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SMITHSONIAN CONTRIBUTIONS TO BOTANY • NUMBER 105

The Mesophotic, Coral Reef–Associated, Marine Algal Flora of Puerto Rico, Caribbean Sea

David L. Ballantine,
Hector Ruiz Torres,
and Nilda E. Aponte

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ABSTRACT

Ballantine, David L., Hector Ruiz Torres, and Nilda E. Aponte. The Mesophotic, Coral Reef-Associated, Marine Algal Flora of Puerto Rico, Caribbean Sea. *Smithsonian Contributions to Botany*, number 105, viii + 41 pages, 5 figures, 3 tables, 2 appendixes, 2016. — Deepwater open-circuit scuba, dredging, submersible, and technical mixed-gas (closed-circuit) rebreather diving collections of marine benthic algae made over the last approximately 30 years in Puerto Rico are summarized in this account. In total, 186 taxa (166 identified to species) comprising 60% Rhodophyta, 11% Phaeophyceae, and 29% Chlorophyta are reported from depths greater than 35 m. Eighty-nine of these (56% of taxa identified to species) from the Puerto Rican mesophotic are thought to be the deepest known distributional records for the species recognized. Forty-three species (8% of the entire benthic flora of Puerto Rico) are mostly or entirely restricted to depths greater than 35 m. KEYWORDS: deepwater algae, mesophotic, Puerto Rico, tropical west Atlantic.

Cover images, from left to right: Edge of insular shelf, offshore from La Parguera; technical divers' descent to the mesophotic; bottom habit, edge of insular shelf, "Weinberg," offshore from La Parguera.

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Contents

LIST OF FIGURES v

LIST OF TABLES vii

INTRODUCTION 1

ENVIRONMENT AND HABITAT 2

MATERIAL AND METHODS 3

RESULTS 3
- Rhodophyta 3
- Heterokontophyta 15
- Chlorophyta 17

DISCUSSION 23

ACKNOWLEDGMENTS 25

APPENDIX A: SUMMARY OF PUERTO RICAN MESOPHOTIC ALGAL SPECIMENS 27

APPENDIX B: COLLECTION LOCALITY DATA 31

REFERENCES 35

INDEX OF GENERA AND SPECIES 39

Figures

1. Map of Puerto Rico and associated islands showing collection locations **4**
2. Encrusting deepwater rhodophyte species **5**
3. Deepwater Rhodophyta species **9**
4. Algal deepwater benthic habitats sampled **13**
5. Deepwater Chlorophyta species **18**

Tables

1. Algal species mostly depth-restricted to the mesophotic realm in Puerto Rico **23**
2. Numbers of genera and species of families represented by four or more species reported from 35 m or greater in depth in Puerto Rico **24**

Appendix A

A1. Identified mesophotic algal specimens from Puerto Rico **27**

The Mesophotic, Coral Reef–Associated, Marine Algal Flora of Puerto Rico, Caribbean Sea

David L. Ballantine,[1,4*] *Hector Ruiz Torres,*[2,4] *and Nilda E. Aponte*[3,4]

INTRODUCTION

The term "mesophotic" is somewhat difficult to define precisely, in part because its depth ranges vary geographically. Nevertheless, Hinderstein et al. (2010:248) characterized mesophotic communities as consisting of light-dependent corals and associated communities "typically found at depths ranging from 30–40 m and extending to over 150 m in tropical and subtropical regions. Due to difference in water transparency, the lower depth limit is to about 90 m in the Caribbean and to greater than 150 m in Hawaii. The dominant communities providing structural habitat in the mesophotic zone can be comprised of coral, sponge, and algal species." Because of the decreased light at these depths, these environments have been referred to as "twilight zones" (Frick and Knauer, 1986; Pyle, 1996; Brokovich et al., 2008).

For the tropical and subtropical western Atlantic, published accounts of deep reef-associated algae are proportionately few, and thus, the benthic flora (>35 m) in the region remains poorly to incompletely known, largely because of logistical difficulties in working in water deeper than is safely accessible by scuba. Scuba collections are limited by decreased bottom time at depth and limits imposed on depth by modern scientific diving safety standards. Collection by dredging is a low-technology alternative that allows access to deeper-water environments; however, such collections are largely indiscriminate because they are conducted remotely from the surface. Dredge collections also suffer from the fact that the process is destructive to the community being sampled and may physically damage collections, particularly delicate forms. Thus, deeper-water studies have historically been largely hampered by existing technology.

The advent of submersible and remotely operated vehicle (ROV) availability to the scientific research community has opened new avenues for examination of previously inaccessible communities. These devices afford direct access to deeper communities and allow for greater time spent at depth. Nevertheless, submersible- and ROV-based collections have their own shortcomings. In the first place, collections made by submersibles have limited fine-scale selectivity as the collector is normally meters away from the substratum collected and hence is unable to see small specimens from close range. Second, the submersible and ROV collection process is relatively crude, utilizing a mechanical arm that frequently results in damage to delicate forms and makes selective removal of closely adherent crustose forms difficult. Successful submersible and ROV collection is reliant on the competent handling of a manipulator arm and the capacity to store and segregate collections made at the bottom. One obvious restriction to the use of submersibles

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and ROVs is related to availability and expense of appropriate support vessels. Earle (1985) discussed the research potential of "one-atmosphere diving" suits as well as one-man microsubmersibles such as *Deep Rover*. However, work from these platforms to date has been largely limited to commercial applications.

In water deeper than that safely accessible by scuba depth, the limitations mentioned above are largely ameliorated by technology that permits an experienced collector close-range access to the environment in which the algae live. Thus, the recently expanding utilization of trimix rebreather (closed-circuit) diving now allows substantially less obstructed access to this environment. Although still of limited practice, it has the advantage of allowing a collector (as is true for a scuba diver) immediate contact with the substratum, which allows selectivity in collection. One of the drawbacks to technical rebreather diving in general is the substantial time that a diver must train to be certified on the equipment. The equipment itself is also expensive, and a diving team requires infrastructure support (Sherman et al., 2013). Deep diving must also still be regarded as inherently dangerous. As might be expected, experienced algal collectors with technical dive training are few.

Historically, extensive systematic collection specifically aimed at deep-water algae in the tropical west Atlantic have been few. The earliest of these was that by Frederick (1963) on the Bermuda platform. Using mostly dredging collections at an average depth of 54 m during 1960 and 1961, Frederick recorded 97 species (exclusive of cyanobacteria), of which 91 were identified to species level. A large-scale scientific dredging program off the east coast of Brazil conducted under the auspices of Laboratório de Ciências do Mar (Lacimar) of the Universidade Federal de Pernambuco (see Ugadim and Pereira, 1978; Guimarães et al., 1981; see also additional references cited in the species accounts) involved numerous collections deeper than 35 m. A series of papers by Schneider and Searles (1973, 1975, 1976) as well as by Schneider (1974, 1975, 1976) based mostly on scuba and dredging collections reported on the deep offshore flora of the Carolinas (east U.S. coast) and yielded a number of new algal species and species distributional records. Also in the western Atlantic, a series of submersible dives on the east Florida shelf (Eiseman, 1979; Eiseman and Blair, 1982; Hanisak and Blair, 1988a) resulted in a substantial increase in our knowledge of the deep algal flora of the region. More recently in the Bahamas, use of submersible-based dive collections also resulted in recognition of new algal species and new geographical records (Aponte and Ballantine, 2001; Ballantine and Aponte, 1996, 2002a, 2003, 2005). Dredging collections to 90 m in the Flower Garden Banks National Marine Sanctuary (Gulf of Mexico) by Fredericq's research group (reported in Gavio and Fredericq, 2003, 2005; Gavio et al., 2005) further resulted in the characterization of new algal species and new species records. More recently, Leichter et al. (2008) reported on distribution and spatial extent of algal communities off the Florida coast based on broad systematic groupings, using ROVs and scuba.

In the tropical western Atlantic (inclusive of Florida, the Bahamas, Jamaica, and Bermuda), only a handful of other submersible-based studies have been conducted in reef environments in water greater than 50 m depth: these include the results of Lang (1974), Huston (1985), and Fricke and Meischner (1985) from Florida; Lang et al. (1975) and Liddell and Olhurst (1988) from Jamaica; Littler et al. (1985, 1986), Blair and Norris (1988), Liddell et al. (1997), and Norris and Olsen (1991) from the Bahamas; and Ballantine (1990) from Puerto Rico. Macintyre et al. (1991) reported a handful of algal species collected from Barbados on the basis of two submersible dives. Littler et al. (1985) reported the deepest known macroalga (to 268 m), an unidentified Corallinales. In a more recent paper based on deployment of a drop camera, Friedlander et al. (2014: "Deep Reefs," paragraph 2) reported the presence of crustose coralline algae "from 312 m depth (and probably from 382 m)" at Pitcairn Island (Pacific Ocean), although specimens presumably were not obtained.

Other noteworthy deepwater algal reports include those by Dawes and Van Breedveld (1969) in the Florida Middle Grounds, Gulf of Mexico, who reported a number of benthic algal species and distributional records based on dredging and trynet collections to 73 m, and by Cheney and Dyer (1974) on the basis of scuba collections to 60 m.

Systematics of deep-water algal flora in Puerto Rico effectively began with the publication of a new deep-water *Halimeda* species variety (*H. cryptica* v. *acerifolia*) by Ballantine (1982) collected utilizing scuba. Wynne and Ballantine (1986) and Ballantine and Wynne (1987, 1988) reported three new species of benthic algae on the basis of scuba collections to 61 m. Subsequently, two species of a previously undescribed deepwater green alga, *Verdigellas*, were obtained utilizing dredging (Ballantine and Norris, 1994). Although these studies have provided insight into the diversity and distribution of deepwater species, initial trimix rebreather dives in southwest Puerto Rico have already yielded a handful of species new to science, particularly among calcified and noncalcified encrusting algae, as well as new geographical and depth records (including Ballantine and Ruiz, 2005, 2008, 2010, 2011; Athanasiadis et al., 2013).

ENVIRONMENT AND HABITAT

Mesophotic reef environments in general are principally noted for depth and, as a consequence, reduced light. For oceanic water off Brazil, there is a sharp decline in photosynthetically active radiation at 30 m, where less than 2% of surface irradiance reaches (Magalhães et al., 2015). In situ sea conditions are thought to be more stable in deeper water than in shallow water, with decreased disturbance and a lower fluctuation in water temperature; however, the presence of internal waves may periodically alter localized temperature regimes (Appeldoorn et al., 2016). Herbivory, which exerts a strong influence on algal populations through most of the euphotic zone, is less important in the mesophotic zone. For example, herbivorous fish populations have been shown to decline with depth in deepwater coral reef environments (Brokovich et al., 2010; Bejarano et al., 2014). Mesophotic reef habitats at the insular shelf break in south Puerto Rico are diverse in physical and geomorphic attributes. The bottom habitat may be slightly to steeply inclined and in some locales nearly vertical.

The substrata available for colonization are either hard-bottom (primarily dead *Agaricia* plates) or sand; however, the extensive sand-bottom mesophotic habitats reported in Spalding (2012) were never seen in Puerto Rico. Downslope sediment transfer grooves, which are extensions of the spur and groove environment at the shelf break, are generally devoid of macroscopic biological growth. As a result, mesophotic community development is largely restricted to topographical highs (Sherman et al., 2010). Living coral cover is occasionally substantial; however, percent bottom cover is often dominated by algal and sponge growth. In terms of composition, few foliose algal species are present, and the flora is made up of mostly encrusting Corallinales species in addition to Peyssonneliaceae species; leafy Phaeophyta, including *Dictyota* spp. and *Lobophora* spp.; and multispecies turf. Photographs of typical bottom habitat show the domination of benthic encrusting organisms at depths of 49 to 76 m (e.g., see in Figure 4).

MATERIAL AND METHODS

The present work is based on dredging and scuba collections and several submersible-based dives over the last three decades by the first author and the more recent deep trimix technical diving by the second author (see Sherman et al., 2013, for the deep technical diving protocols utilized). Species in this report were all collected in coastal waters of Puerto Rico (see Appendix A), with most effort concentrated on the southern coast (Figure 1; see also Appendix B). Additionally, collections have been conducted at Mona Island (66 km west of Puerto Rico) and at "El Seco," southeast of Vieques Island (13 km east of Puerto Rico). Species of algae reported are limited to those collected at 35 m or greater depth. This is a somewhat arbitrary depth, partly because, for Puerto Rico, the depth is recognized as a transitional one between shallow and deeper affinities and is near the recommended limit for nondecompression open-circuit scuba diving on air. Voucher specimens of algae reported are deposited in the Herbario Marino Puertorriqueño of the Department of Marine Sciences, University of Puerto Rico (MSM), and/or in the algae collection of the U.S. National Herbarium, Smithsonian Institution. Authority names are according to Brummitt and Powell (1992). A total of 185 taxa of algae collected in water deeper than 35 m are listed below. An asterisk prior to entries represents what is considered to be the deepest (or equaling the deepest) recorded depths for that species. Species are ordered by presumed phylogenetic position (Guiry and Guiry 2016).

RESULTS

RHODOPHYTA

FLORIDEOPHYCIDEAE, CORALLINOPHYCIDAE, CORALLINALES, CORALLINACEAE

****Amphiroa rigida*** J. V. Lamour.
Specimens: *DLB7357*, 49 m; *DLB7139*, 50 m; *DLB7552*, 62 m; *DLB7629*, 70 m.

Amphiroa rigida is typically a plant of shallow water and reported to 11 m depth (Taylor, 1960).

****Amphiroa tribulus*** (J. Ellis et Sol.) J. V. Lamour.
Specimens: *DLB7358*, 49 m; *DLB7144*, 50 m; *DLB7489*, 61 m.

Amphiroa tribulus is also typically a plant of shallow water and reported to 18 m depth (Taylor, 1960).

****Hydrolithon abyssophila*** Athanas., D. L. Ballant. et H. Ruiz
FIGURE 2I
Specimens: *DLB7691*, 49 m; *Athanas.PR135A*, 73 m; *DLB7824*, 73 m; *DLB7746*, 76 m.

Known from 30 to at least 76 m, the species was recently described from an insular shelf habitat on the south coast of Puerto Rico (Athanasiadis et al., 2013). The species is extremely abundant and is probably to be found at mesophotic depths throughout the Caribbean and, perhaps by cover, is the most common benthic eukaryotic organism in the Caribbean at depths greater than 50 m (Ballantine and Ruiz, unpublished).

Hydrolithon farinosum (J. V. Lamour.) Penrose et Y. M. Chamb. var. *chalicodictyum* (W. R. Taylor) Serio
Specimens: *DLBs.n.*, 55 m; *DLB1711*, 58 m; *DLB1746*, *DLB7506*, 61 m.

Schneider and Searles (1997) reported the species in Bermuda to a maximum depth of 27 to 40 m. The deepest known record for the species remains that of Frederick (1963) from Bermuda at 64 m.

****Jania adhaerens*** J. V. Lamour.
Specimen: *DLB7385*, 50 m.

This extremely broadly distributed species is mostly found in shallow-water environments (Taylor, 1960). It has been reported to 30 m depth in Florida by Hanisak and Blair (1988a) and to 35 m depth in Onslow Bay, North Carolina (Schneider and Searles, 1991).

****Jania cubensis*** Mont. ex Kütz.
Specimens: *DLB4190*, 36 m; DLB7359, 49 m; *DLB7488*, 61 m; *DLB7576*, *DLB7620*, 70 m.

As *Haliptilon cubense* (Mont. ex Kütz.) Garbary et H. W. Johans, Ballantine and Aponte (2005) and Yoneshigue-Valentin et al. (2004) reported the species to 46 and 60 m in the Bahamas and Brazil, respectively.

****Jania subulata*** (J. Ellis et Sol.) Sond.
Specimen: *DLB3736*, 36–46 m.

Jania subulata is typically known from shallow-water habitats (Littler and Littler, 2000).

NEMALIOPHYCIDAE, NEMALIALES, GALAXAURACEAE

Dichotomaria marginata (J. Ellis et Sol.) Lam.
Specimen: *DLB7494*, 61 m.

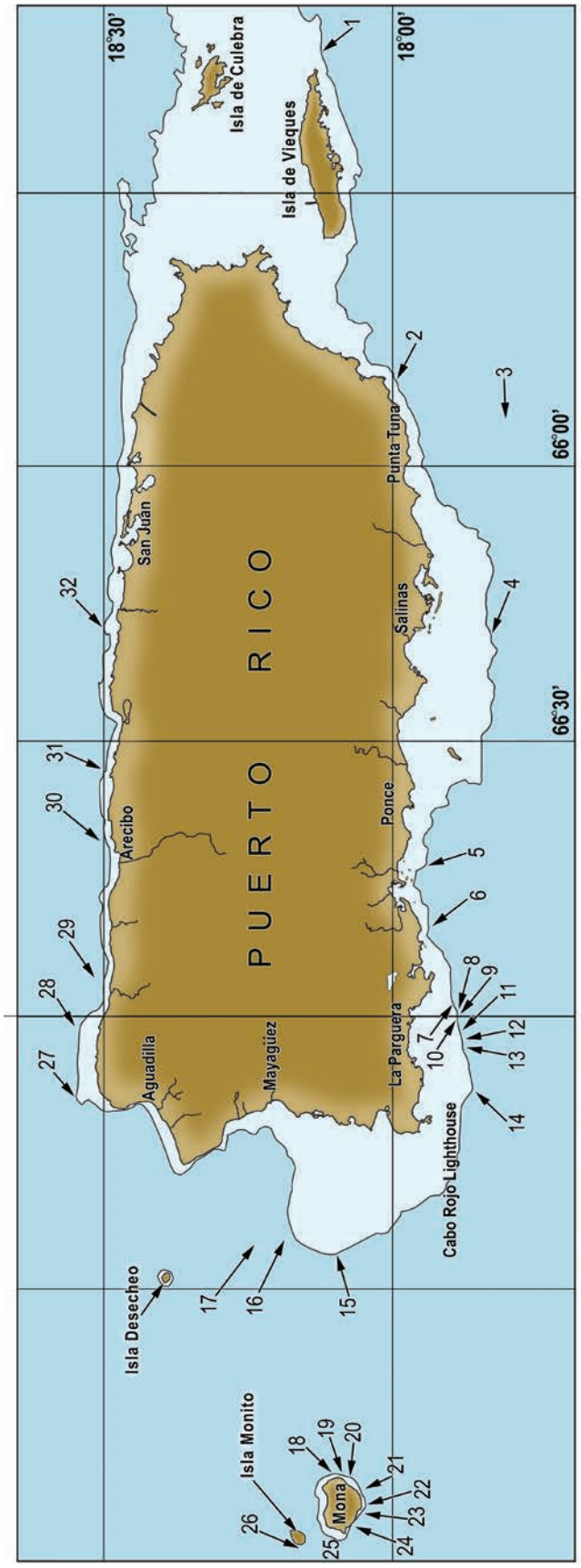

FIGURE 1. Map of Puerto Rico showing sampling sites. The depth contour surrounding the island represents a depth of 50 m. Map by Alice Tangerini for Smithsonian Institution.

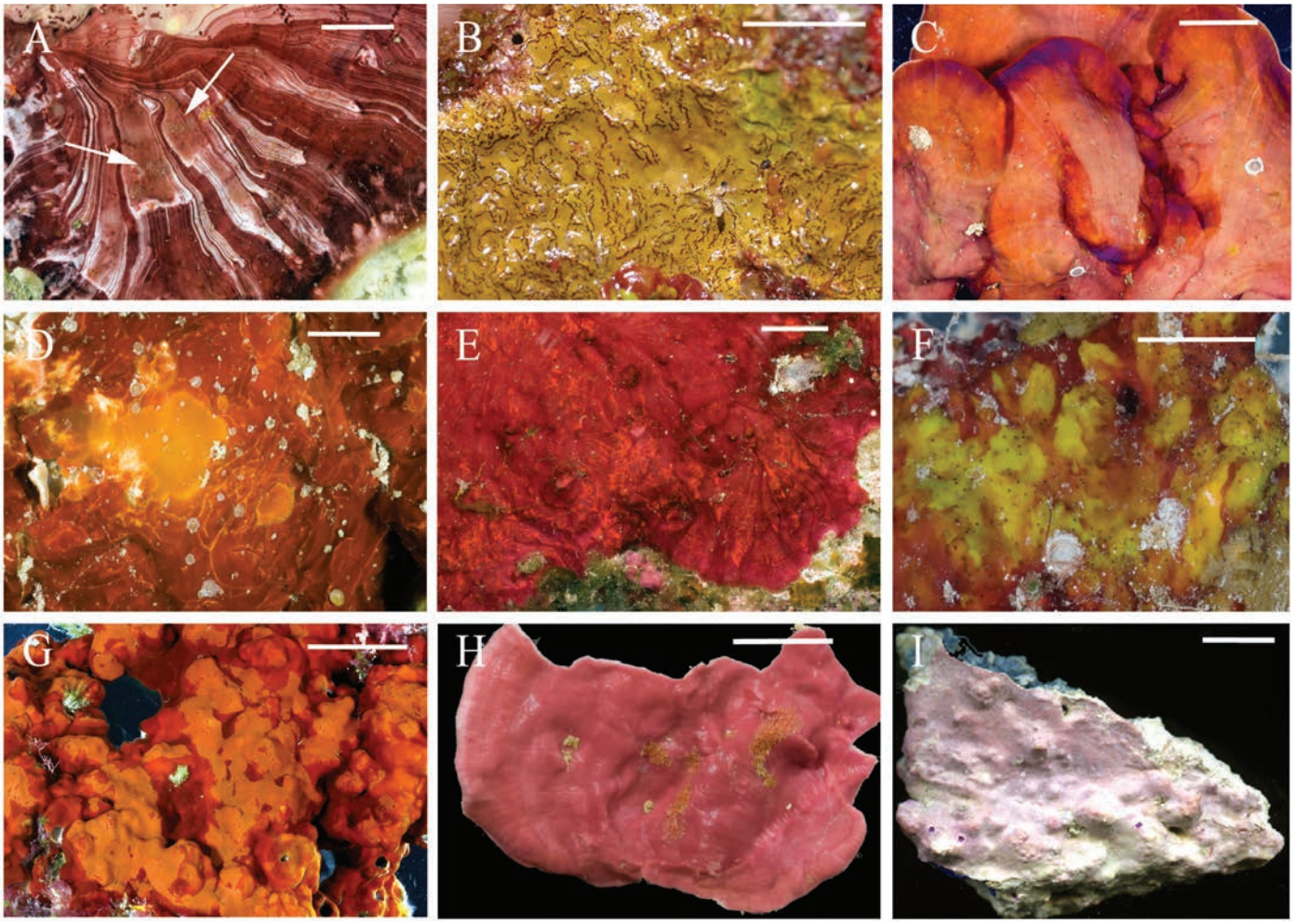

FIGURE 2. Encrusting deepwater rhodophyte species. (A) *Peyssonnelia gigaspora* (*DLB7637*); sporangial sori are denoted by arrowheads. These tetrasporangia are the largest reproductive algal spores known (scale bar = 1.0 cm). (B) *Peyssonnelia flavescens* (*DLB5883*; scale bar = 2.0 cm). (C) *Peyssonnelia iridescens* (*DLB7116*; scale bar = 1.0 cm). (D) *Peyssonnelia incomposita* (*DLB7777*; scale bar = 1.0 cm). (E) *Peyssonnelia* sp. 3 (*DLB7411*; scale bar = 5 mm). (F) *Peyssonnelia* sp. 2 (*DLB7286*; scale bar = 2.0 cm). (G) *Ethelia* sp. (*DLB6355*; scale bar = 2.0 cm). (H) *Polystrata fosliei* (*DLB7912*; scale bar = 2.0 cm). (I) *Hydrolithon abyssophila* (*Athanasiadis PR135A*; scale bar = 2.0 cm). Photos by Hector Ruiz Torres.

Reported by Taylor (1960) as having been dredged to 55 m. The deepest known record for the species remains that of Frederick (1963) from Bermuda at 62 m.

****Dichotomaria obtusata*** (J. Ellis et Sol.) Lam.
Specimen: *DLB7490*, 61 m.

Dichotomaria obtusata was reported to 27 m depth by Schneider and Searles (1973) from the offshore flora of North Carolina. *Galaxaura obtusata* var. *major* W. R. Taylor (1960) was reported as having been dredged to 53 m depth. Mateo-Cid et al. (2013) reported collections from 50 to 56 m from Campeche Banks, Mexico, and Frederick (1963) reported the species to a depth of 59 m from Bermuda.

****Galaxaura rugosa*** (J. Ellis et Sol.) J. V. Lamour.
Specimens: *DLB7153*, 50 m; *DLB3104*, 55–90 m; *DLB7628*, 70 m.

Taylor (1960) indicated that *G. rugosa* is a shallow-water alga that had also been collected to 18 m depth.

****Tricleocarpa fragilis*** (L.) Huisman et R. A. Towns.
Specimens: *DLB7549*, 62 m; *DLB7557*, 70 m.

Taylor (1960) also indicated that *T. fragilis* (as *Galaxaura cylindrica* (J. Ellis et Sol.) J. V. Lamour.) is a shallow-water alga; however, Dawes and Mathieson (2008) reported that the species has been dredged to 30 m in Florida.

Rhodymeniophycidae, Bonnemaisoniales, Bonnemaisoniaceae

Asparagopsis taxiformis (Delile) Trevis.
Specimens: *DLB7362b*, *DLB7722*, 49 m; *DLB7384*, 50 m; *DLB7645*, 70 m.

Asparagopsis taxiformis in Puerto Rican deepwater habitats is represented by the *Falkenbergia* stage (or tetrasporophyte life history alternate of *A. taxiformis*). This growth phase is typically seen in shallow-water environments in the Caribbean and is encountered only occasionally in deep water. The species was reported to 49 m in Bermuda by Frederick (1963), from 50 to 60 m in Brazil (Magalhães et al., 2015), and to 63 m in the Pacific by Gilmartin (1960).

Ceramiales, Callithamniaceae

Aglaothamnion cordatum (Børgesen) Feldm.-Maz.
Specimens: *DLB4429*, 37 m; *DLB8077*, 50 m.

The species (as *Callithamnion cordatum* Børgesen) has been collected by Schneider (1980) offshore North Carolina to 32 m depth and to 74 m by Hanisak and Blair (1988a) from Florida.

Crouania pumila Gavio, Reyes-Gómez et M. J. Wynne
Specimen: *DLB7904*, 55 m.

Reported for Puerto Rico by Ballantine et al. (2015), only small, sterile epiphytic plants were collected. The holotype specimen was from 16 m depth in Colombia (Gavio et al., 2013), and other collections were made by them at 1–2 and 37 m.

Crouanophycus latiaxis (I. A. Abbott) Athanas.
Specimen: *DLB7173*, 50 m.

Depth information was not provided for the species (as *Antithamnionella latiaxis*; Abbott, 1979) from the holotype location in St. Croix, U.S. Virgin Islands; however, it is presumed to have been collected in shallow-water reef environments. Bucher and Norris (1995) reported the species (also as *A. latiaxis*) to a maximum depth of 12 m from Martinique.

Seirospora occidentalis Børgesen
Specimens: *DLB3706*, 36 m; *DLB1214*, *DLB1818*, 40 m; *DLB1802*, *DLB7337*, 50 m; *DLB7503*, 61 m; *DLB7881*, 82 m; *DLB2158*, 87 m.

Seirospora occidentalis is a fairly common element in the deepwater turf flora of Puerto Rico.

Seirospora viridis Aponte et D. L. Ballant.
Specimen: *DLB1721*, 58 m.

This species is currently known only from Puerto Rico, where it was described from shelf edge habitats at 18 m depth (Aponte and Ballantine, 1995).

Ceramiaceae

Antithamnion antillanum Børgesen
Specimens: *DLB7156*, 50 m; *DLB7883a*, 82 m.

Macintyre et al. (1991) reported the species (as *A. lherminieri* (P. Crouan et H. Crouan) Bornet ex Nasr) to 74 m in Barbados.

Antithamnion decipiens (J. Agardh) Athanas.
Specimens: *DLB1212*, 40 m; *DLB7362a*, *DLB7720*, 49 m; *DLB7405*, 50 m; *DLB7689*, 64 m; *DLB7915*, 70 m; *DLB7883b*, 82 m.

Antithamnion decipiens was reported to 76 m in the Bahamas (Ballantine and Aponte, 2005). As *A. ogdeniae* I. A. Abbott, the species was known from 70 m in Hawaii (Agegian and Abbott, 1985).

Antithamnionella breviramosa (E. Y. Dawson) E. M. Woll.
Specimen: *DLB4419*, 37 m.

The original report of the species from Puerto Rico was based on specimens collected at intermediate depths, to ~30 m (Ballantine and Wynne, 1986). *Antithamnionella breviramosa* has been reported to a depth of 87 m in Florida by Hanisak and Blair (1988a).

Antithamnionella graeffei (Grunov) Athanas.
Specimen: *DLB7774*, 61 m.

Antithamnionella graeffei was reported to 45 m from Onslow Bay, North Carolina (Schneider, 1984), and Børgesen (1945) indicated that the species (as *Antithamnion flagellata* Børgesen) occurred to 55 m in Mauritius.

Balliella pseudocorticata (E. Y. Dawson) D. N. Young
Specimens: *DLB3693*, *DLB7959*, 36 m; *DLB7717*, 49 m; *DLB7423*, 50 m; *DLB1720*, 58 m.

As a taxonomic synonym, *Bakothamnion curassavicum* C. Hoek (1978) was based on material collected between 10 and 60 m in coral reef habitats at Curaçao. *Balliella pseudocorticata* has also been reported from 27 to 40 m in Bermuda (Schneider and Searles, 1997).

Ceramium bisporum D. L. Ballant.
Specimens: *DLB3714*, 46–55 m; *DLB7170*, 50 m; *DLB4726*, 60 m; *DLB8025*, 70 m; *DLB3195*, 80 m; *DLB3188*, 80–100 m.

In Puerto Rico, the species is found exclusively in deep water (see Ballantine, 1990); however, *C. bisporum* was recently reported as a shallow-water epiphyte in the Mediterranean Sea (Sartoni and Boddi, 2002) and also in Colombia by Rincon-Diaz et al. (2014) at 12.5 m.

Ceramium leptozonum M. A. Howe
Specimen: *DLB8096*, 50 m.

Ceramium leptozonum was first reported from Puerto Rico by Ballantine et al. (2011). Frederick (1963) reported the species to 62 m in Bermuda, and Hanisak and Blair (1988a) reported *C. leptozonum* to 92 m in Florida.

****Ceramium nitens*** (C. Agardh) J. Agardh
Specimen: *DLB7492*, 61 m.

Ceramium nitens is a very common element of the shallow-water flora in Puerto Rico, frequently found in coral reef environments.

***Ceramium* spp.**
Specimens: *DLB1209*, *DLB7392*, 50 m; *DLB7888*, 82 m.

****Gayliella transversalis*** (Collins et Herv.) Cho et L. McIvor
Specimens: *DLB7554b*, 62 m; *DLB8018*, 70 m.

The species is based on *Ceramium transversalis* Collins et Herv. (1917) from Bermuda without report of depth. As *Ceramium flaccidum* (Harvey ex Kütz.) Ardiss., the species was reported to 33 m by Hanisak and Blair (1988a) from Florida, and as *C. tranversale*, Børgesen (1918) indicated that it was found in the intertidal in the U.S. Virgin Islands. Schneider and Searles (1991) indicated that the species (as *C. byssoideum* Harv.) was collected to 21.5 m depth offshore Onslow Bay, North Carolina.

****Perikladosporon abaxiale*** D. L. Ballant. et Aponte
Specimen: *DLB2173a*, 87 m.

The species was described on the basis of specimens from the Bahamas collected at a depth of 76 m and from a submersible collection in Puerto Rico (Ballantine and Aponte, 2005). These represent the only collections known for the species.

Dasyaceae

***Dasya* sp.**
Specimen: *DLB8079*, 50 m.

****Dictyurus occidentalis*** J. Agardh
Specimen: *DLB3732*, 36–46 m.

Reported by Taylor (1960) as having been dredged to a depth of 30 m. Guimarães et al. (1981) also reported specimens dredged from 40 m in Brazil.

****Heterosiphonia crispella*** (C. Agardh) M. J. Wynne
Specimens: *DLB7073*, 52 m; *DLB8072*, 70 m.

As *Heterosiphonia wurdemannii* (Baily ex Harvey) Falkenberg, this species was reported to 30 m depth from the offshore North Carolina flora (Schneider and Searles, 1973), to 58 m in Bermuda by Frederick (1963), and to 65 m in Hawaii (Agegian and Abbott, 1985).

***Heterosiphonia* sp.**
Specimens: *DLB8097*, 50 m; *DLB8017*, 70 m.

This entity represents an undescribed species that superficially resembles *H. crispella*, differing by the nature of its near-complete axial cortication.

Delesseriaceae

****Apoglossum gregarium*** (E. Y. Dawson) M. J. Wynne
Specimens: *DLB1779*, 61 m; *DLB3122*, 100 m.

In the original report of this species from Puerto Rico, collections were reported from 18 to 30 m (Ballantine and Wynne, 1985). The species has also been reported from 50 m depth in the Mediterranean (Tsiamis and Bellou, 2010).

****Augophyllum wysorii*** S.-M. Lin, Fredericq et Hommersand
Specimen: *DLB7441*, 49 m.

Augophyllum wysorii was described from Caribbean Panama (Lin et al., 2004) at 12–15 m depths. The species was originally reported from Puerto Rico by Ballantine et al. (2015).

****Branchioglossum prostratum*** C. W. Schneid.
Specimen: *DLB1745*, 61 m.

The species is based on collections off North Carolina at 60 m (Schneider, 1974). Eiseman (1979) reported the species from 48 m on the east Florida continental shelf. *Branchioglossum prostratum* was first reported from Puerto Rico by Ballantine and Wynne (1987). Despite the fact that the species is only rarely found in water shallower than 25 m in Puerto Rico, a shallow-water collection from American Samoa was reported by Skelton and South (2007).

****Frikkiella pseudoprostrata*** (D. L. Ballant. et M. J. Wynne) M. J. Wynne et C. W. Schneid.
Specimens: *DLB7074*, 46 m; *DLB1794*, *DLB7429*, 50 m; *DLB7902*, 55 m; *DLB1733*, 58 m; *DLB1755*, 61 m; *DLB7057*, 52 m; *DLB7889*, 82 m.

Frikkiella pseudoprostrata is based on *Branchioglossum pseudoprostratum* D. L. Ballant. et M. J. Wynne (1987), where it was originally reported from 50 m depth in Puerto Rico. It is also known to 76 m in the Bahamas (Ballantine and Aponte, 2005).

Frikkiella searlesii M. J. Wynne et C. W. Schneid.
Specimen: *DLB1733*, 61 m.

Wynne and Schneider (1996) separated *Frikkiella* from *Branchioglossum* on the basis of the origin of lateral branches and the origin of tertiary cell rows. They discerned that the original circumscription of *Branchioglossum pseudoprostratum* included two separate species (i.e., *F. pseudoprostrata* and *F. searlesii*). The generitype was collected from 31 m depth in Mona Island, Puerto Rico (Ballantine and Wynne, 1987). The species has also been collected to 40 and 53 m in Bermuda (Wynne and Schneider, 1996), to 60 m in Brazil (Peruzzi de Oliveira and Yoneshigue-Valentin, 2014), and to 76 m in the Bahamas by Ballantine and Aponte (2005).

**Hypoglossum anomalum* M. J. Wynne et D. L. Ballant.
FIGURE 3C
Specimens: *DLB3705*, 36 m; *DLB1823*, 40 m; *DLB1789*, *DLB8093*, 50 m; *DLB1719*, 55 m; *DLB4685*, 55–60 m; *DLB7455*, 57 m; *DLB7455*, 61 m; *DLB7954*, 67 m; *DLB8023*, *DLB8057*, 70 m; *DLB3200*, 80 m; *DLB7680*, 82 m; *DLB2164*, 87 m; *DLB3127*, 91 m.

Hypoglossum anomalum, originally described from specimens collected at depths of 30 to 60 m in Puerto Rico (Wynne and Ballantine, 1986), is an extremely common element in deepwater habitats in the Caribbean. The species is also known to 91 m in the Bahamas (Ballantine and Aponte, 2005). A shallow-water collection was reported by Skelton and South (2007) from American Samoa as well as by Wynne (2001) from Oman (Arabian Sea).

**Hypoglossum caloglossoides* M. J. Wynne et Kraft
FIGURE 3D
Specimens: *DLB7740*, 49 m; *DLB7149*, *DLB7189*, 50 m; *DLB7903*, 55 m; *DLB7569*, 70 m; *DLB7602*, 77 m.

Hypoglossum caloglossoides was reported from 61 m depth in the Bahamas by Ballantine and Aponte (2005) and originally from Puerto Rico to 70 m depth (Ballantine et al., 2009). The holotype of the species, however, was collected at 11 m depth (Wynne and Kraft, 1985) and is also known from shallow water in the Red Sea and the Mediterranean (Hoffman and Wynne, 2015).

**Hypoglossum hypoglossoides* (Stackh.) Collins et Herv.
Specimens: *DLB3691*, 36 m; *DLB7430*, 50 m; *DLB1750a*, 61 m; *DLB2157a*, 87 m.

Hypoglossum hypoglossoides was reported from Bermuda at 37 m by Schneider (2000) and at 50–56 m at Campeche Banks, Mexico, by Mateo-Cid et al. (2013).

**Hypoglossum rhizophorum* D. L. Ballant. et M. J. Wynne
Specimens: *DLB*1832, 40 m; *DLB7402*, *DLB7737*, 49 m; *DLB7147*, *DLB7193*, 50 m; *DLB7905*, 55 m; *DLB1718*, 58 m; *DLB1750b*, 61 m; *DLB7486*, 63 m; *DLB3206*, 68 m; *DLB7594*, 77 m; *DLB2157b*, 87 m.

The species was originally described from deepwater habitats in Puerto Rico to 61 m depth (Ballantine and Wynne, 1988). Schneider (2000) reported the species from Bermuda to a maximum of 47–50 m.

**Hypoglossum simulans* M. J. Wynne, I. R. Price et D. L. Ballant.
Specimens: *DLB3696*, 36 m; *DLB4728*, 60 m; *DLB*1783, 61 m.

The holotype of *H. simulans* is from 30 m at Guadeloupe, French West Indies (Wynne et al., 1989).

Hypoglossum tenuifolium (Harv.) J. Agardh
Specimens: *DLB1717*, 58 m; *DLB1743*, *DLB7772*, 61 m; *DLB2156*, 87 m.

Reported to 83 m from Brazil (Cordeiro-Marino and Guimarães, 1981) and from 90 m in Florida by Hanisak and Blair (1988a).

**Martensia pavonia* Hering
Specimens: *DLB3703*, 36 m; *DLB7027*, 46 m; *DLB7364*, 49 m; *DLB7318*, 50 m; *DLB1772*, 61 m; *DLB7484*, 63 m; *DLB8004*, 70 m; *DLB7882*, 82 m.

Martensia pavonia is another common deepwater algal turf component. It was reported to 40 m depth by Hanisak and Blair (1988a).

**Myriogramme prostrata* (E. Y. Dawson, Neushul et Wildman) M. J. Wynne
FIGURE 3B
Specimens: *DLB7051*, 52 m; *DLB7948*, 67 m.

Myriogramme prostrata was originally reported from Puerto Rico at 11 m depth by Ballantine et al. (2004).

**Nitophyllum adhaerens* M. J. Wynne
Specimens: *DLB7958*, 36 m; *DLB7032*, 46 m; *DLB7142*, *DLB7346*, 50 m; *DLB449*, 70 m; *DLB7683*, 82 m; *DLB8162*, 90 m.

Schneider (2000) reported *Nitophyllum adhaerens* from Bermuda to 50 m, and Ballantine and Aponte (2005) also reported the species from the Bahamas to a maximum depth of 50 m. Wynne (1997), in part on the basis of Puerto Rican specimens, reported the species from the Bahamas at 61 m depth. The holotype, however, was from shallow water at Quintana Roo, Mexico.

**Taenioma nanum* (Kütz.) Papenf.
Specimen: *DLB7812*, 49 m.

Typically, a shallow-water entity (Taylor, 1960), the species has also been collected at the Puerto Rican insular shelf edge at 21 m depth (Ballantine, unpublished).

Rhodomelaceae

**Amansia multifida* J. V. Lamour.
Specimen: *DLB8457*, 55 m

Amansia multifida is typically a shallow-water alga. Littler and Littler (2000) reported that the alga lives from the intertidal to a depth of 5 m.

Chondria **spp.**
Specimens: *DLB4204*, 36 m; *DLB7344*, *DLB7368*, *DLB7744*, 49 m; *DLB7053*, 52 m; *DLB7887*, 77 m.

These *Chondria* records probably represent multiple species.

**Herposiphonia secunda* (C. Agardh) Ambronn.
Specimen: *DLB7499*, 61 m.

The species is a member of the deepwater algal turf in Puerto Rico. It has been reported to 31 m in the Bahamas (Ballantine

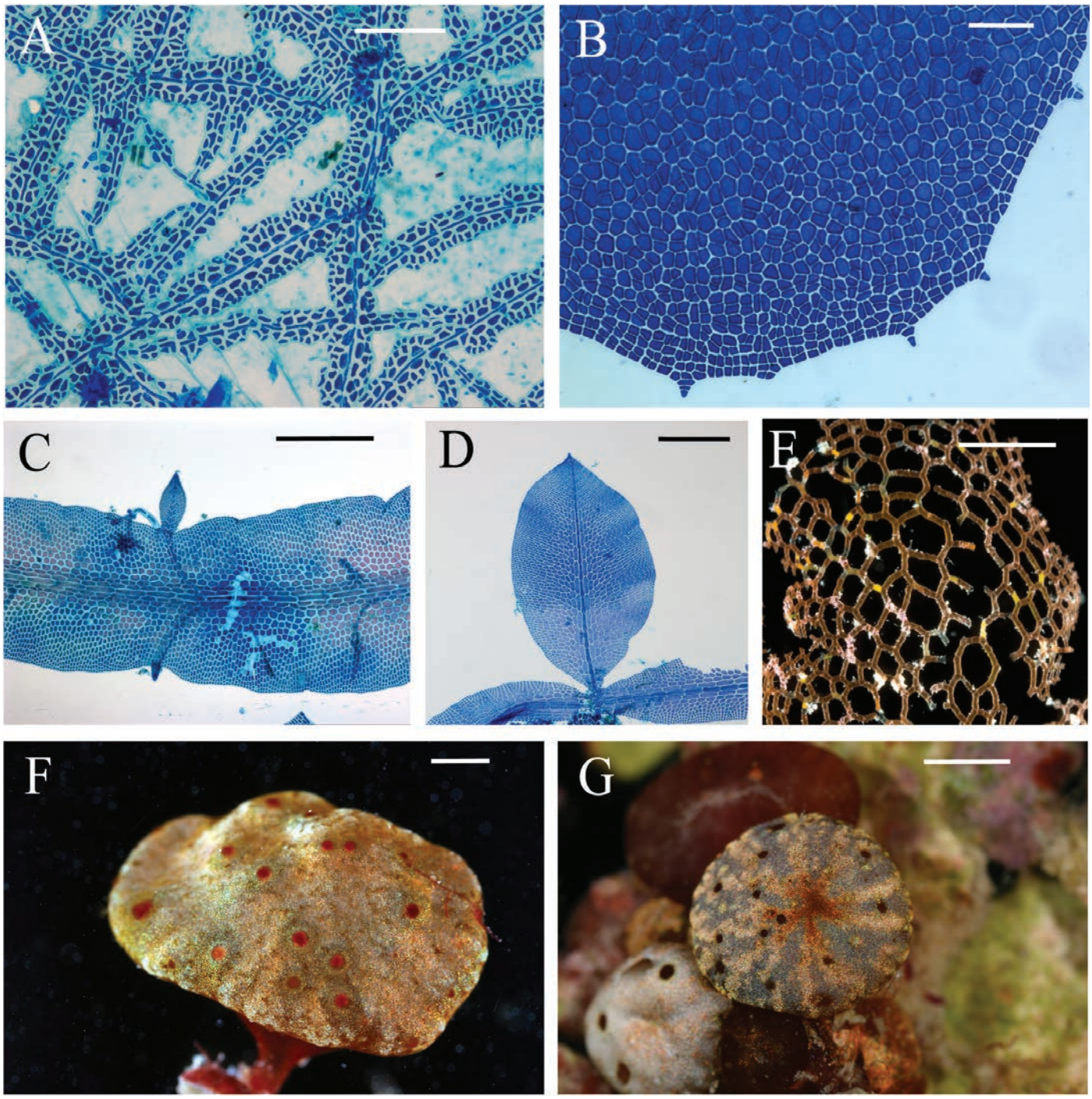

FIGURE 3. Deepwater Rhodophyta algal species. (A) *Hymenoclonium serpens* (*DLB0720*; scale bar = 100 µm). (B) *Myriogramme prostrata* (*DLB6029*; scale bar = 100 µm). (C) *Hypoglossum anomalum* (*DLB7569*; scale bar = 200 µm). (D) *Hypoglossum caloglossoides* (*DLB7569*; scale bar = 200 µm). (E) *Rhododictyon bermudense* (*DLB7527*; scale bar = 1.0 mm). (F) *Cresia opalescens* (*DLB6343*; scale bar = 1.0 mm). (G) *Botryocladia iridescens* (*DLB6307*; scale bar = 2.0 mm). Photos by Hector Ruiz Torres.

and Aponte, 2005) and to 35 m in Bermuda (Schneider and Searles, 1997). The species was also identified from Brazil at 52 m by Guimarães et al. (1981).

***Herposiphonia* sp.**
Specimen: *DLB7222*, 52 m.

***Laurencia intricata* J. V. Lamour.**
Specimens: *DLB4195*, 36 m; *DLB4684*, 55–60 m.

Laurencia intricata is a common shallow-water species (Littler and Littler, 2000), although Taylor (1960) reported that the species had been dredged to a depth of 36 m, and Mateo-Cid et al. (2013) recorded the species from 40 to 49 m at Campeche Banks, Mexico.

***Lophosiphonia cristata* Falkenb.**
Specimen: *DLB8107*, 49 m.

Listed by Taylor (1960) as a shallow-water species, *L. cristata* is a member of the deep-water algal turf in Puerto Rico.

***Polysiphonia* spp.**
Specimens: *DLB7285*, 46 m; *DLB7365*, 49 m; *DLB7398*, 50 m; *DLB8015*, 70 m.

These *Polysiphonia* records probably represent multiple species.

***Wrightiella tumanowiczi* (Gatty ex Harv.) F. Schmitz**
Specimens: *DLB7436*, *DLB7389*, 50 m; *DLB4807*, 55 m.

Puerto Rican inshore plants typically reach to over 30 cm in height, whereas the deepwater specimens are highly reduced, to 5 cm or less. The species has also been collected to 40 m depth offshore North Carolina (Schneider and Searles, 1975) and 50–56 m from the Campeche Banks, Mexico (Mateo-Cid et al., 2013).

Sarcomeniaceae

***Cottoniella filamentosa* (M. Howe) Børgesen**
Specimen: *DLB3130*, 91 m.

Taylor (1960) reported the species to a depth of 92 m.

***Platysiphonia caribaea* D. L. Ballant. et M. J. Wynne**
Specimens: *DLB3698*, 36 m; *DLB3713*, 46–55 m; *DLB1710*, 58 m; *DLB1776*, 61 m; *DLB3199*, 80 m; *DLB3193*, 80–100 m.

This species was originally reported from Puerto Rico at a depth of 18 m as well as from 29 m in Quintana Roo, Mexico (Ballantine and Wynne, 1985). The 100 m depth record exceeds the 92 m depth reported by Ballantine and Aponte (2005) for the Bahamas.

Wrangeliaceae

***Diplothamnion jolyi* C. Hoek**
Specimens: *DLB3735*, 36–46 m; *DLB1811*, 50 m.

The species is based on collections from Curaçao, Netherlands Antilles, to a depth of 55 m (Hoek, 1978) and is also known to 32 m from Bermuda (Schneider and Searles, 1997). A previous account of the species from Puerto Rico was based on occurrence in wave-exposed habitats in very shallow water (Wynne and Ballantine, 1985).

***Grallatoria reptans* M. Howe**
Specimens: *DLB3699*, 36 m; *DLB7936*, 49 m; *DLB7052*, 52 m; *DLB7899*, 55 m.

Grallatoria reptans is typically a shallow-water alga in areas of high turbulence (Taylor, 1960); the species is also reported to 55 m from Florida (Hanisak and Blair, 1988a).

***Griffithsia heteromorpha* Kütz**
Specimens: *DLB7372*, 49 m; *DLB7054*, 52 m.

The species was reported by Schneider (2004) to a maximum depth of 37 m in Bermuda, and Hanisak and Blair (1988a) reported a collection of this species to 38 m in Florida.

***Haloplegma duperreyi* Mont.**
Specimen: *DLB7757*, 49 m.

Ballantine and Aponte (2005) reported the species to 61 m in the Bahamas. The species is also known from Hawaii in deep water at 60 m (Agegian and Abbott, 1985).

***Rhododictyon bermudense* W. R. Taylor**
FIGURE 3E
Specimens: *DLB7527*, 63 m; *DLB7574*, 70 m; *DLB7763*, *DLB7846*, 82 m; *DLB2177*, *DLB8145*, 87 m; *DLB8164*, 90 m; *DLB8147*, 91 m.

Ballantine and Aponte (2005) collected this exclusively deepwater species at a depth of 107 m in the Bahamas. The species was also reported to 100 m by Frederick (1963).

***Spermothamnion investiens* (P. Crouan et H. Crouan) Vickers**
Specimens: *DLB4120*, 55 m; *DLB1714*, 58 m; *DLB1771*, 61 m; *DLB7854*, 82 m; *DLB2168*, 87 m.

Reported by Taylor (1960) to a depth of 27 m, *S. investiens* var. *cidaricola* Børgesen was reported by Schneider (1976) to a maximum depth of 54 m in the Carolinas.

***Spermothamnion* cf. *macromeres* Collins et Herv.**
Specimen: *DLB7854*, 82 m.

Reported as a shallow-water species by Taylor (1960).

***Spongoclonium caribaeum* (Børgesen) M. J. Wynne**
Specimens: *DLB3728*, 36–46 m; *DLB4119*, 55 m; *DLB2155*, 87 m.

As *Mesothamnion caribaeum* Børgesen, the species was reported to 30 m depth in St. John, U.S. Virgin Islands (Børgesen, 1917).

***Wrangelia bicuspidata* Børgesen**
Specimens: *DLB7282*, 46 m; *DLB7360*, *DLB7711*, 49 m; *DLB7317*, *DLB8088*, 50 m; *DLB7070*, 52 m; *DLB1723*,

58 m; *DLB4686*, 55–60 m; *DLB1763*, 61 m; *DLB7974*, 62 m; *DLB7478*, 63 m; *DLB7953*, 67 m; *DLB7562*, *DLB7631*, 70 m; *DLB7593*, 77 m; *DLB7678*, 82 m.

Wrangelia bicuspidata is another common component of the deepwater turf community in Puerto Rico. Taylor (1960) reported that the species has been dredged from 40 m depth.

Wrangelia gordoniae Bucher, D. L. Ballant. et J. N. Norris
Specimens: *DLB7035*, 46 m; *DLB7742*, 49 m; *DLB7315*, *DLB7426*, 50 m; *DLB7445*, 57 m; *DLB4724*, 60 m; *DLB7470*, 61 m; *DLB7974*, 62 m; *DLB7825*, 73 m.

Bucher et al. (2014), in describing the species in part on the basis of the above Puerto Rican collections, reported the species to a maximum depth of 67–73 m at San Salvador Island, Bahamas, equaling the depth of the deepest Puerto Rican collection.

Gigartinales, Cystocloniaceae

Hypnea volubilis Searles in C. W. Schneid. et Searles
Specimen: *DLB7897*, 55 m.

Hypnea volubilis was previously reported from Puerto Rico (Ballantine and Aponte, 1997) to a depth of 60 m. It has also been reported off the east coast of Florida to 40 m by Eiseman (1979).

Kallymeniaceae

Meredithia? caribaea D. L. Ballant, H. Ruiz et J. N. Norris
Specimens: *DLB7947*, 67 m; *DLB7579*, 70 m.

Meredithia? caribaea, only recently described from offshore habitats in Puerto Rico (Ballantine et al., 2015), is known from two deepwater collections as well as from a midshelf algal plain at 17 m.

Meredithia pulchella D. L. Ballant, H. Ruiz et J. N. Norris
Specimens: *DLB7308*, 50 m; *DLB7590*, *DLB7639*, 70 m.

The entity first reported from Puerto Rico between 14 and 70 m by Ballantine et al. (2011) was referred to *Kallymenia limminghei* Montagne. Schneider et al. (2014) indicated that on the basis of molecular evidence, the Puerto Rican entity was an undescribed species of the genus *Meredithia*. The species was subsequently described by Ballantine et al. (2015).

Rhizophyllidaceae

***Contarinia* sp.**
Specimens: *DLB7921*, 49 m; *DLB7839*, 5 m; *DLB7892*, 55 m; *DLB7950*, *DLB7956*, 67 m; *DLB7813*, 73 m; *DLB7891*, *DLB8186*, 82 m.

This noncalcified crust was common in the Puerto Rican deepwater collections and was sequenced by G. W. Saunders' lab (University of New Brunswick, Fredericton, Canada) and listed as *Contarinia* sp. in Schneider et al. (2014).

Solieriaceae

Agardhiella ramosissima (Harv.) Kylin
Specimen: *DLB4683*, 55–60 m.

Agardhiella ramosissima has been reported as dredged to 55 m by Taylor (1960).

Flahaultia tegetiformans W. R. Taylor
Specimens: *DLB1709*, 36 m; *DLB1258*, *DLB1825*, 40 m; *DLB7440*, 49 m; *DLB1765*, 61 m.

The species was previously reported from Puerto Rico by Ballantine and Aponte (1997) to a maximum depth of 61 m. A dredged specimen of *F. tegetiformans* from Jamaica was reported to 24 m depth by Taylor (1974).

Meristotheca gelidium (J. Agardh) E. J. Faye et Masuda
Specimen: DLB4188, 36 m.

Frederick (1963) reported the species as *Eucheuma schrammii* (P. et H. Crouan) J. Agardh from 64 m depth in Bermuda.

Solieria filiformis (Kütz.) P. W. Gabrielson
Specimen: DLB4209, 36 m.

Schneider and Searles (1991) reported that the species has been dredged from 29 to 45 m at Onslow Bay, North Carolina.

Wurdemannia miniata (Spreng.) Feldmann et Hamel
Specimen: *DLB7832*, 52 m; *DLB7532*, 63 m.

A member of the deepwater turf community in Puerto Rico, the species is typically known as being from shallow water (Taylor, 1960), although Hanisak and Blair (1988a) reported *W. miniata* from 26 to 58 m in Florida.

Nemastomatales, Nemastomataceae

Predaea laciniosa Kraft
Specimens: *DLB7505*, *DLB7520*, 61 m; *DLB7472*, 63 m; *DLB7778*, 70 m.

The species as known from Puerto Rico is based on the above collections (Ballantine et al., 2009). The Puerto Rico report remains the species' only occurrence in the Atlantic Ocean. *Predaea laciniosa* was originally described from the Great Barrier Reef, Australia, with the holotype having been collected at 12 m depth (Kraft, 1984). The species is otherwise broadly reported from the Pacific, to 10 m in Hawaii (Abbott, 1999), as well as from the Indian Ocean, with depth records of 21 m in Oman and Yemen (Schils and Coppejans, 2002).

***Predaea* sp.**
Specimen: *DLB7686*, 64 m.

Schizymeniaceae

Titanophora incrustans (J. Agardh) Børgesen
Specimen: *DLB4698*, 60 m.

Littler and Littler (2000) indicated a depth range to 15 m for the species, and Mateo-Cid et al. (2013) reported *Titanophora incrustans* from 50 to 56 m at Campeche Banks, Mexico.

Gracilariales, Gracilariaceae

**Gracilaria isabellana* Gurgel, Frederica et J. N. Norris
Specimens: *DLB3751*, 36–46 m; *DLB4124*, 55 m; *DLB4687*, 55–60 m; *DLB4735b*, 60 m.

The species is based on shallow-water collections in St. Croix, U.S. Virgin Islands (Gurgel et al., 2004).

Peyssonneliales, Etheliaceae

Ethelia **sp.**
FIGURE 2G
Specimens: *DLB7529*, 63 m; *DLB7573*, 70 m; *DLB7814*, 73 m; *DLB7858*, 82 m.

These specimens are recognized to represent an undescribed species, and their description is pending.

Peyssonneliaceae

**Peyssonnelia boergesenii* Weber Bosse
Specimens: *DLB*7401, 49 m; *DLB7323*, 50 m; *DLB7471*, 61 m.

Peyssonnelia boergesenii is more typically a shallow-water alga (Taylor, 1960; Guimarães and Fujii, 1999). It had previously been reported from 0.5 and 22 m in Puerto Rico (Ballantine and Ruiz, 2005).

**Peyssonnelia flavescens* D. L. Ballantine et H. Ruiz
FIGURE 2B
Specimens: *DLB7166*, 50 m; *DLB8053*, 70 m; *DLB7819*, 73 m; *DLB7872*, 82 m.

The original and only report of the species is from Puerto Rico by Ballantine and Ruiz (2005).

**Peyssonnelia gigaspora* D. L. Ballant. et H. Ruiz
FIGURE 2A
Specimens: *DLB7830*, 52 m; *DLB7468*, *DLB7521*, 61 m; *DLB7477*, 63 m; *DLB7943*, *DLB7945*, 67 m; *DLB7612*, *DLB7637*, *DLB7907*, 70 m; *DLB7816*, 73 m; *DLB7859*, *DLB7890*, 82 m; *DLB8160*, 90 m; *DLB8150*, 91 m.

The original and only report of the species is from Puerto Rico by Ballantine and Ruiz (2010). The species is very common in deepwater coral reef habitats.

Peyssonnelia inamoena Pilg.
Specimens: *DLB*7278, 46 m; *DLB1229*, 49 m; *DLB7817*, 73 m.

Ballantine and Aponte (2005) reported the species to 91 m depth in the Bahamas, and Hanisak and Blair (1998a) reported the species in Florida to 98 m.

**Peyssonnelia incomposita* D. L. Ballant. et H. Ruiz
FIGURE 2D
Specimens: *DLB7830*, 52 m; *DLB7987*, 62 m; *DLB7777*, *DLB8039*, 70 m; *DLB7818*, 73 m; *DLB7859*, 82 m.

The original and only report of the species is from Puerto Rico by Ballantine and Ruiz (2011).

**Peyssonnelia iridescens* D. L. Ballant. et H. Ruiz
FIGURES 2C, 4C
Specimens: *DLB7277*, 46 m; *DLB7116*, *DLB 7759*, 49 m; *DLB7316*, *DLB7329*, 50 m; *DLB7518*, *DLB9769*, 61 m; *DLB7547*, 62 m; *DLB7474*, *DLB7530*, 63 m; *DLB7687*, 64 m; *DLB7558*, *DLB7914*, 70 m; *DLB7609*, 77 m; *DLB7670*, *DLB7855*, 82 m; *DLB8143*, 87 m.

The original and only report of the species is from Puerto Rico by Ballantine and Ruiz (2010). Because of its iridescence and loosely attached habit, the species is a visually conspicuous element of the Puerto Rican mesophotic community.

Peyssonnelia **sp. 1**
Specimens: *DLB7440*, 49 m; *DLB7334*, 50 m; *DLB7454*, 57 m; *DLB7986*, 62 m; *DLB8043*, 70 m.

The crust possesses hypothallial filaments that do not laterally cohere.

Peyssonnelia **sp. 2**
FIGURE 2F
Specimens: *DLB7286*, 46 m; *DLB7727*, 49 m; *DLB7444*, 57 m; *DLB7519*, *DLB7522*, 61 m; *DLB7479*, 63 m.

Peyssonnelia **sp. 3**
FIGURE 2E
Specimens: *DLB7548*, 62 m; *DLB7570*, *DLB7606*, *DLB7624*, *DLB8042*, 70 m; *DLB7865*, 82 m.

This species as well as the other above *Peysso**nnelia* species are reasonably abundant on the deep Puerto Rican insular shelf; unfortunately, reproductive specimens were never collected for any of these taxa. They all probably represent additional undescribed species.

**Polystrata fosliei* (Weber Bosse) Denizot
FIGURE 2H
Specimen: *DLB7912*, 70 m.

Ballantine et al. (2011) reported this species from Puerto Rico in deep water and at 17 m depth. Kato et al. (2006) reported the species from Japanese coastal waters to be a species of shallow to intermediate depths.

Halymeniales, Halymeniaceae

Cryptonemia crenulata (J. Agardh) J. Agardh
Specimens: *DLB3701*, 36 m; *DLB1208*, 40 m; *DLB7026*, 46 m; *DLB436*, *DLB7756*, 49 m; *DLB7836*, 52 m; *DLB7452*,

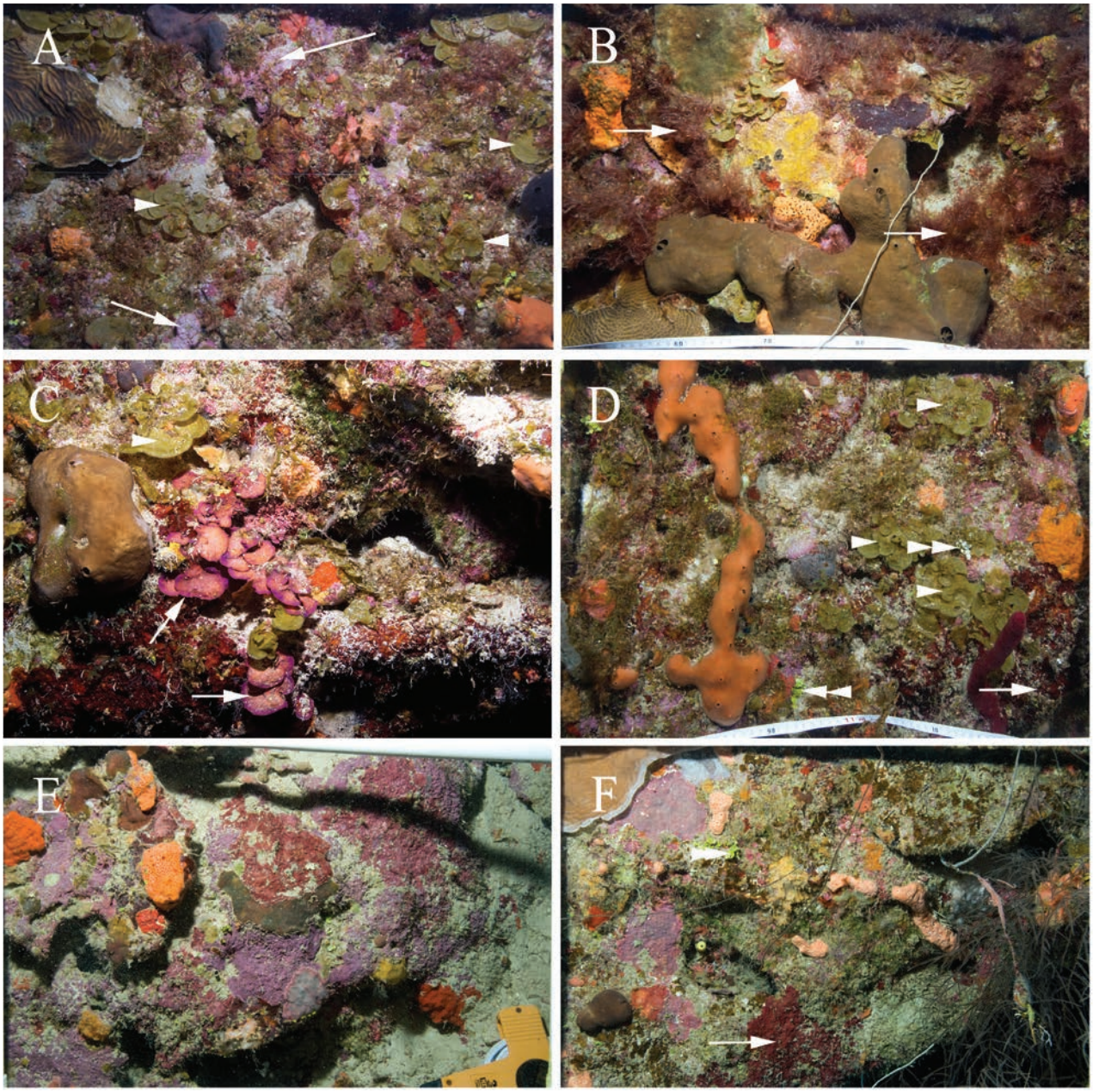

FIGURE 4. Bottom habits at edge of insular shelf south of La Parguera (all 1 m^2). (A) "Weinberg," 47 m. Pinkish background growths are Corallinales, mostly *Hydrolithon abyssophila* (arrows); also present are leafy *Lobophora* (probably *L. guadeloupensis*) (arrow heads) and several small *Halimeda* sp. in the lower right; orange growths are sponges; and at the far upper left is a colony of *Agaricia lamarcki* Milne Edwards et Haime. (B) "Hole in the wall," 47 m. The frame is dominated by a brown sponge (bottom); the large yellow incrustation at center is *Peyssonnelia flavescens*; algal turf (including *Wrangelia* spp.) is indicated by arrows; and leafy *Lobophora* (probably *L. guadeloupensis*) is shown by the arrowhead. (C) "Hole in the wall," 67 m. Nearly free blades of *Peyssonnelia iridescens* dominate the center of the frame (arrows); crustose coralline algae (some covered with sediment) appear as pink encrustations; the deep maroon encrustation at lower left is *Peyssonnelia* sp.; and leafy *Lobophora* (probably *L. guadeloupensis*) is shown by the arrowhead. (D) El Hoyo Terrace, 59 m. Coralline algae are pinkish encrustations; maroon encrustations (arrow) are *Peyssonnelia* sp.; leafy *Lobophora* (probably *L. guadeloupensis*) are shown by arrowheads; and *Halimeda cryptica* is indicated by double arrowheads. (E) "Hole in the wall," 76 m. Bottom is dominated by encrusting coralline red algae, *Peyssonnelia* sp., and sponges. (F) "El Precipicio," 70 m. Bottom is similarly dominated by encrusting coralline red algae, *Peyssonnelia* sp. (arrow), and sponges; *Halimeda cryptica* is indicated by a double arrowhead; and a portion of an *Agaricia* plate is in the upper left corner. Photos by Hector Ruiz Torres.

57 m; *DLB7525*, 63 m; *DLB8003*, 70 m; *DLB7623*, 70 m; *DLB7875*, 82 m.

Ballantine and Aponte (2005) reported the species to 61 m in the Bahamas, and Hanisak and Blair (1988a) reported the species to 93 m from Florida.

***Cryptonemia* sp.**
Specimen: *DLB1800*, 50 m.

Halymenia hancockii W. R. Taylor
Specimen: *DLB8458*, 55 m.

The species was described from dredged material at 24 m depth in Colombia (Taylor, 1942). Frederick (1963) reported the species to 64 m from Bermuda, and Hanisak and Blair (1988a) recorded the species from 34 to 93 m off the east coast of Florida.

Halymenia pseudofloresii Collins et M. Howe
Specimens: *DLB4206*, 36 m; *DLB*4692, 55–60 m.

Halymenia pseudofloresii was reported to 60 m (as *Halymenia floresii* (Clemente) Agardh) by Leichter et al. (2008) from Florida and to the same depth from Bermuda by Frederick (1963). Dawes and Van Breedveld (1969) also reported the species (as *H. floresii*) from Florida at 73 m.

Rhodymeniales, Champiaceae

Champia parvula (C. Agardh) Harv.
Specimens: *DLB7314*, *DLB7381*, 50 m; *DLB7056*, 52 m; *DLB7509*, 61 m; *DLB8071*, 70 m.

Taylor (1960) indicated that the species was primarily restricted to shallow water; however, he also reported that dredged material had been collected to 37 m. Gilmartin (1960) reported *C. parvula* from 63 m in Eniwetok, and Joly and Yoneshigue Braga (1966) reported the species from 120 m in Brazil. Lozada-Troche and Ballantine (2010) indicated that specimens identified as *C. parvula* in the western Atlantic may represent multiple cryptic species.

Champia vieillardii Kütz.
Specimens: *DLB1253*, 40 m; *DLB7377*, *DLB7928*, 49 m; *DLB7338*, *DLB7404*, 50 m; *DLB7081*, 55 m.

Ballantine and Aponte (2005) reported the species to 61 m in the Bahamas. The species has also been reported from 55 to 60 m at St. Paul Archipelago (Mid-Atlantic Ridge, Brazil) by Magalhães et al. (2015).

Faucheaceae

****Gloiocladia atlantica*** (Searles) R. E. Norris
Specimens: *DLB7464*, 41 m; *DLB7933*, 40 m; *DLB7151*, 50 m; *DLB7553*, 62 m; *DLB7556*, 70 m; *DLB3121*, 100 m.

Originally reported from Puerto Rico (as *Gloioderma atlanticum* Searles) by Ballantine and Norris (1989) from a maximum depth of 36 m, *Gloiocladia atlantica* is relatively rarely reported in the tropical western Atlantic. Hanisak and Blair (1988a) reported the species from a maximum depth of 60 m in Florida, and Ballantine and Aponte (2005) reported the species to 76 m from the Bahamas.

Hymenocladiaceae

Asteromenia peltata (W. R. Taylor) Huisman et A. Millar
Specimens: *DLB3692*, 36 m; *DLB4689*, 55–60 m; *DLB4719*, 60 m.

Reported from the Gulf of Mexico to 50–65 m by Gavio and Fredericq (2005) and to 64 m (as *Halichrysis peltata* (W. R. Taylor) P. Huvé et H. Huvé) in the Canary Islands by Haroun et al. (1993). Dawes and Van Breedveld (1969) reported the species as *Fauchea peltata* W. R. Taylor from Florida to 73 m. The deepest known report for the species is by Ballantine and Aponte (2005), who reported *A. peltata* to 76 m in the Bahamas.

Lomentariaceae

***Lomentaria* sp.**
Specimen: *DLB7378*, 49 m.

Lomentaria divaricata (Durant.) M. J. Wynne was reported (as *L. baileyana* (Harv.) Farlow) to 71 m by Hanisak and Blair (1988a).

Rhodymeniaceae

****Botryocladia iridescens*** D. L. Ballant. et H. Ruiz
FIGURE 3G
Specimens: *DLB7036*, 47 m; *DLB7335a*, 50 m; *DLB7563*, 70 m; *DLB7853*, 82 m.

The species was originally reported from moderate (23 m) depth habitats in Puerto Rico and Grenada (Ballantine and Ruiz, 2008) and has not been elsewhere reported.

Botryocladia pyriformis (Børgesen) Kylin
Specimens: *DLB4674*, 55–60 m; *DLB4714*, 60 m.

Botryocladia pyriformis was reported to 60 m in Florida by Leichter et al. (2008) and to 70 m by Gavio and Fredericq (2005). The deepest depth report for the species is 73 m by Frederick (1963) at Bermuda.

****Botryocladia spinulifera*** W. R. Taylor et I. A. Abbott
Specimens: *DLB1251*, 40 m; *DLB7037*, 47 m; *DLB1218*, *DLB7748*, 49 m; *DLB7326*, 50 m; *DLB7944*, 67 m; *DLB7618*, 70 m; *DLB7876*, 82 m.

The species was originally reported from Puerto Rico by Ballantine (1985) to a maximum depth of 49 m as well as by Bucher et al. (1990) to a maximum depth of 40–49 m in Florida. Mateo-Cid et al. (2013) reported the species from 50 to 56 m at Campeche Banks, Mexico.

**Botryocladia wynnei* D. L. Ballant.
Specimen: DLB7475, 63 m.

The type locality for the species is a 17-m-deep algal plain in Puerto Rico (Ballantine, 1985). Schneider and Searles (1991) reported the species from 30 to 35 m depth at Onslow Bay, North Carolina.

Chrysymenia **cf.** *ventricosa* (J. V. Lamour.) J. Agardh
Specimen: *DLB 8422*, 37 m.

Ballantine et al. (2015) reinstated the presence of the species in Puerto Rico on the basis of a collection at 37 m. Taylor (1960:479) indicated that *C. ventricosa* was "probably a deep-water species" that has been dredged to 90 m, and Rodriguez y Femenías (1888) reported the species growing at 130 m at Puerto de Mahón (Menorca, Spain) in the Mediterranean.

Chrysymenia **sp.**
Specimen: *DLB7403*, 50 m.

Coelarthrum cliftonii (Harv.) Kylin
Specimens: *DLB7932*, 49 m; *DLB7339*, *DLB7425*, 50 m; *DLB450*, 70 m.

Gavio and Fredericq (2005) also collected the species from 50 to 70 m in the Gulf of Mexico, and Frederick (1963) reported the species to 73 m depth in Bermuda. The deepest known depth for the species is 76 m in the Bahamas (Ballantine and Aponte, 2005).

**Cresia opalescens* D. L. Ballant., Lozada-Troche et H. Ruiz
FIGURE 3F
Specimen: *DLB7729*, 49 m.

To date, *Cresia opalescens* is known only from its type locality in Puerto Rico, where it is most frequently collected in coral reef habitats at moderate depths (Lozada-Troche et al., 2010).

**Halichrysis corallinaria* D. L. Ballant., G. W. Saunders et H. Ruiz
Specimen: *DLB7133*, 50 m.

Halichrysis corallinaria was reported from Puerto Rico to a maximum depth of 23 m by Ballantine et al. (2007) and has not been collected elsewhere.

Leptofauchea? rhodymenioides W. R. Taylor
Specimens: *DLB7747*, *DLB7927*, 49 m; *DLB7305*, *DLB*7328 50 m; *DLB7837*, 52 m; *DLB 7451*, 57 m; *DLB7590*, 70 m; *DLB7766*, 82 m.

As no reproductive material was collected, this record is unconfirmed. *Leptofauchea rhodymenioides* was reported to 93 m by Hanisak and Blair (1988a) and 95 to 155 m in the Gulf of Mexico by Gavio and Fredericq (2005).

Other Rhodophyta

**Hymenoclonium serpens* (P. Crouan et H. Crouan) Batters
FIGURE 3A
Specimens: *DLB7833*, 52 m; *DLB7453*, 57 m; *DLB2153*, 87 m.

This species was first reported for Puerto Rico by Ballantine and Norris (1989), following the listing of Taylor (1960) as a species of uncertain assignment. The Puerto Rican entity is occasionally seen in water as shallow as 20 m depth. It forms prostrate crusts with elongate, branched vein-like cells to 53 µm in length. Small irregularly shaped cells fill in the crust between the branched axes (see also Ballantine and Norris, 1989:6, fig. 9).

The species was originally described as *Callithamnion serpens* P. Crouan et H. Crouan (1859) from material dredged at Brest, France, at 20 m depth and later transferred to the genus *Hymenoclonium* by Batters (1895), who noted that his material was "dredged from deep water" in Plymouth Bay. *Hymenoclonium serpens* is now considered to be the tetrasporophytic life history alternate of *Bonnemaisonia asparagoides* (Woodward) C. Agardh, although Åsen (1980) reported the entity growing directly from its basophyte. The only two members of the Bonnemaisoniales in the western Atlantic (Wynne, 2011) are *Asparagopsis taxiformis* (Delile) Trevis. and *Bonnemaisonia hamifera* Harv. The tetrasporophytic life history alternate of the former in the western Atlantic is well known to be the filamentous *Falkenbergia hillebrandii* (Bornet) Falkenberg. The life history alternate of the latter is *Trailliella intricata* Batters (1896).

Other possible relationships with *Hymenoclonium* include the life history alternate of *Acrosymphyton purpuriferum* (J. Agardh) Sjöstedt. Cortel Breeman (1975) provided evidence that a *H. serpens*–like prostrate filamentous form represented the tetrasporophyte of *A. purpuriferum*. Although *A. purpuriferum* is not known from Puerto Rico, *A. caribaeum* (J. Agardh) Sjözsedt has been reported from the island (Ballantine and Aponte, 2002b). Another possibility is the carpospore germination product of *Meredithia microphylla* (J. Agardh) J. Agardh. Guiry and Maggs (1984), in investigating the life history of that species, reported that the tetrasporophyte germinated and formed a complex system of prostrate filaments (figs. 11–21) resembling the above-cited fig. 9 in Ballantine and Norris (1989). The genus *Meredithia* is represented in Puerto Rico by the above-listed deepwater species *M.? caribaea* and *M. pulchella*.

Heterokontophyta

Phaeophyceae, Dictyotales, Dictyotaceae

Canistrocarpus cervicornis (Kütz.) De Paula et De Clerck
Specimens: *DLB7743*, 49 m; *DLB7159*, 50 m.

Ballantine and Aponte (2003) reported the species from the Bahamas as *Dictyota cervicornis* Kütz. from 77 m.

**Dictyopteris delicatula* J. V. Lamour.
Specimens: *DLB3704*, 36 m; *DLB7029*, 46 m; *DLB7111*, 49 m; *DLB7333*, 50 m; *DLB7500*, 61 m; *DLB7561*, *DLB7630*, *DLB8006*, 70 m; *DLB7598*, 77 m; *DLB7878*, 82 m.

This alga is extremely common in shallow-water coral reef environments throughout the Caribbean. It is also very common in deepwater turf communities and was previously reported to a depth of 61 m in the Bahamas by Ballantine and Aponte (2003) and to 74 m by Macintyre et al. (1991) from Barbados.

Dictyopteris justii J. V. Lamour.
Specimens: *DLB3716*, 36–46 m; *DLB4114*, 55 m; *DLB4717*, 60 m.

Dictyopteris justii was reported by Taylor (1960) to range from the intertidal to 40 m depth. It has also been reported from 46 m depth in the Bahamas (Ballantine and Aponte, 2003). The deepest known record of the species is 110 m reported by Guimarães et al. (1981) from Brazil.

Dictyota bartayresiana J. V. Lamour.
Specimen: *DLB7775*, 61 m.

In the western Atlantic, *Dictyota bartayresiana* was also reported to 61 m by Ballantine and Aponte (2003) from the Bahamas and to 60 m from Brazil by Yoneshigue-Valentin et al. (2004). The deepest known depth record for the species is 118 m from Johnston Atoll, Pacific Ocean (Agegian and Abbott, 1985).

Dictyota ciliolata Sond. ex Kütz.
Specimen: *DLB3749*, 36–46 m.

Dictyota ciliolata was reported by Taylor (1960) to generally be an alga of shallow water, ranging to 24 m depth, but was reported to 50 m by Schneider (1976). Suárez et al. (2015) reported that *D ciliolata* is known to a depth of 55 m; however, the depth is reported without citation or location.

****Dictyota humifusa*** Hörnig, Schnetter et Coppejans
Specimens: *DLB7028*, 46 m; *DLB7039*, 46 m; *DLB7138*, 50 m; *DLB7482*, 63 m; *DLB7572*, 70 m; *DLB7884*, 82 m.

This alga is easily recognized because of its blue and green iridescent bands and is extremely abundant at the southwestern Puerto Rican insular shelf break in approximately 18 m of water. De Clerck (2003) indicated that the species typically lives in the shallow subtidal in the Indian Ocean.

****Dictyota jamaicensis*** W. R. Taylor
Specimen: *DLB3719*, 36–46 m.

Taylor (1960) reported that the species was limited to shallow water.

Dictyota pulchella Hörnig et Schnetter
Specimens: *DLB7160*, *DLB8090*, 50 m; *DLB7485*, 63 m; *DLB7504*, 61 m; *DLB8064*, 70 m.

Dictyota pulchella was reported to a depth of 76 m in the Bahamas by Ballantine and Aponte (2003). This species, as *D. divaricata* Lamour., although not appearing in his species list, was nevertheless reported by Frederick (1963) as the most abundant brown alga on the Bermuda platform to 63 m.

Dictyota stolonifera E. Y. Dawson
Specimens: *DLB7989*, 62 m; *DLB8063*, 70 m.

The species was first reported from Puerto Rico and the Caribbean region by Ballantine et al. (2011). De Clerck (2003) indicated that the species ranged from shallow depths to intermediate (to 20 m) throughout its distribution, although Spalding (2012) reported *D. stolonifera* to 93 m in Hawaii.

****Lobophora canariensis*** (Sauv.) C. W. Vieria, De Clerck et Payri.
Specimens: *DLB4179*, 37–38 m; *DLB1817*, 40 m; *DLB1798*, *DLB8082*, 50 m; *DLB3090*, 55–90 m; *DLB7491*, 61 m; *DLB7973*, 62 m; *DLB7868*, 82 m.

For virtually every deep-water collection on which this report is based, *Lobophora* specimens were obtained. Until the work reported by Shultz et al. (2015), all of these Caribbean collections were assumed to be *Lobophora variegata*. On reexamination of deepwater herbarium specimens in MSM identified as *L. variegata*, both *L. canariensis* and *L. guadeloupensis* (below) proved to be abundant. Shultz et al. (2015) described as a new segregate species *Lobophora payriae* N. E. Schultz, C. W. Schneid. et F. Rousseau on the basis of algae collected in Bermuda to depths of 35–36 m and from Guadeloupe. Vieira et al. (2016) subsequently regarded *L. payriae* as a synonym of *Cutleria canariensis* (Sauvageau) I. A. Abbott et J. M. Juisman and transferred the species to *Lobophora*. The present report is the first known occurrence in Puerto Rico. Some of the Puerto Rican specimens were extremely small, with flabella measuring 9.0 mm high and 10 mm across; larger specimens measured to 4 cm high and 5 cm broad. All were 3 cell layers thick and measured 33 to 40 µm thick. Further examination of herbarium specimens will probably reveal that *L. canariensis* is not restricted to depths greater than 35 m in Puerto Rico.

Lobophora guadeloupensis N. E. Schultz, F. Rousseau et L. Le Gall
Specimens: *DLB1817*, 40 m; *DLB3717*, 40–50 m; *DLB7136*, 49 m; *DLB4130*, 56 m; *DLB4716*, 60 m; *DLB8055*, 70 m.

Lobophora guadeloupensis represents a new species record for Puerto Rico. Flabella measured to 5.5 cm high and to 8.0 cm across. In section, Puerto Rican specimens possessed a single medullary layer with two cortical rows both above and below, averaging 82 µm in thickness. In radial section, the cortical cells located immediately outside medullary cells are covered by two elongate outer cortical cells. Collections at MSM also reveal that *L. guadeloupensis* is found in Martinique (*DLB3546*) at 50 m and the Bahamas (*DLB4341* and *DLB4518*) at 33–35 and 46–53 m, respectively. The greatest known depth for the species is reported to be 135 m from Guadeloupe (Schultz et al., 2015). Once herbarium records attributable to *L. variegata* in deep water are reexamined, the broader occurrence of both

L. guadeloupensis and *L. payriae* will undoubtedly be confirmed, and the depth records reported here will be exceeded.

Lobophora variegata (J. V. Lamour.) Womersley ex E. C. Oliveira
Specimen: *DLB4031*, 36–37 m.

The species, as originally circumscribed, was broadly distributed worldwide. Vieira et al. (2014), employing molecular tools, concluded that species diversity in Pacific *Lobophora* was underestimated, and they suggested that Atlantic species required reexamination as well. In Puerto Rico, until the recent revision by Shultz et al. (2015), *Lobophora variegata* was thought to be a very common element from shallow nearshore environments and extending across the insular shelf into deeper water. It has been considered to have a broad worldwide tropical distribution; however Vieiria et al. (2016) concluded that it is restricted to the Caribbean.

Historical records of *Lobophora variegata* from deepwater must now be accepted with caution. The species was reported to a depth of 76 m in the Bahamas by Ballantine and Aponte (2003), although unattached thalli were regularly observed deeper than 100 m (DLB and NEA, unpublished observations). The species is also known from 90 m in San Salvador Island, Bahamas (Hanisak and Blair, 1988b). Littler and Littler (2000) further reported that species has been collected to 120 m. Although Agegian and Abbott (1985) reported a maximum depth of 140 m for the species at Johnston Atoll, Pacific Ocean, Spalding (2012) regarded these reports as probably being *Distromium flabellata* Womersley. In light of Shultz et al.'s (2015) treatment, we have confirmed only a single specimen deeper than 35 m to be *L. variegata*. Nevertheless, *L. variegata* is still probably abundant in shallower mesophotic environments.

Padina* cf. *sanctae-crucis Børgesen
Specimen: *DLB4441*, 37 m.

Reported by Taylor (1960) as a plant of shallow water; however, Dawes and Van Breedveld (1969) reported the species from 73 m in Florida.

Stypopodium zonale (J. V. Lamour.) Papenf.
Specimens: *DLB7141*, *DLB7176*, 50 m.

Frederick (1963) reported the species to 64 m in Bermuda, and Littler and Littler (2000) reported a maximum depth of 80 m.

Sphacelariales, Sphacelariaceae

***Sphacelaria* sp.**
Specimen: *DLB8019*, 70 m.

Puerto Rican deepwater specimens were without vegetative propagules.

Ectocarpales, Scytosiphonaceae

***Rosenvingea* sp.**
Specimen: *DLB1215*, 40 m.

The three known species of the genus from the Caribbean are all known from shallow water, although *R. intricata* Børgesen is also known from a dredge collection at 35 m depth (Taylor, 1960).

Sporochnales, Sporochnaceae

Sporochnus bolleanus Mont.
Specimens: *DLB3723*, 36–46 m; *DLB4117*, 55 m.

Sporochnus bolleanus was reported to 59 m by Hanisak and Blair (1988a) and to 90 m by Taylor (1960).

Fucales, Sargassaceae

****Sargassum filipendula*** C. Agardh
Specimen: *DLB4118*, 55 m.

Sargassum filipendula was reported by Taylor (1960) to a depth of 33 m. Schneider (1975) also reported the species to 55 m from the North Carolina continental shelf.

Sargassum hystrix J. Agardh
Specimen: *DLB8046*, 70 m.

Littler and Littler (2000) reported that the species had been dredged to 137 m. This specimen may very well have been unattached and drifted from shallower water.

****Sargassum ramifolium*** Kütz.
Specimen: *DLB4042*, 36 m.

Littler and Littler (2000) indicated a shallow-water distribution for the species.

***Sargassum* sp.**
Specimen: *DLB7163*, 50 m.

Chlorophyta

Palmophyllophyceae, Palmophyllales, Palmellopsidaceae

****Verdigellas fimbriata*** D. L. Ballant. et J. N. Norris
Specimen: *DLB3711*, 46–55 m; *DLB3606*, 55–65 m.

Verdigellas fimbriata, the generitype, had been collected only in deepwater habitats in Puerto Rico (Ballantine and Norris, 1994) prior to the report by Moura (2010) from Brazil.

Verdigellas peltata D. L. Ballant. et J. N. Norris
FIGURE 5A
Specimen: *DLB3710*, 46–55 m; *DLB3605*, 55–65 m; *DLB3189*, 80–100 m.

Ballantine and Aponte (2003) collected the species to 122 m from a submersible in the Bahamas. It is also known from a depth of 97 m in Florida (Hanisak and Blair, 1988a). Littler and Littler (2000) indicated a maximum depth of 157 m for the species, and Bravin et al. (1999) reported the species from Brazil at

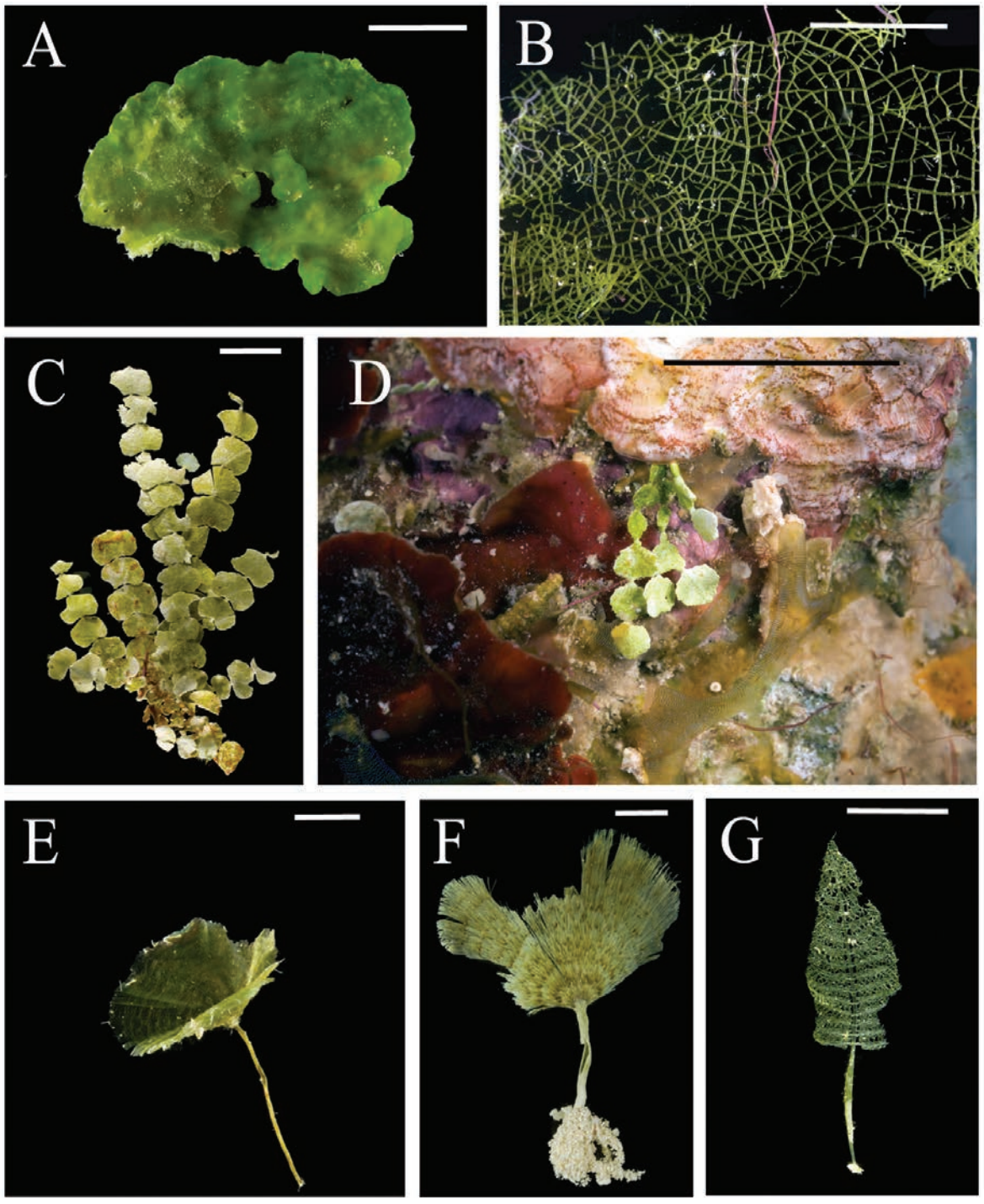

FIGURE 5. Deepwater Chlorophyta species. (A) *Verdigellas peltata* (*DLB8029*, *DLB8029*; scale bar = 1.0 cm). (B) *Microdictyon boergesenii* (*DLB7422*; scale bar = 5 mm). (C) *Halimeda copiosa* (*DLB7502*; scale bar = 1.0 cm). (D) *Halimeda pumila* (*DLB7867*; scale bar = 1.0 cm). (E) *Rhipiliopsis profunda* (*DLB3607*; scale bar =1.0 cm). (F) *Udotea unistratea* (*DLB8047*; scale bar = 1.0 cm). (G) *Phyllodictyon pulcherrimum* (*DLB8056*; scale bar = 1.0 cm). Photos by Hector Ruiz Torres.

a depth of 110 m. Although most collections are in water deeper than 50 m, Schneider et al. (2010) has reported the species from 2 to 3 m in a shaded grotto in Bermuda.

Chlorophyceae, Ulvales, Gayraliaceae

**Gayralia oxysperma* (Kütz.) K. L. Vinogr. ex Scagel, P. W. Gabrielson, Garbary, Golden, M. W. Hawkes, S. C. Lindstrom, J. C. Oliveira et Widd.
Specimen: *DLB7847*, 82 m.

A few very small specimens were collected at the edge of the Puerto Rican insular shelf. In deepwater, small individuals were also reported in 49 and 60 m of water by Frederick (1963) from Bermuda.

Phaeophilaceae

**Phaeophila dendroides* (P. Crouan et H. Crouan) Batters
Specimen: *DLB2170*, 65 m.

Reported from shallow water in the Florida Dry Tortugas by Taylor (1928). This deepwater specimen was identified by Dr. Ruth Nielsen.

Cladophorales, Anadyomenaceae

Anadyomene lacerata D. Littler et Littler
Specimens: *DLB8111*, *DLB3391*, 40 m; *DLB8465*, 46 m; *DLB4677*, 55–60 m; *DLB7977*, 62 m.

The species is based on a collection to 40 m at Monito Island in Puerto Rico (Littler and Littler, 1991). It is also known from 65 m in Brazil (Alves et al., 2011). The deepest known record for the species is also from Brazil at 180 m (Yoneshigue-Valentin et al., 2004).

Anadyomene saldanhae A. B. Joly et E. C. Oliveira
Specimens: *DLB3690*, 36 m; *DLB7957*, 49 m; *DLB3712*, 46–55 m; *DLB3203*, 68 m; *DLB8182*, 83 m; *DLB3124*, 100 m.

Anadyomene saldanhae is a common member of deepwater turfs in mesophotic coral reef habitats. The species was originally described from Brazilian material, being dredged from 79 m (Joly and De Oliveira Filho, 1969 [1968]) and subsequently reported from Brazil to 91 m by Alves et al. (2011) as well as to 180 m by Yoneshigue-Valentin et al. (2004).

Anadyomene stellata (Wulfen) C. Agardh
Specimens: *DLB7331*, *DLB7174*, 50 m; *DLB4116*, 55 m; *DLB4733*, 60 m; *DLB3202*, 68 m; *DLB7581*, 70 m; *DLB7665*, 82 m; *DLB3190*, 80–100 m; *DLB3114*, 100 m.

Although it is generally considered to be a shallow-water alga, Ballantine and Aponte (2003) collected the species to 46 m in the Bahamas, and Littler and Littler (1991) observed small clumps of the species to 91.5 m depth. The species is also known to 100 m in Bermuda (Frederick, 1963) and to about 160 m by Guimarães et al. (2008) and 180 m by Yoneshigue-Valentin et al. (2004) from Brazil.

Microdictyon boergesenii Setch.
FIGURE 5B
Specimens: *DLB1242*, 49 m; *DLB7422*, 50 m; *DLB4678*, 55–60 m; *DLB4697*, *DLB7465*, *DLB7773*, 61 m; *DLB8040*, 70 m; *DLB7764*, *DLB7845*, 82 m; *DLB3120*, 100 m.

Microdictyon boergesenii is another very common element in the deepwater algal turf community in Puerto Rico, as well as in the Bahamas, where Ballantine and Aponte (2003) reported it to 77 m. Taylor (1928) reported the species to 159 m from Florida, and Littler and Littler (2000) reported the species from a depth of 160 m in the Caribbean region.

Siphonocladales, Boodleaceae

Cladophoropsis **sp.**
Specimens: *DLB8033*, 70 m; *DLB7863*, 82 m.

Schneider and Searles (1975) reported another *Cladophoropsis* species, *C. membranacea*, to 33 m on the Carolina continental shelf.

Phyllodictyon anastomosans (Harvey) Kraft et M. J. Wynne
Specimen: *DLB3697*, 36 m.

Phyllodictyon anastomosans is typically a species of shallow water in Puerto Rico and the Caribbean. However, the species is reported from 50 to 56 m in Campeche Banks, Mexico (Mateo-Cid et al., 2013), and (as *Struvea anastomosans* (Harvey) Picc. et Grunov ex Picco.) to 61 m by Norris and Olsen (1991) from the Bahamas.

Phyllodictyon pulcherrimum J. E. Gray
FIGURE 5G
Specimens: *DLB8075*, 50 m; *DLB4715*, 60 m; *DLB8056*, 70 m.

As pointed out by Norris and Olsen (1991), the species is typically a common shallow-water element. Nevertheless, they reported the species to 85 m in the Bahamas. As *Struvea pulcherrima* (J. E. Gray) Murray et Boodle, Dawes and Van Breedveld (1969) reported collections to 73 m from Florida, and Humm and Cerame-Vivas (1964) dredged the species from 60 to 120 m in the Gulf of Mexico and North Carolina.

Struvea elegans Børgesen
Specimens: *DLB7284*, 46 m; *DLB1224*, 47 m; *DLB4691*, 55–60 m; *DLB1766*, 61 m; *DLB7578*, 70 m.

Struvea elegans is mostly restricted to deepwater habitats in the western Atlantic. From the Bahamas, it has been collected to 76 m (Ballantine and Aponte, 2003).

Cladophoraceae

**Cladophora coelothrix* Kütz.
Specimen: *DLB7861*, 82 m.

Norris and Olsen (1991) reported the species to 76 m at San Salvador, Bahamas; Ballantine and Aponte (2003) also reported *Cladophora coelothrix* from the Bahamas at 82 m at Lee Stocking Island, Bahamas.

Siphonocladaceae

Valonia macrophysa Kütz.
Specimen: *DLB7857*, 82 m.

Ballantine and Aponte (2003) reported the species, also typically a shallow-water species, to 76 m at Lee Stocking Island, and Norris and Olsen (1991) reported *Valonia macrophysa* to 92 m at San Salvador Island, Bahamas.

Valonia ventricosa J. Agardh
Specimens: *DLB3748*, 36–46 m; *DLB7755*, 49 m; *DLB7165*, 50 m; *DLB7991*, 62 m; *DLB3116*, 100 m.

Eiseman and Blair (1982) reported the species from 69 m in the Gulf of Mexico, and Norris and Olsen (1991) reported it to 90 m in the Bahamas. *Valonia ventricosa* is a common shallow-water element in the Puerto Rican and Caribbean algal flora. The deepest record for the species (as *Ventricaria ventricosa* (J. Agardh) J. L. Olsen et J. A. West) is ~160 m by Guimarães et al. (2008) from Brazil.

Bryopsidales, Bryopsidaceae

***Bryopsis* sp.**
Specimens: *DLB7898*, 55 m; *DLB7815*, *DLB7828*, 73 m.

**Derbesia osterhoutii* (L. R. Blinks et A. C. H. Blinks) Page
Specimens: *DLB7349*, 49 m; *DLB7087*, 56 m; *DLB7844*, *DLB7852*, 82 m.

Derbesia osterhoutii is a life history alternate that in deep-water collections in Puerto Rico, and also, the Bahamas are represented by the *Halicystis* stage, where it was reported to 61 m by Ballantine and Aponte (2003).

Caulerpaceae

Caulerpa ambigua Okamura
Specimen: *DLB1829*, 40 m.

Despite the single collection referenced above, *Caulerpa ambigua* (as *Caulerpa vickersiae* Børgesen), although never abundant, is commonly found in the Puerto Rican deeper-water flora. *Caulerpa ambigua* was reported from the Gulf of Mexico to 37 m (as *Caulerpa vickersiae*) by Dawes and Van Breedveld (1969) and from 51 m at Eniwetok (also as *C. vickersiae*) by Gilmartin (1960).

Caulerpa chemnitzia (Esper) J. V. Lamour.
Specimens: *DLB7971*, 62 m; *DLB8035*, 70 m; *DLB8054*, 70 m.

This entity has had a confused taxonomic history. Species assignation follows Belton et al. (2014), who listed the Indian Ocean as the type locality while regarding *C. racemosa* var. *peltata* (J. V. Lamour.) Eubank and *C. peltata* Lamouroux (both from the Caribbean) as heterotypic synonyms. Taylor (1960) reported the species as *C. peltata* J. V. Lamour., having been dredged to over 30 m depth. The species has also been reported to 73 m in the Gulf of Mexico by Eiseman and Blair (1982) as well as to 73 m by Norris and Olsen (1991) in the Bahamas.

Caulerpa mexicana Sond. ex Kütz.
Specimens: *DLB3721*, 36–46 m; DLB7276, 46 m; *DLB7351*, *DLB7735*, 49 m.

Caulerpa mexicana was reported as dredged to 73 m and "probably to 110 m" by Taylor (1960:141) in the tropical west Atlantic. In Pacific Hawaii, *C. mexicana* was reported to 129 m by Spalding (2012).

Caulerpa microphysa (Weber van Bosse) Feldmann
Specimens: *DLB1810*, *DLB8089*, 50 m; *DLB4121*, 55 m; *DLB7448*, 57 m; *DLB7952*, 67 m; *DLB7566*, 70 m; *DLB7877*, 82 m.

The species has been reported from 61 to 70 m at San Salvador Island, Bahamas (Norris and Olsen, 1991) and to 110 m in Bermuda by Frederick (1963).

Caulerpa racemosa (Forssk.) J. Agardh
Specimens: *DLB7158*, *DLB7179*, 50 m.

In Puerto Rico, *Caulerpa racemosa* is a common species in exposed reef flat habitats and has been relatively rarely collected in deeper water. Taylor (1960) reported the species to 55 m. In deep water, the species is also known from Hawaii at 60 m (Agegian and Abbott, 1985) and Eniwetok to 63 m (Gilmartin, 1960).

**Caulerpa verticillata* J. Agardh
Specimens: *DLB7730*, 49 m; *DLB7421*, 50 m; *DLB7895*, 55 m; *DLB7447*, 57 m; *DLB1233*, *DLB7571*, *DLB1715*, 58 m; *DLB1748*, 61 m; *DLB7917*, 70 m; *DLB7600*, 77 m; *DLB3123*, 100 m.

In Puerto Rico, *Caulerpa verticillata* is a very common shallow-water epiphyte on mangrove prop roots, moderately common in offshore algal plains at intermediate depths, as well as being a not uncommon element in deeper-water algal turfs. Norris and Bucher (1982) also indicated that the species lived both in shallow-water and deeper-water habitats to 12 m.

**Caulerpa webbiana* Mont.
Specimens: *DLB7135*, 50 m; *DLB3205*, 68 m; *DLB3117*, 100 m.

Taylor (1960) indicated that the species is found from the littoral to a depth of 50 m.

Codiaceae

Codium isthmocladum Vickers ssp. *clavatum* (Collins et Herv.) P. C. Silva
Specimens: *DLB4197*, 36 m; *DLB4681*, 55–60 m.

Norris and Olsen (1991) reported the subspecies to 73 m in the Bahamas. The deepest known report of *C. isthmocladum* is 75 m by Joly and Yoneshigue Braga (1966) from Brazil.

Codium taylorii P. C. Silva
Specimens: *DLB4199*, 36 m; *DLB7180*, 50 m.

Taylor (1960) indicated that the species was limited to shallow water; however, Hanisak and Blair (1988a) also reported *Codium taylorii* to 50 m in Florida. The deepest report for the species is that by Suárez et al. (2015), who reported *C. taylorii* to a depth of 55 m; however, the depth is reported without citation or location.

Rhipiliaceae

Rhipiliopsis profunda (Eiseman et S. A. Earle) J. N. Norris et S. Blair
FIGURE 5E
Specimens: *DLB8073*, 50 m; *DLB3607*, 55–65 m; *DLB3607*, 55–65 m; *DLB8009*, *DLB8067*, 70 m.

Rhipiliopsis profunda was reported to 92 m in the Bahamas by Norris and Olsen (1991).

Rhipiliopsis reticulata (C. Hoek) Farghaly et Denizot
Specimens: *DLB7718*, *DLB7733*, 49 m; *DLB7633*, 70 m; *DLB7870*, 82 m.

The species, as *Udotea reticulata* Hoek (1978), was originally described from Curaçao as a coral reef–associated alga and was collected to 60 m. Norris and Olsen (1991) reported the species to 92 m in the Bahamas.

Rhipiliopsis stri (S. A. Earle et J. R. Young) Farghaly et Denizot
Specimens: *DLB1234*, 49 m; *DLB1808*, 165 m; *DLB8010*, 70 m.

Rhipiliopsis stri was reported to a depth of 76 m in the Bahamas by Ballantine and Aponte (2003).

Udoteaceae

Avrainvillea asarifolia Børgesen
Specimens: *DLB8099*, 50 m; *DLB8016*, 70 m.

Taylor (1960) indicated that *Avrainvillea asarifolia* is a deepwater species and had been dredged to 90 m, although it is not uncommon at an offshore 17-m-deep algal plain in southwest Puerto Rico.

****Avrainvillea elliotii*** A. Gepp et E. Gepp
Specimen: *DLB4115*, 55 m.

Joly et al. (1965) reported the species (as *A. atlantica* A. B. Joly et Yamaguishi) from 2 to 3 m depth in Brazil. Dawes and Mathieson (2008) reported the species to 10 m from the Florida Keys.

Cladocephalus luteofuscus (P. Crouan et H. Crouan) Børgesen
Specimen: *DLB4127*, 55 m.

Taylor (1960) reported the species to 72 m, and the species is also known from very shallow water, less than 1 m in depth in Bermuda (Schneider et al., 2010).

Halimeda copiosa Goreau et E. A. Graham
FIGURE 5C
Specimens: *DLB7140*, 50 m; *DLB7181*, 50 m; *DLB7550*, 62 m; *DLB7559*, 70 m; *DLB7856*, 82 m; *DLB3125*, 91 m; *DLB3112*, 100 m.

Ballantine and Aponte (2003) reported *Halimeda copiosa* to a maximum depth of 107 m in the Bahamas, where it commonly formed long pendant chains hanging from shelf wall ledges, as illustrated by Suárez et al. (2015:179, fig. 195). Blair and Norris (1988) commented that *H. copiosa* was the most common *Halimed*a species in the deep-water algal community at San Salvador, where they indicated a maximum depth of 152 m.

Halimeda cryptica Colinvaux et E. A. Graham
Specimens: *DLB7610*, *DLB446*, *DLB8070*, 70 m; *DLB7841*, *DLB7862*, 82 m.

The species was reported between 61 and 152 m from San Salvador Island, Bahamas (Blair and Norris, 1988). *Halimeda cryptica* as var. *acerifolia* D. L.Ballant. (*DLB1755*, 61 m; *DLB7638*, 70 m) was initially collected in Puerto Rico (Ballantine, 1982) from 53 m.

Halimeda discoidea Decne.
Specimens: *DLB4189*, 36 m; *DLB7145*, 50 m; *DLB4679*, 55–60 m; *DLB8051*, 70 m.

Blair and Norris (1988) and Littler and Littler (2000) reported maximum depths of 73 and 80 m, respectively, for the species in the tropical western Atlantic. Spalding (2012) reported *H. discoidea* to 86 m in Pacific Hawaii. The deepest known depth for the species is 115 m (Suárez et al., 2015); however, the depth is reported without citation or location.

Halimeda goreaui W. R. Taylor
Specimens: *DLB3688*, 36 m; *DLB7432*, *DLB7728*, 49 m; *DLB7049*, 52 m; *DLB7466*, *DLB7507*, 61 m; *DLB7473*, 63 m; *DLB7946*, 67 m; *DLB8092*, 70 m; *DLB7826*, 73 m.

Halimeda goreaui was described from Jamaica (Taylor, 1962) on the basis of collections to a depth of 42 m. In Puerto Rico, *H. goreaui* is extremely common at the insular shelf edge break (18 m) and becomes less abundant with depth. The deepest known depth for the *H. goreaui* is 80 m (Suárez et al., 2015); however, the depth is reported without citation or location.

Halimeda gracilis Harv. ex J. Agardh
Specimens: *DLB4680*, 55–60 m; *DLB7502*, 61 m; *DLB7972*, 62 m; *DLB8037*, 70 m.

In Puerto Rico, *Halimeda gracilis* is rarely collected at depths shallower than 17 m. Joly et al. (1968) reported the species to a depth of 75 m in Brazil, and Blair and Norris (1988) collected the species to 122 m in the Bahamas. The deepest known reported record for *Halimeda gracilis* is that by Agegian and Abbott (1985), who reported the species to 125 m from Hawaii and Johnson Atoll.

****Halimeda hummii*** D. L. Ballant.
Specimens: *DLB7555*, 62 m; *DLB8044*, 70 m.

The species was based on collections from both shallow and moderate depths in Puerto Rico (Ballantine, 1982) and is also known from moderate depths in Panama (Wysor and Kooistra, 2003).

Halimeda pumila Verbruggen, D. Littler et Littler
FIGURE 5D
Specimens: *DLB7115*, *DLB7396*, 59 m; *DLB7867*, 82 m.

Verbruggen et al. (2007) described the species on the basis of their Bahamian collections to 50 m depth and regarded the Littler and Littler (2000) report of *Halimeda cryptica* var. *acerifolia* (to a maximum depth of 174 m) to be *H. pumila*. The first report of the species in Puerto Rico was by Ballantine et al. (2011).

Halimeda tuna (J. Ellis et Sol.) J. V. Lamour.
Specimen: *DLB8030*, 70 m.

Taylor (1960) reported *H. tuna* to 80 m, and Blair and Norris (1988) reported the species to 100 m depth at San Salvador Island, Bahamas.

****Penicillus capitatus*** J. V. Lamour.
Specimen: *DLB3191*, 80–100 m.

In Puerto Rico, this alga is extremely common in shallow-water seagrass habitats and in moderate-depth algal plain habitats. Sangil et al. (2010) reported the species growing in large stands to 50 m depth in the Canary Islands; however, deep-water Puerto Rico specimens were always collected as solitary individuals.

****Rhipocephalus oblongus*** (Decne) Kütz.
Specimen: *DLB8469*, 36 m.

The species was only recently recognized from Puerto Rico (Ballantine et al., 2015); however, it is typically found in shallow water (Taylor, 1960).

Rhipocephalus phoenix (J. Ellis et Sol.) Kütz.
Specimens: *DLB3687*, 36 m; *DLB3389*, 40 m; *DLB7162*, *DLB8074*, 50 m.

Rhipocephalus phoenix was reported to 60 m in the Florida Keys by Leichter et al. (2008). Taylor (1960) indicated a maximum depth of 72 m for the species.

****Udotea abbottiorum*** D. Littler et Littler
Specimen: *DLB3744*, 36–46 m.

This species is normally a plant of shallow water; the holotype is from 5 m depth (Littler and Littler, 1990).

****Udotea caribaea*** D. Littler et Littler
Specimen: *DLB8455*, 46–55 m.

Prior to the report from 55 m in Bermuda by Schneider et al. (2010), the species was typically reported from depths of less than 7 m. Ballantine et al. (2015) first reported the species from Puerto Rico.

****Udotea conglutinata*** (J. Ellis et Sol.) J. V. Lamour.
Specimen: *DLB7971*, 62 m.

Udotea conglutinata was reported to a depth of 40 m by Littler and Littler (1990), to 52 m from Bermuda by Schneider et al. (2010), and to a depth of 55 m by Dawes and Van Breedveld (1969) in the Florida Gulf of Mexico.

Udotea cyathiformis **Decne. var.** ***flabellifolia*** D. Littler et Littler
Specimens: *DLB4201*, 36 m; *DLB3745*, 36–46 m; *DLB8179*, 45 m.

Udotea cyathiformis was reported to 56 m by Eiseman and Blair (1982) as *U. cyathiformis* f. *infundibulum* (J. Agardh) Littler et D. S. Littler. The maximum known depth for the species is 73 m (Frederick, 1963). The deepwater collections from Puerto Rico all possessed a peltate flabellum. Flabellum filaments were free of lateral appendages, and those from stipe filaments were as illustrated by Littler and Littler (1990) for the variety.

Udotea dixonii D. Littler et Littler
Specimens: *DLB3390*, 40 m; *DLB4676*, 55–60 m.

Littler and Littler (1990, 2000) characterized this species as typically being from deepwater habitats, with the holotype from 46 m. *Udotea dixonii* has also been reported from 50 to 56 m by Mateo-Cid et al. (2013). The deepest report for the species is by Suárez et al. (2015), who reported it to a depth of 55 m (although without citation or location).

Udotea flabellum (J. Ellis et Sol.) J. V. Lamour.
Specimens: *DLB4186*, 36 m; *DLB4722*, 60 m.

Normally a plant of shallow water (Littler and Littler 1990), this species has been reported by Taylor (1960) to have been dredged from greater than 70 m depth and reported to 40 m by Schneider (1976) from the North Carolina continental shelf. The deepest report of the species is to ~160 m from Brazil by Guimarães et al. (2008).

****Udotea occidentalis*** A. Gepp et E. Gepp
Specimen: *DLB8048*, 70 m.

Udotea occidentalis is another typically shallow-water plant, although the species was reported to have been dredged to 36 m in St. Thomas, U.S. Virgin Islands (Littler and Littler, 1990), and Mateo-Cid et al. (2013) reported the species from 50 to 56 m from Campeche Banks, Mexico.

Udotea spinulosa M. Howe
Specimen: *DLB8440*, 37–46 m.

The species was reported from Puerto Rico by Littler and Littler (1990) and has been reported as being dredged from over 90 m depth (Taylor, 1960).

****Udotea unistratea*** D. Littler et Littler
FIGURE 5F
Specimen: *DLB8047*, 70 m.

The holotype of *U. unistratea* was collected from Belize at 46 m depth (Littler and Littler, 1990), and Mateo-Cid et al. (2013) reported the species from 50 to 56 m from Campeche Banks, Mexico.

Dasycladales, Dasycladaceae

Neomeris annulata Dickie
Specimen: *DLB3742*, 36–46 m.

Although this species is typically reported from shallow-water habitats, Taylor (1960) and Dawes and Mathieson (2008) indicated a maximum depth of 50 m for the species. Joly (1953) reported dredged specimens taken from between 30 and 50 m at Trindade Island, off the western coast of Brazil. The deepest known depth for *Neomeris annulata* is from Hawaii at 60 m (Agegian and Abbott, 1985).

Polyphysaceae

****Parvocaulis pusillus*** (M. Howe) S. Berger, Fettweiss, Gleissberg, Liddle, U. Richter, Sawitzky et Zuccarello
Specimens: *DLBs.n.*, 40 m; *DLB1222*, 49 m.

Parvocaulis pusillus is based on collections from shallow water in Jamaica and the Bahamas (Howe, 1909).

DISCUSSION

Our collections of algae from water deeper than 35 m (listed above) comprise 59% Rhodophyta, 31% Chlorophyta, and 10% Phaeophyceae. Species reported with depth ranges collected are summarized in Appendix A. These 185 species constitute a third of the total algal flora known from Puerto Rico (Ballantine and Aponte, 2002b; Ballantine et al., 2015). Puerto Rican algal species restricted to depths greater than 35 m (Table 1)

TABLE 1. Algal species mostly depth-restricted to the mesophotic realm in Puerto Rico, grouped by higher taxa. (Numbers in parentheses in column headings are counts of species listed.)

Rhodophyta (23)	Phaeophyceae (3)	Chlorophyta (17)
Botryocladia iridescens	*Dictyota stolonifera*	*Anadyomene lacerata*
Branchioglossum prostratum	*Lobophora canariensis*	*Anadyomene saldanhae*
Ceramium bisporum	*Lobophora guadeloupensis*	*Avrainvillea elliotii*
Ceramium leptozonum		*Caulerpa ambigua*
Ethelia sp.		*Cladocephalus luteofuscus*
Flahaultia tegetiformans		*Cladophora coelothrix*
Frikkiella pseudoprostrata		*Halimeda copiosa*
Frikkiella searlesii		*Halimeda cryptica*
Gloiocladia atlantica		*Halimeda pumila*
Hydrolithon abyssophila		*Microdictyon boergesenii*
Hypoglossum anomalum		*Rhipiliopsis profunda*
Hypoglossum caloglossoides		*Rhipiliopsis reticulata*
Hypoglossum rhizophorum		*Rhipiliopsis stri*
Hypoglossum simulans		*Udotea dixonii*
Perikladosporon abaxiale		*Udotea unistratea*
Peyssonnelia gigaspora		*Verdigellas fimbriata*
Peyssonnelia incomposita		*Verdigellas peltata*
Peyssonnelia iridescens		
Peyssonnelia sp. 1		
Peyssonnelia sp. 2		
Peyssonnelia sp. 3		
Predaea laciniosa		
Rhododictyon bermudense		

are dominated by members of Rhodophyta and Chlorophyta; only three species of Phaeophyceae listed are depth restricted. However, further examination of herbarium specimens of *Lobophora canariensis* and *L. guadeloupensis* is required to determine if those species are restricted to depths greater than 35 m in Puerto Rico. *Lobophora canariensis*, as *L. payriae*, is known from shallow water in Guadeloupe and Bermuda (Schultz et al., 2015). Species such as *Ceramium leptozonum*, *Flahaultia tegetiformans*, *Gloiocladia atlantica*, *Hypoglossum caloglossoides*, *Peyssonnelia incomposita*, and *Verdigellas peltata* are mostly restricted to mesophotic depths in Puerto Rico and are rarely encountered in shallower water. *Ceramium bisporum* and *Dictyota stolonifera*, although restricted to the mesophotic zone in Puerto Rico, have been reported from shallow water from different geographical locations (Sartoni and Boddi, 2002; De Clerck, 2003; Rincon-Diaz et al., 2014).

Among each major division of algae, several families are disproportionately represented (Table 2). For example, among Rhodophyta, 27 species of Ceramiaceae (sensu lato), 17 species of Delesseriaceae (sensu lato), 11 species of Peyssonneliaceae (included here is one species of Etheliaceae), and 11 species of Rhodymeniaceae were identified. Among Phaeophyceae, Dictyotaceae comprised 14 species. Deepwater Chlorophyta included 7 species of Caulerpaceae and 26 species of Udoteaceae. Although these two latter families were species rich and conspicuous because of their size, they were generally represented by only one or two individuals per collection. The most visually conspicuous members of the deepwater flora were coralline Rhodophyta (Hapalidiaceae) and Peyssonneliaceae species in addition to turfs. Many of the deepwater species, generally small statured, were identified as members of the species-rich and ubiquitous turf flora.

TABLE 2. Numbers of genera and species of families represented by four or more species reported from 35 m or greater in depth in Puerto Rico.

Family	No. Genera	No. Species
Rhodophyta		
Ceramiaceae (sensu lato)	7	13
Dasyaceae	3	4
Callithamniaceae	4	5
Delesseriaceae (sensu lato)	9	15
Galaxauraceae	3	4
Hapalidiaceae	3	7
Halymeniaceae	3	4
Peyssonneliaceae and Etheliaceae	3	11
Rhodomelaceae	7	8
Rhodymeniaceae	7	11
Solieriaceae	4	4
Wrangeliaceae	7	9
Heterokontophyta		
Dictyotaceae	6	14
Sargassaceae	1	4
Chlorophyta		
Boodleaceae	3	4
Caulerpaceae	2	7
Cladophoraceae	3	4
Udoteaceae	7	26

Three depth distributional groups may be thought of as comprising the mesophotic flora. Nearly half of the species (81) that are found in depths of 35 m or greater are found across the entire shelf, ranging from shallow nearshore habitats to the offshore mesophotic zone. There is a tendency for many of these species to drop out of the flora toward the shallower mesophotic region (for example, only approximately a quarter of these species are found in water deeper than ~60 m). A second distributional group consists of algae (~42 species) that are found ranging from intermediate depths to the mesophotic realm. More than half of these are also found at depths greater than ~60 m. An only slightly smaller group of algae (with a few minor exceptions), made up by 38 taxa identified to species (and accounting for 7% of the total Puerto Rican algal flora), appears to be restricted to water greater than 35 m in depth (see Table 1). Thus, community composition gradually changes with depth, both by the elimination of shallow species and the inclusion of mesophotic-restricted species. It is important to note that some species included in Table 1 may be found in shallower habitats in locations other than Puerto Rico.

Ballantine et al. (2010) reported that the principal calcium carbonate–producing organisms in the deep-water algal flora (>50 m depth) off the southwest coast of Puerto Rico were principally *Peyssonnelia* spp. and Corallinales. Similarly, many of the macroscopic species recognized at depths of 50 to 100 m in other studies (see Larkum et al., 1967; Littler et al., 1986; Aponte and Ballantine, 2001) were also dominated by Peyssonneliaceae and Corallinales. The coralline/*Peyssonnelia* dominance at mesophotic depths in tropical and warm temperate Atlantic regions may be a universal deepwater distributional pattern.

Hanisak and Blair (1988a) listed 157 species of algae from deeper than 40 m in Florida, and roughly a third of these species are the same as the above-reported deepwater species from Puerto Rico. Of these, only 20% had a deeper distribution in Florida than in Puerto Rico, possibly a function of greater water clarity in coastal Puerto Rico than coastal Florida.

On the basis of his study at Eniwetok (Pacific Ocean), Gilmartin (1960:218) concluded that there was not a "specifically distinct deep water algal flora" with a relatively large percentage of species also occurring in littoral and infralittoral environments. Conversely, Spalding (2012) indicated that 45% of the 76 total algae identified in Hawaiian mesophotic habitats were restricted to those depths. For the Puerto Rican mesophotic zone, the fact that there are 20 species (Rhodophyta and Chlorophyta) essentially restricted to the mesophotic realm (Table 1) and the fact that most Puerto Rican algal species are never found

in deep water are indicative that there is also a distinct deepwater flora in Puerto Rico. Within the mesophotic region, algal species composition changed with depth between approximately 30 and 70 m. There was a fairly high similarity in species composition between 30 and 50 m (68%). The species similarity between 30 and 70 m falls to 54%; in other words, roughly half of the species are cosmopolitan across these depths. There was also a fairly high similarity between 50 and 70 m (67%). This similarity would suggest an approximate depth of rapid change at about 50 m.

Fifty-one percent of the algae reported herein (identified to species) are most likely the deepest known distributional depths for those species. This proportion may be slightly high as certainly not every depth record for each species has been located, and unfortunately, the literature is replete with species names accompanied by little data, particularly concerning depth. On the other hand, some of the deepwater algae reported herein at the generic level probably, or, in some cases, certainly, represent new species to science that would increase the proportion of obligate deepwater species. One frustration in working with algae from deep environments is that some species are rare enough that it is difficult to obtain more than a few individuals. Furthermore, it is not uncommon for the deep algae to be vegetative, lacking reproductive characters to support description. Frederick's (1963) unpublished dissertation remarkably still includes many of the region's deepest algal records despite the fact that the work was conducted over 50 years ago.

With the present report of Puerto Rican deepwater algae, we still feel that the mesophotic flora of the western Atlantic remains essentially only partially characterized. The geographical areas studied at any depth represent only a fraction of deepwater communities, and the percentage of deepwater floras studied in the Puerto Rico (and the Caribbean as a whole) is thus extremely small. Furthermore, even in areas that have been studied, the observation by Gilmartin (1960) broadly applies. He concluded that in his sampling at Eniwetok at depth, although species saturation curves were never calculated, probably not a single sampled site was adequately collected such that most species could be accounted for. This is probably true worldwide of most deepwater habitats sampled, which is understandable given limitations inherent in most deepwater sampling.

Many of the deeper-water studies to date have generally focused on a single systematic group (i.e., sponges, corals, algae) or have provided only broad systematic categories in characterization of deep communities. Historically, relatively few systematic collections of algae at any one site have been undertaken; thus, many records of the deepwater algae are based on incidental reports. Despite increased deepwater collection in recent decades with more sophisticated equipment, our overall understanding of deepwater algae is still limited. This limitation is due to several factors, one being that such studies have been limited to restricted geographical areas and another being that most of the region remains effectively unsampled. Virtually all deepwater excursions to date have resulted in the discovery of new species as well as important geographical distribution records. Further, given that the known mesophotic algal flora is rich floristically, it is virtually certain that sampling new mesophotic environments will continue to yield new species to science.

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Appendix A: Summary of Puerto Rican Mesophotic Algal Specimens

TABLE A1. Identified mesophotic algal specimens from Puerto Rico and their depth ranges.

Species	Mesophotic depth range (m)
Rhodophyta	
Agardhiella ramosissima	55–60
Aglaothamnion cordatum	55–60
Amansia multifida	55
Amphiroa rigida	49–70
Amphiroa tribulus	49–61
Antithamnion antillanum	50–82
Antithamnion decipiens	40–82
Antithamnionella breviramosa	37
Antithamnionella graeffei	61
Apoglossum gregarium	61–100
Asparagopsis taxiformis	49–70
Asteromenia peltata	36–60
Augophyllum wysorii	49
Balliella pseudocorticata	36–58
Branchioglossum prostratum	61
Botryocladia iridescens	47–82
Botryocladia pyriformis	55–60
Botryocladia spinulifera	40–82
Botryocladia wynnei	63
Ceramium bisporum	46–100
Ceramium leptozonum	50
Ceramium nitens	61
Champia parvula	50–70
Champia vieillardii	40–55
Chrysymenia cf. *ventricosa*	37
Coelarthrum cliftonii	49–70
Cottoniella filamentosa	91
Cresia opalescens	49
Crouania pumila	55
Crouanophycus latiaxis	50
Cryptonemia crenulata	36–82

(*Continued*)

TABLE A1. (*Continued*)

Species	Mesophotic depth range (m)
Rhodophyta	
Dichotomaria marginata	*61*
Dichotomaria obtusata	*61*
Dictyurus occidentalis	36–46
Diplothamnion jolyi	36–50
Flahaultia tegetiformans	36–61
Frikkiella pseudoprostrata	46–82
Frikkiella searlesii	61
Galaxaura rugosa	50–70
Gayliella transversalis	62–70
Gloiocladia atlantica	41–100
Gracilaria isabellana	36–60
Grallatoria reptans	36–55
Halichrysis corallinaria	50
Griffithsia heteromorpha	49–52
Haloplegma duperreyi	49
Halymenia hancockii	*55*
Halymenia pseudofloresii	36–60
Herposiphonia secunda	61
Heterosiphonia crispella	52–70
Hydrolithon abyssophila	49–76
Hydrolithon farinosum	55–61
Hymenoclonium serpens[a]	52–87
Hypnea volubilis	*55*
Hypoglossum anomalum	36–91
Hypoglossum caloglossoides	49–77
Hypoglossum hypoglossoides	36–87
Hypoglossum. rhizophorum	40–87
Hypoglossum simulans	36–61
Hypoglossum tenuifolium	58–87
Jania adhaerens	50
Jania cubensis	36–70
Jania subulata	36–46
Leptofauchea? rhodymenioides	49–82
Laurencia intricata	36–60
Lophosiphonia cristata	49
Martensia pavonia	36–82
Meredithia? caribaea	67–70
Meredithia pulchella	50–70
Meristotheca gelidium	36
Myriogramme prostrata	52–67
Nitophyllum adhaerens	36–90
Perikladosporon abaxiale	87
Peyssonnelia boergesenii	49–61
Peyssonnelia flavescens	50–82
Peyssonnelia gigaspora	52–91
Peyssonnelia inamoena	46–73
Peyssonnelia incomposita	52–82
Peyssonnelia iridescens	46–87

Species	Mesophotic depth range (m)
Rhodophyta	
Platysiphonia caribaea	36–100
Polystrata fosliei	70
Predaea laciniosa	61–70
Rhododictyon bermudense	63–91
Seirospora occidentalis	36–87
Seirospora viridis	58
Solieria filiformis	36
Spermothamnion investiens	55–87
Spermothamnion cf. *macromeres*	82
Spongoclonium caribaeum	36–87
Taenioma nanum	49
Titanophora incrustans	60
Tricleocarpa fragilis	62–70
Wrangelia bicuspidata	46–82
Wrangelia gordoniae	46–73
Wrightiella tumanowiczi	50–55
Wurdemannia miniata	52–63
Heterokontophyta	
Canistrocarpus cervicornis	49–50
Dictyopteris delicatula	36–82
Dictyopteris justii	36–60
Dictyota bartayresiana	61
Dictyota ciliolata	36–46
Dictyota humifusa	46–82
Dictyota jamaicensis	36–46
Dictyota pulchella	50–70
Dictyota stolonifera	62–70
Lobophora canariensis	37-82
Lobophora guadeloupensis	40–70
Lobophora variegata	36–37
Padina cf. *sanctae-crucis*	37
Stypopodium zonale	50
Sporochnus bolleanus	36–55
Sargassum filipendula	55
Sargassum hystrix	70
Sargassum ramifolium	36
Chlorophyta	
Anadyomene lacerata	40–62
Anadyomene saldanhae	36–100
Anadyomene stellata	50–100
Avrainvillea asarifolia	50–70
Avrainvillea elliotii	55
Caulerpa ambigua	40
Caulerpa chemnitzia	62–70
Caulerpa mexicana	36–49
Caulerpa microphysa	50–82
Caulerpa racemosa	50

(*Continued*)

TABLE A1. (*Continued*)

Species	Mesophotic depth range (m)
Chlorophyta	
Caulerpa verticillata	49–100
Caulerpa webbiana	50–100
Cladocephalus luteofuscus	55
Cladophora coelothrix	82
Codium isthmocladum	36–60
Codium taylorii	36–50
Derbesia osterhoutii	49–82
Gayralia oxysperma	82
Halimeda copiosa	50–100
Halimeda cryptica	70–82
Halimeda discoidea	36–70
Halimeda goreaui	36–73
Halimeda gracilis	55–70
Halimeda hummii	62–70
Halimeda pumila	59–82
Halimeda tuna	70
Penicillus capitatus	80–100
Microdictyon boergesenii	49–100
Neomeris annulata	36–46
Parvocaulis pusillus	40–49
Phaeophila dendroides	65
Phyllodictyon anastomosans	36
Phyllodictyon pulcherrimum	50–70
Rhipiliopsis profunda	50–70
Rhipiliopsis reticulata	49–82
Rhipiliopsis stri	49–70
Rhipocephalus oblongus	36
Rhipocephalus phoenix	36–50
Struvea elegans	46–70
Udotea abbottiorum	36–46
Udotea caribaea	46–55
Udotea conglutinata	62
Udotea cyathiformis	36–45
Udotea dixonii	40–60
Udotea flabellum	36–60
Udotea occidentalis	70
Udotea spinulosa	37–46
Udotea unistratea	70
Valonia macrophysa	82
Valonia ventricosa	36–100
Verdigellas fimbriata	46–65
Verdigellas peltata	46–100

[a] The species is listed as a form genus.

Appendix B: Collection Locality Data

Locations of collection sites sampled around Puerto Rico are provided here, grouped by geographic area. Numbers for sites correspond to collection site numbers in Figure 1.

EAST

1. Vieques "El Seco" [approximately 18°7′N, 65°15′W]
70 m: *DLB8038–8053*, *DLB8092–8094*

SOUTH

2. Southeast, Puerto Rico, National Oceanic and Atmospheric Administration R/V *Seward Johnson* collected from DSV *Johnson-Sea-Link* [approximately 17°59′N, 65°49′W]
66 m: *DLB2321*

3. Grappler Bank (SE Puerto Rico), collected by University of Puerto Rico technical diving team and dredged from R/V *Oregon II* [17°47′56.63″N, 65°54′39.53″W]
55–90 m: *DLB3089–3104*, *DLB3201–3206*, *DLB8381–8382*
100 m: *DLB3111–3124*

4. Edge of insular shelf, offshore Salinas [approximately 17°52′N, 66°18′W]
49 m: *DLB1245–1249*

5. Edge of insular shelf, Ponce [approximately 17°56′N, 66°40′W]
55 m: *DLB8254*

6. Edge of insular shelf, Guanica, collected in submersible *Johnson-Sea-Link* [approximately 17°56′N, 66°50′W]
50 m: *DLB2152–2179*

7. Edge of insular shelf, "Baranca" [approximately 17°54′N, 66°59′W]
49 m: *DLB7432–7442*
61 m: *DLB7522–7523*
70 m: *DLB7615–7616*

8. Edge of insular shelf, "Weinberg" [17°53.423′N, 66°59.320′W]
50 m: *DLB7314–7347*, *DLB7380–7394*, *DLB7403–7409*

9. Edge of insular shelf, "Buoy" [17°53.292′N, 66°59.872′W]
36 m: *DLB8430*
37 m: *DLB1705–1709*
40 m: *DLB1208–1215*, *DLB1250–1258, DLB1817–1832*
46 m: *DLB7026–7033*
49 m: *DLB435–436*, *1218–1242*, *DLB7011–7124*
50 m: *DLB1786–1813*, *DLB7305–7308*
52 m: *DLB7048–7059*, *DLB7070–7073*
55 m: *DLB7080–7087*
58 m: *DLB1710–1738*, *DLB7514–7517*
61 m: *DLB1740–1783*, *DLB7518–7521*
70 m: *DLB446–450*

10. Edge of insular shelf, "Black Wall" [17°53.090′N, 67°00.863′W]
46 m: *DLB7074*, *DLB7276–7287*
49 m: *DLB7800*
57 m: *DLB7444–7455*
70 m: *DLB7635–7645*
82 m: *DLB7675–7685*, *DLB7866–7891*

11. Edge of insular shelf, "Hole in the Wall" [17°53.077′N, 67°1.315′W]
37 m: *DLB7219–7225*
41 m: *DLB7464*
49 m: *DLB7709–7746*, *DLB7811–7812*, *DLB7956–7957*
50 m: *DLB7420–7431*
55 m: *DLB7892–7905*
61 m: *DLB7465–7471*
63 m: *DLB7472–7486*
67 m: *DLB7942–7955*
70 m: *DLB7618–7634*
73 m: *DLB7813–7828*
77 m: *DLB7590–7609*
91 m: *DLB8160–8169*

12. Edge of insular shelf, "El Hoyo" [17°52.537′N, 67°2.648′W]
46 m: *DLB8719*
49 m: *DLB7348–7379*, *DLB7747–7760*, *DLB7395–7402*, *DLB7920–7936*
50 m: *DLB8177*
52 m: *DLB7829–7839*, *DLB8181*
61 m: *DLB7772–7775*
62 m: *DLB7547–7555*
63 m: *DLB7525–7532*, *DLB7686–7692*
70 m: *DLB7610–7614*, *DLB7776–7779*, *DLB7906–7918*
73 m: *DLB7646*
82 m: *DLB7664–7674*, *DLB7761–7771*, *DLB7840–7848*, *DLB7850–7865*, *DLB8192–8186*
87 m: *DLB8143–8146*
91 m: *DLB8147–8154*

13. Edge of insular shelf, "El Precipico" [17°52.510′N, 67°2.929′W]
61 m: *DLB7487–7513*
70 m: *DLB7556–7581*

14. Edge of insular shelf, South La Parguera, dredged R/V *Oregon II* (station 46003) [approximately 17°52′N, 67°6′W]
40 m: *DLB2903–2916*

WEST

15. Tourmaline Reef [approximately 18°6′N, 67°24′W]
37 m: *DLB8422–8424*

16. West of Mayaguez, dredged R/V *Oregon II* (station 45998) [approximately 15°11′N, 67°24′W]
91 m: *DLB2896–2902*, *DLB3125–3130*

17. Bajo de Sico [approximately 18°13′N, 67°21′W]
50 m: *DLB7133–7199*

MONA ISLAND

18. East Mona Island [approximately 18°6′N, 67°50′W]
46–55 m: *DLB8455–8456*, *DLB8468*
61–82 m: *DLB8470*

19. Southeast Mona Island [approximately 18°5′N, 67°50′W]
70 m: *DLB8026–8037*

20. South Mona Island [approximately 18°5′N, 67°51′W]
62 m: *DLB7971–7993*

21. South Mona Island [18°3′N, 67°53′W]
50 m: *DLB8095–8101*
70 m: *DLB8003–8025*
80–100 m: *DLB3188–3200*

22. South Mona Island, dredged from R/V *Isla Magueyes* [approximately 18°3′N, 67°55′W]
45–65 m: *DLB3605–3607*, *DLB3710–3715*

23. Mona Island, Carabinero [18°3′54.93″N, 67°55′36.65″W]
35–37 m: *DLB3686–3708*, *DLB8469*
50 m: *DLB8073–8091*

24. Mona Island (wall) [approximately 18°4′N, 67°56′W]
70 m: *DLB8054–8072*

25. West Mona Island [approximately 18°6′N, 67°57′W]
46 m: *DLB8465–8467*

26. West Monito [18°9′30″N, 67°56′99″W]
40 m: *3389–3391*

NORTH COAST

27. Punta Aguyereada, Aguadilla [approximately 18°33′N, 67°8′W]
36 m: *DLB4178–4212*
60 m: *DLB4694–4698*, *DLB4712–4733*

28. Isabela, dredged R/V *Isla Magueyes* [approximately 18°32′N, 67°1′W]
37 m: *DLB4410–4441*
55–60 m: *DLB4673–4693*

29. Guajataca, Quebredillas, dredged [approximately 18°30′N, 66°56′W]
55 m: *DLB8457–8459*

30. Punta Caracoles, Arecibo, dredged [approximately 18°29′N, 66°42′W]
36 m: *DLB4031–4074*
55 m: *DLB4114–4129*

31. Islote, Arecibo [approximately 18°30′N, 66°36′W]
55 m: *DLB4802–4808*
37–46 m: *DLB8440–8441*

32. Between Punta Cerro Gorda and Punta Fraile (north coast), dredged [approximately 18°30′N, 66°18′W]
36–46 m: *DLB3716–3751*

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Index of Genera and Species

Acrosymphyton, 15
  caribaeum, 15
  purpuriferum, 15
Agardhiella, 11, 27
  ramosissima, 11, 27
Agaricia, 13
  lamarcki, 13
Aglaothamnion, 6, 27
  cordatum, 6, 27
Amansia, 8, 27
  multifida, 8, 27
Amphiroa, 3, 27
  rigida, 3, 27
  tribulus, 3, 27
Anadyomene, 19, 23, 29
  lacerata, 19, 23, 29
  saldanhae, 19, 23, 29
  stellata, 19, 23, 29
Antithamnion, 6, 28
  antillanum, 6, 28
  decipiens, 6, 28
  flagellata, 6
  lherminieri, 6
  ogdeniae, 6
Antithamnionella, 6, 28
  breviramosa, 6, 28
  graeffei, 6, 28
  latiaxis, 6
Apoglossum, 7, 27
  gregarium, 7, 27
Asparagopsis, 6, 15, 27
  taxiformis, 6, 15, 27
Asteromenia, 14, 27
  peltata, 14, 27
Augophyllum, 7, 27
  wysorii, 7, 27
Avrainvillea, 21, 23, 29
  asarifolia, 21, 23, 29
  elliotii, 21, 23, 29
Bakothamnion, 6
  curassavicum, 6
Balliella, 6, 27
  pseudocorticata, 6, 27
Bonnemaisonia, 15
  asparagoides, 15
  hamifera, 15
Botryocladia, 9, 14, 15, 23, 27
  iridescens, 9, 14, 23, 27
  pyriformis, 14, 27
  spinulifera, 14, 27
  wynnei, 15, 27
Branchioglossum, 7, 23, 27
  prostratum, 7, 23, 27
  pseudoprostratum, 7, 28
Bryopsis sp., 20

Callithamnion, 6, 15
  cordatum, 6
  serpens, 15
Canistrocarpus, 15, 29
  cervicornis, 15, 16, 29
Caulerpa, 20, 23, 29
  ambigua, 20, 23, 29
  chemnitzia, 20, 29
  mexicana, 20, 29
  microphysa, 20, 29
  peltata, 20
  racemosa, 20, 29
  verticillata, 20, 30
  vickersiae, 20
  webbiana, 20, 30
Ceramium, 6, 7, 23, 24, 27
  bisporum, 6, 23, 24, 27
  byssoideum, 7
  flaccidum, 7
  leptozonum, 7, 23, 24, 27
  nitens, 7, 27
  spp., 7

Ceramium (*continued*)
transversale, 7
transversalis, 7
Champia, 14, 27
parvula, 14, 27
vieillardii, 14, 27
Chondria, 8
spp., 8
Chrysymenia, 15, 27
cf. *ventricosa*, 15, 27
sp., 15
Cladocephalus, 21, 23, 30
luteofuscus, 21, 23, 30
Cladophora, 20, 23, 30
coelothrix, 20, 23, 30
Cladophoropsis, 19
membranacea, 19
sp., 19
Codium, 21, 30
isthmocladum, 21, 30
ssp. *clavatum*, 21
taylorii, 21, 30
Coelarthrum, 15, 27
cliftonii, 15, 27
Contarinia sp., 11
Cottoniella, 10, 27
filamentosa, 10, 27
Cresia, 9, 15, 27
opalescens, 9, 15, 27
Crouania, 6, 27
pumila, 6, 27
Crouanophycus, 6, 27
latiaxis, 6, 27
Cryptonemia, 12, 14, 27
crenulata, 12, 27
sp., 14

Dasya sp., 7
Derbesia, 20, 30
osterhoutii, 20, 30
Dichotomaria, 3, 5, 28
marginata, 3, 28
obtusata, 5, 28
Dictyopteris, 15, 16, 29
delicatula, 15, 29
justii, 16, 29
Dictyota, 3, 15, 16, 23, 24, 29
bartayresiana, 16, 29
cervicornis, 15
ciliolata, 16, 29
divaricata, 16
humifusa, 16, 29
jamaicensis, 16, 29
pulchella, 16, 29
stolonifera, 16, 23, 24, 29
Dictyurus, 7, 28
occidentalis, 7, 28
Diplothamnion, 10, 28
jolyi, 10, 28

Ethelia sp., 5, 12, 23
Eucheuma, 11
schrammii, 11

Falkenbergia, 6, 15
hillebrandii, 15
Fauchea, 14
peltata, 14
Flahaultia, 11, 23, 24, 28
tegetiformans, 11, 23, 24, 28
Frikkiella, 3, 7, 23, 28
pseudoprostrata, 3, 7, 23, 28
searlesii, 3, 7, 23, 28

Galaxaura, 5, 6, 28
cylindrica, 6
obtusata var. *major*, 5
rugosa, 5, 28
Gayliella, 7, 28
transversalis, 7, 28
Gayralia, 19, 30
oxysperma, 19, 30
Gloiocladia, 14, 23, 24, 28
atlantica, 14, 23, 24, 28
Gracilaria, 12, 28
isabellana, 12, 28
Grallatoria, 10, 28
reptans, 10, 28
Griffithsia, 10, 28
heteromorpha, 10, 28

Halichrysis, 14, 15, 28
corallinaria, 15, 28
peltata, 14
Halicystis, 20
Halimeda, 13, 18, 21, 22, 23, 30
copiosa, 18, 21, 23, 30
cryptica, 13, 21, 23, 30
var. *acerifolia*, 21, 22
discoidea, 21, 30
goreaui, 21, 30
gracilis, 22, 30
hummii, 22, 30
pumila, 18, 22, 23, 27, 30
tuna, 22, 30
Haliptilon, 3
cubense, 3
Haloplegma, 10, 23
duperreyi, 10, 23
Halymenia, 14, 28
hancockii, 14, 28
pseudofloresii, 14, 28
Herposiphonia, 8, 10, 28
secunda, 8, 28
sp., 10
Heterosiphonia, 7, 28
crispella, 7, 28
sp., 7
wurdemannii, 7
Hydrolithon, 3, 5, 13, 23, 28
abyssophila, 3, 5, 13, 23, 28
farinosum, 3, 28
var. *chalicodictyum*, 3
Hymenoclonium, 9, 15, 28
serpens, 9, 15, 28
Hypnea, 11, 28
volubilis, 11, 28

Hypoglossum, 8, 9, 23, 24, 28
anomalum, 8, 9, 23, 28
caloglossoides, 8, 9, 23, 24, 28
hypoglossoides, 8, 28
rhizophorum, 8, 23, 28
simulans, 8, 23, 28
tenuifolium, 8, 28

Jania, 3, 28
adhaerens, 3, 28
cubensis, 3, 28
subulata, 3, 28

Kallymenia, 11
limminghei, 11

Laurencia, 10, 28
intricata, 10, 28
Leptofauchea, 15, 28
rhodymenioides, 15, 28
Lobophora, 3, 13, 16, 17, 23, 24, 29
canariensis, 16, 23, 24, 29
guadeloupensis, 13, 16, 17, 23, 24, 29
payriae, 16, 17, 24
variegata, 16, 17, 29
Lomentaria, 14
baileyana, 14
divaricata, 14
sp., 14
Lophosiphonia, 10, 18, 28
cristata, 10, 18, 28

Martensia, 8, 28
pavonia, 8, 28
Meredithia, 11, 15, 28
caribaea, 11, 28
microphylla, 15
pulchella, 11, 28
Meristotheca, 11, 28
gelidium, 11, 28
Mesothanmion, 10
caribaeum, 10
Microdictyon, 18, 19, 23, 30
boergesenii, 18, 19, 23, 30
Myriogramme, 8, 9, 28
prostrata, 8, 9, 28

Neomeris, 23, 30
annulata, 23, 30
Nitophyllum, 8, 28
adhaerens, 8, 28

Padina, 17, 29
cf. *sanctae-crucis*, 17, 29
Parvocaulis, 23, 30
pusillus, 23, 30
Penicillus, 22, 30
capitatus, 22, 30
Perikladosporon, 7, 23, 28
abaxiale, 7, 23, 28
Peyssonnelia, 5, 6, 12, 13, 23, 24, 28
boergesenii, 12, 28
flavescens, 5, 6, 12, 13, 28

gigaspora, 5, 12, 23, 28
inamoena, 12, 28
incomposita, 5, 12, 23, 24, 25, 28
iridescens, 5, 6, 12, 13, 23, 28
sp. 1, 12, 23
sp. 2, 5, 12, 23
sp. 3, 5, 12, 23
Phaeophila, 19, 30
dendroides, 19, 30
Phyllodictyon, 18,19, 30
anastomosans, 19, 30
pulcherrimum, 18, 19, 30
Platysiphonia, 10, 29
caribaea, 10, 29
Polysiphonia, 10
spp., 10
Polystrata, 5, 12, 29
fosliei, 5, 12, 29
Predaea, 11, 23, 29
laciniosa, 11, 23, 29
sp., 11

Rhipiliopsis, 18, 21, 23, 30
profunda, 18, 21, 23, 30
reticulata, 21, 23, 30
stri, 21, 23, 30
Rhipocephalus, 22, 30
oblongus, 22, 30
phoenix, 22, 30
Rhododictyon, 9, 10, 23, 29
bermudense, 9, 10, 23, 29
Rosenvingea sp., 17

Sargassum, 17, 29
filipendula, 17, 29
hystrix, 17, 29
ramifolium, 17, 29
sp., 17
Seirospora, 6, 29
occidentalis, 6, 29
viridis, 6, 29
Solieria, 11, 29
filiformis, 11, 29
Spermothamnion, 10, 29
investiens, 10, 29
var. *cidaricola*, 10
cf. *macromeres*, 10, 29
Sphacelaria sp., 17
Spongoclonium, 10, 29
caribaeum, 10, 29
Sporochnus, 17, 29
bolleanus, 17, 29
Struvea, 19, 30
elegans, 19, 30
Stypopodium, 17, 29
zonale, 17, 29

Taenioma, 8, 29
nanum, 8, 29
Titanophora, 11, 12, 29
incrustans, 11, 12, 29
Trailliella, 15
intricata, 15
Tricleocarpa, 5, 29
fragilis, 5, 6, 29

Udotea, 21, 22, 30
abbottiorum, 22, 30
caribaea, 22, 30
conglutinata, 22, 30
cyathiformis, 22, 30
f. *infundibulum*, 22
var. *flabellifolia*, 22
dixonii, 22, 30
flabellum, 22, 30
occidentalis, 22, 30
reticulata, 21
spinulosa, 22, 30
unistratea, 18, 22, 30

Valonia, 20, 30
macrophysa, 20, 30
ventricosa, 20, 30
Ventricaria, 22
Verdigellas, 2, 17, 18, 23, 24, 30
fimbriata, 17, 23, 30
peltata, 17, 18, 23, 24, 30

Wrangelia, 10, 11, 13, 29
bicuspidata, 10, 11, 29
gordoniae, 11, 29
Wrightiella, 10, 29
tumanowiczi, 10, 29
Wurdemannia, 11, 20, 29
miniata, 11, 20, 29

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