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An annotated list of marine Chlorophyta from the Caribbean coast of the Republic of Panama

by

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With 31 figures and 2 tables

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Abstract: An updated species list has been compiled for the green algae of the Caribbean coast of the Republic of Panama based on available literature and our own collections. Of the 277 specimens of green algae reported herein, 41 taxa (31 species, 10 subspecies, varieties or forms) represent new records for Caribbean Panama. These discoveries and others from the literature bring the total number of green algae known for this region to 79 species and 16 sub-specific entities, an increase in known green algal diversity of 179% from the last published account. The green algal flora of Caribbean Panama is as rich as neighboring floras, but earlier reports had suggested it was impoverished. Earlier surveys probably underestimated diversity due to limited time spent in the field and limited coverage of various coastal habitats.

Key words: Caribbean, Chlorophyta, *Halimeda hummii*, macroalgal diversity, Panama, species list.

Resume: En el presente reporte hemos compilado una lista actualizada de las especies de algas verdes del Caribe Panameño basada en la literatura disponible y en nuestras propias colectas realizadas. De las 277 especies de algas verdes reportadas aquí, 41 taxa (31 especies, 10 subespecies, variedades o formas) representan nuevos registros para la República de Panamá. Estos descubrimientos, y otras desde la literatura, suman un número total de algas verdes conocidas para esta region de 79 especies

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y 16 entidades sub-especificas, un incremento del 179% en la diversidad conocida de algas verdes a partir del último reporte publicado. La flora de algas verdes del Caribe Panameño es de una riqueza comparable con las floras adyacentes, a pesar de que los reportes iniciales habian sugerido una flora empobrecida. Los estudios iniciales probablemente subestimaron la diversidad real debido al tiempo limitado empleado en el área y a una cobertura limitada de los variados hábitats costeros.

Introduction

Knowledge of the Caribbean marine flora of Central America is limited in comparison with the long history of phycological collections made throughout the eastern Caribbean Sea. The available literature seems to indicate that the marine flora of Caribbean Central America is relatively impoverished, but these estimates of diversity probably reflect limited collection and research effort. Knowledge of macroalgal diversity in the Republic of Panama is based primarily on collections made during very brief visits to the country (e.g., Howe 1910, Taylor 1929, Earle 1972) or collections focused on a restricted part of the diversity (e.g., Hay & Gaines 1984, Clifton & Clifton 1999, Kooistra et al. 1999). The most concerted effort to document macroalgal diversity in Panama was undertaken by Earle (1972), who spent approximately six weeks (pers. comm.) collecting seaweeds. She listed 118 taxa from the Caribbean coast including 38 Chlorophyta. Recent macroalgal inventories conducted in neighboring countries uncovered over twice as many Caribbean species: 263 from Costa Rica (Soto & Ballantine 1986) and 472 from Colombia (Bula-Meyer 1998). Only Puerto Rico, with 492 macroalgal species, has a more richly documented marine flora (Ballantine & Aponte 2002) in the Caribbean Sea.

Methods used for collecting may also affect reported diversity. Prior to Earle's work, all collections from Caribbean Panama were obtained by dredging, wading or snorkeling. Earle (1972) collected the majority of her newly recorded species (17) using SCUBA. Nevertheless, it is likely that marine macroalgal diversity for Panama has been underestimated because efforts have mainly concentrated on a few sites (Earle 1972) or on a restricted part of the taxonomic diversity (Hay & Gaines 1984, Hay & Norris 1984, Kilar & Norris 1988, Clifton & Clifton 1999).

In the present study, based on nearly 55 man-hours of SCUBA diving collections made in 1999, 277 specimens of marine Chlorophyta were examined. Thirty-one species and 10 varieties, forms or subspecies constitute new records for Panama.

Materials and methods

The Caribbean coastline of Panama extends over 900 km with gulfs and archipelagos contributing to coastal complexity and habitat diversity. Shores are dominated by coral reefs behind which seagrass beds and mangroves abound in protected lagoons. Outside the reef slope, the substratum consists of limestone platforms and sand and mud plains. Forty-six independent collections were made from 38 different sites in the Bocas del Toro Province in the northwestern part of the country, the Colón Province in the central region and the Comarca de San Blas in the northeastern region (Fig. 1, Table 1). We sampled diverse habitat types at each collection site in order to obtain a representative census of algal diversity. Permission to collect specimens was granted by the Autoridad Maritima de Panama, Direccíon General de Recursos Marinos y Costeros.

Samples were collected from February to November 1999 by snorkeling and wading, or by SCUBA diving to a maximum depth of 35 m. Additional samples were obtained from dredging collections of other researchers at the Smithsonian Tropical Research Institute (STRI). Field collections were held in flow-through seawater aquaria until preliminary identifications were made. Samples were preserved in 5-10% Formalin/seawater and pressed and air-dried on herbarium sheets for archiving. Additional material, when available, was preserved in silica gel desiccant or 95% ethanol for future molecular genetic studies. A complete set of specimens is archived at the University of Louisiana at Lafayette Herbarium (LAF); duplicate material has been deposited in the Algal Collection of the US National Herbarium (US) and the Smithsonian Tropical Research Institute (STRI).

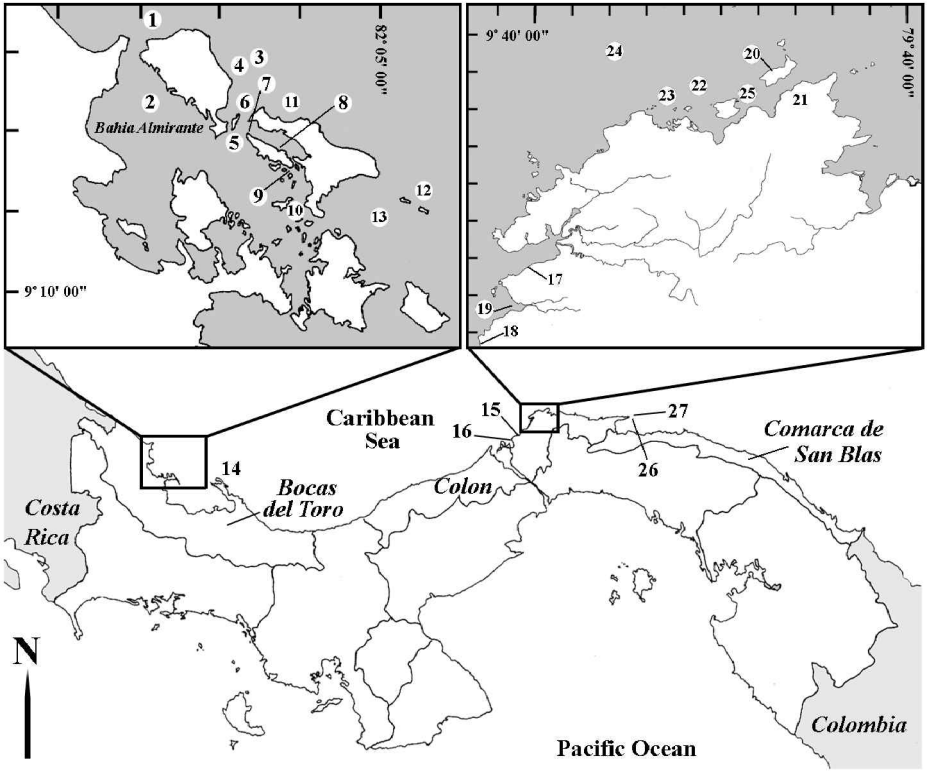


Fig. 1. Map of collecting sites for Caribbean Panama. Ticks along the margins of the Bocas del Toro (left) and Colón (right) insets mark 5' and 1' intervals, respectively. Sail Rock, 1; Knapps Hole, 2; NE Canal de Bocas del Toro, 3; Long Bay Point, 4; Shepard Bank, 5; Porvenir Point, 6; Hospital Point, 7; Hospital Bight Mangrove Fringe, 8; Cayo Nancy mangrove key, 9; Isla Bastimentos mangrove key, 10; Barren Rock, 11; Cayos Zapatillas, 12; Laguna de Zapatilla, 13; Peninsula Valiente, 14; Galeta Point, 15; For Randolph, 16; Nautilus Dive Club, 17; roadside, west of Portobelo, 18; Bahia de Buena Ventura, 19; Isla Grande, 20; Mainland, across from Isla Grande, 21; north of Pedro Pelada, 22; Between Pedro Pelada and Punta Cacique, 23; Las Farallones, 24; western point of Isla Mamey, 25; Sail Rock (San Blas), 26; STRI research station at San Blas, 27). Political boundary map after National Geographic (1999). Bocas del Toro inset after Instituto Geográfico Nacional "Tommy Guardia" (1998). Colón inset after Defense Mapping Agency (1995).

Table 1. Collection sites from 1998 survey of Caribbean Panama marine flora. Collections were made across diverse habitats within and between sites. Names designated for collection sites reflect closest meaningful landmarks. Latitude and longitude co-ordinates were determined using nautical charts for the region.

Province	Site Name	Lat. (°N)	Long. (°W)	Notes
Bocas del Toro	Sail Rock	9° 27.4	82° 17.8	Algae-covered reef and rock outcrops interspersed with sandy patches.
	Knapps Hole	9° 23.3	82° 18.5	Shallow sand plain, mangroves and well-developed coral reef.
	Northeast of Canal de Bocas del Toro	9° 24.8	82° 12.5	Limestone dome at ~23 m drops off to a sandy plain at 33-35 m.
	Long Bay Point	9°24.0	82° 13.7	Extensive limestone platforms with intermittent sandy patches.
	Shepard Bank	9° 19.8	82° 13.6	Silty sand and rock substrata, devoid of corals.
	Porvenir Point	9° 21.8	82° 13.3	Rock rubble, corals and patches of silty-sand.
	Hospital Point	9° 20.1	82° 13.0	Poorly-developed corals in shallows, dropping off to silty sand bottom at 15 m.
	Hospital Bight Mangrove Fringe	9° 19.4	82° 11.4	Large (live and dead) coral heads among mangrove fringe, extensive meadows of *Thalassia* and *Syringodium*. Mangrove fouling light.
	Cayo Nancy mangrove key	9° 18.0	82° 10.2	Extensive meadows of *Thalassia* and *Syringodium*. Mangrove fouling heavy.
	Isla Bastimentos mangrove key	9° 16.0	82° 10.5	Similar to Cayo Nancy mangrove key.
	Barren Rock	9° 21.7	82 ° 11.1	Vertical rock wall to 10 m, covered with invertebrates and few algae. Rock and sand substrata, with interspersed corals.
	Cayos Zapatillas	9° 16.0	82° 02.5	Barrier reef separating shallow seagrass meadow from sandy plain with well-developed corals.
	Laguna de Zapatilla	9° 15.0	82° 05.5	Sheltered sea grass meadows with heavy siltation.
	Peninsula Valiente	9° 11.5	81° 54.0	Dredging to a depth of 29 m over coarse sand bottom.
Colón	Galeta Point	9° 24.4	79° 52.0	Fringing reef, sandy plain, protected lagoon, seagrass meadows and mangroves. For detailed site information see Glynn (1972), MacIntyre & Glynn (1976), Hay & Norris (1984), Kilar & Norris (1988), Garrity et al. (1994)

Province	Site Name	Lat. (°N)	Long.(°W)	Notes
	Fort Randolph	9° 23.3	79° 52.9	Similar to Galeta point, but reef flat inundated with 1-2 m deep canals.
	Nautilus Dive Club	9° 32.9	79° 40.2	Abundant heads of well-developed corals often cemented into a unified structure, sandy plain at greater depths.
	Roadside, 11.4 km west of Portobelo	9° 30.7	79° 41.5	Reef flat and fringing reef with a sand shoreline.
	Bahia de Buena Ventura	9° 32.0	79° 40.8	Small shallow lagoon with small coral heads and sparse seagrass beds, coral rubble and muddy sand.
	Isla Grande	9° 38.0	79° 33.8	Large reef/rock platforms, 'spur and groove' system with caverns and overhangs, rocky and sandy shorelines.
	Mainland, across from Isla Grande	9° 37.2	79° 34.0	Sandy shore and reef flat covered by <1m water.
	North of Pedro Pelada	9° 37.6	79° 35.3	Gently sloping terrain to 20 m. Predominant substratum includes rock, dead coral, coral rubble and sand.
	Between Pedro Pelada and Punta Cacique	9° 36.8	79° 36.2	Submerged bedrock rising abruptly from muddy bottom.
	Las Farallones	9° 39.0	79° 37.8	A small group of rocks northwest of Isla Grande. Predominant substratum consists of rock and dead coral.
	Western point of Isla Mamey	9° 32.0	79° 37.5	Wave exposed boulder field with extensive algal turfs at the western tip of the island and sheltered, landward-facing reef.
Comarca de San Blas	Dog Island	9° 33.6	78° 52.8	Conglomerate and isolated corals surrounding island. Fragmented reef flat with sparse seagrass to North. Expansive sand plain sloping to ~15 m and steep reef to East. Mangrove islands in vicinity.
	Sail Rock	9° 33.3	78° 56.7	Wishbone shaped, periodically emergent reef. Sloping reef leads to sandy plain with scattered seagrasses.
	Grass Island	9° 33.0	78° 54.5	Extended fragmented reef flat on protected side. Exposed shoreline dominated by large coral heads and patchy seagrass meadows.
	Pelican Island	9° 34.5	78° 52.8	Similar to Dog Island and Grass Island.
	Former STRI Research Station	9° 33.1	78° 57.3	Similar to other San Blas sites. For detailed information on the site see Robertson (1987), Wulff (1995) and Clifton & Clifton (1999).

Annotated Species List

The annotated list presented here serves as a catalogue of marine green macroalgal species known to the Caribbean coast of Panama. For each species we report the type locality, references to previous reports from Panamanian waters and other pertinent information relating to morphology or ecological distribution. The list below follows the taxonomic scheme of Wynne (1998); species records documented from previous accounts reflect nomenclatural changes as indicated therein. New records for Panama are denoted with an "*". Collection numbers for voucher specimens are labeled "BW-" followed by a 5-digit number. Under each species, curated specimens are reported along with associated collection information (e.g., substratum and depth).

ULVALES

Ulvaceae

Enteromorpha Link ex Nees

*__Enteromorpha flexuosa__ (Wulfen) J. Agardh (1883: 126-128)

Type Locality: Adriatic Sea.

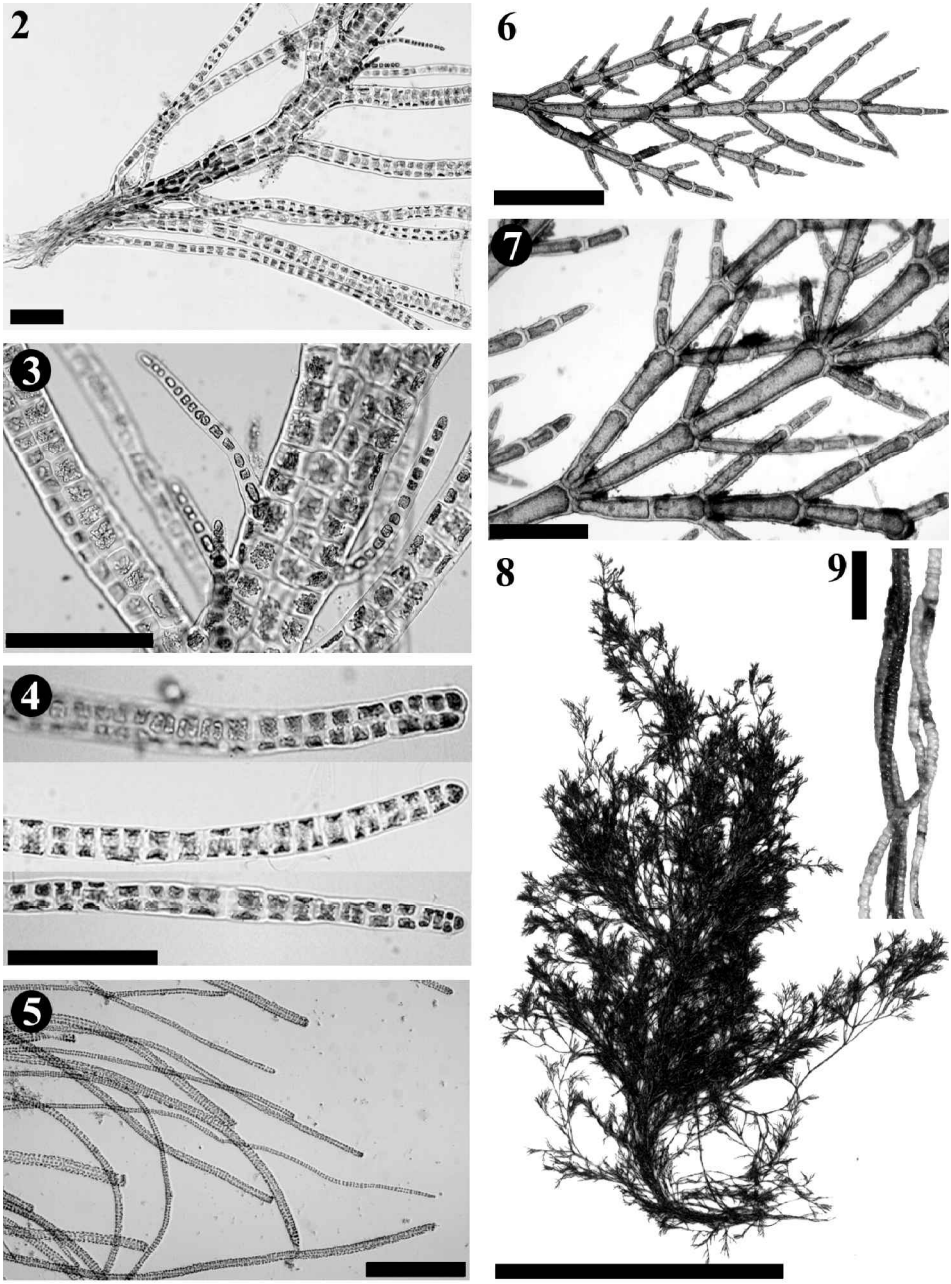
Collections: BW-00096 Fort Randolph, on drift wood floating in 0.5 m water next to shore; BW-00185 Fort Randolph, on shell fragment covered by sand, ~3 m; BW-00876 Galeta, S. lagoon and reef flat, epiphytic on *Acetabularia crenulata* Lamouroux (BW-00875); BW-01117 near Knapps Hole, collected from submerged boat engine on a boat docked at the Smithsonian Research Station.

*__Enteromorpha flexuosa__ subsp. __paradoxa__ (C. Agardh) Bliding (1963: 79, figs 42-45)

Type Locality: Tennstedt, Thüringen, Germany.

Collections: BW-00236 Buena Ventura, associated with *E. flexuosa* (BW-00096) on drift wood floating in 0.5 m water next to shore.

Notes: This taxon shares with the species the feature of branching limited to the lower portions of the thallus (Figs 2-3), but differs in its finely branched nature. The subspecies is characterized by the presence of uniseriate branchlets (Littler & Littler 2000), but these were not exclusively uniseriate in this specimen (Figs 3-5). Uniseriate filaments were born on the lower portion of the axis (Fig. 3), and most filament tips were multiseriate, or uniseriate for only a short distance (Figs 4-5), and unbranched. These features, along with the presence of 3-8 series of longitudinally arranged cells distinguish the Panamanian specimen from *E. chaetomorphoides,* which it resembles in gross morphology but which is characterized by only 3-4 series of longitudinally arranged cells and uniseriate, branched apical filaments. Børgesen (1913) illustrated a cross section of the latter species showing 10 cells but noted the rarity of that condition.



Figs 2-5. *Enteromorpha flexuosa* subsp. *paradoxa* (BW-00236). Fig. 2. Branching in the lower part of the thallus. Fig. 3. Uniseriate branchlets borne off the main axis. Fig. 4-5. Multiseriate, unforked branch tips. Scale bars: Figs 2-4: 100 mm, Fig. 5: 500 mm). Figs 6-9. *Cladophora ordinata* (BW-01312). Fig. 6. Branch apex showing opposite branching. Fig. 7. Portion of branch showing trichotomous branching and younger developing branchlets between two trichotomies. Fig. 8. Habit. Fig. 9. Annular constrictions. Scale bars: Fig. 6: 1 mm, Fig. 7: 500 mm, Fig. 8: 5 cm.

Ulva Linnaeus

Ulva lactuca Linnaeus aff. var. **latissima** (sensu Taylor, 1960: 65)

Type Locality: Europe.

Collections: BW-00106 Sail Rock, San Blas, on rock, <0.2 m.

Other Panamanian records: Taylor (1929, 1960).

Notes: Confusion exists with regard to the application of the specific names *lactuca* and *latissima* in *Ulva* (Silva et al. 1996). This specimen conformed well to Taylor's (1960) account of *U. lactuca* var. *latissima*.

CLADOPHORALES

ANADYOMENACEAE

Anadyomene Lamouroux

***Anadyomene saldanhae** A.B. Joly et E.C. Oliveira (1969: 30, figs 1-3)

Type Locality: Banco Dogareza, off the coast of Victoria, Espirito Santo State, Brazil.

Collections: BW-01232 Long Bay Point, on hard substratum, ~8-10 m; BW-01252 Sail Rock, ~8 m; BW-01483 Northeast of Canal de Bocas del Toro, on rock; BW-01488 Cayos Zapatilla Islet Trio, on hard substratum.

Anadyomene stellata (Wulfen) C. Agardh (1822-1823: 400)

Type Locality: Adriatic Sea.

Collections: BW-00001 mainland, across from Isla Grande, on reef flat in sand; BW-00038 roadside, ~11.4 km west of Portobelo; BW-00078 Fort Randolph, in rocks in 0.3 m water, next to shore; BW-00280 Nautilus Dive Club, in protected nook of coral, 1-2 m; BW-00394 Galeta, on coral, ~3 m; BW-00799 Galeta, on coral, ~5-8 m; BW-01072 Rampa Privada, on cement bulkhead at waterline; BW-01205 Northeast of Canal de Bocas del Toro, on hard substratum, ~25m; BW-01367 Cayos Zapatilla, exposed side of reef, on hard substratum, 13-15 m.
Other Panamanian records: Taylor (1929, 1942, 1960); Littler & Littler (1991).

Microdictyon Decaisne

Microdictyon boergesenii Setchell (1925: 106)

Type Locality: St. John, Virgin Islands.

Collections: BW-00392 Galeta, tangled with various other taxa, 3-8 m; BW-00945 Galeta, unattached drifting over bottom, 7-10 m; BW-01020 Galeta, on dead coral, 12-15 m.

Other Panamanian records: Kilar & Norris (1988).

Chaetomorpha Kützing

Chaetomorpha antennina (Bory de Saint-Vincent) Kützing (1847: 166)

Type Locality: Réunion Island (Indian Ocean).

Other Panamanian records: Taylor (1929, 1942, 1960) as *C. media* (C. Agardh) Kützing.

Chaetomorpha brachygona Harvey (1858: 87-88, pl. XLVIA)

Syntype Localities: Key West, Florida, USA; mouth of Rio Bravo [Rio Grande], border of Mexico and Texas, USA.

Collection: BW-01114 near Knapps Hole, from seagrass bed near mangrove fringe, 0.5 m.

Other Panamanian records: Taylor (1929, 1942, 1960).

***Chaetomorpha gracilis** Kützing (1845: 203).

Type Locality: Trieste, Italy.

Collection: BW-01110 near Knapps Hole, from seagrass bed near mangrove fringe, 0.5 m.

Chaetomorpha linum (O.F. Müller) Kützing (1845: 204).

Syntype Localities: Nakskov and Rødby, Denmark.

Collections: BW-00040 roadside, ~11.4 km west of Portobelo; BW-00865 Galeta, north lagoon and reef flat, floating in tangled mass, <0.2 m in *Halodule* Endlicher seagrass bed.

Other Panamanian records: Taylor (1942, 1960).

Cladophora Kützing

Cladophora coelothrix Kützing (1843: 272).

Type Locality: Golfo di Genova, Italy.

Collections: BW-00866 Galeta, south lagoon and reef flat, growing on log washed ashore. BW-01082 mainland, across from Isla Grande, growing on mud at base of mangroves. BW-01083 and BW-01084 mainland across from Isla Grande, growing in mud at base of mangroves.

Other Panamanian records: Taylor (1929, 1960) as *C. repens* (J. Agardh) Harvey.

Notes: BW-01083 and –01084 were tangled masses of variously sized filaments representing a range of sizes that is consistent with previous accounts of this species (van den Hoek 1982).

*__Cladophora dalmatica__ Kützing (1843: 268-269)

Type Locality: Split, Croatia.

Collection: BW-01030 Galeta.

*__Cladophora ordinata__ (Børgesen) van den Hoek (1982: 123-125, pl. 22: figs 231-237)

Type Locality: Dwarka, Okha Port NW India.

Collections: BW-1290 Long Bay Point, on hard substratum in sand, ~15 m; BW-1292 Long Bay Point, on hard substratum, 15 m; BW-01312 NE of Canal de Bocas del Toro, on rock, ~20 m.

Notes: These specimens exhibited pseudo-trichotomous and opposite branching (Figs 6-7) that is characteristic of the species. Individual branches were planar, which is similar to *Phyllodictyon,* but the presence of tenaculae in the latter ultimately results in the development of a reticulum which *C. ordinata* never forms. Undulations in the cell wall, reminiscent of annular constrictions, typical of other Cladophoralean taxa (e.g., *Chamaedoris peniculum* (Ellis et Solander) Kuntze and *Cladophora prolifera* (Roth) Kützing), were apparent at the base of the thallus in some individuals (Fig. 8). This rarely reported species is also recorded from Venezuela (van den Hoek & de Rios 1972, as *Willeella ordinata*) and the east coast of Africa (Sartoni 1992). The Panamanian material was encountered in a restricted area in Panama, but these large and bushy specimens (Fig. 9) were very conspicuous in the vicinity of Isla Colón, Bocas del Toro. Originally described as *Willeella ordinata* Børgesen (1930), van den Hoek (1982) reduced the genus to the rank of section within *Cladophora*. Silva et al. (1996) continued to recognize *Willeella* on grounds that molecular data would show it to be a genus genetically distinct from *Cladophora*, which subsequently was not supported (Wysor 2002).

*__Cladophora pellucidoidea__ van den Hoek (1982: 179-182, pl. 36: figs 358-362; pl. 37: 365)

Type Locality: Bogue Beach, Beaufort, North Carolina, USA.

Collections: BW-00951 Galeta, in sand, ~10 m; BW-01028 Galeta, tangled with *Haliptilon subulatum* (J. Ellis et Solander) Johansen (BW-01027); BW-01301 NE of Canal de Bocas del Toro, on hard substratum, ~15-20 m. BW-01455 Hospital Bight mangrove fringe, on rock, <0.5 m.

*__Cladophora socialis__ Kützing (1849: 416)

Type Locality: Tahiti.

Collection: BW-01357 mangrove cay flanking channel at east end of Cayo Nancy, forming large turfs over bottom, 1-2 m.

Rhizoclonium Kützing

Rhizoclonium africanum Kützing (1853: 21, pl. 67 fig. 2)

Type Locality: 'Senegambien' (Senegal or Gambia).

Other Panamanian records: Taylor (1929, 1960) as *R. hookeri* Kützing.

Boodleaceae

Phyllodictyon J.E. Gray

***Phyllodictyon anastomosans** (Harvey) Kraft et M.J. Wynne (1996: 139)

Type Locality: Freemantle, Western Australia.

Collections: BW-00095 Fort Randolph, epiphytic on *Chondrophycus papillosa* (C. Agardh) Garbary and Harper (BW-00089); BW-00304 Western point of Isla Mamey, on coral; BW-00747 Galeta, growing among coralline red algae, ~6-8 m; BW-00847 Galeta, on coral ~6 m; BW-01021 Galeta, on dead coral, 12-15m; BW-01078 Isla Grande, epiphytic on *Digenea simplex* (Wulfen) C. Agardh on exposed bedrock along shoreline in breaking waves, <1 m; BW-01116 near Knapps Hole; BW-01386 Cayos Zapatilla Islet Trio, on shaded side of rock islet, <2 m; BW-01426 Isla Bastimentos, on mangrove prop-root, <1 m.

Siphonocladaceae

Chamaedoris Montagne

***Chamaedoris peniculum** (Ellis et Solander) Kuntze (1898: 400)

Type Locality: Antilles.

Collections: BW-01148 Long Bay Point, on hard substratum, ~10-12 m; BW-01368 Cayos Zapatilla, exposed side of reef on hard substrate, 13-15 m.

Cladophoropsis Børgesen

Cladophoropsis membranacea (Bang ex C. Agardh) Børgesen (1905: 289, figs 8-13)

Type Locality: St. Croix, Virgin Islands.

Collection: BW-00004 mainland, across from Isla Grande, in reef flat, tangled with *Acanthophora spicifera*.

Other Panamanian records: Taylor (1929, 1960).

*__Cladophoropsis sundanensis__ Reinbold (1905: 147)

Syntype Localities: various in Indonesia, including Solor and Semau.

Collection: BW-01080 Isla Grande, epiphytic on *Digenea simplex* on exposed bedrock along shoreline in breaking waves, <1 m.

Dictyosphaeria Decaisne

Dictyosphaeria cavernosa (Forrskål) Børgesen (1932: 2, pl. 1, fig. 1)

Syntype Localities: 'Gomfodae' [Al-Qunfudhah], Saudi Arabia; Mokha, Yemen.

Collections: BW-00135 Grass Island, on coral; BW-00828 Galeta, south lagoon and reef flat; BW-01069 Isla Grande, on dead coral, ~7 m; BW-01457 Hospital Bight, in seagrass bed at mangrove fringe, 1-2 m.

Other Panamanian records: Taylor (1929, 1960).

Siphonocladus Schmitz

*__Siphonocladus tropicus__ (P. Crouan et H. Crouan in Schramm et Mazé) J. Agardh (1887: 105)

Syntype Localities: various in Guadeloupe, West Indies.

Collection: BW-01376 Cayos Zapatilla, exposed side of reef on hard substratum, 15 m.

Ventricaria Olsen et J. West

Ventricaria ventricosa (J. Agardh) J.L. Olsen et J.A. West (1988: 104).

Lectotype Locality: Guadeloupe, West Indies.

Collections: BW-00077 Fort Randolph; BW-00110 Sail Rock, on coral; BW-00823 Galeta, in crevices of coral, 3-8 m; BW-00824 Galeta, in crevices of coral, ~7 m; BW-01122 near Knapps Hole, on hard substratum from seagrass bed near mangrove fringe; BW-01346 Cayo Nancy, unattached, over bottom in ~2 m.

Other Panamanian records: Taylor (1929, 1960) as *Valonia ventricosa* J. Agardh.

VALONIACEAE

Ernodesmis Børgesen

*__Ernodesmis verticillata__ (Kützing) Børgesen (1912: 259, figs 10-12)

Type Locality: St. Croix, Virgin Islands.

Collections: BW-01014 Galeta, on dead coral, 12-15m; BW-01115 near Knapps Hole, over sand near mangrove fringe; BW-01233 Long Bay Point; BW-01446 off Porvenir Point, unattached, over sand, ~10-13 m; BW-01456 Hospital Bight, in sand near mangrove fringe, <0.5 m.

Valonia C. Agardh

***Valonia macrophysa** Kützing (1843: 307)

Type Locality: Lessina [Hvar], Croatia.

Collections: BW-00408 Galeta, under coral overhang, ~4 m; BW-00825 Galeta, south lagoon and reef flat, growing among corals, ~3-7 m; BW-00826 Galeta, south lagoon and reef flat; BW-00988 Isla Grande, on coral, ~1 m.

Valonia utricularis (Roth) C. Agardh (1823: [1822-1823]: 431)

Type Locality: Mediterranean Sea.

Collection: BW-00988 Isla Grande, on coral, ~1 m.

Other Panamanian records: Taylor (1929, 1960).

BRYOPSIDALES

BRYOPSIDACEAE

Bryopsis Lamouroux

***Bryopsis hypnoides** Lamouroux (1809: 333)

Type Locality: Mediterranean coast of France.

Collection: BW-01388 Cayos Zapatilla Islet Trio, <2 m.

***Bryopsis pennata** Lamouroux (1809: 333)

Type Locality: Antilles, West Indies.

Collections: BW-00784 Galeta, on coral; BW-00870 Galeta, in breaking waves on reef flat; BW-00871 on coral; BW-01119, BW-01121, near Knapps Hole, from mangrove prop-root; BW-01387 Cayos Zapatilla Islet Trio, shaded side of rock, <2 m.

***Bryopsis plumosa** (Hudson) C. Agardh (1823: [1822-1823]: 448.

Type Locality: Exmouth, Devon, England.

Collections: BW-00783 Galeta, on coral; BW-01172 Long Bay Point, on hard substratum, ~10-12 m.

Caulerpaceae

Caulerpa Lamouroux

Caulerpa cupressoides (H. West in Vahl) C. Agardh (1817: 23)

Type Locality: St. Croix, Virgin Islands.

Other Panamanian records: Clifton & Clifton (1999)

*__Caulerpa cupressoides__ var. **flabellata** Børgesen (1907: 368, figs 18, 19)

Syntype Localities: St. John and St. Thomas, Virgin Islands.

Collections: BW-00125 Grass Island, in sand ~8 m; BW-01434 near Shepard Bank, in sand, 10 m; BW-01453 Hospital Bight mangrove fringe, in sand, ~1 m.

*__Caulerpa cupressoides__ var. **lycopodium** Weber-van Bosse (1898: 335, pl. 27, figs 8-13 pl. 28, figs 10-12, 14)

Type Locality: "e mari Brasiliae et Indiae Occidentalis".

Collections: BW-00052 Buena Ventura, in sand, 2 m.; BW-01054 Fort Randolph, in muddy sand, 6 m; BW-01101 Peninsula Valiente, dredged from ~29m; BW-01423 Cayos Zapatilla Islet Trio, in sand, 10 m.

Caulerpa cupressoides var. **mammillosa** (Montagne) Weber-van Bosse (1898: 332, pl. 27, figs 2-7)

Syntype Localities: Agalega Islands; Mangareva, Îles Gambier, French Polynesia.

Collections: BW-00074 Fort Randolph, in sand; BW-00169 Fort Randolph, on coral, ~1 m; BW-01410 Cayos Zapatilla Islet Trio, in sand, ~1.5 m.

Other Panamanian records: Taylor (1942, 1960).

Caulerpa fastigiata Montagne (1837: 353-354)

Type Locality: Cuba.

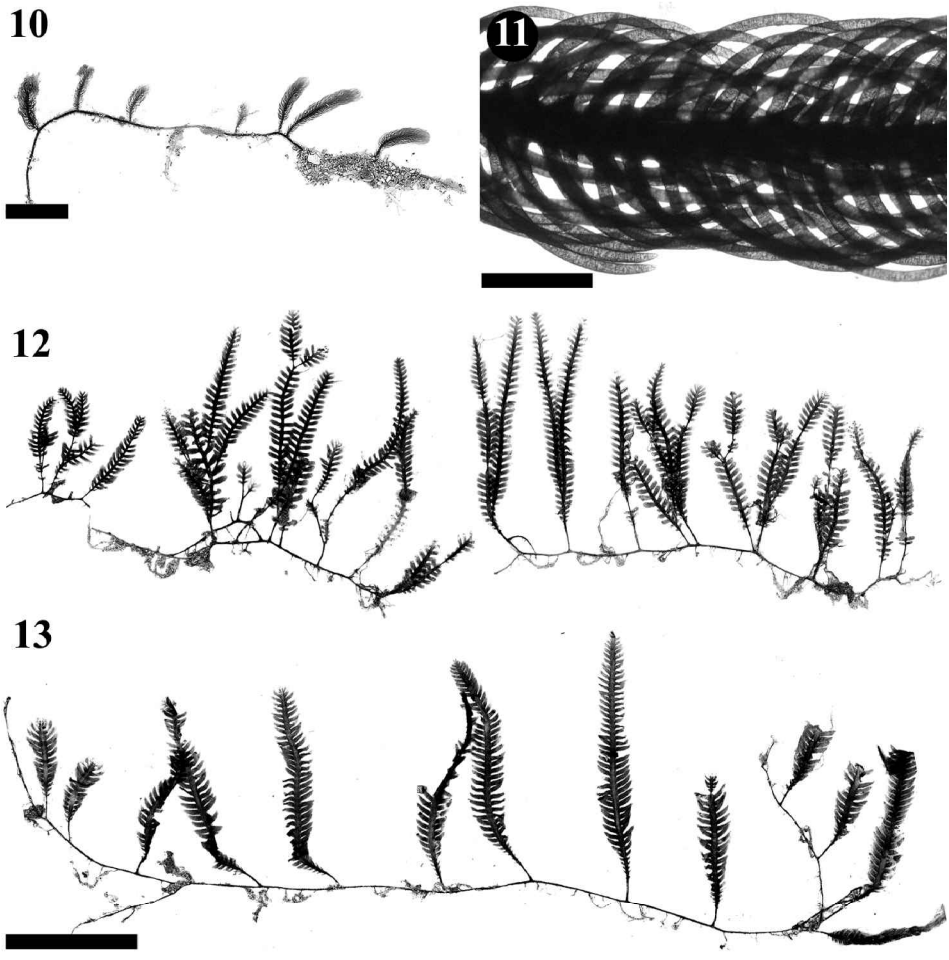
Other Panamanian records: Taylor (1929, 1960).

*__Caulerpa lanuginosa__ J. Agardh (1873: 28)

Type Locality: Key West, Florida, USA.

Collection: BW-01377 Cayos Zapatilla, exposed side of reef, on rock, ~15 m.

Notes: This specimen (Figs 10-11) was similar to that pictured by Littler & Littler (2000) and rather unlike the tomentose appearance of typical specimens encountered in the vicinity of the type locality. DNA sequence analysis clearly allied this specimen with another specimen of this species collected from near the type locality (Famà et al. 2002).



Figs 10-11. *Caulerpa lanuginosa* (BW-01377). Fig. 10. Habit. Fig. 11. Enlargement of vertical axis showing the random arrangement of pinnules around the main axis. Scale bars: Fig. 10: 1 cm, Fig. 11: 100 mm. Fig. 12. *Caulerpa mexicana* (BW-01340). Distinctive forkings of the vertical axes and widely spaced pinnules distinguish this specimen from the more typical morphology commonly collected throughout Caribbean Panama. Scale bar: 5 cm. Fig. 13. *Caulerpa mexicana* f. *pectinata* (BW-01333). Acute tips and widely spaced pinnules distinguish this form from the nominate form. Scale bar: 5 cm.

Caulerpa mexicana Sonder ex Kützing (1849: 496)

Type Locality: Mexico.

Collections: BW-00061 Buena Ventura, in sand; BW-00168 Fort Randolph, in muddy sand; BW-00750 Galeta; BW-01015 Galeta, on coral, ~5 m; BW-01340 Cayo Nancy, in sand, 2-6 m.

Notes: Vouchers of BW-001340 were characterized by distinctive forkings arising from just above the denuded assimilator, or more distally where the frond may have suffered damage (Fig. 12). On all assimilators, the branchlets were widely separated, in some cases by as much as the branchlet width (~2 mm).

Other Panamanian records: Clifton & Clifton (1999).

*__Caulerpa mexicana__ f. __pectinata__ (Kützing) W.R. Taylor (1960: 141, 142)

Type Locality: La Guayra, Mexico.

Collections: BW-01180 Long Bay Point, in sand, ~10-12m; BW-01333 Hospital Point, in sand, ~15 m.

Notes: These specimens exhibited distinctive, acute branchlet tips (Fig. 13) that were less crowded than in other specimens in the collection (compare with Fig. 12). These features are consistent with Taylor's (1960) description of this form.

Caulerpa microphysa (Weber-van Bosse) J. Feldmann (1955: 430)

Type Locality: Macassar [Ujung Pandang], Celebes, Indonesia.

Collections: BW-00418 Galeta, on rock, 8-12 m; BW-00787 on coral, ~5 m; BW-01016 Galeta, on dead coral and rock, 12-15 m; BW-01186 01226 Long Bay Point, on hard substratum, ~10-12 m, BW-01226 Long Bay Point, on hard substratum in dense mat; BW-01242 NE of Canal de Bocas del Toro, on hard substratum, ~25 m.

Other Panamanian records: Earle (1972).

*__Caulerpa prolifera__ (Forsskål) Lamouroux (1809: 332)

Type Locality: Alexandria, Egypt.

Collection: BW-01151 Long Bay Point, in sand, ~10-12 m.

*__Caulerpa prolifera__ f. __zosterifolia__ Børgesen (1907: 359, fig. 6)

Type Locality: West Indies (St. John, St. Croix, St. Thomas).

Collection: BW-01291 Long Bay Point, in sand 15 m (fig. 14).

Notes: This specimen was abundantly branched from the primary blades. The breadth (~7 mm) of the linear-lanceolate blades was slightly greater than that described in Taylor (1960) ("hardly 6 mm wide", p. 140), but the prolific stand of this specimen and its repeatedly branched nature are features consistent with Taylor's (1960) account of this form as "interrupted and richly proliferous" (p. 140). This specimen, however, does not show the "distinct twisting" that Børgesen (1913) reported as often occurring in this form.

Caulerpa racemosa (Forsskål) J. Agardh (1873: 35-36)

Type Locality: Suez, Egypt.

Collections: BW-00003 mainland, across from Isla Grande, on coral on reef crest; BW-00037 roadside, ~11.4 km west of Portobelo, on reef crest in breaking waves; BS-00161 Fort Randolph, on reef crest in breaking waves and commonly on *Halimeda opuntia*; BW-00409 Galeta, unattached over bottom, ~3 m; BW-01454 Hospital Bight mangrove fringe, in coarse sand, ~1 m.

Other Panamanian records: Taylor (1929, 1942, 1960) as *C. racemosa* var. *clavifera* (Turner) Weber-van Bosse and *C. racemosa* var. *uvifera* (Turner) Weber-van Bosse.

***Caulerpa racemosa** var. **lamourouxii** (Turner) Weber-van Bosse (1898: 369, pl. 32: figs 1-4)

Type Locality: Red Sea.

Collections: BW-01204 NE of Canal de Bocas del Toro, ~25 m; BW-01334 Cayo Nancy, in sand, ~6 m.

Caulerpa racemosa var. **macrophysa** (Sonder ex Kützing) W.R. Taylor (1928: 101).

Type Locality: Central America.

Collections: BW-00002 mainland, across from Isla Grande, on coral on reef crest; BW-00076 Fort Randolph, in sand; BW-00170 Fort Randolph, on reef crest, in breaking waves.

Other Panamanian records: This taxon is pictured in Clifton & Clifton (1999) where it is recorded simply as *C. racemosa*.

***Caulerpa racemosa** var. **occidentalis** (J. Agardh) Børgesen (1907: 379, figs 28-29)

Type Locality: upper Gulf of Mexico to Recife, Brazil.

Collections: BW-01109 near Knapps Hole, in sand and on mangrove prop-roots; BW-01337 Cayo Nancy, in sand, ~2-6 m.

Notes: Both specimens exhibited a peltate tendency in certain ramuli. In shaded thalli of BW-01109, branchlets exhibited a peltate morphology while those exposed to more direct sunlight were hemispherical to spherical.

Caulerpa racemosa var. **peltata** (Lamouroux) Eubank in Stephenson (1944: 349)

Type Locality: Antilles, West Indies.

Collections: BW-00109 Dog Island, on coral; BW-00303 Western Point of Isla Mamey on coral; BW-00879 Galeta, creeping over coral, ~5-8 m.

Other Panamanian records: Earle (1972) as *C. peltata* Lamouroux; Taylor (1960) as *C. racemosa* var. *laetevirens* (Montagne) Weber-van Bosse.

Caulerpa serrulata (Forsskål) J. Agardh (1837: 174)

Type Locality: Mokha, Yemen.

Collections: BW-00100 Sail Rock, on coral, ~7 m; BW-00116 Dog Island, in sand, on reef flat; BW-00702 Dog Island, on coral, ~1 m; BW-00981 on rock, between Pedro Pelada and Punta Cacique, ~8 m.

Other Panamanian records: Clifton & Clifton (1999).

Caulerpa sertularioides (S.G. Gmelin) M. Howe (1905: 576)

Type Locality: "in coralliis americanis" (Gmelin 1768).

Collections: BW-00062 Buena Ventura, in sand <2 m; BW-00075 Fort Randolph, in sand; BW-00107 Sail Rock, in sand; BW-00172 Fort Randolph, muddy sand, ~3 m; BW-01070 Isla Grande, in seagrass bed in southwestern cove near hotel (Fig. 15); BW-01108 Knapps Hole, in sand along mangrove fringe; BW-01120 in sand in seagrass bed near mangrove fringe; BW-01331 Barren Rock, on rock submerged in sand, ~22 m; BW-01335 Cayo Nancy, in sand, ~2-6 m (Figs 16-17); BW-01408 Cayos Zapatilla Islet Trio; BW-01449 Off Porvenir Point, in sand ~7 m.

Other Panamanian records: Taylor (1929, 1942, 1960); Clifton & Clifton (1999).

Notes: Specimens collected from the Bocas del Toro region of Panama were morphologically distinct from eastern Panama collections in that the fronds tended to be broader and the distance between pinnules greater (Figs 15-17). It remains to be determined whether there is a genetic basis for these differences.

Caulerpa sertularioides f. **brevipes** (J. Agardh) Svedelius (1906: 114-115, figs 7, 8)

Syntype Localities: West Indies, Pacific Ocean, Sri Lanka, Red Sea.

Other Panamanian records: Taylor (1929, 1942, 1960).

***Caulerpa sertularioides** f. **longiseta** (Bory) Svedelius (1906: 114, fig. 10)

Type Locality: not specified.

Collections: BW-00006 mainland, across from Isla Grande, on reef flat, in breakers; BW-00171 Fort Randolph, muddy sand, ~3 m; BW-00822 Galeta, south lagoon and reef flat, in sand near pier, ~1 m.

***Caulerpa taxifolia** (H. West in Vahl) C. Agardh (1817: 22)

Type Locality: St. Croix, Virgin Islands.

Collection: BW-01336 Cayo Nancy, in sand, 1-6 m.

Caulerpa verticillata J. Agardh (1847: 6)

Type Locality: not specified.

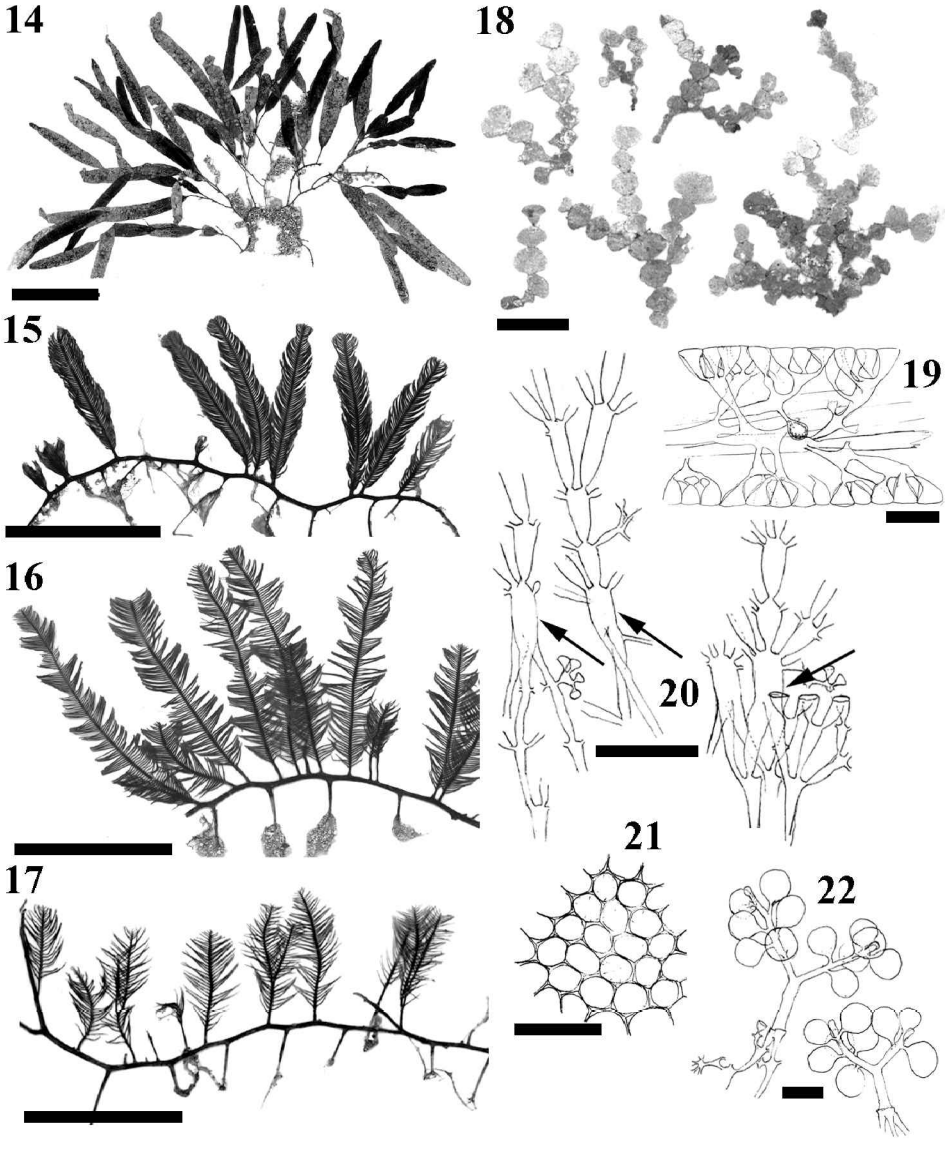


Fig. 14. *Caulerpa prolifera* f. *zosterifolia*. Narrow blades and numerous proliferations of the blades distinguish this form from the nominate form. Scale bar: 5 cm. Figs 15-17. *Caulerpa sertularioides*. Fig. 16. Specimen BW-01070 from eastern Panama. Fig. 16-17. Two individuals of BW-01335 from western Panama that exhibit a wider frond and an overall larger habit but with apparently fewer pinnules per length of frond. Scale bars: Figs 16-18: 5 cm. Figs 18-22. *Halimeda hummii*. Fig. 18. Habit of specimen BW-01300. Fig. 19. Section through a distal segment showing a single layer of secondary utricles. Fig. 20. Fusion of medullary filaments at internodes (arrows). Fig. 21. Surface view of a portion of a de-calcified segment showing rounded utricles. Fig. 22. Gametangia. Scale bars: Fig. 18: 1 cm, Figs 19, 21: 100 mm, Fig. 20: 500 mm, Fig. 22: 200 mm.

Collections: BW-00058 Buena Ventura, in sand < 2 m; BW-00788 Galeta, on mangrove prop-root at surface; BW-01033 Galeta, S. lagoon and reef flat, on mangrove prop-root; BW-01355 Cayo Nancy, on mangrove prop-root.

Other Panamanian records: Clifton & Clifton (1999).

*__Caulerpa verticillata__ f. __charoides__ Weber-van Bosse (1898: 267-268)

Lectotype Locality: Tonga.

Collections: BW-00314 Western Point of Isla Mamey, on coral fragment; BW-00419 Galeta on coral and rock, 7-12 m; BW-01017 Galeta, on rock, 12-15 m; BW-01060 Fort Randolph, epiphytic on *Halimeda opuntia,* over muddy sand, 6 m; BW-01314 Barren Rock, growing over rock, 10-16 m.

Caulerpella Prud'homme van Reine et Lokhorst

*__Caulerpella ambigua__ (Okamura) Prud'homme van Reine et Lokhorst (1992: 114)

Type Locality: Ogasawara-gunto [Bonin Islands], Japan.

Collection: BW-00982 reef flat on western end of Isla Grande.

Notes: Famà et al. (2002) provided the first molecular evidence supporting the recognition of this taxon as belonging to a genus distinct from *Caulerpa* (Prud'Homme van Reine & Lokhorst 1992).

CODIACEAE

Codium Stackhouse

*__Codium intertextum__ Collins et Hervey (1917: 54)

Type Locality: Bermuda.

Collections: BW-00126 Grass Island, on coral; BW-01136 Long Bay Point, tightly adhering to hard substratum, ~10-12 m; Cayos Zapatilla Islet Trio, tightly adhering to rock on bay side of islets.

__Codium isthmocladum__ Vickers (1905: 57)

Type Locality: Barbados.

Collections: BW-00182 Fort Randolph, on coral rubble in sand, ~3 m; BW-00279 Nautilus Dive Club, on coral, ~2 m; BW-00770 Galeta, on coral; BW-00878 Galeta, on coral, ~6-8 m; BW-01090 Peninsula Valiente, dredged from ~29m; BW-01133 Long Bay Point, on hard substratum, ~10-12m; BW-01303 Northeast of Canal de Bocas del Toro, on rock, ~20 m; BW-01411 Cayos Zapatilla Islet Trio, on hard substratum, ~1.5 m.

Other Panamanian records: Taylor (1942, 1960).

*__Codium repens__ P. Crouan et H. Crouan in Vickers (1905: 56-57)

Type Locality: Vieux-Fort, Guadeloupe, West Indies.

Collections: BW-00971 Las Farallones, over dead coral and rock, ~7 m; BW-01071 Isla Grande, on dead coral, ~3-7 m.

OSTREOBIACEAE

Ostreobium Bornet & Flahault

*__Ostreobium quekettii__ Bornet et Flahault (1889: CLXI, pl. IX: figs 5-8)

Lectotype Locality: Le Croisic, Loire-Atlantique, France.

Collection: BW-01123 near Knapps Hole, growing through dead coral.

UDOTEACEAE

Avrainvillea Decaisne

Avrainvillea hayi D. Littler et M. Littler (1992: 390, fig. 9)

Type Locality: Galeta, Panama.

Collections: BW-001187 Long Bay Point, in sand, ~10-12 m; BW-01372 Cayos Zapatilla, exposed side of reef; in sand, 15 m.

Other Panamanian records: Littler & Littler (1992).

*__Avrainvillea longicaulis__ (Kützing) G. Murray et Boodle (1889: 70)

Type Locality: Antilles.

Collection: BW-00986 Galeta.

*__Avrainvillea nigricans__ Decaisne (1842: 108)

Type Locality: West Indies near Guadeloupe.

Collection: BW-00113 Sail Rock, in sand ~7 m.

Avrainvillea rawsonii (Dickie) M. Howe (1907: 510)

Type Locality: Barbados.

Collections: BW-00798 Galeta, on reef flat; BW-00874 Galeta, on reef flat east of station.

Other Panamanian records: Taylor (1942).

Halimeda Lamouroux, nom. cons.

Halimeda copiosa Goreau et E.A. Graham (1967: 433, figs 1-10)

Type Locality: Jamaica.

Collections: BW-00154 Dog Island, among coral; BW-00964 Galeta, on dead coral, ~8 m; BW-01199 Northeast of Canal de Bocas del Toro, ~25 m; BW-01299 Northeast of Canal de Bocas del Toro, in coarse sand, ~15-20 m; BW-01364 Cayos Zapatilla, exposed side of reef, 13-15 m.

Other Panamanian records: Kooistra et al. (1999, 2002).

Halimeda discoidea Decaisne (1842: 102)

Type Locality: stated as "Kamtshatka", but true provenance not known.

Collections: BW-00278 Nautilus Dive Club, on coral, ~6-8 m; BW-00965 Galeta, on dead coral, 8-10 m; BW-01197 Northeast of Canal de Bocas del Toro, ~25 m; BW-01298 Northeast of Canal de Bocas del Toro, on hard substratum under coarse sand, ~15-20 m.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999), Kooistra et al. (1999, 2002).

Halimeda goreaui W.R. Taylor (1962: 173, figs 1-7)

Type Locality: Jamaica.

Collections: BW-00122 Grass Island, on coral, ~5 m; BW-00156 Dog Island, on coral; BW-00797 Galeta, on coral, ~6-8 m; BW-00966 Galeta, on dead coral, ~8-10m; BW-01361 Cayos Zapatilla, exposed side of reef, 10-15 m.

Other Panamanian records: Clifton & Clifton (1999), Kooistra et al. (1999).

Halimeda gracilis Harvey ex J. Agardh (1887: 82)

Type Locality: Sri Lanka.

Collections: BW-00863 Galeta, ~5-8 m; BW-01142 Long Bay Point; BW-01277 Long Bay Point, ~12-15 m; BW-01302 Northeast of Canal de Bocas del Toro, ~15-20 m; BW-01363 Cayos Zapatilla, exposed side of reef.

Other Panamanian records: Kooistra et al. (1999, 2002).

Halimeda hummii D.L. Ballantine (1982: 87-89, figs 1-6, 10)

Type Locality: Puerto Rico.

Collections: BW-00849 Galeta, 5-8 m; BW-01023 Galeta, on rock and dead coral, 10-15 m; BW-01207 Northeast of Canal de Bocas del Toro, on hard substratum, ~25 m; BW-01212 Long Bay Point, ~7-10 m; BW-01300 Northeast of Canal de

Bocas del Toro, on hard substratum, ~15-20 m; BW-01326 Barren Rock, on hard substratum; BW-01373 Cayos Zapatilla, exposed side of reef on hard substratum, 15 m.

Notes: While the anatomical and gross morphological features of these specimens are consistent with the original species description, some ambiguities exist which may encompass the range in variability in this rarely reported species. Basal segments of our specimens were irregularly shaped and similar to those reported by Ballantine (1982), but upper segments of larger thalli were more rounded (Fig. 18). Medullary siphons were as described in Ballantine (1982). Internodal medullary siphons were typically fused at the nodes between segments (Fig. 19), but occasionally traversed the nodes without fusing. This is consistent with the original description in which an "inconsistent disposition" was reported for internodal medullary siphons (Ballantine, 1982, p. 87). From the medulla, secondary utricles branched off, ramifying into either smaller secondary utricles or directly into peripheral utricles (Fig. 20). Ballantine (1982, p. 87) described the secondary utricles as "one, two, or rarely three series of utricles." In *Halimeda* species with thicker segments, the secondary utricles often form a distinct layer between the medulla and the peripheral utricles. However, segments of *H. hummii* are too thin to accommodate space for such a layer and therefore are interwoven among the medullary siphons. In young segments, peripheral utricles appeared rounded in surface view (Fig. 21) becoming polygonal in mature, calcified segments as previously reported. Gametangia, which have not been reported previously for this species, occur as racemose branchlets from distal blade siphons (Fig. 22). This species was originally reported as rare from deep water and nearshore shallow water locales in Puerto Rico, yet it was common along moderately exposed shores in Panama. It can be easily overlooked because its small size may be confused with juveniles of other species of *Halimeda.*

Other Panamanian record: Kooistra et al. 2002.

Halimeda incrassata (Ellis) Lamouroux (1816: 307)

Type Locality: West Indies.

Collections: BW-00071 Fort Randolph, in sand; BW-00175 Fort Randolph, in muddy sand, ~1-3 m; BW-00235 Buena Ventura, in sand; BW-01397 Cayos Zapatilla Islet Trio.

Other Panamanian records: Clifton & Clifton (1999), Kooistra et al. (1999).

Halimeda incrassata f. **tripartita** E.S. Barton (1901: p. 27, fig. 43)

Type Locality: no locality cited; Siboga Expedition.

Collection: BW-01339 Cayo Nancy, in sand, ~2-6 m

Other Panamanian records: Taylor (1929) as *H. tridens* var. *tripartita* Barton; Taylor (1960).

Halimeda monile (Ellis et Solander) Lamouroux (1816: 306)

Type Locality: Jamaica.

Collections: BW-00056 Buena Ventura, in sand; BW-00073 Fort Randolph, in sand; BW-00174 For Randolph, in muddy sand, ~2 m; BW-00199 Grass Island, in sand.

Other Panamanian records: Taylor (1929, 1960); Clifton & Clifton (1999), Kooistra et al. (1999, 2002).

Halimeda opuntia (Linnaeus) Lamouroux (1816: 308)

Lectotype Locality: Jamaica.

Collections: BW-00023 mainland, across from Isla Grande, on reef slope, ~3-5 m; BW-00039 ~11.4 km west of Portobelo, in drift; BW-00176 Fort Randolph on coral, ~1 m; BW-01124 Knapps Hole; BW-01126 Knapps Hole; BW-01466 Cayos Zapatilla Islet Trio; BW-01469 Isla Bastimentos mangrove cay; BW-01487 Knapps Hole.

Other Panamanian records: Taylor (1929, 1942, 1960); Clifton & Clifton (1999), Kooistra et al. (1999, 2002).

***Halimeda opuntia** f. **triloba** (Decaisne) J. Agardh (1887: 84)

Type Locality: Indian Ocean.

Collections: BW-00855 Galeta, on coral, ~5-8 m; BW-01338 Cayo Nancy, in sand, ~2-6 m.

Halimeda simulans M. Howe (1907: 503, pl. 29)

Type Locality: Isla de Culebra, Puerto Rico.

Collections: BW-00123 Grass Island, in sand; BW-01451 Hospital Bight mangrove fringe in sand.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999), Kooistra et al. (1999, 2002).

Halimeda tuna (Ellis et Solander) Lamouroux (1816: 309)

Type Locality: Mediterranean Sea.

Collections: BW-00005 mainland, across from Isla Grande, on coral on reef slope, ~3.5 m; BW-00072 Fort Randolph, on coral; BW-00108 Sail Rock, on coral; BW-00132 Grass Island; BW-00155 Dog Island, on coral; BW-00173 Fort Randolph, on coral,1-3 m; BW-01138 Long Bay Point; BW-01465 Cayos Zapatilla Islet Trio.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999), Kooistra et al. (1999, 2002).

Penicillus Lamarck

Penicillus capitatus Lamarck (1813: 299)

Type Locality: Antilles.

Collections: BW-00063 Buena Ventura, in sand; BW-00084 Fort Randolph, in sand; BW-00177 Fort Randolph, in sand, ~1 m; BW-01343 Cayo Nancy, in sand, 1-4 m; BW-01409 Cayos Zapatilla Islet Trio, in sand, 1-2 m.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999).

Penicillus dumetosus (Lamouroux) Blainville (1834: 553)

Type Locality: Antilles.

Collections: BW-01514 STRI research station, in seagrass beds (*Thalassia*), ~3 m.

Other Panamanian records: Clifton & Clifton (1999).

Penicillus lamourouxii Decaisne (1842: 97)

Type Locality: Bahamas.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999).

Penicillus pyriformis A. Gepp et E. Gepp (1905: 1, pl. 468, fig. 1)

Type Locality: Bahamas.

Collections: BW-00060 Buena Ventura, in sand; BW-00083 Fort Randolph, in sand; BW-00178 Fort Randolph, in sand, ~1 m; BW-01483 Cayos Zapatilla Islet Trio, in sand on bayside of islets; BW-01468 Hospital Bight mangrove fringe, in sand.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999).

Rhipidosiphon Montagne

***Rhipidosiphon floridensis** D. Littler et M. Littler (1990a: 34, figs 1-5)

Type Locality: Northwest of Loggerhead Key, Dry Tortugas, Monroe County, Florida, USA.

Collections: BW-00952 Galeta, in coarse sand, ~10 m; BW-01322 Barren Rock, on coral rubble, 22 m.

Notes: At 3 cm from blade tip to the rhizoidal mass (Fig. 23), specimen BW-00952 was three times larger than the high end of the size range reported by Littler & Littler (1990a). The monosiphonous stipe (Fig. 24), the unistratose blade composed of dichotomously dividing blade siphons, the presence of equal constrictions above the siphon dichotomies and the absence of lateral connections between siphons

(Fig. 25) are features consistent with the species description (Littler & Littler 1990a). While there were many small, hyaline rhizoids which provide additional anchors for adhesion to the coarse sand substratum (Fig. 26), the rhizoidal mass did not branch di- or trichotomously as is depicted in Littler & Littler (1990a). Measurements of the siphons differed from published accounts. The width of siphons in this specimen ranged from 80 mm to 150 mm just below the dichotomies and 50 mm to 70 mm just above the dichotomies. The width of siphons at the margins or tips of the blade ranged from 75 mm to 90 mm below the dichotomy and 45 mm to 50 mm above the dichotomy, while at the base the range was 105 mm to115 mm below the dichotomy and 50 mm to 75 mm above the dichotomy. The width of the stipe was 115 mm. These measurements overlapped with those reported by Littler & Littler (1990a), but the obvious tapering of the siphons which they observed is much more subtle in this specimen.

Rhipiliopsis Kützing

***Rhipiliopsis reticulata** (van den Hoek) Farghaly et Denizot (1979: 181 pl. 8, figs 23-24)

Type Locality: Curaçao, Netherlands Antilles.

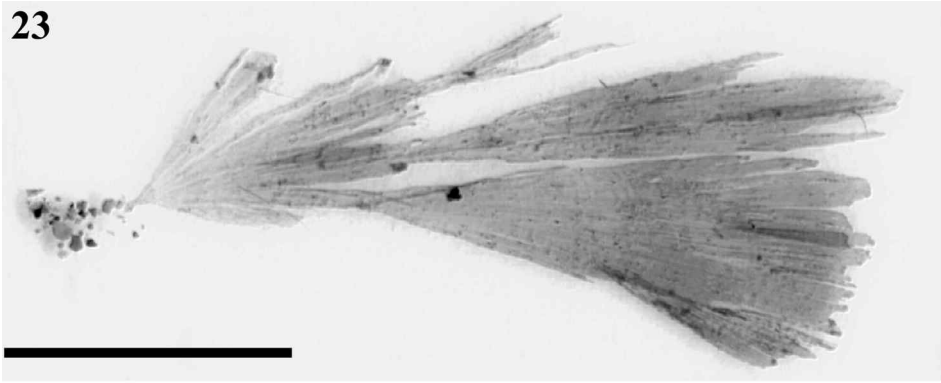
Collections: BW-00420 Galeta, on coral and rock, under ledge, 8-10m; BW-00989 Isla Grande, on dead coral, ~8 m.

Notes: These individuals were easily distinguished from *R. stri* because the lateral siphons tended to be much longer and because the blade is multistratose (Figs 27-28). The longer lateral siphons gave the blade a spongy habit, the open spaces of which tended to accumulate detritus. Littler & Littler (2000) recognized *R. reticulata* as a distinct species from *R. stri*, however Wynne (1998) considered it a synonym of *R. stri*. Phylogenetic analysis of the Udoteaceae based on nuclear ribosomal DNA indicated that there is a genetic basis for the separation of *R. stri* and *R. reticulata* (Kooistra, unpublished data).

Rhipiliopsis stri (S. Earle et J.R. Young) Farghaly et Denizot (1979: 182, pl. 8, fig. 25)

Type Locality: Galeta, Panama.

Figs 23-26. *Rhipidosiphon floridensis* (BW-00952). Fig. 23. Habit. Fig. 24. The monosiphonous stipe of this genus distinguishes it from *Udotea*. Fig. 25. Unistratose blade with equal constrictions above siphon dichotomies. Fig. 26. Monosiphonous rhizoid with fine hyaline rhizoidal extensions. Scale bars: Fig. 23: 1 cm, Figs 24-26: 100 mm. Figs 27-28. *Rhipiliopsis reticulata* (BW-00420). Fig. 27. Portion of thallus at the distal margin of the blade showing the multi-layered blade siphons (compare to the unistratose *R. stri* (Fig. 29). Fig. 28. Portion of blade showing elongate lateral blade siphons and large open spaces. Scale bars: Figs 27-28: 100 mm. Fig. 29. *Rhipiliopsis stri* (BW-00985). Portion of blade showing a single layer of dichotomously branched blade siphons with short laterals. Short lateral blade siphons creates a tighter blade in contrast to the comparatively open blade of *R. reticulata* (compare to Figs 27-28). Scale bar: 100 mm.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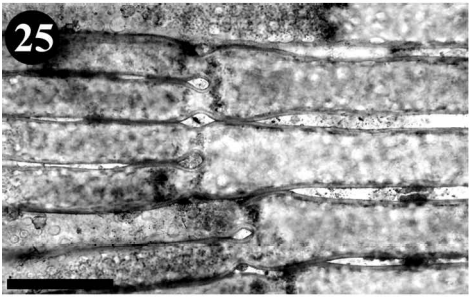
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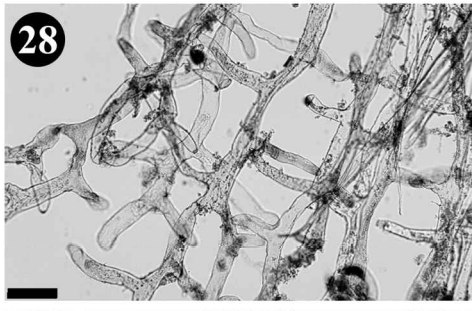
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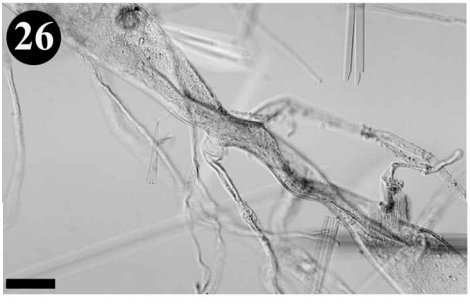
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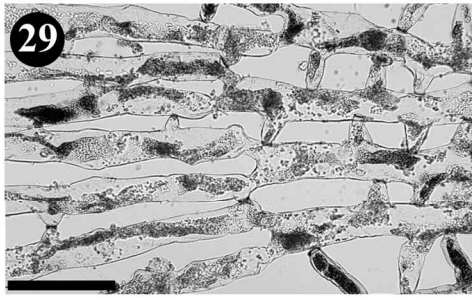
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Collections: BW-00868 Galeta, on shell fragment, ~6-8 m; BW-00985 Las Farallones, on vertical face of rock, ~7 m (Fig. 29); BW-01031 Galeta, on sponge, coral and rock, ~12-15 m.

Other Panamanian records: Earle & Young (1972) as *Siphonoclathrus stri* S. Earle et J.R. Young.

Rhipocephalus Kützing

Rhipocephalus phoenix (J. Ellis et Solander) Kützing (1843: 311)

Type Locality: Antilles.

Collection: BW-01515 tip of San Blas Peninsula near Porvenir, in sand, ~0.25 m, among abundant *Penicillus capitatus.*

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999).

Udotea Lamouroux

Udotea abbottiorum D. Littler et M. Littler (1990b: 210, fig. 1)

Type Locality: Content Keys, Monroe County, Florida, USA.

Collection: BW-00751 Galeta, in sand.

Other Panamanian records: Littler & Littler (1990b); Clifton & Clifton (1999).

Udotea caribaea D. Littler et M. Littler (1990b: 211, fig. 2)

Type Locality: Tobacco Range, Belize.

Other Panamanian records: Clifton & Clifton (1999).

Udotea conglutinata (Ellis et Solander) Lamouroux (1816: 312)

Lectotype Locality: Bahamas.

Other Panamanian records: Taylor (1942, 1960).

Udotea cyathiformis Decaisne (1842: 106)

Type Locality: Guadeloupe, Lesser Antilles.

Collections: BW-01416 Cayos Zapatilla Islet Trio, in sand, 10 m; BW-01439 near Shepard Bank, in sand, 10 m.

Other Panamanian records: Clifton & Clifton (1999).

Udotea cyathiformis var. **flabellifolia** D. Littler et M. Littler (1990b: 220, fig. 7)

Type Locality: San Blas Islands, Republic of Panama.

Other Panamanian records: Littler & Littler (1990b).

*__Udotea dotyi__ D. Littler et M. Littler (1990b: 223, figs 9d, e, 10)

Type Locality: Tobago Cays, Grenadines, Lesser Antilles.

Collections: BW-01182 Long Bay Point, in sand, ~10-12 m; BW-01381 Barren Rock, in sand, 22 m.

Udotea flabellum (Ellis et Solander) M. Howe (1904: 94)

Type Locality: West Indies.

Collections: BW-00081 Fort Randolph, in sand, BW-00082 Fort Randolph, in sand; BW-00133 Grass Island, in sand; BW-00180 Fort Randolph, in sand, ~1 m; BW-01304 Northeast of Canal de Bocas del Toro, in sand, ~15-20m; BW-01351 Cayo Nancy, in sand, 2-6 m.

Other Panamanian records: Taylor (1942, 1960); Clifton & Clifton (1999).

Udotea looensis D. Littler et M. Littler (1990b: 232, fig. 15)

Type Locality: Looe Key, Monroe County, Florida, USA.

Other Panamanian records: Littler & Littler (1990b).

*__Udotea luna__ D. Littler et M. Littler (1990b: 232-235, fig. 15)

Type Locality: Content Keys, Monroe County, Florida, USA.

Collections: BW-00059 Buena Ventura in sand; BW-00134 Grass Island, in sand.

Udotea wilsonii A. Gepp, E. Gepp et M. Howe in A. Gepp et E. Gepp (1911: 130-131, 144-145, pl. 7; fig. 66; pl. 8 figs 67-68)

Type Locality: North End, Salt Key Bank, Anguilla Isles, Bahamas.

Other Panamanian records: Littler & Littler (1990b).

DASYCLADALES

DASYCLADACEAE

Neomeris Lamouroux

Neomeris annulata Dickie (1874: 198)

Type Locality: Mauritius.

Collections: BW-00111 Sail Rock, on coral; BW-00179 Fort Randolph, on coral rubble in sand, ~3 m; BW-01059 Fort Randolph, on sunken log and coral rubble in muddy sand, 6 m.

Other Panamanian records: Taylor (1929, 1960).

POLYPHYSACEAE

Acetabularia Lamouroux, nom. cons.

Acetabularia crenulata Lamouroux (1816: 249, pl. 8: fig. 1)

Type Locality: Caribbean Sea.

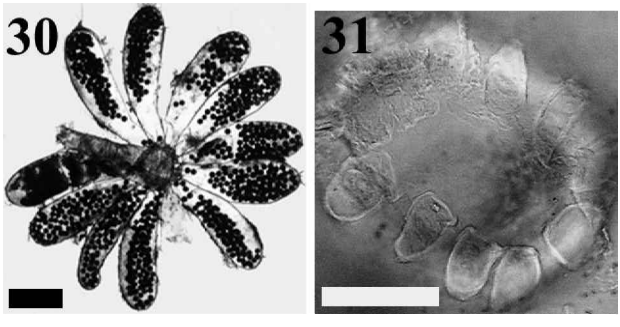
Collections: BW-00875 Galeta, South lagoon and reef flat, on rock over sand; BW-01344 Cayo Nancy, on mangrove prop-roots and coral rubble, 1-2 m.

Other Panamanian records: Earle (1972) reported this taxon and an undetermined species.

***Acetabularia polyphysoides** P. Crouan et H. Crouan in Mazé et Schramm (1878: 42)

Type Locality: Pointe-à-Pitre, Guadeloupe, Lesser Antilles.

Collection: BW-00192 Fort Randolph, on coral fragment in sand among *Codium isthmocladum*, *Agardhiella subulata* (C. Agardh) Kraft et M. J. Wynne and *Polysiphonia* sp., ~3 m (Fig. 30).



Figs 30-31. *Acetabularia polyphysoides* (BW-00192). Fig. 31. Cap morphology showing unfused rays and gametangia. Fig. 32. Corona superior showing elliptically arranged protrusions. Scale bars: Fig. 31: 1 mm, Fig. 32: 40 mm.

Notes: The number of gametangia per ray in this specimen was ~60 (Fig. 30), which is considerably greater than the 15-40 gametangia per ray reported by Berger & Kaever (1992). It also differed from the features reported by Berger & Kaever

(1992) in having blunt versus triangular tips, and a cap diameter of 5 mm versus 2 mm to 4 mm. Consistent features included unfused rays (Fig. 30), and 6-9 protuberances per segment of the corona superior arranged elliptically (Fig. 31). Because this species is the only one that has so few rays and so many protuberances, we simply regard this specimen as a variant of the typical morphotype.

Acicularia D'Archiac

***Acicularia schenkii** (K. Möbius) Solms-Laubach (1895: 33, pl. 3 figs 4, 9, 11, 12, 14, 15)

Type Locality: Cabo Frio, Brazil.

Collection: BW-01345 Cayo Nancy, 4-6 m.

Discussion

Green algal diversity along the Caribbean coastline of Panama has been underestimated previously, a finding that Wysor & DeClerck (2003) also reported with regard to marine phaeophyte diversity in Panama. Earle (1972) reported 34 taxa of marine Chlorophyta (excluding taxa identified only to genus). In this updated list of the Caribbean green algae of Panama, 31 species and 10 sub-specific entities are reported new for Panama. An additional 20 taxa not appearing in Earle's (1972) comprehensive list are reported from the literature, bringing the total number of green algae known for this area to 79 species and 16 varieties/forms.

The increase in algal diversity relative to Earle's (1972) compilation represents an increase in known algal diversity of approximately 179%. Despite the increase, this figure probably represents an underestimation of chlorophyte diversity based on diversity comparisons with nearby floras. Table 2 shows a short list of comparisons of species diversity along coastlines of nearby countries as well as Puerto Rico. Soto & Ballantine (1986) listed 58 green algal species and 9 sub-specific entities (varieties or forms) for the Caribbean coast of Costa Rica. Of these records, 23 are not known in the Panama flora. Similarly, in a report on the marine flora of the Chocoano region of Colombia (Bula-Meyer & Schnetter 1988) in which 31 species of green algae are reported, 12 species are unknown in the Caribbean Panama flora. Five additional green algal records appear in an earlier report (Bula-Meyer 1986) that are also absent from the present study. Bula Meyer (1998) reported 120 Chlorophyta from the Caribbean coast of Colombia, a flora nearly half again as rich as that of neighboring Panama.

The increase in known algal diversity is attributed to sampling over an extended period of time (10 months), to the extensive use of SCUBA diving, and to logistical services provided by STRI field stations at Bocas del Toro and Galeta, which allowed exploration of habitats previously difficult to access. Another factor related to sampling effort is the care with which small and cryptic species were sought. Since we were

Table 2. Documented green algal diversity of selected countries bordering the Caribbean Sea. Note, sub-specific taxa have been excluded from diversity estimates.

Country	# Chlorophyta	# species not represented in flora of Panama	Source
Puerto Rico	136	66	Ballantine & Aponte (2002)
Colombia	120	no list available	Bula-Meyer (1998)
Panama	83	—	this study
Belize	72	26	Littler & Littler (1997)
Costa Rica	58	24	Soto & Ballantine (1986)
Honduras	38	3	Ogden (1998)
Nicaragua	34	9	Phillips et al. (1982)

not only interested in algal diversity, but also the evolution of particular groups present in the Panamanian flora (e.g., Kooistra et al. 2002, Wysor 2002), special attention was paid to diminutive species in select genera (e.g., *Cladophoropsis*, *Halimeda, Phyllodicyton, Rhipiliopsis*). For example, we collected many specimens believed to be juveniles of *Halimeda goreaui*. Microscopic examination revealed these specimens to be *Halimeda hummii*, a species previously only recorded from deep water off Puerto Rico (Ballantine 1982). We encountered this species frequently and suspect that it has a much broader distribution throughout the Caribbean Sea.

Conclusions

The large number of species from nearby floras that are absent from the Panamanian flora suggests that many species have been overlooked or remain unidentified in available collections. Nevertheless, Panama's green algal flora is among the richest of Central America and the Caribbean Sea in general. Continued investigation of the marine flora of Panama will undoubtedly reveal more species, especially when particularly smaller sized species, as well as epi- and endophytes become the focus of detailed study.

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