

## An annotated list of marine Chlorophyta from the Pacific Coast of the Republic of Panama with a comparison to Caribbean Panama species

by

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**Abstract:** Recent study of marine macroalgal diversity of the Republic of Panama has led to a substantial increase in the number of seaweed species documented for the country. In this updated list of marine algae based on collections made in 1999 and reports from the literature, 44 Chlorophyta (43 species and one variety) are documented for the Pacific coast of Panama, including 27 new records. A comparison of chlorophyte diversity along Caribbean and Pacific coasts revealed greater diversity at nearly all taxonomic levels in the Caribbean flora. Differences in environmental regime (e.g., absence of sea grasses, lower abundance and diversity of hermatypic corals, and greater tidal range along the Pacific coast) explained some of the discrepancy in diversity across the isthmus. Fifteen taxa were common to Caribbean and Pacific coasts, but the number of amph-isthmian taxa nearly doubled when taxa from nearby floras were included in the estimate. These taxa may represent daughter populations of a formerly contiguous population that was severed by the emerging Central American Isthmus. As indicated by their distribution throughout all tropical oceans, survivors of this transition are probably species that tolerate a broad range of environmental conditions, but some may represent recent introductions mediated by natural or anthropogenic vectors.

**Key words:** amph-isthmian species, Central American Isthmus, Chlorophyta, eastern tropical Pacific, macroalgal diversity, Panama, species list, *Struveopsis robusta*.

**Resume:** Un estudio reciente de la diversidad de macroalgas marinas de la República de Panamá ha incrementado el número de especies de algas marinas reportadas para este país. En esta lista actualizada de algas marinas basada en colectas realizadas en 1999 y reportes bibliográficos, 44 Chlorophyta son reportadas para la costa del Pacífico de Panamá, incluyendo 27 registros nuevos. Una comparación entre la diversidad de clorofitas a lo largo de las costas del Pacífico y del Caribe revelaron una diversidad mas grande en la flora Caribeña en casi todos los niveles taxonómicos. Diferencias en los regímenes ambientales (por ej. Ausencia de pastos marinos, menor abundancia y diversidad de corales hermatípicos, y un rango intermareal mas grande a lo largo de la costa del Pacífico) explican en parte la discrepancia entre la diversidad a través del istmo. Quince taxa fueron comunes a las

costas Caribeña y del Pacifico, pero el numero de taxa anfi-ístmicos casi se duplicó cuando taxa de floras cercanas fueron incluidos en la estimación. Estos taxa podrian representar poblaciones descendientes de una poblacion originalmente contigua que fue separada por la emergencia del istmo Centro Americano. Como es indicado por sus distribuciones a lo largo de los océanos tropicales, los sobrevivientes de esta transicion son probablemente especies que toleran un amplio rango de condiciones ambientales, pero algunos pueden representar introducciones recientes por medio de vectores naturales o antropogénicos.

## Introduction

The state of knowledge regarding Panama's Pacific marine flora is indicative of the relatively poorly studied floras of tropical Pacific America in general. Taylor's (1945) and Dawson's (Dawson & Beaudette 1959; Dawson 1960, 1961, 1962) contributions to documenting algal species distributions in Central America were significant; however, there have been few subsequent attempts to fill in the geographic sampling gaps throughout tropical Pacific America (here defined as the region between Guatemala in the north, to Ecuador in the south, including the Galápagos Islands). Approximately 100 green algal species are known from this region (Howe 1914, Taylor 1945, Dawson 1960, Dawson 1961, Dawson 1962, Dawson 1964, Bird & McIntosh 1979, Schnetter & Bula Meyer 1982). Nevertheless, the best documented floras, El Salvador, Colombia and Ecuador (including the Galápagos Islands), harbour only a fraction of that diversity: 18, 29 and 37 species respectively. One of the few reports published on marine algae from this region in the past three decades is Earle's (1972) compilation of the marine algae of Panama, which included 14 Chlorophyta (excluding genera not identified to species) for the Pacific coast. Given the small number of investigations and greater macroalgal diversity in neighboring Colombia, and elsewhere throughout tropical Pacific America, Earle's estimate of green algal diversity was likely to have been an underestimate of actual diversity.

In the present study, 44 green algal taxa are documented for the Pacific coast of the Republic of Panama, including 27 new records and all previously documented species. This list, in combination with the updated list of marine Chlorophyta of Caribbean Panama (Wysor & Kooistra 2003), provides a foundation for studying the biogeography of tropical marine floras in the vicinity of the Central American Isthmus. The Panamanian flora is of particular interest because it probably represents the most recent stage of geographic isolation as the Central American Isthmus emerged. The Caribbean and Pacific marine floras are compared, and differences and similarities discussed in the light of environmental and evolutionary processes.

## Materials and methods

Qualitative sampling of algal diversity was undertaken across diverse habitats throughout Pacific Panama (Fig. 1, Table 1). Most habitats that were sampled have been described in detail in terms of coral composition, coral ecology and physical environmental characteristics (e.g., Glynn 1972, Glynn & Stewart 1973, Glynn 1982, D'Croz & Robertson 1997, Glynn & Maté 1997). Additional information regarding community composition of tropical intertidal systems is documented in Menge & Lubchenco (1981) and Menge et al. (1986a, b). In addition to coral habitats, extensive mangrove forests are common, but sea grasses are absent altogether. Brief habitat descriptions of collection sites (Fig. 1) are provided in Table 1.

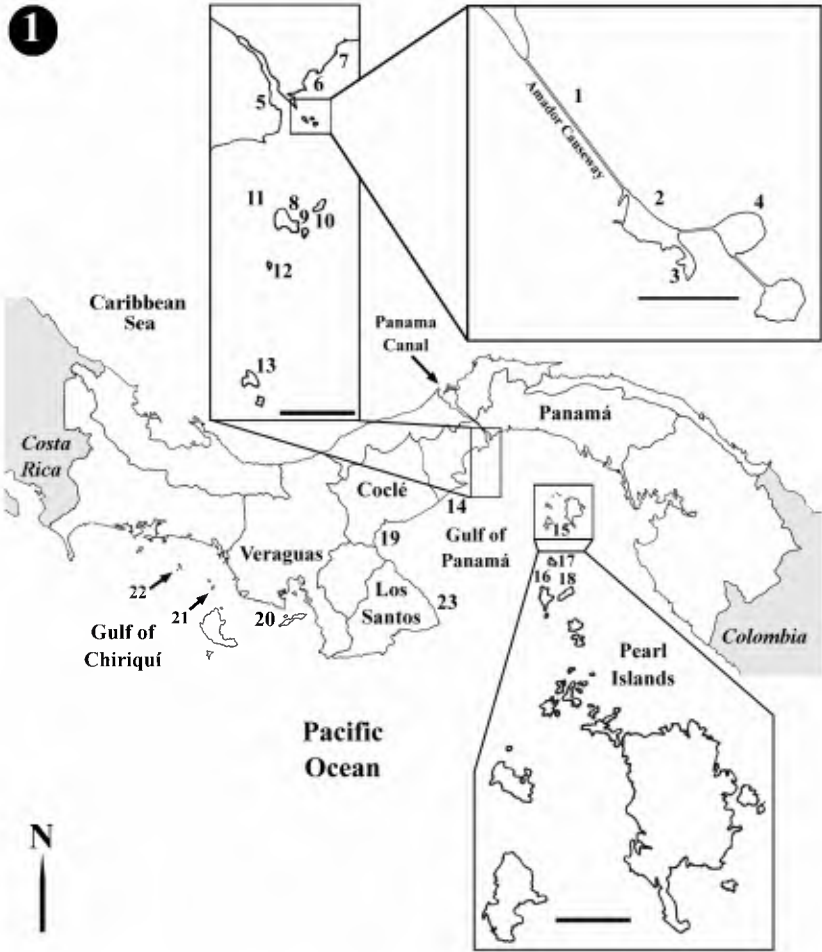


Fig. 1. Map of collecting sites for Pacific Panama. Amador Causeway, 1; Naos Island, 2; Culebra Point, 3; Perico Island, 4; Fort Rodman, 5; Paitilla Point, 6; Costa del Este, 7; Taboga Island, 8; Urabá Island, 9; Tobaguilla Island, 10; Melones Island, 11; Chama Island, 12; Otoque Island, 13; Rio Mar, 14; Pearl Islands, 15; Saboga Island, 16; Pacheca Island, 17; Contadora Island, 18; Tres Piscinas, 19; Cebaco Island, 20; Uva Island, 21; Secas Islands, 22; Iguana Island, 23. Naos Island inset after Defense Mapping Agency (1995). Pearl Islands and Taboga Islands inset after Instituto Geográfico Nacional “Tommy Guardia” (1998). Political boundary map after National Geographic (1999).

Collection excursions were staged from the Smithsonian Tropical Research Institute (STRI) laboratories on Naos Island, Panama where samples could be maintained in running seawater aquaria following collection. A total of 44 independent collections were made from 36 different sites. Permission to collect specimens was granted by Autoridad Marítima de Panamá, Dirección General de Recursos Marinos y Costeros.

Samples were collected from February to November 1999 by snorkeling and wading throughout the intertidal to the splash zone and by SCUBA diving to a maximum depth of 20 m. Nearly 40 man-

Table 1. Collection sites from 1998 survey of Pacific 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. For detailed site descriptions of the Perlas, Contreras and Secas Islands see Glynn & Maté (1997) and Glynn & Stewart (1973).

Province	Site Name	Lat. (°N)	Long. (°W)	Notes
Panama	East side Amador Causeway, Balboa, Panama	8° 55.7'	79° 33.7'	An elevated causeway lined with large boulders, flanking Pacific entrance to Panama Canal.
	Naos Island	8° 55.2'	79° 31.8'	Large boulders and sandy shores
	Culebra Point	8° 46.9'	79° 31.9'	Small sandy beach facing Panama Canal entrance, flanked by barnacle-encrusted boulders and numerous tide pools.
	Perico Island	8° 55.1'	79° 31.5'	Cobble beach and tide pools to the North and South. Emergent bedrock rises steeply out of the water to the East.
	Fort Rodman	8° 56.5'	79° 34.1'	Extensive mudflat on low tide fringed by dense mangroves.
	Paitilla Point	8° 58.1'	79° 31.0'	Emergent bedrock and tidepools near Panama Harbor.
	Costa del Este	9° 01.5'	79° 29.0'	Muddy banked, mangrove-fringed river mouth.
	Taboga Island	8° 47.9'	79° 33.2'	Ahermatypic corals, coral and rock rubble fields over sand, and discarded steel beams near harbor.
	Urabá Island	8° 46.8'	79° 32.4'	Gradually sloping rock and coral rubble field between Urabá and Taboga
	Tobaguilla Island	8° 48.1'	79° 31.2'	Protected cove on south side with steep rock facies and boulders at the waterline sloping abruptly to sandy bottom.
	Melones Island	8° 48.9'	79° 37.5'	Bean-shaped island with subtle cove on north side and sandy beach extending into subtidal zone.
	Chama Island	8° 48.0'	79° 39.5'	Small rock outcrops with steep slopes below waterline and swift currents. Black corals and sponges abundant.
	Otoque Island	8° 35.1'	79° 36.5'	Rock cobble and boulders interspersed among fine muddy sand.
	Rio Mar	8° 30.5'	79° 57.1'	Expansive sand and cobble beach with shallow (<0.5 m) tide pools.

Province	Site Name	Lat. (°N)	Long. (°W)	Notes
	Pearl Islands			Archipelago southeast of Panama City in Gulf of Panama.
	Bartolome Island	8° 38.8'	79° 02.1'	Dredging over coarse sandy bottom.
	Between Contadora Island and Chapera Island	8° 37.0'	79° 02.0'	Dredging over coarse sandy bottom.
	Between Chapera Island and Mogo Mogo Island	8° 34.7'	79° 02.2'	Dredging over coarse sandy bottom.
	Saboga Island	8° 36.0'	79° 03.5'	Extensive sand plain with <i>Pocillopora</i> and occasional <i>Gardineroseris</i> corals.
	Contadora Island	8° 38.0'	79° 02.5'	Similar to Saboga Island.
	Pacheca Island	8° 44.0'	79° 03.0'	Similar to Saboga Island.
Coclé	Tres Piscinas, near Aguadulce	8° 13.5'	80° 27.5'	Shallow (<0.5 m) tidepools with lush algal vegetation, in expansive intertidal zone of ~2 km. Dense mangroves with heavy algal fouling fringed high tide mark.
Veraguas	Cebaco Island	7° 32.0'	81° 16.0'	Elongate island near entrance to Gulf of Montijo.
	Uva Island (Contreras Islands)	7° 47.5'	81° 46.0'	2.5 ha patch reef (Glynn & Maté 1997). sand, mud and rubble bottom.
Chiriquí	Unnamed Island (Secas Islands)	7° 59.0'	82° 1.0'	Fringing pocilloporid coral reef and sloping rock/coral rubble plain.
	Cavada Island (Secas Islands)	8° 02.0'	82° 01.0'	Pocilloporid coral reef, in places overgrown with <i>Acanthophora spicifera</i> . Extensive turfs of macrophytic red algae formed around cores of coral rubble

hours were logged underwater for collecting seaweeds using SCUBA. Additional samples were obtained from dredging excursions of other researchers at STRI. 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 molecular genetic studies (e.g., Famà et al. 2002, Wysor 2002, Kooistra 2002). 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).

## Annotated Species List

This annotated list serves as a comprehensive catalogue of all marine green macroalgal species known to the Pacific coast of the Republic of Panama. For each species, the type locality, references to previous reports from Panamanian waters and other pertinent information relating to morphology or ecological distribution are listed. New records for the Republic of 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).

### PHAEOPHILALES

#### PHAEOPHILACEAE

#### **Phaeophila** Hauck

**Phaeophila dendroides** (P. Crouan et H. Crouan) Batters (1902: 13)

Type Locality: Brest, Finistère, France.

Other Panamanian records: Taylor (1945) as *P. engleri* Reinke.

### ULVALES

#### ULVACEAE

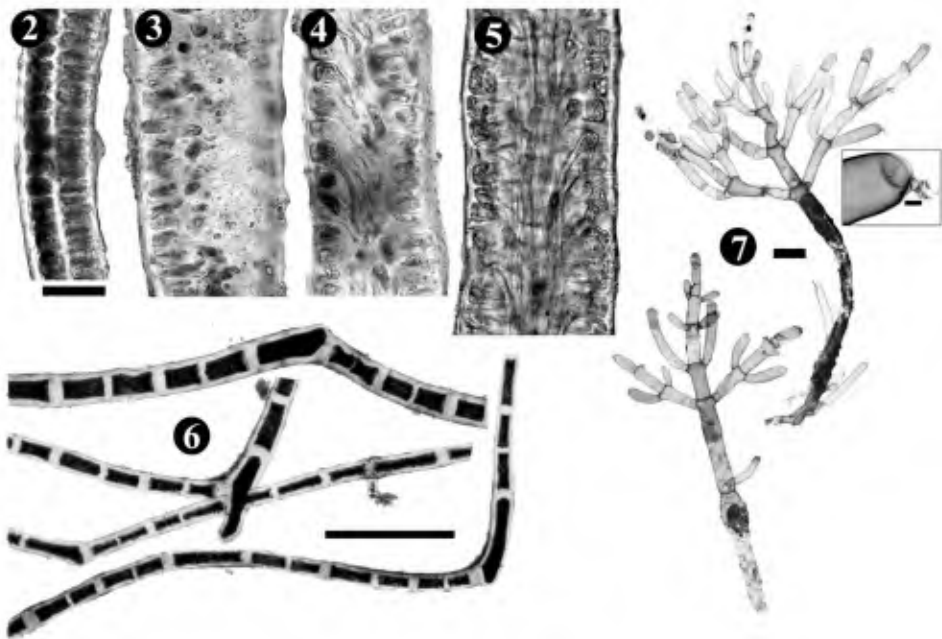
#### **Chloropelta** Tanner

\***Chloropelta caespitosa** Tanner (1980: 130, figs 2-49)

Type Locality: Point Fermin, San Pedro, California, USA.

Collections: BW-00045 east side Amador Causeway, on emergent rock; BW-00213, BW-00257 Culebra Point, on boulder in tidepool.

Notes: Bi-stratose blades (Fig. 2), which measured 3-7 mm in diameter and approximately 35  $\mu\text{m}$  in thickness, developed from a central point of attachment and were composed of isodiametrical cells with a single peripheral chloroplast. In surface view the cells appeared to be paired, with chloroplasts appressed to the unshared wall. A cross section through the central region of specimen BW-00257 (Fig. 3) revealed multiple cell layers consisting of cortical cells that elongated periclinally towards the central part of the thallus (Fig. 4). The arrangement of cortical cells resembled cortical cells at the base of *E. lingulata* thalli (Fig. 5). The similarity in morphology between *Chloropelta* and *Enteromorpha*, suggests that the loose generic boundary between *Ulva* and *Enteromorpha* (e.g., Blomster et al. 1998, Blomster et al. 1999, Tan et al. 1999) also encompasses the genus *Chloropelta*. This idea was recently substantiated on the basis of DNA sequence data (Hayden & Waaland 2003). These records represent a significant range extension for this species, which has not otherwise been recorded south of La Jolla, CA, USA (Tanner 1980).



Figs 2-4. Cross sections of *Chloropelta caespitosa* (BW-00257). Fig. 2. Bi-stratose blade. Fig. 3. Rhizine-like appearance of cells in the central part of the thallus, near the point of attachment. Fig. 4. Cortical cell extensions projecting periclinally into the central portion of the blade. Scale bar: Figs 2-4: 40  $\mu$ m. Fig. 5. Cortical cell extensions in the basal region of *Enteromorpha lingulata* (BW-00228), resembling the central portion in a specimen of *Chloropelta caespitosa* (Fig. 4). Scale bar as in Figs 2-4. Fig. 6. *Rhizoclonium rhizophyllum* (BW-00997) filaments showing distinctive deflections in the unbranched filaments. Scale bar: 0.5 mm. Fig. 7. *Struveopsis robusta* (BW-00657). Two specimens each bearing a pseudo-reticulum in which second- and third-branches are not united by tenacula; only a single tenaculum was observed in these specimens (inset). It is clearly distinct from a torn or degraded branchlet and bears rhizoidal outgrowths. Scale bar: 1 mm, inset: 100  $\mu$ m.

### Enteromorpha Link ex Nees

\**Enteromorpha flexuosa* (Wulfen) J. Agardh (1883: 126-128)

Type Locality: Adriatic Sea.

Collections: BW-00258 Culebra Point, on pebble in tidepool; BW-00514; BW-00575 Unnamed Island, on coral rubble; BW-01044 Culebra Point, from algal turf on emergent rock at low tide.

Notes: In general, specimens were very small, rarely reaching more than 1 cm in height.

*Enteromorpha lingulata* J. Agardh (1883: 143)

Syntype Localities: North Atlantic, Gulf of Mexico, Tasmania, New Zealand.

Collections: BW-00228 Culebra Point, on emergent rock at low tide.

Other Panamanian records: Taylor (1945).

Notes: Specimen BW-00228 was abundantly branched near the base and was composed of rectangular cells that were arranged in a nearly linear fashion. This species is difficult to distinguish from *E. flexuosa* subsp. *paradoxa* (C. Agardh) Bliding in gross morphology, but the lack of uniseriate branches in *E. lingulata* seems to distinguish the two species. Littler & Littler (2000) noted that branches in *E. lingulata* are indistinguishable from the primary axes. In the Panamanian material, however, the diameter of the primary axes tends to be greater and increases towards the apex, as noted by Taylor (1945).

**Enteromorpha prolifera** (Müller) J. Agardh (1883: 129 pl. 4)

Type Locality: Denmark.

Other Panamanian records: Glynn & Stewart (1973).

## CLADOPHORALES

### CLADOPHORACEAE

#### **Chaetomorpha** Kützing

**Chaetomorpha indica** (Kützing) Kützing (1849: 376)

Type Locality: Tranquebar, Tamil Nadu, India.

Other Panamanian records: Dawson (1960).

\***Chaetomorpha javanica** Kützing (1847: 773)

Type Locality: Java, Indonesia.

Collections: BW-00814 Melones Island, growing on rusting food can, ~3 m.

Notes: These specimens were shorter than those of Schnetter & Bula Meyer (1982) at 3-5 cm, but the lack of constrictions and cells one to two times longer than wide are features consistent with their interpretation of this species.

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

Syntype Localities: Nakskov and Rødby, Denmark

Collections: BW-00936 Tres Piscinas, on mangrove trunk.

#### **Cladophora** Kützing

\***Cladophora coelothrix** Kützing (1843: 272)

Type Locality: Golfo di Genova, Italy.

Collections: BW-00935 Tres Piscinas, forming dense mounds and sometimes meadows below mangroves, near mangrove fringe.



\***Cladophora flexuosa** (O.F. Müller) Kützing (1843: 270)

Type Locality: Denmark.

Collections: BW-00898 This specimen was collected from a running seawater aquarium at STRI fed by the Bay of Panama.

\***Cladophora laetevirens** (Dillwyn) Kützing (1843: 267)

Type Locality: Swansea, Glamorgan, Wales.

Collections: BW-00249 Culebra Point; BW-00901 from running seawater aquarium at STRI fed by the Bay of Panama.

\***Cladophora microcladioides** Collins (1909a: 17-18, pl. 78: figs 2, 3)

Type Locality: San Pedro, CA, USA.

Collections: BW-00229 Culebra Point, from turf on emergent rock at low tide; BW-00246, BW-00247, BW-00248, BW-00306 Culebra Point, in rock crevices.

\***Cladophora montagneana** Kützing (1849: 415)

Type Locality: Cuba.

Collections: BW-00233 Taboga Island, on floating dock at ferry landing, above water line, BW-00250 Culebra Point, tangled at base of *C. microcladioides* in rock crevice.

**Cladophora panamensis** W.R. Taylor (1945: 56-57)

Type Locality: Bahía Honda, Panama.

\***Cladophora socialis** Kützing (1849: 416)

Type Locality: Tahiti.

Collections: BW-00234 Taboga Island, turf on rock, ~1 m at low tide; BW-00449, BW-00463, BW-00466, BW-00487, BW-00500, BW-00512, BW-00533, Uva Island, on coral; BW-00618 Unnamed Island, epiphytic on *Galaxaura rugosa* (Ellis et Solander) Lamouroux., BW-00625 Unnamed Island, on coral, BW-00667 west side Iguana Island; BW-00903 running seawater aquarium at STRI fed Bay of Panama seawater.

### **Rhizoclonium** Kützing

\***Rhizoclonium rhizophilum** W.R. Taylor (1945: 55)

Type Locality: Archipiélago de Colón, on an old stump on the open beach at Pta. Albemarle, I. Isabela, Galápagos Islands, Ecuador.

Collections: BW-00937 Tres Piscinas, on mangrove; BW-00997 Fort Rodman, on mangrove prop roots, branches and pneumatophores.

Notes: These specimens are consistent with Taylor's description of a large diameter *Rhizoclonium*. Filaments measured approximately 100 µm in diameter and consist of cells about 1.1-2.1 times long as broad. Filaments were unbranched but often deflect from a distinct barrel-shaped cell (Fig. 6).

**Rhizoclonium riparium** (Roth) Harvey (1849 [1846-1851]: pl. CCXXXVIII)

Type Locality: Norderney, East Frisian Islands, Germany.

Collections: BW-01003 Fort Rodman, on mangrove trunk ~1.25 m above mud flat (probably rarely submerged); BW-01004 Fort Rodman, ~1.25 m above mud flat on wooden tower

Notes: Specimen BW-01003 may represent *R. riparium* var. *implexum* (Dillwyn) Rosenvinge, which is characterized by fewer, shorter branchlets. In contrast to BW-01003, specimen BW-01004 was much more abundantly branched. The inflated apical cell that has been reported in Caribbean material (e.g., Littler & Littler 2000) was rarely observed in Panamanian material of this species.

Other Panamanian records: Dawson (1960) as *R. kochianum* Kützing.

#### BOODLEACEAE

##### **Boodlea** G. Murray et De Toni

\***Boodlea cf. composita** (Harvey) F. Brand (1905: 187-190, pl. 6 figs 28-35)

Type Locality: Mauritius.

Collections: BW-00480 Uva Island, epiphytic on *Galaxaura* sp. The three dimensional, reticulate thallus of this specimen is consistent with the morphological concept of *Boodlea composita* (e.g., Taylor 1960). Recent molecular studies of reticulate cladophoralean taxa (Wysor 2002), however, have revealed that morphological features of the reticulum do not necessarily correspond to phylogenetically defined species. In the absence of molecular evidence, this taxonomic designation is considered equivocal.

##### **Phyllocladyon** J.E. Gray

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

Type Locality: Freemantle, Western Australia.

Collections: BW-00920 Urabá Island, on coral rubble.

#### SIPHONOCLADACEAE

##### **Cladophoropsis** Børgesen

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

Type Locality: St. Croix, Virgin Islands.

Collections: BW-00043, BW-00044 east side Amador Causeway, turfs on emergent rocks; BW-00230 Culebra Point, in turf on emergent rock at low tide; BW-01481 Rio Mar, on emergent rocks at low tide.

Other Panamanian records: Earle (1972).

### **Struveopsis** Rhyne et H. Robinson

\***Struveopsis robusta** (Setchell et Gardner) Rhyne et H. Robinson (1968: 470)

Type Locality: Isla Tortuga, Baja California Sur, Mexico.

Collections: BW-00657 west side Iguana Island; BW-01505 Santa Catalina, Perlas Islands.

Notes: Specimen BW-00657 (Fig. 7) conformed to the description of a *Struvea*-like species that fails to form a reticulate thallus due to the rarity of tenacula (Rhyne & Robinson 1968). Only one tenaculum was observed among the Panamanian material (Fig. 7 inset). The taxonomic status of this genus has been questioned (Egerod 1975, Kraft & Wynne 1996), but comparative DNA sequence analysis revealed these specimens to be distinct from *Phyllocladion anastomosans*, *P. pulcherrimum* J.E. Gray, *Cladophoropsis membranacea* and *Struvea elegans* Børgesen (Wysor 2002). No intercalary cell divisions were observed in the Panamanian material, suggesting that it undergoes segregative cell division and that it is more closely allied with *Struvea* than either *Phyllocladion* or *Cladophoropsis*. As noted by Kraft & Wynne (1996), careful studies are needed to clarify the relationship of this rarely reported species with other members of the Siphonocladaceae.

## BRYOPSIDALES

### BRYOPSIDACEAE

#### **Bryopsis** Lamouroux

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

Type Locality: Mediterranean coast of France.

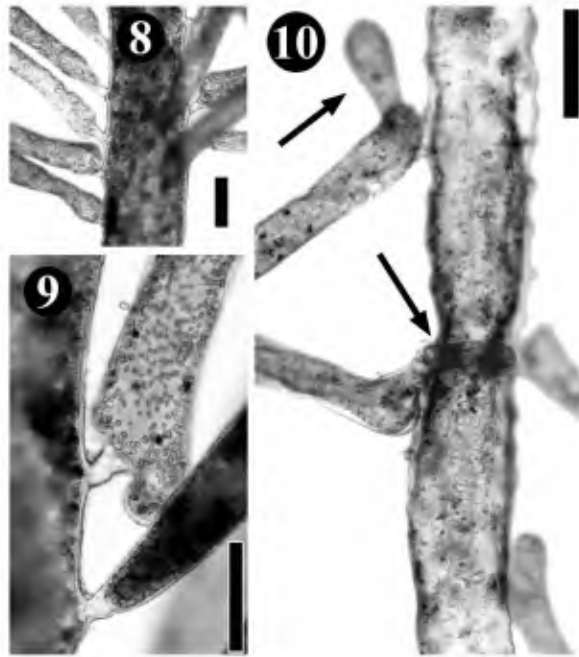
Collections: BW-00569 west Cove, Uva Island, epizoic on *Strombus*; BW-00687 south of Pacheca Island, in sand, ~12-15 m.

Other Panamanian records: Taylor (1945).

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

Type Locality: Antilles, West Indies.

Collections: BW-00317 Tobaguilla Island, on boulder, ~8 m. BW-00374 Urabá Island, on coral, 2 m; BW-00586 Unnamed Island, on dead *Pocillopora* coral; BW-00648 south side Iguana Island; on *Pocillopora* coral, ~3-5 m; BW-00806 Chama Island, on rock, ~10 m.



Figs 8-10. Pinnules of *Bryopsis rhizophora*. In the upper region of the primary axis, pinnules gradually taper to an acute attachment (Fig. 8 and 9). Pinnules frequently elongate from the proximal end (Fig. 9, upper pinnule), growing into a rhizoidal extension that can wrap around the primary axis (Fig. 10, arrows). Scale bars: 100  $\mu\text{m}$ .

Notes: Taylor (1945) described *B. galapagensis* as a “parallel species” (p. 61) to *B. pennata*, but designated the former a distinct entity on the basis of its deeper water distribution, smaller size, lighter green color and lack of iridescence. Bula-Meyer (1995) synonymized these taxa, noting that differences in iridescence and size were within the range of morphological variability of a single taxon across different habitats. Most of the Panamanian specimens exhibited distinctive pinnule scars that led Dawson (1961) to suggest that the pinnules were deciduous.

\**Bryopsis rhizophora* M. Howe (1914: 48)

Type Locality: Islas Pescadores, Ancon, Peru.

Collections: BW-00707 Urabá Island, on coral rubble; BW-00998 Fort Rodman, on metal pontoons of a floating dock.

Notes: Specimen BW-00707 matured in an aquarium where it grew into a dense but loose turf, with many erect axes emerging from a prostrate rhizoid. The large diameter of the main axis of this species was striking; Dawson (1964) listed the range of measurements from 300  $\mu\text{m}$  to 800  $\mu\text{m}$ . This specimen measured 360  $\mu\text{m}$  at the tip,

435  $\mu\text{m}$  in the middle of the axis and 525  $\mu\text{m}$  near the base. Pinnules were 1.0-2.8 mm long and approximately 100  $\mu\text{m}$  in diameter. Distal pinnules were highly constricted (Fig. 8). Frequently, near the base of the main axis, and elsewhere throughout the thallus, the pinnules formed a basal extension that wrapped around the axis (Figs 9-10). This feature is also present in *B. salvadoreana* Dawson, but that is an alga of much smaller size (see below).

\****Bryopsis salvadoreana*** Dawson (1961: 405, pl. 5, fig. 2, pl. 6)

Type Locality: Intertidal, on Sacate reef, off Punta Chiriquín, Golfo de Fonseca, El Salvador.

Collections: BW-00307 Culebra Point, on rock; BW-00812 Melones Island, growing on rusting food can; BW-01479 Rio Mar, on emergent rock at low tide; BW-01556 Unnamed Island, tangled in turf of *Derbesia*.

Notes: The axis width of specimen BW-00307 (~425  $\mu\text{m}$ ) was greater than that reported for this species (200-300  $\mu\text{m}$ ); however, the presence of indeterminate, forked pinnules (Figs 11-12) is consistent with the species description (Dawson 1961). The large axis diameter of *B. rhizophora* and the distinctive forked, papillate and indeterminate pinnules of *B. salvadoreana*, seem to distinguish these species, but an apparent broad range in morphological character states observed in Panamanian material obscures species boundaries. Taxonomic revision of eastern tropical Pacific species of *Bryopsis* based on a combination of molecular, biochemical and morphological data will help clarify species relationships in this phenotypically variable genus (see Krellwitz et al. 2001).

### ***Derbesia* Solier**

***Derbesia attenuata*** Dawson (1954: 390, figs 9a, b)

Type Locality: Nha Trang Bay, Vietnam.

Other Panamanian records: Dawson (1960).

\****Derbesia fastigiata*** W.R. Taylor (1928: 94, pl. 11, figs 1-3)

Type Locality: Dry Tortugas, Florida, USA.

Collection: BW-00665 west side Iguana Island, from damselfish garden.

\****Derbesia hollenbergii*** W.R. Taylor (1945: 75-76, pl. 1, figs 7-9)

Type Locality: Archipiélago de Colón, Black Beach Anchorage, I. Santa María, Ecuador.

Collection: BW-00634 Unnamed Island, on dead coral.

Notes: Specimen BW-00634 formed tufts emanating from a central holdfast of overlapping and contorted siphons. Sporangia were infrequent, separated by a double wall from the main siphon when mature, and measured 160-175  $\mu\text{m}$  long and 100-

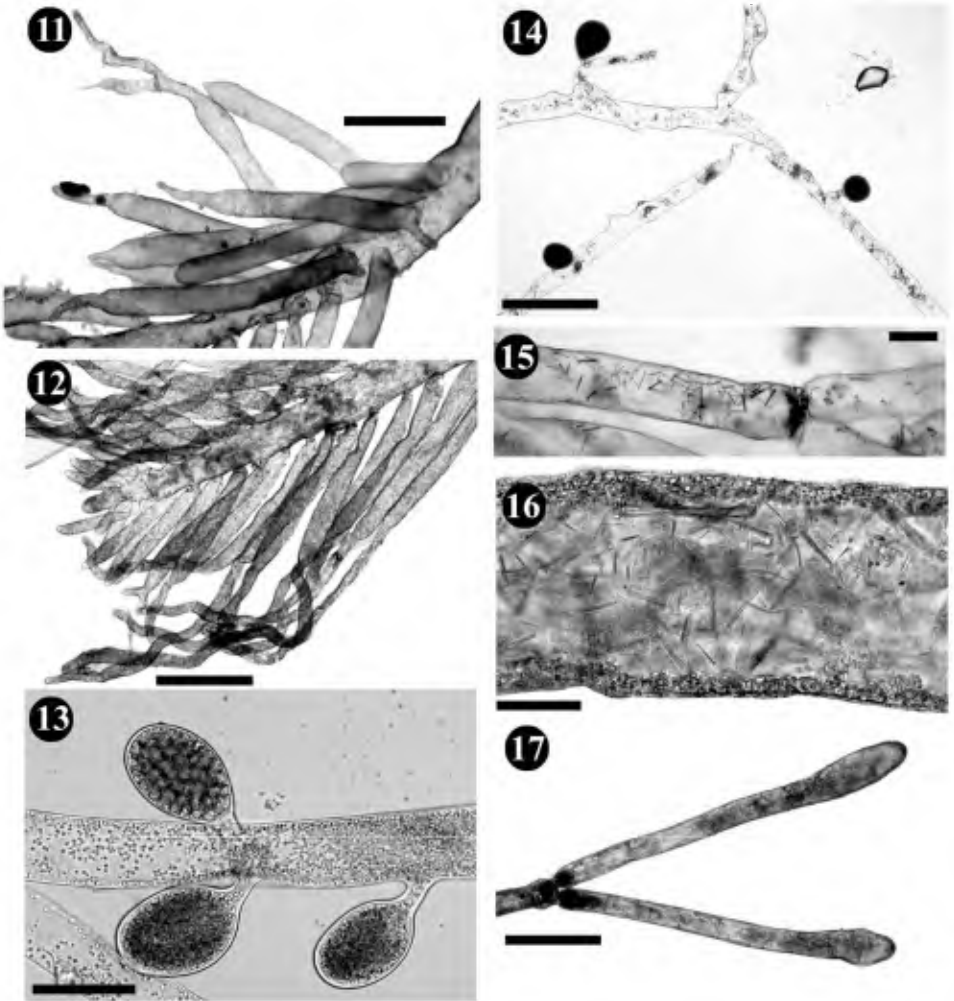


Fig. 11. Forked and papillate tips of *Bryopsis salvadoreana* (BW-01479) pinnules. Scale bar: 0.5 mm. Fig. 12. Indeterminate pinnules of *Bryopsis salvadoreana* (BW-01556). Scale bar: 0.5 mm. Fig. 13. Sporangia of *Derbesia hollenbergii* (BW-00634). Scale bar: 100  $\mu$ m. Fig. 14. Spherical sporangia of *Derbesia marina* (BW-00900). Scale bar: 0.5 mm. Figs 15-17. *Chlorodesmis caespitosa*. Intracellular crystals (Figs 16-17), distally swollen siphons and equally constricted siphons above the dichotomies (Fig. 18). Scale bars: Fig. 15: 100  $\mu$ m, Fig. 16: 40  $\mu$ m, Fig. 17: 500  $\mu$ m.

125  $\mu$ m wide. Sporangia occurred singly, or were sometimes arranged oppositely in groups of 2-3 (Fig. 13). In some features, including size and shape of the sporangia, this species resembles *D. turbinata* M. Howe et Hoyt (Littler & Littler 2000), but the larger diameter, overall habit and distribution of sporangia distinguish the two species (Taylor 1945).

\***Derbesia marina** (Lyngbye) Solier (1846: 452)

Type Locality: Denmark.

Collection: BW-00900 tangled among *Cladophora* sp.

Notes: This specimen was collected from a running seawater aquarium at STRI fed by Bay of Panama water. The diameter of the primary siphons, 75-90  $\mu\text{m}$ , was slightly greater than the 50-70  $\mu\text{m}$  range commonly reported (e.g., Dawson 1960, Taylor 1960). Numerous obovoid to spherical stalked sporangia, 160-185  $\mu\text{m}$  in diameter (Fig. 14), were borne laterally from the main siphons or shorter, lateral branches which is consistent with the description of this species. Taylor (1945) described *D. prolifica* from the Galápagos Islands, a species that is very similar to *D. marina* with regard to branching pattern and the size and shape of sporangia. *Derbesia prolifica* differs in siphon diameter, reaching 120-150  $\mu\text{m}$ , or about twice that of *D. marina*. This specimen may represent a larger *D. marina* or a somewhat smaller *D. prolifica*. Mateo-Cid & Mendoza-Gonzalez (1993) recognized both of these species in the Pacific Mexico flora.

\***Derbesia turbinata** Howe et Hoyt (1916: 106, pl. 11, figs 10-16)

Type Locality: Beaufort, North Carolina, USA.

Collections: BW-00813 Melones Island, growing on rusted food can.

Notes: Branching was pseudo-dichotomous, becoming irregular distally. The diameter of the axes ranged from 35 to 60  $\mu\text{m}$  and these bore pear-shaped to ovoid sporangia, 110-170  $\mu\text{m}$  in length and 200-250  $\mu\text{m}$  in width. Sporangia were attached by a short stalk 17-25  $\mu\text{m}$  long and about half as wide. These features are generally consistent with Taylor's (1945) description of *D. hollenbergii* with the exception of narrower filaments. The narrow filament size, branching pattern and sporangium shape and size seem to be in closer agreement with descriptions of *D. turbinata* (Littler & Littler 2000).

#### CAULERPACEAE

### **Caulerpa** Lamouroux

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

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

Other Panamanian records: Earle (1972).

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

Type Locality: Suez, Egypt.

Collection: BW-01520 Uva Island, on coral.

Other Panamanian records: Earle (1972).

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

Type Locality: Antilles, West Indies.

Collections: BW-00210, BW-00242 Culebra Point, on boulder in tidepool; BW-00218 Taboga Island, on rock in subtidal; BW-00316 Tobaguilla Island, on boulder surface, ~8 m; BW-00355 Perico Island, on bedrock, ~1 m at low tide; BW-00596 Unnamed Island, on coral; BW-00638 Cavada Island, on *Pocillopora* coral. This specimen exhibited both racemose and peltate morphologies. BW-00659 south side Iguana Island, on dead coral, ~5 m; BW-00673 Saboga Island.

Other Panamanian records: Earle (1972) as *C. peltata* Lamouroux; Glynn & Maté (1997) as *C. peltata* Lamouroux.

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

Type Locality: Mokha, Yemen.

BW-00434 Cebaco Island, on rock.

Notes: This taxon has been reported from the Indian Ocean (Silva et al. 1996), western Atlantic (e.g., Littler & Littler 2000), western Pacific (e.g., N'Yeurt 2001) and Indian Oceans (e.g., Silva et al. 1996). This specimen appears to represent the first report of the species in the eastern Pacific.

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

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

Collections: BW-00065, BW-00215, BW-00237, Taboga Island, on coral and rock rubble; BW-00336 Pacheca Island, on boulder, ~3 m; BW-00502 Uva Island; BW-00516 Lazarus Cove, Uva Island, in sand ~15 m; BW-00628 Unnamed Island, in sand; BW-00679 west side Contadora Island, on coral, ~5 m; BW-00692 south of Pacheca Island, in sand, ~8-13 m; BW-00801 Melones Island, in sand, ~3 m; BW-01472 Rio Mar, in small tidepool on tube worm colony; BW-01490, BW-01497 southwest of Bartolome Island, ~16 m; BW-01492, BW-01501, BW-01503 between Contadora and Chapera Islands, ~13 m.

Other Panamanian records: Earle (1972); Glynn & Maté (1997).

#### CODIACEAE

#### **Codium** Stackhouse

\***Codium isabelae** W.R. Taylor (1945: 70, pl. 1, figs 10-13; pl. 7 fig. 1)

Type Locality: Tagus Cove, Isabela Isla, Ecuador.

Collection: BW-00353 Perico Island, on boulder, ~1 m at low tide; BW-00712 Culebra Point, in crevice of emergent boulder.



**Codium picturatum** F.F. Pedroche et P.C. Silva (1996: 2-7, figs 1-6)

Type Locality: Playa La Audiencia [close to Manzanillo], Colima, México.

Collection: BW-00241 Culebra Point, on vertical face of rock at waters edge at low tide.

Notes: This may be the species that Earle (1972) and Schnetter & Bula-Meyer (1982) reported as *C. setchellii* Gardner (see Pedroche & Silva 1996).

#### UDOTEACEAE

### **Boodleopsis** A. Gepp et E. Gepp

**Boodleopsis verticillata** Dawson (1960: 32, Figs 1, a-d)

Type Locality: Bahía San Telmos, Isla del Rey, Pearl Islands, Panama.

### **Chlorodesmis** Harvey et Bailey

\***Chlorodesmis caespitosa** J. Agardh (1887: 49-50).

Type Locality: Colombo, Sri Lanka.

Collection: BW-00328, BW-00329 Tobaguilla Island, on boulder, ~4 m; BW-00352 Perico Island, on bedrock in <1 m at low tide; BW-00534 Lazarus Cove, Uva Island, on rock; BW-00585 Unnamed Island; BW-01502 between Chapera and Mogo Mogo Islands.

Notes: This species has been recorded for Pacific Colombia (Schnetter & Bula-Meyer 1982) and is distinguished from other species in the genus (Ducker 1967) by the presence and abundance of crystals within the cells (Figs 15-16), swollen tips and equal constrictions at dichotomies (Fig. 17). Dawson (1961) recorded *C. hillebrandtii* A. Gepp et E. Gepp from El Salvador which superficially resembles this species but lacks abundant crystals.

### **Halimeda** Lamouroux, nom. cons.

\***Halimeda discoidea** Decaisne (1842: 102)

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

Collections: BW-00493 Uva Island, on coral rubble, ~5-7 m; BW-00881 Montuosa Island, on vertical rock wall, 6.4 m.

Notes: Atlantic and Indo-Pacific specimens of *H. discoidea* represent genetically distinct species on the basis of molecular data (Kooistra et al. 2002). Morphologically, there are small differences in the degree to which terminal utricles adhere. In the Indo-Pacific material they adhere for a distance of several micrometers, whereas in the Atlantic material they only touch at the periphery. Eastern Pacific specimens

often exhibited small secondary utricles that approached the size range of secondary utricles in *H. tuna* (Hillis-Colinvaux 1980). It remains unclear whether the variations in utricle size observed in Pacific Panama specimens distinguishes them from Atlantic and Indo-Pacific *H. discoidea* (Kooistra pers. comm.), which were shown to be phylogenetically distinct on the basis of DNA sequence data (Kooistra et al. 2002)..

## DASYCLADALES

### POLYPHYSACEAE

#### **Acetabularia** Lamouroux, nom. cons.

\***Acetabularia parvula** Solms-Laubach (1895: 29, pl. 2: Figs 3, 5)

Syntype Localities: “Tropical India”; Celebes, Indonesia.

Collections: BW-00654 west side Iguana Island; BW-01480 Rio Mar, on emergent rock at low tide.

**Acetabularia pusilla** (Howe) Collins (1909b: 379)

Type Locality: Montego Bay, Jamaica.

Other Panamanian records: (Earle 1972).

#### **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-00066 Taboga Island, on coral rubble.

Notes: Previously recorded only from Pacific Colombia (Bula-Meyer 1995), this is the second report of *A. schenkii* from the Pacific Ocean.

## Discussion

The physical complexity of the eastern tropical Pacific Ocean led Howe (1910) to expect a greater abundance and diversity of marine macroalgae throughout the extensive rocky intertidal shoreline of Panama than he actually encountered. He commented that above and below the low tide mark, rocks and pools, which harbour a rich algal flora elsewhere at that latitude, were virtually “destitute of plant life” (Howe 1910, p. 31). Howe (1910) and Dawson (1962) attributed the absence of a substantial marine flora to extreme tides, an idea that Hay & Gaines (1984) later expanded. They argued that the extreme tidal range and general lack of coral reef structure allowed herbivores access to the entire range of the intertidal zone. Herbivory coupled with wide temperature fluctuations on a daily (due to tidepool heating on

low tides) and seasonal (due to coastal upwelling) basis constitute a stressful physical regime. Algal turfs are known to be a response to stressful environments (Menge & Lubchenco 1981, Menge et al. 1986a) and this may explain their common presence throughout the subtidal zone.

Despite the lack of an obvious macrophytic flora, macroalgal diversity was substantial. In this report 44 chlorophyte taxa are documented including 27 new records for Panama. This increase in known macroalgal diversity, from 14 (excluding genera unidentified to species) (Earle 1972) to 44 taxa (~214%), is attributed to greater sampling and paying close attention to algal turfs. Previous studies of the Panamanian marine flora were primarily opportunistic. Taylor's (1945) Pacific Panama collections were somewhat a matter of convenience when a port call in Ancon, Panama was made, and Dawson's (1959) collections were but one aspect of a multi-faceted project to study biodiversity in tropical Pacific America. Earle (1972) added eight new records for the country in her compilation based on short-term visits to the country. She also noted that some 30 new records awaited formal publication, an eventuality that was never realized.

This updated list indicates that Panama's marine flora, at least in terms of green algae, is one of the richest floras of tropical Pacific America. This estimate is likely an underestimate of actual chlorophyte diversity, as numerous species represented in nearby floras are not yet recorded for Panama (Table 2). Continued study in Panama and throughout tropical Pacific America is still needed to fully understand the distribution and range of macroalgal species in this region of the world.

AMPHI-ISTHMIAN GREEN ALGAL DIVERSITY. The marine green algal flora of Panama (Caribbean and Pacific) includes 16 varieties, forms or subspecific taxa (predominantly of the genus *Caulerpa*), and 107 species, representing 37 genera, 14 families, five orders and a single class (Ulvophyceae). The green algal flora of the Caribbean harboured greater diversity than that of the Pacific at nearly all taxonomic levels with the exception of orders (Fig. 18). A total of 15 taxa were encountered on both coasts encompassing one variety, 14 species, nine genera, eight families and four orders. Five additional genera and one additional family were represented along both coasts, but by different species (Appendix).

One of the most striking features of the Panamanian marine flora was the marked difference in species diversity across the Central American Isthmus (Fig. 18). The environmental regimes along both coasts differ markedly from one another; the Pacific coastline is characterized by both spatial and temporal heterogeneity, whereas the Caribbean is comparatively uniform (Glynn 1972). The clearest example of the effect of environment on diversity is in the Udoteaceae. While 37 taxa (34 species, two forms, one variety) represented the Udoteaceae in the Caribbean, only three representatives were present in the Pacific flora (*Boodleopsis verticillata*, *Chlorodesmis caespitosa*, and *Halimeda discoidea*). This may be explained by the lack of sandy habitats on the Pacific coast. Most species in the family produce prolific rhizoidal masses that facilitate attachment. Such an adaptation is ill-served on the Pacific coast where sandy habitats are limited or exposed by tides on a regular basis. Indeed, two of three species of Pacific Udoteaceae (*C. caespitosa* and *H. discoidea*) inhabit

Table 2. Documented green algal diversity of tropical eastern Pacific marine floras. Sub-specific taxa have been excluded from diversity estimates.

Country	Number of Chlorophyta	Number of species not represented in flora of Panama	Source
El Salvador	18	11	Dawson (1961)
Nicaragua	6	3	Dawson (1962)
Guatemala	6	3	Bird & McIntosh (1979)
Costa Rica	11	7	Taylor (1945), Dawson (1960, 1962)
Panama	45	-	this study
Colombia	29	15	Schnetter & Bula-Meyer (1982), Bula-Meyer (1995)
Ecuador	37	26	Taylor (1945)

hard substratum. When 33 sand-dwelling Udoteaceae were removed from the trans-isthmian comparison, the number of Caribbean species was reduced to 46, just three species more than are currently known in the Pacific.

Numerous species that are present in the Caribbean Panama flora are also part of western and central Pacific tropical marine floras (Appendix). The absence of these species from the eastern tropical Pacific suggests that these species may have been unable to survive environmental changes (Weaver 1990) associated with the emergence of the Central American Isthmus. Cooler waters associated with seasonal upwelling (Glynn 1972) may be below the survival or reproductive limits of species that may have been part of a homogeneous regional flora prior to the final closure of the Central America Seaway. These species would have perished in the eastern Pacific, while maintaining viability in the Caribbean where sea surface temperatures have remained largely unchanged in the last 3.0-3.5 million years (Cronin & Dowsett 1996).

In addition to changes in temperature associated with the emergence of the Central American Isthmus, associated changes in current patterns may have also affected the dispersal patterns of marine macroalgae. Prior to the emergence of the Central American Isthmus, the eastern tropical Pacific was fed by the westerly flowing equatorial current; today it is fed by the northward flowing Peru current and the eastward flowing equatorial under current (see Pickard & Emery 1990). Though evidence of long distance dispersal of marine macroalgae via ocean currents is limited, it can be expected that successful establishment of macroalgae dispersed in this way would be limited to eurythermal species that can tolerate the cooler waters of Peru and Ecuador as well as the comparatively warmer waters of Panama. The equatorial under current may play a negligible role in algal dispersal because it crosses few areas in which it could pick up algal propagules. In the Caribbean, the situation differs considerably because islands are numerous, the distance between them is relatively small and gross environmental features (including temperature) are very similar. These features may promote dispersal and possibly inflate diversity through the rescue effect (Stevens 1989).

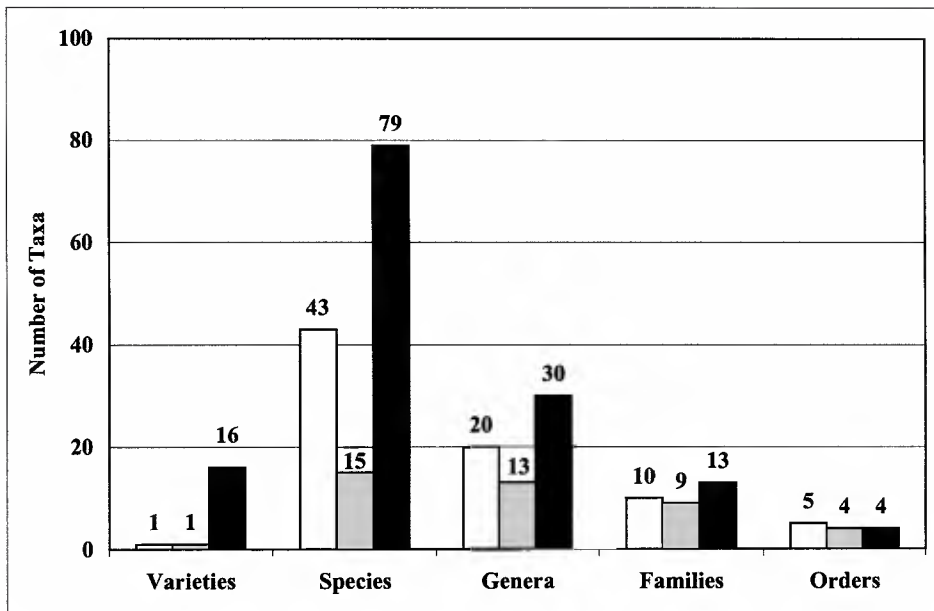


Fig. 18. Algal biodiversity at different taxonomic levels for the Caribbean (black) and Pacific (white) floras of Panama. Amphi-isthmian taxa are represented in gray. Numbers over bars indicate the total number of taxa.

The rescue effect describes a situation in which species survive beyond their geographic range and inflate diversity even though they are not established as reproducing populations. The presence of the species outside of their natural range is re-enforced by dispersal from the home range. The idea was originally conceived as an explanation for the latitudinal species diversity gradient, in which high latitude species were shown to have a wider geographic range than species of low latitudes (Stevens 1989). A general corollary of this rule is that regions of high diversity are characterized by greater climatic stability, while regions of low diversity are characterized by greater climatic variability. Santelices & Marquet (1998) found no support for the corollary for the Atlantic European or Pacific South American marine floras, but it is a provocative explanation for differences in diversity across the Panamanian isthmus, where substantial environmental differences exist (Glynn 1972). Support for this hypothesis requires rigorous analysis of dispersal potential, latitudinal range, and other growth characteristics (Santelices & Marquet 1998) among species of Panamanian marine algae.

The discussion to this point has focused on the differences in the floras separated by the Central American Isthmus, but consideration of the similarities in the two floras may also be instructive in understanding extant species distributions. In general, amphi-isthmian species have a broad distribution world-wide (Table 3); only three species (*Acicularia schenckii*, *Caulerpa microphysa* and *C. serrulata*) of the 15 have

Table 3. List of amphi-isthmian species documented for the Republic of Panama. The world-wide distribution of each species is documented with representative literature in Guiry & Nic Dhonncha (2002). IO: Indian Ocean; EP: eastern Pacific; WP: western Pacific; EA: eastern Atlantic; WA: western Atlantic. Taxa in bold have a disjunct world distribution; x's indicate presence of species.

Taxon	Distribution				
	IO	EP	WP	EA	WA
<i>Acicularia schenkii</i>		<b>x</b>			<b>x</b>
<i>Bryopsis hypnoides</i>	x	x	x	x	x
<i>Bryopsis pennata</i>	x	x	x	x	x
<i>Caulerpa microphysa</i>	<b>x</b>	<b>x</b>	<b>x</b>		<b>x</b>
<i>Caulerpa racemosa</i>	x	x	x	x	x
<i>Cladophora racemosa</i> var. <i>peltata</i>	x	x	x	x	x
<i>Caulerpa serrulata</i>	<b>x</b>	<b>x</b>	<b>x</b>		<b>x</b>
<i>Caulerpa sertularioides</i>	x	x	x	x	x
<i>Chaetomorpha linum</i>	x	x	x	x	x
<i>Cladophora coelothrix</i>	x	x	x	x	x
<i>Cladophora socialis</i>	x	x	x	x	x
<i>Cladophoropsis membranacea</i>	x	x	x	x	x
<i>Enteromorpha flexuosa</i>	x	x	x	x	x
<i>Halimeda discoidea</i> <sup>1</sup>	x	x	x	x	x
<i>Phyllocladion anastomosans</i>	x	x	x	x	x

<sup>1</sup>See notes under *H. discoidea* regarding genetic differences between Atlantic and Indo-Pacific *H. discoidea*.

a disjunct world-wide distribution. *Acicularia schenkii* is a diminutive alga that could be easily overlooked (Littler & Littler 2000) or confused with species of the genus *Acetabularia* from which it differs only in producing a mass of lime within the rays (Taylor 1960). That *Acicularia* is apparently only found in the western Atlantic and eastern Pacific suggests that it may be endemic to the region, having diverged from an *Acetabularia*-like sister taxon prior to the emergence of the Central American Isthmus. Alternatively, eastern Pacific populations, which were documented for the first time by Bula-Meyer (1995), may represent a recent introduction across the isthmus, or perhaps a chance dispersion through a short-lived breach in the isthmus 2.3-2.0 million years ago (Cronin & Dowsett 1996).

Dispersal of marine organisms across the Central American Isthmus could be facilitated in a variety of ways. The distance across the isthmus is relatively short (~80 km), a distance that shore birds could easily cross in one day. Shore birds may transfer algal propagules (fragments, spores or gametes) from their feathers and on their bills or feet between coastal feeding grounds. Numerous freshwater microalgae are believed to be transported in this way (Kristiansen 1996), and zebra mussel veligers are also potentially dispersed in this manner (Johnson and Carlton 1996). Other natural vectors include surviving gut passage in trans-isthmian, euryhaline fish (Paya and Santelices 1989), or by rafting on mangrove logs or other debris through the Panama Canal. All of these seem unlikely vectors because (wind-blown) bird feathers and fish guts are probably extremely harsh environments for marine macroalgal propagules. Additionally, the large size of Gatún Lake, the bi-directional outflow of

the Panama Canal, and the small, gated entrances to the Panama Canal inhibit passive migration of debris across the isthmus.

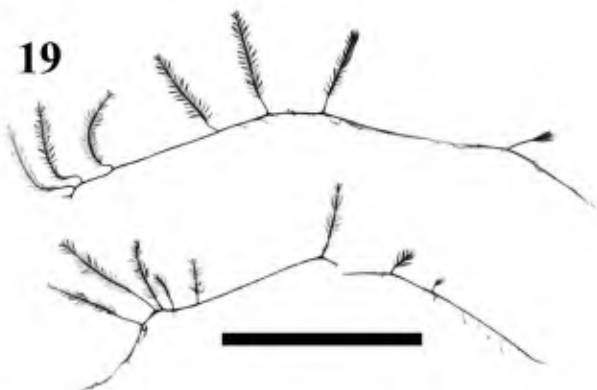
More likely trans-isthmian dispersal vectors are those associated with human activities such as seafood shipments, ship hull fouling and ballast water discharge. Hay and Gaines (1984) proposed the idea that recreational sailing yachts may be an important vector in transporting fouling species from one coast of Panama to the other, and Menzies (1968) conservatively estimated that some 252,000 kg of fouling biota could be transported between oceans via the Panama Canal. Despite the advent of anti-fouling paints, green fouled hulls have been observed in the Canal (pers. obs.), and fouling could easily be dislodged during lockage operations.

Ballast water exchanges in the vicinity of the Panama Canal were apparently a very common practice at one point (Chesher 1968, Glynn 1982, Carlton 1985). However, the frequency of interoceanic ballast water exchange in the vicinity of the Panama Canal today is unclear, and only two published ballast water surveys have documented marine macroalgae from anywhere in the world. Carlton and Geller (1993) list two chlorophytes and two rhodophytes, while Smith et al. (1999) list a single rhodophyte species; all macroalgae were listed as rare occurrences in the samples.

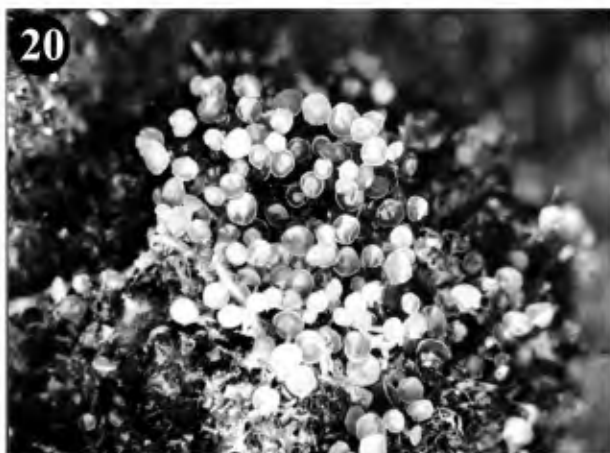
Despite the challenges of interoceanic dispersal via the Panama Canal or natural vectors, trans-isthmian dispersal has been documented in amph-isthmian and geographically disjunct seaweeds. McCosker & Dawson (1975) reported *Cladophora montagneana* (as *Cladophora delicatula* Montagne) in the outermost lock of the Pacific terminus to the Panama Canal. This is an alga with a predominantly Atlantic distribution (Guiry & Nic Dhonncha 2002), but Dawson (1944) also recorded it (as *Cladophora delicatula*) for the Gulf of California. Intraspecific phylogenetic studies of this species could reveal whether Gulf of California and third-lock Panama Canal specimens have an Atlantic origin. Such studies have revealed a recent Atlantic origin for a Pacific Panama isolate of *Phyllocladon anastomosans* (Wysor 2002), while Kooistra et al. (2002) have suggested a recent Indo-Pacific origin for *Halimeda opuntia* in the Caribbean Sea. Of these species, only *P. anastomosans* has been found on both coasts of Panama (Appendix).

Of the 12 amph-isthmian species that are broadly distributed throughout the world (Table 3) most show little morphological variation between Caribbean and Pacific Panama habitats. These may be eurytolerant species that exhibit a simple morphology under variable conditions throughout their range. Three taxa (*Caulerpa sertularioides*, *C. racemosa* var. *peltata*, and *Halimeda discoidea*) exhibit different morphologies in opposite ocean basins. Specimens of *C. sertularioides* on the Pacific coast (Fig. 19) are always much finer and more delicate relative to Caribbean specimens (see Wysor & Kooistra 2003, figs 15-17). Specimens of *C. racemosa* var. *peltata* form distinctly flattened to concave branchlets in the Pacific (Fig. 20) where the organism exists as a tightly adherent and tangled turf. In contrast, branchlets of Caribbean material were never as compressed, frequently remained slightly convex and never occurred as adherent turfs (Fig. 21). Caribbean and Pacific specimens were genetically identical based on *tufA* sequence data (Famá et al. 2002), suggesting that differences in morphology may be environmentally triggered as has been shown

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in a number of other studies (Peterson 1972, Ohba & Enomoto 1987, Ohba et al. 1992). Lastly, as discussed previously, *Halimeda discoidea* in the Pacific, may be a species distinct from its counterpart in the Atlantic (Kooistra pers. comm.).

Over 15% (15 species) of the green algal diversity represented in Panama is common to both coasts. When green algal diversity from nearby floras is considered, the number of amphi-isthmian green algae climbs to 30 taxa (Appendix). Furthermore, when amphi-isthmian diversity is considered for all of Central America across red, green and brown algae the number of amphi-isthmian taxa nearly triples (Wysor unpublished data). The number of amphi-isthmian marine algae appears to greatly exceed the number of amphi-isthmian species among other groups of organisms (bivalve and gastropod molluscs, decapod crustaceans, polychaetes (Vermeij 1978); sea urchins (Lessios 1979, Lessios & Cunningham 1990, Lessios et al. 1999, Lessios et al. 2001); isopod crustaceans (Weinberg & Starczak 1989); fish (Bermingham & Lessios 1993, Banford et al. 1999, Bowen et al. 2001, Muss et al. 2001); and snapping shrimp (Knowlton 1993, Knowlton et al. 1993, Knowlton & Weigt 1998)). It remains to be studied whether this is the result of inadequate algal taxonomy, reduced rate of speciation in seaweeds, or incomplete species inventories in general.

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Fig. 19. A typical specimen of *Caulerpa sertularioides* from the Pacific coast of Panama. Compare size to Figs 15-17 (Wysor & Kooistra, in press). Scale bar: 5 cm. Fig. 20-21. *Caulerpa racemosa* var. *peltata* from Pacific (Fig. 20) and Caribbean (Fig. 21) shores of Panama. Note the cup shaped branchlets in the Pacific material versus the hemispherical, bulging branchlets that are more typical of the variety on the Caribbean coast. The diameter of a peltate branchlet is approximately 3 mm. Scale bar for Fig. 22, 1 mm.

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Appendix. Comprehensive list of marine Chlorophyta recorded for the Republic of Panama. Taxa listed in bold occur on both the Caribbean (C) and Pacific (P) coasts of the country.

An “•” in the C or P column indicates that the taxon has been reported outside of Panama in the Western Atlantic or Pacific Ocean, respectively, but has not been reported in Panamanian waters. The total number of amphi-isthmian taxa, 15 (14 species, 1 varieties), increases to 30 when this number includes extra-Panamanian taxa from nearby floras. Taxa with an “x” in the Western Pacific (WP) column, are recorded for tropical Pacific marine floras (Guiry & Nic Dhonncha 2002).

C	P	ORDER: FAMILY: Genus species	WP
		<b>PHAEOPHILALES</b>	
		<b>PHAEOPHILACEAE</b>	
	x	<i>Phaeophila dendroides</i> (P. Crouan et H. Crouan) Batters	x
		<b>ULVALES</b>	
		<b>ULVACEAE</b>	
	x	<i>Chloropelta caespitosa</i> Tanner	
x	x	<i><b>Enteromorpha flexuosa</b></i> (Wulfen) J. Agardh	x
x		subsp. <i>paradoxa</i> (C. Agardh) Bliding	x
•	x	<i>Enteromorpha lingulata</i> J. Agardh	x
•	x	<i>Enteromorpha prolifera</i> (Müller) J. Agardh	x
x		<i>Ulva lactuca</i> aff. var. <i>latissima</i> sensu (Taylor, 1960)	x
		<b>CLADOPHORALES</b>	
		<b>ANADYOMENACEAE</b>	
x		<i>Anadyomene saldanhae</i> A.B. Joly et E.C. Oliveira	
x		<i>Anadyomene stellata</i> (Wulfen) C. Agardh	x
x		<i>Microdictyon boergesenii</i> Setchell	
		<b>CLADOPHORACEAE</b>	
x		<i>Chaetomorpha antennina</i> (Bory) Kützing	x
x	•	<i>Chaetomorpha brachygona</i> Harvey	x
x		<i>Chaetomorpha gracilis</i> Kützing	x
	x	<i>Chaetomorpha indica</i> (Kützing) Kützing	x
	x	<i>Chaetomorpha javanica</i> Kützing	x
x	x	<i><b>Chaetomorpha linum</b></i> (Müller) Kützing	x
x	x	<i><b>Cladophora coelothrix</b></i> Kützing	x
x		<i>Cladophora dalmatica</i> Kützing	x
	x	<i>Cladophora flexuosa</i> (Müller) Kützing	x
	x	<i>Cladophora laetevirens</i> (Dillwyn) Kützing	x
	x	<i>Cladophora microcladioides</i> Collins	
	x	<i>Cladophora montagneana</i> Kützing	x
x		<i>Cladophora ordinata</i> Børgesen	x
	x	<i>Cladophora panamensis</i> W.R. Taylor	
	x	<i>Cladophora pellucidoidea</i> van den Hoek	
x	x	<i><b>Cladophora socialis</b></i> Kützing	x
x		<i>Rhizoclonium africanum</i> Kützing	x
	x	<i>Rhizoclonium rhizophyllum</i> W.R. Taylor	
•	x	<i>Rhizoclonium riparium</i> (Roth) Harvey	x
		<b>BOODLEACEAE</b>	
•	x	<i>Boodlea composita</i> (Harvey) F. Brand	x
x	x	<i><b>Phyllocladion anastomosans</b></i> (Harvey) Kraft et M. J. Wynne	x
		<b>SIPHONOCLADACEAE</b>	
x		<i>Chamaedoris peniculum</i> (Ellis et Solander) Kuntze	
x	x	<i><b>Cladophoropsis membranacea</b></i> (Bang ex C. Agardh) Børgesen	x
x		<i>Cladophoropsis sundanensis</i> Reinbold	x
x		<i>Dictyosphaeria cavernosa</i> (Forrskål) Børgesen	x
x		<i>Siphonocladus tropicus</i> (P. Crouan et H. Crouan in Schramm et Mazé) J. Agardh	x

C	P	ORDER: FAMILY: Genus species	WP
	x	<i>Struveopsis robusta</i> (Setchell et Gardner) Rhyne et H. Robinson	
x		<i>Ventricaria ventricosa</i> (J. Agardh) Olsen et J. A. West	x
		VALONIACEAE	
x	•	<i>Ernodesmis verticillata</i> (Kützing) Børgesen	x
x		<i>Valonia macrophysa</i> Kützing	x
x		<i>Valonia utricularis</i> (Roth) C. Agardh	x
		BRYOPSIDALES	
		BRYOPSIDACEAE	
x	x	<b><i>Bryopsis hypnoides</i> Lamouroux</b>	x
x	x	<b><i>Bryopsis pennata</i> Lamouroux</b>	x
x	•	<i>Bryopsis plumosa</i> (Hudson) C. Agardh	x
	x	<i>Bryopsis rhizophora</i> Howe	x
	x	<i>Bryopsis salvadoreana</i> Dawson	
	x	<i>Derbesia attenuata</i> Dawson	x
•	x	<i>Derbesia fastigiata</i> W.R. Taylor	x
	x	<i>Derbesia hollenbergii</i> W.R. Taylor	
•	x	<i>Derbesia marina</i> (Lyngbye) Solier	x
	x	<i>Derbesia turbinata</i> Howe et Hoyt	
		CAULERPACEAE	
x	•	<i>Caulerpa cupressoides</i> (H. West in Vahl) C. Agardh	x
x		var. <i>flabellata</i> Børgesen	x
x		var. <i>lycopodium</i> Weber-van Bosse	x
x		var. <i>mammillosa</i> (Montagne) Weber-van Bosse	x
x		<i>Caulerpa fastigiata</i> Montagne	x
x		<i>Caulerpa lanuginosa</i> J. Agardh	
x		<i>Caulerpa mexicana</i> Sonder ex Kützing	x
x		f. <i>pectinata</i> Kützing	
x	x	<b><i>Caulerpa microphysa</i> (Weber-van Bosse) J. Feldmann</b>	x
x		<i>Caulerpa prolifera</i> (Forsskål) Lamouroux	x
x		f. <i>zosterifolia</i> Børgesen	
x	x	<b><i>Caulerpa racemosa</i> (Forsskål) J. Agardh</b>	x
x		var. <i>lamourouxii</i> (Turner) Weber-van Bosse	x
x		var. <i>macrophysa</i> (Sonder ex Kützing) W.R. Taylor	x
x		var. <i>occidentalis</i> (J. Agardh) Børgesen	x
x	x	<b>var. <i>peltata</i> (Lamouroux) Eubank</b>	x
x	x	<b><i>Caulerpa serrulata</i> (Forsskål) J. Agardh</b>	x
x	x	<b><i>Caulerpa sertularioides</i> (S.G. Gmelin) Howe</b>	x
x		f. <i>brevipes</i> (J. Agardh) Svedelius	x
x		f. <i>longiseta</i> (Bory) Svedelius	x
x		<i>Caulerpa taxifolia</i> (H. West in Vahl) C. Agardh	x
x		<i>Caulerpa verticillata</i> J. Agardh	x
x		f. <i>charoides</i> Weber-van Bosse	x
x	•	<i>Caulerpella ambigua</i> (Okamura) Prud'homme van Reine et Lokhorst	
		CODIACEAE	
x		<i>Codium intertextum</i> Collins et Hervey	
	x	<i>Codium isabellae</i> W.R. Taylor	
x		<i>Codium isthmocladum</i> Vickers	
	x	<i>Codium picturatum</i> Pedroche et P.C. Silva	
x		<i>Codium repens</i> P. Crouan et H. Crouan ex Vickers	x
		OSTREOBIACEAE	
x	•	<i>Ostreobium quekettii</i> Bornet et Flahault	x
		UDOTEACEAE	
x		<i>Avrainvillea hayi</i> D. Littler et M. Littler	
x		<i>Avrainvillea longicaulis</i> (Kützing) G. Murray et Boodle	x



C	P	ORDER: FAMILY: Genus species	WP
x		<i>Avrainvillea nigricans</i> Decaisne	x
x		<i>Avrainvillea rawsonii</i> (Dickie) Howe	
	x	<i>Boodleopsis verticillata</i> Dawson	x
	x	<i>Chlorodesmis caespitosa</i> J. Agardh	
x		<i>Halimeda copiosa</i> Goreau et E. Graham	x
x	x	<b><i>Halimeda discoidea</i> Decaisne</b>	x
x		<i>Halimeda goreau</i> W.R. Taylor	
x		<i>Halimeda gracilis</i> Harvey ex J. Agardh	x
x		<i>Halimeda hummii</i> Ballantine	
x		<i>Halimeda incrassata</i> (Ellis) Lamouroux	x
x		f. <i>tripartita</i> Barton	
x		<i>Halimeda monile</i> (Ellis et Solander) Lamouroux	
x	•	<i>Halimeda opuntia</i> (Linnaeus) Lamouroux	x
x		f. <i>triloba</i> (Decaisne) Barton	x
x		<i>Halimeda simulans</i> Howe	x
x		<i>Halimeda tuna</i> (Ellis et Solander) Lamouroux	x
x		<i>Penicillus capitatus</i> Lamouroux	
x		<i>Penicillus dumetosus</i> (Lamouroux) Blainville	
x		<i>Penicillus lamourouxii</i> Decaisne	
x		<i>Penicillus pyriformis</i> A. Gepp et E. Gepp	
x		<i>Rhipidosiphon floridensis</i> D. Littler et M. Littler	
x		<i>Rhipiliopsis reticulata</i> (van den Hoek) Farghaly et Denizot	
x		<i>Rhipiliopsis stri</i> (S.A. Earle et J. R. Young) Farghaly et Denizot	
x		<i>Rhypocephalus phoenix</i> (Ellis et Solander) Kützing	
x		<i>Udotea abbotiorum</i> D. Littler et M. Littler	
x		<i>Udotea caribaea</i> D. Littler et M. Littler	
x		<i>Udotea conglutinata</i> (Ellis et Solander) Lamouroux	x
		<i>Udotea cyathiformis</i> Decaisne	
x		var. <i>flabellifolia</i> D. Littler et M. Littler	
x		<i>Udotea dotyi</i> D. Littler et M. Littler	
x		<i>Udotea flabellum</i> (Ellis et Solander) Lamouroux	
		<i>Udotea looensis</i> D. Littler et M. Littler	
x		<i>Udotea luna</i> D. Littler et M. Littler	
x		<i>Udotea wilsonii</i> A. Gepp, E. Gepp et Howe in A. Gepp et E. Gepp	
		<b>DASYCLADALES</b>	
		<b>DASYCLADACEAE</b>	
x		<i>Neomeris annulata</i> Dickie	x
		<b>POLYPHYSACEAE</b>	
x		<i>Acetabularia crenulata</i> Lamouroux	x
•	x	<i>Acetabularia parvula</i> Solms-Laubach	x
x		<i>Acetabularia polyphysoides</i> P. Crouan et H. Crouan in Mazé et Schramm	
	x	<i>Acetabularia pusilla</i> (Howe) Collins	x
x	x	<b><i>Acicularia scheukii</i> (Möbius) Solms-Laubach</b>	