; US Alg. Coll.-40783).
- Halicystis*-phase (Figure 39A,B): Isla Willard, Bahía de San Luis Gonzaga, Baja California, Coll. J. N. Norris and K. E. Bucher (*JN-5732*; US Alg. Coll.-157764).
- Codium amplivesiculatum* (Figure 40): Isla San Esteban, Coll. J. N. Norris, with J. Paul and K. Robertson (*JN-5700*; US Alg. Coll.-157600).
- Codium brandegeei* (Figure 42): “*Codium macdougalii*-form” of *C. brandegeei*, Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and R. W. Hoshaw (*JN-5020*; US Alg. Coll.-157629).
- Codium simulans* (Figure 43): SE side of Isla San Esteban, Coll. J. N. Norris, with J. Paul and K. Robertson (*JN-5713*; US Alg. Coll.-157676).
- Codium* sp.? (Figure 44): cf. *Codium cuneatum*-form of *C. simulans*, off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris, with J. Paul and K. Robertson (*JN-5286*; US Alg. Coll.-157616).
- Caulerpa mexicana* f. *pectinata* (Figure 45): Playa Estación, Puerto Peñasco, Sonora, Coll. N.J. Lang (*JN-5861*; US Alg. Coll.-157510).
- Caulerpa sertularioides* (Figure 46A): N side of bay, Bahía Bocochoibampo, Guaymas, Sonora, Coll. M. Helvey (*JN-4471*; US Alg. Coll.-157509).
- Caulerpa sertularioides* (Figure 46B): Bahía de San Carlos, Nueva Guaymas, Sonora, coll. D. Evanson (*JN-4277*; US Alg. Coll.-157507).
- Caulerpa vanbosseae* (Figure 47A): El Desemboque de San Ignacio, Sonora, Coll. J. N. Norris, K. E. Bucher and D. Coon (*JN-6562*; US Alg. Coll.-157529).
- Caulerpa vanbosseae* (Figure 47B): Punta Pelicano, vicinity of Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (*JN-4981*; US Alg. Coll.-157521).

Halimeda discoidea (Figure 48B,C): 3 miles [4.8 km] south of Punta Mangles, Baja California Sur, Coll. J. Bleck (EYD-25921; US Alg. Coll.-36518 and slide 8477 and slide 8478).

Acetabularia caliculus (Figure 49A): Bahía Cholla, vicinity of Punta Peñasco, Sonora, Coll. A. E. Dennis (EYD-27569; US Alg. Coll.-40937 and vial 3442, jar 406).

Acetabularia caliculus (Figure 49B): Bahía Cholla, vicinity of Puerto Peñasco, Sonora, Coll. R. W. Hoshaw (US Alg. Coll.-95320 and slide 5533).

II. PHAEOPHYCEAE

Ishige sinicola (Figure 50A): Specimens, from left to right: La Mona, Bahía de los Ángeles, Baja California, Coll. J. N. Norris (JN-2980; US Alg. Coll.-158148); Puerto Calamajué, Baja California, Coll. J. N. Norris and K. E. Bucher (JN-4621; US Alg. Coll.-158165); and Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4166; US Alg. Coll.-158160).

Ishige sinicola (Figure 50B): Northwest of rock window on shore, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris and K. E. Bucher (JN-5824; US Alg. Coll.-158176 and slide 8481).

Sphacelaria rigidula (Figure 51A): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4041; US Alg. Coll.-158531 and slide 4201).

Sphacelaria rigidula (Figure 51B): Bahía San Francisco, Baja California, Coll. J. N. Norris (JN-3271; US Alg. Coll.-158528 and slide 4194).

Sphacelaria rigidula (Figure 51C): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris (JN-3715; US Alg. Coll.-158514 and slide 4196).

Sphacelaria tribuloides (Figure 53A-C): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4038; US Alg. Coll.-158525 and slide 4198 and slide 4199).

Dictyopteris undulata (Figure 55): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (JN-5801; US Alg. Coll.-157994).

Dictyota concrescens (Figure 56A): Punta Hughes, vicinity of Bahía Magdalena, about 3½ miles [5.6 km] southeast of Cabo San Lazaro, Baja California Sur (Pacific Mexico), Isotype (W. R. Taylor 34-598; US Alg. Coll.-56360).

Dictyota concrescens (Figure 56B): North side of Puerto Calamajué, Baja California, Coll. J. N. Norris and K. E. Bucher (JN-4695; US Alg. Coll.-158074).

Dictyota coriacea (Figure 57): Off southeast end of Isla San Esteban, Coll. K. E. Bucher (JN-5522; US Alg. Coll.-158202).

Dictyota crenulata (Figure 58A): Playa between San Jose del Cabo and Cabo San Lucas, Baja California Sur, Coll. J. N. Norris and H. Sleeper (JN-4091a; US Alg. Coll.-158007).

Dictyota crenulata (Figure 58B): Playa between San Jose del Cabo and Cabo San Lucas, Baja California Sur, Coll. J. N. Norris and K. E. Bucher, and H. Sleeper (JN-4114; US Alg. Coll.-158009).

Dictyota dichotoma var. *intricata* (Figure 59A): Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and H. Sleeper (JN-4087; US Alg. Coll.-158034).

Dictyota dichotoma var. *intricata* (Figure 59B): In front of Laboratorio de Biología Marina, Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris (JN-5630; US Alg. Coll.-158042).

Dictyota dichotoma var. *intricata* (Figure 59C): Playa between San Jose del Cabo and Cabo San Lucas, Baja California Sur, Coll. J. N. Norris and H. Sleeper (JN-4094; US Alg. Coll.-158016).

Dictyota flabellata (Figure 60): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-3474; US Alg. Coll.-158049).

Dictyota stolonifera (Figure 61A): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-3865a; US Alg. Coll.-158031).

Dictyota stolonifera (Figure 61B): Playa between San Jose del Cabo and Cabo San Lucas, Baja California Sur, Coll. J. N. Norris, K. E. Bucher and H. Sleeper (JN-4113a; US Alg. Coll.-158017).

Dictyota stolonifera (Figure 61C): C. In front of marine laboratory, vicinity of Puerto Peñasco, Sonora, Coll. E. Y. Dawson (EYD-27409; US Alg. Coll.-40641).

Dictyota vivesii (Figure 62): Punta Prieta, outer Bahía Topolobampo, Sinaloa, Coll. E. Y. Dawson (EYD-10938; US Alg. Coll.-39951).

Padina caulescens (Figure 63A,B): Islas de los Gemelos, Bahía de los Ángeles, Baja California, Coll. J. N. Norris, H. Sleeper and W. Baines (JN-4748; US Alg. Coll.-158312).

- Padina crispata* (Figure 64A–C): Isla Grande, Guerrero (Pacific Mexico), Coll. E. Y. Dawson (EYD-20957; US Alg. Coll.-6160).
- Padina durvillei* (Figure 65): Punta Pelicano, Puerto Peñasco, Sonora, Coll. M. and D. Littler, *s.n.* (US Alg. Coll.-163415).
- Padina gymnospora* (Figure 66): Playa Arenosa, east of Punta Pelicano, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-3425*b*; US Alg. Coll.-158298).
- Padina mexicana* var. *mexicana* (Figure 67): Photo of live specimen from Playa Estación, Puerto Peñasco, Sonora.
- Rugulopteryx okamurae* (Figure 68A): Cabeza Ballena, Baja California Sur, Coll. J. N. Norris and H. Sleeper (JN-4086; US Alg. Coll.-158127).
- Rugulopteryx okamurae* (Figure 68B): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris (JN-3724; US Alg. Coll.-158125 and slide 4204).
- Spatoglossum subflabellatum* (Figure 70): Punta Lobos, north side of point, vicinity of Puerto Lobos, Sonora, Coll. J. N. Norris (JN-5902; US Alg. Coll.-158512).
- Desmarestia filamentosa* (Figure 71): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (JN-5271; US Alg. Coll.-157950).
- Desmarestia filamentosa* (Figure 72A,B): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris, with J. Paul and K. Robertson (JN-5271; US Alg. Coll.-157950 and slide 4183).
- Desmarestia munda* subsp. *mexicana* (Figure 73): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (JN-5283; US Alg. Coll.-157944).
- Sporochnus anomalus* (Figure 74): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (JN-5264; US Alg. Coll.-158494).
- Sporochnus anomalus* (Figure 75A,B): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (JN-5264; US Alg. Coll.-158494; US Alg. Coll. vial 5824, jar 568, and slide 4210).
- Sporochnus neushulii* J. N. Norris *sp. nov.* (Figure 76A–E): Off west side of Roca Blanca, Puerto Refugio, Isla Ángel de la Guarda, Coll. J. N. Norris (A–E. Holotype: JN-5262, US Alg. Coll.158492; B. US Alg. Coll. vial 5823, jar 568; C. US Alg. Coll. slide 4208; D. US Alg. Coll. slide 4209; and E. US Alg. Coll. slide 8474).
- Hapterophycus anastomosans* (Figure 77A,B): Isla Raza, Gulf of California (A,B. Holotype: EYD-26110; US Alg. Coll.-37228 and vial 2479, jar 296).
- Cutleria hancockii* (Figure 79A): Gametophyte, Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4953; US Alg. Coll.-209237).
- Cutleria hancockii* (Figure 79B): Gametophyte, epizoid on carapace of female black sea turtle (*Chelonia mydas agassizii*), vicinity of Campo Ona, Canal de Infiernillo, Sonora, Coll. R. S. Felger and E. Moser (JN-4786; US Alg. Coll.-157912 and slide 4182).
- Cutleria hancockii* (Figure 79C): Gametophyte, Puerto Lobos, Sonora, Coll. J. N. Norris and M. Helvey (JN-6040; US Alg. Coll.-157937 and slide 8471).
- Cutleria hancockii* (Figure 79D): Gametophyte, Camp Dolar, Cabo Tepopa, Sonora, Coll. J. N. Norris (JN-7065; US Alg. Coll.-157942 and slide 8473).
- Cutleria hancockii* (Figure 79E): Sporophyte (“*Aglaozonia*-phase”), Punta Pelicano–Playa Arenosa area, vicinity of Puerto Peñasco, Sonora, Coll. E. Y. Dawson (EYD-27365; US Alg. Coll.-40713 and slide 8469).
- Cutleria hancockii* (Figure 79F): Sporophyte (“*Aglaozonia*-phase”), epiphytic on *Sargassum*, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris (JN-3691*b*; US Alg. Coll. slide 4158).
- Hincksia mitchelliae* (Figure 82): Epizoid on black sea turtle (*Chelonia mydas agassizii*) carapace, vicinity of Campo Ona, Canal de Infiernillo, Sonora, Coll. R. S. Felger and E. Moser (JN-4774; US Alg. Coll.-158145 and slide 4223).
- Chnoospora pacifica* (Figure 83A–C): Binnars Cove, Isla Socorro, Revillagigedo Arch. (Pacific Mexico), Coll. E. Y. Dawson (EYD-12121; US Alg. Coll.-5794 and vial 784, jar B88).
- Hecatonema streblonematoides* (Figure 84A,B): Playa Hermosa, Puerto Peñasco, Sonora, Coll. K. Bucher and J. N. Norris (JN-4033; US Alg. Coll. slide 5350).
- Nemacystus brandegeei* (Figure 85A): Epiphytic on *Sargassum*, Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-3985; US Alg. Coll.-158192).

- Nemacystus brandegeei* (Figure 85B,C): Isla San Jose, Baja California Sur (EYD-25847; US Alg. Coll.-36453; B. US Alg. Coll. slide 8479 and C. US Alg. Coll. jar 269, vial 2271).
- Streblonema transfixum* (Figure 86): Epiphytic on *Gracilaria textorii*, north end of Isla Coronado, Bahía de los Ángeles, Baja California, Coll. H. Sleeper and M. Helvey (JN-4411c; US Alg. Coll. slide 4257).
- Leathesia nana* (Figure 90A-C): Epiphytic on leaflike blade of *Sargassum sinicola*, El Coloradito, Baja California, Coll. R. Aguilar-Rosas, L. Aguilar-Rosas, L. E. Mateo-Cid, C. Mendoza-Gonzalez and C. E. Gutierrez-Villaseñor (BC95-S/N3; CMMEX-6447).
- Colpomenia phaeodactyla* (Figure 91A): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (drawing of JN-4759; US Alg. Coll.-157841).
- Colpomenia ramosa* (Figure 91B): North side of Puerto Calamajué, Baja California, Coll. J. N. Norris and K. E. Bucher (drawing of JN-4697; US Alg. Coll.-157854).
- Colpomenia sinuosa* (Figure 92A): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (drawing of JN-4580; US Alg. Coll.-60062).
- Colpomenia tuberculata* (Figure 92B): Photo of living specimen from Playa Estación, Puerto Peñasco, Sonora.
- Hydroclathrus clathratus* (Figure 94): Isla Pichilingue, La Paz, Baja California Sur, Coll. O. Holguin Q. (PhP-1536; US Alg. Coll.-36619).
- Roseningea floridana* (Figure 95A,B): Punta la Gringa, Bahía de los Ángeles, Baja California, Coll. J. N. Norris and K. E. Bucher (JN-5471; US Alg. Coll.-158327).
- Roseningea intricata* (Figure 96): Punta Bufo, Baja California, Coll. M. and D. Littler, *s.n.* (US Alg. Coll.-163441).
- Sargassum johnstonii* (Figure 97A): Bahía Cholla, vicinity of Punta Peñasco, Sonora, Coll. E. Y. Dawson (EYD-27204).
- Sargassum johnstonii* (Figure 97B): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4559; US Alg. Coll.-158429).
- Sargassum johnstonii* f. *gracile* (Figure 98): Guaymas, Sonora, Coll. Daisy R. Marchant (Isotype, *D. R. Marchant-28a*; US Alg. Coll.-56958).
- Sargassum lapazeanum* (Figure 99A,B): La Paz, Baja California Sur, Coll. Daisy R. Marchant (Isotype, *D. R. Marchant-21*; US Alg. Coll.-56961).
- Sargassum acinacifolium* (Figure 100B,C): Cast ashore, Guaymas (?), Sonora (Isotype, *T. S. Brandegee-2*; UC-221158).
- Sargassum macdougallii* (Figure 101A): Cabo Tepoca, Puerto Lobos, Sonora, Coll. J. N. Norris (JN-5975; US Alg. Coll.-158398).
- Sargassum macdougallii* (Figure 101B): Punta Lobos, Cabo Tepoca, SE side of Puerto Lobos, Sonora, Coll. J. N. Norris (drawing of JN-5944; US Alg. Coll.-158397).
- Sargassum sonorensis* (Figure 102): Northeast side of cove, Isla San Pedro Nolasco, Coll. N. P. Yensen (JN-5205; US Alg. Coll.-158399).
- Sargassum sinicola* subsp. *sinicola* (Figure 103): Isla San Esteban, Coll. E. Y. Dawson (EYD-21568; US Alg. Coll.-6284).
- Sargassum sinicola* subsp. *sinicola* (Figure 104): West side of large rock, Rocas Consag, coll. D. G. Lindquist (JN-3119; US Alg. Coll.-158447).
- Sargassum sinicola* subsp. *sinicola* (Figure 105A): West side of large rock, Rocas Consag, coll. D. G. Lindquist (drawing of JN-3119; US Alg. Coll.-158447).
- Sargassum sinicola* subsp. *camouii* (Figure 105B): Playa Hermosa, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (drawing of JN-3250; US Alg. Coll.-158450).
- Sargassum sinicola* subsp. *camouii* (Figure 106): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-6064; US Alg. Coll.-158477).
- Sargassum herporhizum* (Figure 107): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-4963; US Alg. Coll.-158382).
- Sargassum herporhizum* (Figure 108A): Playa Estación, Puerto Peñasco, Sonora, Coll. J. N. Norris and K. E. Bucher (JN-5870b; US Alg. Coll.-158346).
- Sargassum herporhizum* (Figure 108B): West side of large rock, Rocas Consag, Coll. D. G. Lindquist, drawing of (JN-3117; US Alg. Coll.-158356).
- Sargassum brandegeei* (Figure 109A): North side of point Punta Lobos, Puerto de Lobos, Sonora, coll. M. Helvey (JN-6034; US Alg. Coll.-158392).
- Sargassum brandegeei* (Figure 109B,C): Punta Robinson, west side about 2.4 km east of Puerto Libertad, Sonora, Coll. J. N. Norris and K. B. Bucher (JN-4829; US Alg. Coll.-158377).

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