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DIVERSITY, ECOLOGY, BIOGEOGRAPHY, AND EVOLUTION OF THE PREVALENT BROWN ALGAL GENUS *LOBOPHORA* IN THE GREATER CARIBBEAN SEA, INCLUDING THE DESCRIPTION OF FIVE NEW SPECIES[1]

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Distributed in tropical and warm-temperate waters worldwide, *Lobophora* species are found across the Greater Caribbean (i.e., Caribbean sensu stricto, Gulf of Mexico, Florida, the Bahamas, and Bermuda). We presently discuss the diversity, ecology, biogeography, and evolution of the Greater Caribbean *Lobophora* species based on previous studies and an extensive number of samples collected across the eastern, southern, and to a lesser extent western Caribbean. A total of 18 *Lobophora* species are now documented from the Greater Caribbean, of which five are newly described (*L. agardhii* sp. nov., *L. dickiei* sp. nov., *L. lamourouxii* sp. nov., *L. richardii* sp. nov., and *L. setchellii* sp. nov.). Within the Greater Caribbean, the eastern Caribbean and the Central Province are the most diverse ecoregion and province (16 spp.), respectively. Observed distribution patterns indicate that *Lobophora* species from the Greater Caribbean have climate affinities (i.e., warm-temperate vs. tropical affinities). In total, 11 *Lobophora* species exclusively occur in the Greater Caribbean; six are present in the western Atlantic; two in the Indo-Pacific; and one in the eastern Pacific. Biogeographic analyses support that no speciation occurred across the Isthmus of Panama, and that the Greater Caribbean acted as a recipient region for species from the Indo-Pacific and as a region of diversification as well as a donor region to the North-eastern Atlantic. The Greater Caribbean is not an evolutionary dead end for *Lobophora*, but instead generates and exports diversity. Present results illustrate how sampling based on DNA identification is reshaping biogeographic patterns, as we know them.

*Key index words: cox*3; eastern Caribbean; Greater Caribbean; *Lobophora*; molecular taxonomy; western Caribbean

***Abbreviations*: BI, Bayesian inference; *cox*3, mitochondrial-encoded cytochrome c oxidase III gene; DNA, deoxyribonucleic acid; ML, maximum likelihood**

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Until recently, it was assumed that the Greater Caribbean – the Caribbean sensu stricto, Gulf of Mexico, Florida, the Bahamas, and Bermuda – comprised only one species of the brown algal genus *Lobophora*, *L. variegata*, whose holotype was collected from the "West Indies," presumably from Guadeloupe (Vieira et al. 2016). Further species identifications were never explored after the first *Lobophora* species description as *Dictyota variegata*, later interpreted as displaying different morphological forms (e.g., crust, decumbent, ruffled, and erect forms; De Ruyter van Steveninck et al. 1988, Littler and Littler 2000). However, J.V.F. Lamouroux's actual interpretation was "*exhibiting different colors longitudinally*" ("*longitudinaliter variegatâ*"; Lamouroux 1809). *Lobophora variegata* presented not only different morphotypes but also inhabited several ecological niches. This erroneous taxonomic interpretation is now acknowledged two centuries later, with the help of DNA sequencing (Vieira et al. 2016). Sun et al. (2012), Vieira et al. (2014) and Camacho et al. (2019) demonstrated that different morpho- or ecotypes represent different species. Sun et al. (2012) were the first to sequence a *Lobophora* specimen from the Caribbean s.s. (Curaçao, Netherland Antilles), but did not assign it to the specific epithet *L. variegata*, implicitly suggesting that more than one species occurred in the Greater Caribbean. Schultz et al. (2015) followed by Vieira et al. (2016, 2017) and Camacho et al. (2019) subsequently confirmed that the diversity in the Greater Caribbean was much higher than previously assumed (Table 1, Fig. 1) with the report of nine (Schultz et al. 2015) and five (Camacho et al. 2019) additional species, bringing the number of known species in this region to 15 (Table 1). Identifying more than one species raised the question, which of these Greater Caribbean species was the genuine *L. variegata*. After some debate, *L. variegata* was finally identified as a species geographically restricted to a part of the Greater Caribbean including, so far, Mexico (Quintana Roo), Bahamas, Florida Keys, Grand Cayman, Guadeloupe, Jamaica, and St Kitts and Nevis (Vieira et al. 2016, Godínez-Ortega et al. 2018, Camacho et al. 2019), based on molecular and morphological evidence established from type material (Vieira et al. 2016). *Lobophora* is found across the Greater Caribbean, in warm-temperate and tropical regions, with the northernmost distribution of *L. dispersa* at Cape Lookout, North Carolina (34°23′34.6″ N; Camacho et al. 2019). The increasingly detailed distribution data from the Greater Caribbean enable us to redraw species distribution and diversity patterns within this region.

Complementing previous taxonomic efforts on the genus *Lobophora* in the Greater Caribbean, the present study aims to (i) test completeness of our current knowledge on diversity by expanding the sampling to the eastern, southern, and western Caribbean, (ii) examine to what extent the distribution patterns of *Lobophora* spp. reflect currently defined biogeographic regions, (iii) examine range sizes of *Lobophora* spp. from the Greater Caribbean at regional and global scales, and (iv) discuss the evolution of the Greater Caribbean *Lobophora* species.

MATERIALS AND METHODS

Sampling localities. Sampling was performed in the framework of several campaigns in the Lesser Antilles (French and Dutch Caribbean) and Belize (Fig. 1, Tables S1 and S2 in the Supporting Information). In all, 37 *Lobophora* specimens were collected by SCUBA between 0 and 30 m depth, in the Lesser Antilles (Antigua, Bequia, Guadeloupe, Martinique, Saba, Saint Barthelemy, Saint Lucia, Saint Martin, and Saint Vincent) in 2015 during the PACOTILLES research expedition (April 21 to May 10, and May 13 to June 2, 2015), with the IRD N/O ANTEA research vessel. Over one thousand specimens were collected around Curaçao (Netherland Antilles, February 3 and 16, 2017), of which 126 specimens were selected based on their morphology and habitat for DNA sequencing. Another 156 specimens were collected haphazardly from other Dutch and French Antilles islands (i.e., Bonaire, Saba, Saint Barthelemy, Saint Martin, and Sint Eustatius) and in Belize. Specimens were preserved in silica gel for DNA sequencing, and herbarium specimens were mounted and later deposited in either the Herbarium of the Botanic Garden Meise in Belgium (BR) or the Herbarium of New Caledonia (NOU) registered in the Index Herbariorum (Thiers 2020).

Molecular and morphological analyses. Total genomic DNA was extracted from tissue samples dried in silica gel using a cetyl-trimethyl ammonium bromide (CTAB) extraction method. Sequences were generated from the mitochondrial-encoded cytochrome c oxidase III gene (*cox*3), the most commonly used barcode marker for this genus (Vieira et al. 2014, 2016), following Vieira et al. (2014). New sequences were added to the datasets from Vieira et al. (2016) and Camacho et al. (2019), and aligned using MUSCLE (Edgar 2004). Phylogenetic trees were reconstructed using Bayesian (BI) and maximum likelihood (ML) methods based on the mitochondrial *cox*3 gene following Vieira et al. (2016). Morphological observations of *Lobophora* specimens included analyses of the external and internal structures of the specimens following Vieira et al. (2014).

Biogeographic analyses. We used Robertson and Cramer (2014) provinces and Spalding et al. (2007) ecoregions to look into *Lobophora* diversity patterns in the Greater Caribbean at large and fine spatial scales. We performed hierarchical clustering analyses to determine how these ecoregions and provinces relate to each other. We investigated whether the biogeographic scheme proposed by Robertson and Cramer (2014; three provinces delimited based on the distribution of shore-fish fauna of the Greater Caribbean) is reflected in the distribution patterns of *Lobophora*. To determine how the provinces and ecoregions relate to each other, two commonly used hierarchical clustering methods were performed, that is, the Euclidean distance with Ward's clustering method, and the Jaccard index with the unweighted pair-group method with arithmetic averages (UPGMA). Analyses were performed using the R package FactoMineR (Lê et al. 2008).

RESULTS

Molecular phylogenetic analyses. Sequence data were generated for 325 specimens. Specimens collected

TABLE 1. List of the 15 *Lobophora* species from the Greater Caribbean prior this study and the countries of collections.

	Bermuda	Bahamas	Colombia	Costa Rica	Curaçao	Dry Tortugas	Ewing Bank	Florida Keys	Grand Cayman	Guadeloupe	Jamaica	North Carolina	Panama	Saint Croix	
L. canariensis	x									x					Schultz et al. (2015)
L. colombiana[a]			x												Camacho et al. (2019)
L. crispata[b]				x						x			x		Camacho et al. (2019)
L. declerckii	x				x			x		x				x	Schultz et al. (2015)
L. delicata[c]	x						x			x					Schultz et al. (2015), Camacho et al. (2019)
L. dispersa[d]				x	x		x					x	x		Camacho et al. (2019)
L. guadeloupensis															Schultz et al. (2015)
L. littlerorum															Schultz et al. (2015)
L. schneideri[e]	x													x	Schultz et al. (2015)
L. spWA02[f]	x														Schultz et al. (2015)
L. sp64[g]										x					Schultz et al. (2015)
L. sp85															Vieira et al. (2016)
L. sp86[h]														x	Schultz et al. (2015)
L. tortugensis[i]						x									Camacho et al. (2019)
L. variegata		x	x	x		x	x	x	x	x	x				Vieira et al. (2016)

[a] *L.* sp65 in Vieira et al. (2016).
[b] *L.* sp78 in Vieira et al. (2016).
[c] WA04 in Schultz et al. (2015) and *L.* sp40 in Vieira et al. (2016)
[d] *L.* sp44 in Vieira et al. (2016).
[e] *L.* sp39 in Vieira et al. (2016) and *L. variegata* in Schultz et al. (2015).
[f] WA02 in Schultz et al. (2015).
[g] WA03 in Schultz et al. (2015).
[h] WA01 in Schultz et al. (2015).
[i] and *L.* sp77 in Vieira et al. (2016).

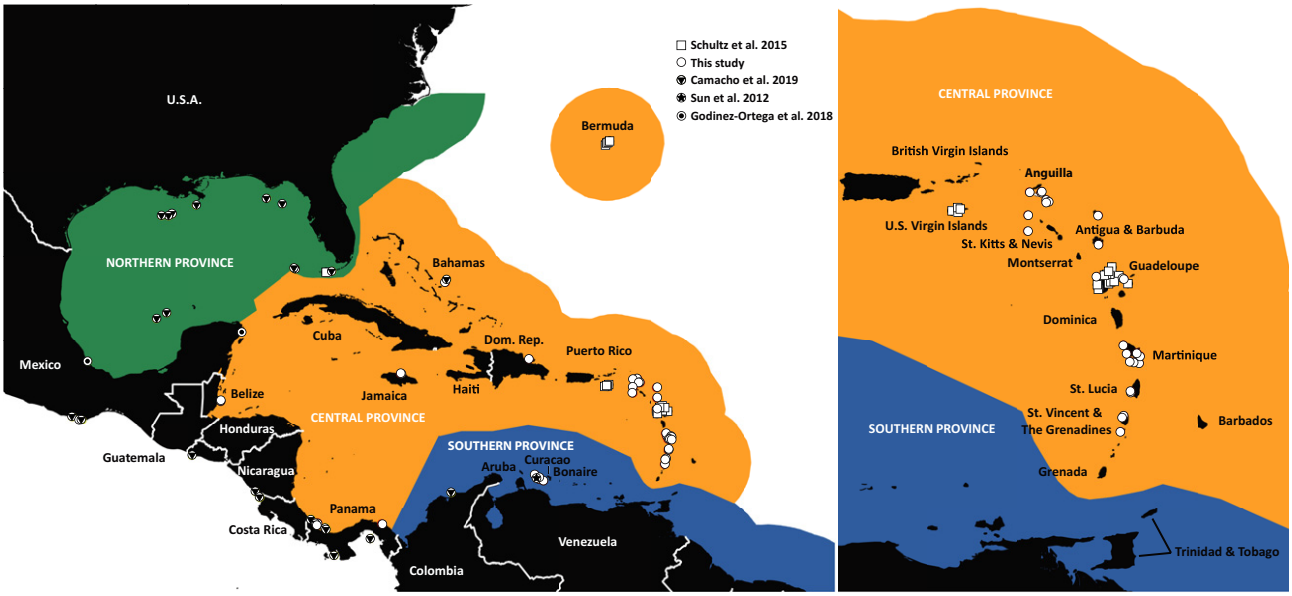


FIG. 1. Map of sampling localities in the Greater Caribbean from previous (Sun et al. 2012, Schultz et al. 2015, Camacho et al. 2019) and current studies. The regions correspond to Robertson and Cramer (2014) provinces. [Color figure can be viewed at wileyonlinelibrary.com]

in this study positioned in 16 highly supported lineages in ML and BI analyses (Fig. 2; Figure S1 in the Supporting Information). Of these 16 lineages, 13 were previously reported from the Greater Caribbean by Schultz et al. (2015), Camacho et al. (2019), and Vieira et al. (2016) including nine described: *Lobophora canariensis*, *L. colombiana*, *L. declerckii*, *L. delicata*, *L. dispersa*, *L. guadeloupensis*, *L. littlerorum*, *L. schneideri*, and *L. variegata*; and four undescribed species: *L.* spWA02, *L.* sp64, *L.* sp85, and *L.* sp86. An additional species recently described from Cape Verde, *L. caboverdeana* (Vieira et al. 2019b), is reported from the Greater Caribbean for the first time. In addition, two lineages are newly reported for the Caribbean, *L.* sp10, previously reported from Kavieng, Papua New Guinea (Vieira et al. 2019a), and *L.* sp90, reported for the first time from the Greater Caribbean. We formally describe five new species (Tables 2, 3; Figs. 3 and 4), previously identified using sequence-based species delineation methods (Generalized Mixed Yule Coalescent, Automatic Barcode Gap Discovery, Poisson Tree Processes) by Schultz et al. (2015), Vieira et al. (2017), and Camacho et al. (2019; i.e., *L.* sp10, *L.* sp64, *L.* sp85, *L.* sp86, and *L.* spWA02). We also provide a more detailed description of *L. variegata*. The remaining lineage *L.* sp90 is not formally described here because we lack enough material at present.

Distribution. We examined the distribution of *Lobophora* species within the Greater Caribbean (Fig. 5) at two geographic scales, that is, ecoregion level (Fig. 5; Spalding et al. 2007) and province level (Fig. 5; Robertson and Cramer 2014). No species was found in all ecoregions, but *L. declerckii*, *L. schneideri*, and *L. dispersa* were present in all three provinces (Fig. 5). The last is the only species reported from the Carolinian ecoregion so far. Additionally, *L. declerckii*, reported from Belize, Curaçao, Saba, Saint Croix, Saint Lucia, and Sint Eustatius, stands out as the most widespread species in the Greater Caribbean. *Lobophora tortugensis* O.Camacho & Fredericq was only found in the Northern Province. In all, 12 species were at least present in two provinces, and mainly the Central and Southern Provinces. Confined to the Greater Caribbean, *L. variegata* was further reported from the Dominican Republic, and appears to be restricted to Mexico (Quintana Roo), Florida (Florida Keys), the Bahamas, and the Lesser and Greater Antilles.

Biogeographic analyses. Regionalization within the Greater Caribbean based on the ecoregions was performed using two hierarchical clustering methods (Fig. 6; Jaccard/UPGMA and Euclidean/Ward). The clustering of regions varied to some extent according to the methods used. The Euclidean Ward HC method presented the highest cophenetic correlation coefficient (CP = 0.8135). The Euclidean/Ward HC and Jaccard/Ward methods concordantly combined the following ecoregions: Carolinian and southern Gulf of Mexico; Floridian and northern Gulf of Mexico; Bahamian and Greater Antilles; and eastern Caribbean, southern Caribbean, and Bermuda. In the latter case, the methods diverged in the relationships among the three ecoregions. These methods showed inconsistence in the placement of the

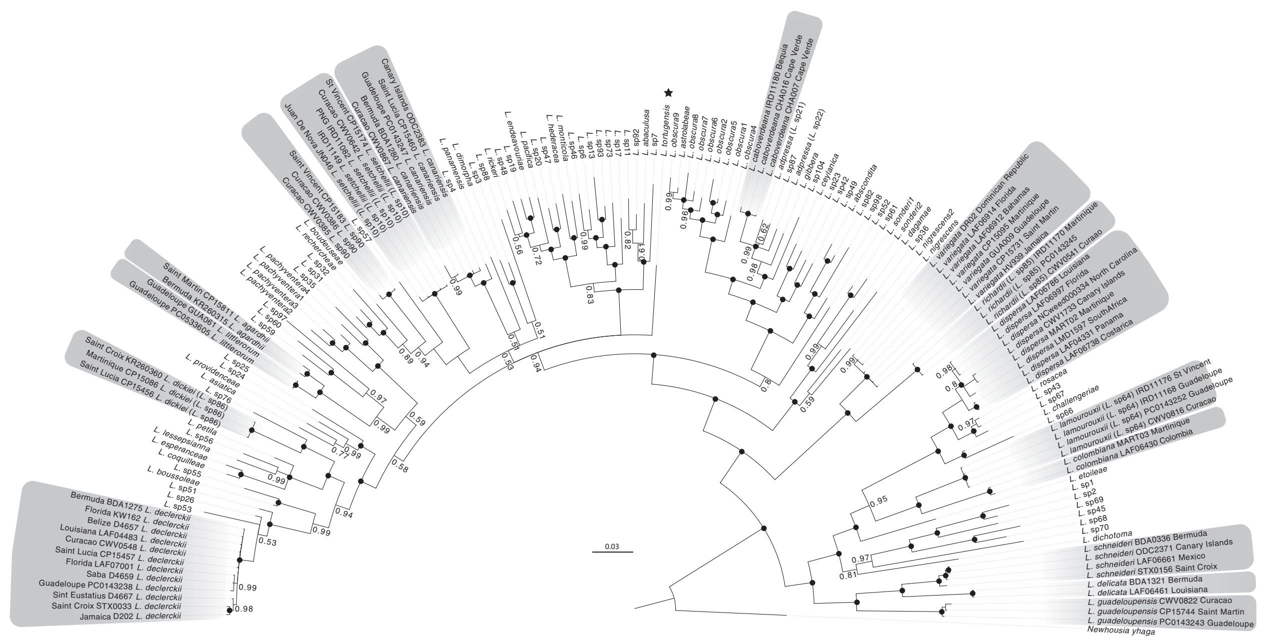


FIG. 2. Phylogenetic tree of the genus *Lobophora* using Bayesian method, generated with MrBayes v3, and based on *cox*3 sequences. The values shown at each node represent posterior probabilities. A black filled circle represents full support. Two species from the Greater Caribbean were not identified in our study, *L. crispata,* for which no *cox*3 sequences are available, and *L. tortugensis* indicated by a star in the tree.

western Caribbean and southwest Caribbean. Except for the presence of the southwest Caribbean, clustering of the Floridian, northern and southern Gulf of Mexico, and Carolinian corresponds to the Northern Province of Robertson and Cramer (2014). Spalding et al. (2007) do not include the Floridian in the Greater Caribbean warm-temperate region. In the two analyses, the ecoregions composing the Central Province of Robertson and Cramer (2014) do not cluster together. Furthermore, the southern Caribbean, part of the Southern Province of Robertson and Cramer (2014), clusters with the eastern Caribbean and Bermuda in both analyses.

In all, 11 *Lobophora* species exclusively occur in the Greater Caribbean (Fig. 5), six are shared with other regions in the Atlantic (*L. caboverdeana*, *L. canariensis*, *L. delicata*, *L. dispersa, L. littlerorum*, and *L. schneideri*), two are shared with the Indo-Pacific (*L. dispersa* and *L. setchellii* sp. nov.), and one is shared with the eastern Pacific (*L. schneideri*; Clipperton Island). The last, however, could be an introduction (Vieira et al. 2018). *Lobophora dispersa* is not only found across the Greater Caribbean but also across the Atlantic (Macaronesia, Brazil) and in the southwestern Indo-Pacific (Madagascar, South Africa). Reported across the Indo-Pacific (Juan de Nova, Kavieng, Tuvalu), *L. setchellii* sp. nov. displays a broad distribution spanning three Oceans (Atlantic, Indian, and Pacific Oceans).

DISCUSSION

Diversity patterns. This is the third major taxonomic study of the genus *Lobophora* in the Greater Caribbean and the first largest sampling in the eastern, southern, and western Caribbean (Belize). Of the 16 species recognized in this study, 13 were previously reported in the Greater Caribbean, and three species (*L. caboverdeana*, *L. setchellii* sp. nov., and *L.* sp90) were newly identified from this region. These new data bring the total number of known species in the Greater Caribbean to 18, and to 19 in the Atlantic. Interestingly, the diversity now confirms a previous estimate of 18 species in the Atlantic by Vieira et al. (2017). This study confirms that the Greater Caribbean and more broadly the Atlantic with 18 species is far less diverse than the Indo-Pacific with 95 species (Vieira et al. 2017). The Greater Caribbean stands out as a diversity hotspot for *Lobophora* in the North Atlantic Ocean.

The eastern Caribbean is the most diverse ecoregion from the Greater Caribbean with 16 species. This is also in line with the theory that the first Caribbean *Lobophora* species came exclusively from the Indo-Pacific – and not from the eastern Pacific – by founder events, leading to additional speciation events in this region (Vieira et al. 2017). Alternatively, these results may also be due to a larger sampling effort in this ecoregion. On a broader scale, the Central Province sensu Robertson and Cramer (2014) is the most diverse region with 16 species

TABLE 2. Descriptions of new *Lobophora* species and *L. variegata* from the Greater Caribbean.

Lobophora agardhii sp. nov. Payri & C.W.Vieira
Figures 3J and 4A
Description: Thallus coarse, predominantly crustose, dark brown in color, leather-looking. Margin entire. Attached to substratum by scattered ventral rhizoids. Thallus of single- to double-cell-layered medulla, two-cell-layered cortex on dorsal and ventral sides, 211–245 μm thick and composed of five-cell to six-cell layers. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN240122.
Holotype (designated here): NOU 201772 [CP15811]
Type locality: Rocher Alizé (18.1173, −63.226333), Saint Martin, Leeward Islands, Lesser Antilles, West Indies
Habitat: Growing on *Avrainvillea nigricans* on coarse sand bottom 3 m deep, forming a sleeve around the stipe.
Distribution: Bermuda, Saint Martin.
Etymology: Named after the Swedish botanist, phycologist, and taxonomist Jacob Georg Agardh (December 8, 1813–January 7, 1901) who described the genus *Lobophora*.Specimens examined: Rocher Alizé, Saint Martin, May 7, 2015 *leg.* C. Payri (CP15811).
Remarks: This species corresponds to *Lobophora* spWA02 (BDA3424, Bermuda) of Schultz et al. (2015)

Lobophora dickiei sp. nov. Payri & C.W.Vieira
Figures 3, C and K, 4C
Description: Thallus flabellate, to 3 cm wide and 2.5 cm tall, procumbent to crustose, orange to light green radial gradient in color speckled with darker small spots. Attached to substratum by numerous ventral rhizoids. Margin entire. Thallus of single-cell-layered medulla, two-and one-cell-layered cortex on the dorsal and ventral sides, respectively, 129–142 μm thick and composed of four-cell to five-cell layers. Distinguished from related species by its orange-green color speckled with darker small spots and procumbent habit. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN240119.
Holotype (designated here): NOU 201781 [CP15473]
Type locality: Trou du Diable(13.860833, −61.074167), Saint Lucia, Windward Islands, Lesser Antilles, West Indies
Habitat: Growing on hard substrate; corals and reef wall on shallow habitats.
Distribution: Curaçao, Saint Lucia.
Etymology: named after the Scottish botanist who specialized in algae, George Dickie (December 21, 1812–June 10, 1882), and described *Lobophora obscura*, as *Zonaria obscura*.Specimens examined: Rocroy Val de l'Orge, Guadeloupe, October 10, 2014, *leg.* C. Payri (IRD11142); Case Pilote, Martinique, April 24, 2015, *leg.* C. Payri (CP15086); Trou du Diable, Saint Lucia, April 30, 2015, *leg.* C. Payri (CP15456); Trou du Diable, Saint Lucia, April 30, 2015, *leg.* C. Payri (CP15473); Wallibou, Saint Vincent, April 26, 2015, *leg.* C. Payri (IRD11175); Château Bel Air Bay, Saint Vincent, April 26, 2015, *leg.* C. Payri (CP15178).
Remarks: This species corresponds to *Lobophora* spWA01 (STX0024, Saint Croix) of Schultz et al. (2015) and *L.* sp86 of Vieira et al. (2016)

Lobophora lamourouxii sp. nov. Payri & C.W.Vieira
Figures 3, E and L; 4D
Description: Large circular thallus, to 5 cm wide and 2.5 tall, predominantly procumbent, distal margin free, light green transparent in color. Attached to substratum by ventral rhizoids. Margin entire. Thallus of single-cell-layered medulla, one-cell-layered cortex on the dorsal and ventral sides, respectively, 110–124 μm thick and composed of three-cell to four-cell layers. Distinguished from related species by its translucent blades and prostrate growth form. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN240030.
Holotype (designated here): NOU 201665 [IRD11176, CP15166]
Type locality: Wallibou (13.333, −61.221617), Saint Vincent, Windward Islands, Lesser Antilles, West Indies
Habitat: Growing on shallow rocky shore.
Distribution: Curaçao, Guadeloupe, Saint Vincent.
Etymology: named after the French biologist and naturalist Jean Vincent Félix Lamouroux (May 3, 1779–March 26, 1825) who described the first species of *Lobophora, Lobophora variegata*, as *Dictyota variegata*.Specimens examined: Wallibou, Saint Vincent, April 26, 2015, *leg.* C. Payri (IRD11176); Rocher La Perle, Guadeloupe, April 23, 2015, *leg.* C. Payri (IRD11168); Canoa, Curaçao, February 11, 2017, *leg.* C. Vieira (CWV0816).
Remarks: This species corresponds to *Lobophora* spWA03 (PC0143252, Guadeloupe) of Schultz et al. (2015) and *L.* sp64 of Vieira et al. (2016)

Lobophora richardii sp. nov. C.W.Vieira & Payri
Figures 3, F and M; 4E
Description: Thallus circular, to 10 cm wide, predominantly erect and ruffled, light green in color with darker small spots forming concentric lines. Attached to the substratum by basal mound of rhizoids. Margin entire. Thallus of single-cell-layered medulla, three-cell-layered cortex on the dorsal and ventral sides, 215–248 μm thick and composed of seven-cell layers. Distinguished from related species by its ruffled growth form and light green color with darker small spots forming concentric lines. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN240034.
Holotype (designated here): NOU 201785 [IRD11170, CP15127]
Type locality: Diamant (14.6579, −61.15755), Martinique, Windward Islands, Lesser Antilles, West Indies
Habitat: Growing in deep water (30 m deep) with other large algae, fixed on sand-covered substrate.
Distribution: Martinique, Curaçao.
Etymology: named after the French botanist and botanical illustrator Louis Claude Marie Richard (September 19, 1754–June 6, 1821) who collected the type specimen of *Lobophora variegata*.
Specimens examined: Diamant, Martinique, April 25, 2015, *leg.* C. Payri (IRD11170); Klein Curaçao, Curaçao, February 9, 2017, *leg.* C. Vieira (CWV0541).
Remarks: This species corresponds to *L.* sp85 of Vieira et al. (2016)

(continued)

Lobophora setchellii sp. nov. C.W.Vieira & Payri
Figures 3, I and N; 4F
Description: Thallus small, to 1 cm wide, predominantly procumbent, light green in color. Attached to substratum by basal mound of rhizoids. Thalli overlapping forming a mat. Margin entire. Thallus of single-cell-layered medulla, two-cell and one-cell-layered cortex on the dorsal and ventral sides, respectively, 123–139 μm thick and composed of four-cell layers. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN240043.
Holotype (designated here): NOU 206223 [CP15174]
Type locality: Château Bel Air Bay (13.29955, −61.2483), Saint Vincent, Windward Islands, Lesser Antilles, West Indies
Habitat: Growing on bedrock and epiphytic on calcareous red algae.
Distribution: Saint Vincent, Curaçao.
Etymology: named after the American phycologist William Albert Setchell (April 15, 1864–April 5, 1943) who collected the type specimen of *Lobophora pacifica*.
Specimens examined: Château Bel Air Bay, Saint Vincent, April 26, 2015, *leg.* C. Payri (CP15174); Klein Curaçao, Curaçao, February 9, 2017, *leg.* C. Vieira (CWV0642).
Remarks: This species corresponds to *L.* sp10 of Vieira et al. (2016).

Lobophora variegata **(J.V.Lamour.) Womersley ex E.C.Oliveira**
Figures 3, G and O; 4H
Basionym: *Dictyota variegata* J.V.Lamour.
Diagnosis: Thallus fan-shaped, erect, with a basal mound of rhizoids and in some individuals a rudimentary stipe, to 8 cm wide and 6 cm tall, forming clusters of ruffled yellowish brown to dark brown and green blades. Blades 112–197 μm thick, composed of five-cell to seven-cell layers, a single medullary layer and cortex of two- to three-cell layers on the dorsal and ventral sides. Mitochondrial-encoded *cox*3 sequence = GenBank accession KU364222, KU364223, KU353160, KX061443, MN240037-MN240037; chloroplast-encoded *rbc*L sequences KU364182, KU364183, KU352998, KU352999, KX061445; chloroplast-encoded *psb*A sequences and KU364269, KU364270, KU352855, KU352856, KX061444.
Habitat: *Lobophora variegata* occurs in shallow water, to 7 m depth on hard substratum or coral rubble mixed among numerous other algae including *Dictyota* J.V.Lamour., *Sargassum* J.Agardh, *Jania* J.V.Lamour., and *Caulerpa* J.V.Lamour., and was also found growing on the holdfast and basal branches of *Sargassum pteropleuron* Grunow, gorgonian corals, and *Thalassia testudiunum* Banks ex K.D.Koenig leaves in the Florida Keys and sponges in the Martinique.
Type specimen: CN C7F100 (CN, Herbarium of the Université de Caen, France)
Type locality: 'Antilles', Caribbean Sea; presumably Guadeloupe (see Vieira et al. 2016).
Distribution: Bahamas, Dominican Republic, Florida, Guadeloupe, Jamaica, Martinique, Mexico, Saint Martin.
Specimens examined: Pointe de la Baleine, Martinique, April 24, 2015, *leg.* C. Payri (CP15095); Ile de Tintamare, Saint Martin, May 6, 2015, *leg.* C. Payri (CP15729); Ile de Tintamare, Saint Martin, May 6, 2015, *leg.* C. Payri (CP15730); Ile de Tintamare, Saint Martin, May 6, 2015, *leg.* C. Payri (CP15731); El Portillo, Dominican Republic, July 1, 2016, *leg.* E. Serrão (DR01); El Portillo, Dominican Republic, July 1, 2016, *leg.* E. Serrão (DR02; El Portillo, Dominican Republic, July 1, 2016, *leg.* E. Serrão (DR03).
Specimens from previous studies: MW11719, Bahamas (Vieira et al. 2016); MW11793, Bahamas (Vieira et al. 2016); LAF6912, Bahamas (Vieira et al. 2016); LAF6914, Florida (Vieira et al. 2016); IRD11140, Guadeloupe (Vieira et al. 2016); HV939, Jamaica (Vieira et al. 2016).

followed by the Southern Province with 10 species. With only six species, the diversity in the Northern Province, which is a warm-temperate region, is twofold to threefold lower than the other two provinces. This lower diversity is likely due to the lower temperature (<25°C), which is unsuitable for most *Lobophora* species with tropical affinities.

Biogeography. Contrary to previous ideas associated with the name *Lobophora variegata* – considered to be a widespread species – most likely not all Greater Caribbean *Lobophora* species are present across this region. Some species appear more widespread than others, and *L. variegata* as far as we know is restricted to the Floridian, Bahamian, western Caribbean, Greater Antilles, and eastern Caribbean ecoregions. Only three species are present across the Greater Caribbean (i.e., Southern, Central, and Northern Provinces; *L. declerckii*, *L. dispersa*, and *L. schneideri*). Eight species are restricted to the Central and Southern Provinces (tropical region), and only one species was exclusively found in the Northern Province, *L. tortugensis* (Fig. 5).

Observed distribution patterns indicate that *Lobophora* species from the Greater Caribbean have climate affinities. Of the 18 Greater Caribbean *Lobophora* species, four clearly have warm-temperate affinities, namely *L. delicata*, *L. dispersa*, *L. schneideri*, and *L. tortugensis*. Rare in the tropical Greater Caribbean (reported in the eastern and southwest Caribbean), *L. schneideri* is a common species in the Canary Islands (warm-temperate climate) where it can dominate benthic assemblages, as well as in the eastern Mediterranean Sea (Vieira et al. 2018). Common in the temperate Greater Caribbean (i.e., Northern Province), *L. dispersa* was previously reported from warm-temperate localities (South Africa, Madagascar, and the Canary Islands). *Lobophora tortugensis* was only reported from the Northern Province in the Greater Caribbean. The other 14 species present tropical affinities, and *L. declerckii* stands as the most common species in the tropical Greater Caribbean and was recorded at the southern edge of the Northern Province in the Floridian ecoregion. Restrictions to either warm-temperate or tropical regions reflect differences in physiological tolerance among species. Cold adaptation is a process with little success for members of the genus *Lobophora* as demonstrated by the limited number of species that have adapted to temperate conditions over evolutionary time (Vieira et al. 2017) in comparison to other Caribbean taxa such as *Dictyota* (Dictyotales, Phaeophyceae; Tyberghein 2012).

TABLE 3. Comparison of morphological characters among species of *Lobophora* from the Greater Caribbean.

	L. agardhii sp. nov.	*L. canariensis*	*L. caboverdeana*	*L. colombiana*	*L. crispata*	*L. declerckii*	*L. delicata*	*L. dickiei* sp. nov.
Thickness								
Average	228.3 ± 10.8	102 ± 8	183.7 ± 13.7	86	112	N/A	58	134.0 ± 5.4
Min–Max	211–245	80–112	170–215	74–94	100–122	55–85	48–65	129–142
Number of cells								
Average	6	5	8	5	6	N/A	3	5
Min–Max	5–6	5	7–9	5	5–7	3–5	3–4	4–5
Number of dorsal cells								
Average	2	2	4	2	2	N/A	1	2
Min–Max	2	2	3–4	2	2–3	1–2	1	2
Number of ventral cells								
Average	2	2	3	2	2	N/A	1	2
Min–Max	2	2	3–4	2	2–3	1–2	1	1–2
Medulla length								
Average	128.0 ± 14.7	79 ± 12	70.0 ± 5.0	80	76	N/A	70	86.8 ± 8.3
Min–Max	195–147	60–100	65–75	62–92	58–101	62–100	59–81	76–103
Medulla height								
Average	92.9 ± 13.1	45 ± 6	60.0 ± 7.1	39	49	N/A	26	60.4 ± 7.8
Min–Max	77–119	30–54	50–75	34–49	32–63	30–50	20–34	49–69
Medulla width								
Average	61.5 ± 3.9	33 ± 4	37. 0 ± 6.3	25	23	N/A	27	65.7 ± 3.1
Min–Max	56–64	30–40	30–50	20–28	20–26	25–45	25–29	59–68
Dorsal height								
Average	69.4 ± 6.2	30 ± 3	70.7 ± 5.3	N/A	N/A	N/A	N/A	42.6 ± 4.1
Min–Max	60–80	26–34	30–80	N/A	N/A	15–22*	N/A	38–47
Ventral height								
Average	66.0 ± 5.6	27 ± 3	53.0 ± 9.6	N/A	N/A	N/A	N/A	31.0 ± 7.4
Min–Max	57–75	20–32	40–70	N/A	N/A	14–20*	N/A	20–37
Thallus								
Growth-form	Crustose	Crustose to decumbent	Crustose	Decumbent	Decumbent	Decumbent	Crustose, procumbent, dececumbent	Procumbent, crustose
Color	Dark brown	Orange-brown	Light brown	Brown	Dark brown	Light green	Translucent light green	Orange to light green
References	a	b	a	c	c	e	c	a

(continued)

TABLE 3. (continued)

	L. dispersa	*L. guadeloupensis*	*L. lamourouxii* sp. nov.	*L. littlerorum*	*L. richardii* sp. nov.	*L. schneideri*	*L. setchellii* sp. nov.	*L. variegata*	*L. sp90*
Thickness									
Average	131.8 ± 17.2 (98°)	N/A	116.8 ± 5.8	N/A	229.7 ± 10.0	167.0 ± 8.6	139.4 ± 16.5	152 ± 19	160.4 ± 20.1
Min–Max	78–164	65–95	110–124	95–140	215–248	156–180	123–139	124–197	149–172
Number of cells									
Average	7 (6°)	N/A	3	N/A	7	7	4	6	5
Min–Max	5–8	5–7	3–4	5–6	7	6–7	4	5–7	3–5
Number of dorsal cells									
Average	3 (3*)	N/A	1	N/A	3	3	2	3	2
Min–Max	2–4	2	1–2	2–3	3	3	2	2–3	1–2
Number of ventral cells									
Average	3 (2°)	N/A	1	N/A	3	3	1	3	2
Min–Max	2–3	3–2	1	2	3	2–3	1	2–3	1–2
Medulla length									
Average	82.0 ± 8.4 (87°)	N/A	130.9 ± 17.4	N/A	174.1 ± 22.8	117.2 ± 13.3	133.5 ± 10.1	81 ± 6	110.9 ± 17.1
Min–Max	48–125	55–105	95–145	60–80	165–190	106–140	120–154	68–94	75–124
Medulla height									
Average	45.6 ± 9.8 (33°)	N/A	57.4 ± 12.3	N/A	61.8 ± 11.4	68.4 ± 8.1	57.1 ± 11.2	70 ± 11	85.4 ± 9.1
Min–Max	23–60	34–50	41–74	38–40	48–83	60–80	46–77	50–94	79–97
Medulla width									
Average	22.4 ± 2.6 (22°)	N/A	31.5 ± 4.7	N/A	53.8 ± 5.3	27.6 ± 2.6	53.7 ± 4.0	33 ± 10	46.3 ± 8.7
Min–Max	18–28	25–32	25–38	32–46	50–61	24–30	48–57	23–43	38–63
Dorsal height									
Average	45.6 ± 7.8	N/A	34.4 ± 11.6	N/A	88.6 ± 3.7	50.4 ± 3.1	50.7 ± 3.7	16 ± 3	41.6 ± 8.7
Min–Max	40–60	18–26*	24–51	24–32*	83–95	44–56	47–57	13–25	32–49
Ventral height									
Average	40.6 ± 1.9	N/A	25.1 ± 1.8	N/A	79.3 + 9.9	48.2 ± 4.8	31.5 ± 4.7	17 ± 2	33.3 ± 9.6
Min–Max	38–44	20–25*	23–27	24–32*	58–88	40–56	25–38	13–21	23–43
Thallus									
Growth-form	Erect, procumbent	Erect	Procumbent	Crustose	Decumbent ruffled	Decumbent ruffled	Procumbent, crustose	Erect, ruffled	Procumbent
Color	Light to dark brown	Brown	Light green transparent	Greenish to brown	Light green	Light green	Light green	Dark orange brown to dark green	Brown
References	c,d	e	a	e	a	f	a	b	a

N/A: not available; °Average from Camacho et al. 2019; * sum of cortex and "subcortex" in Schultz et al. (2015).
[a]This study
[b]Vieira et al. (2016).
[c]Camacho et al. (2019).
[d]Vieira et al. (2019b).
[e]Schultz et al. (2015).
[f]Vieira et al. (2018).

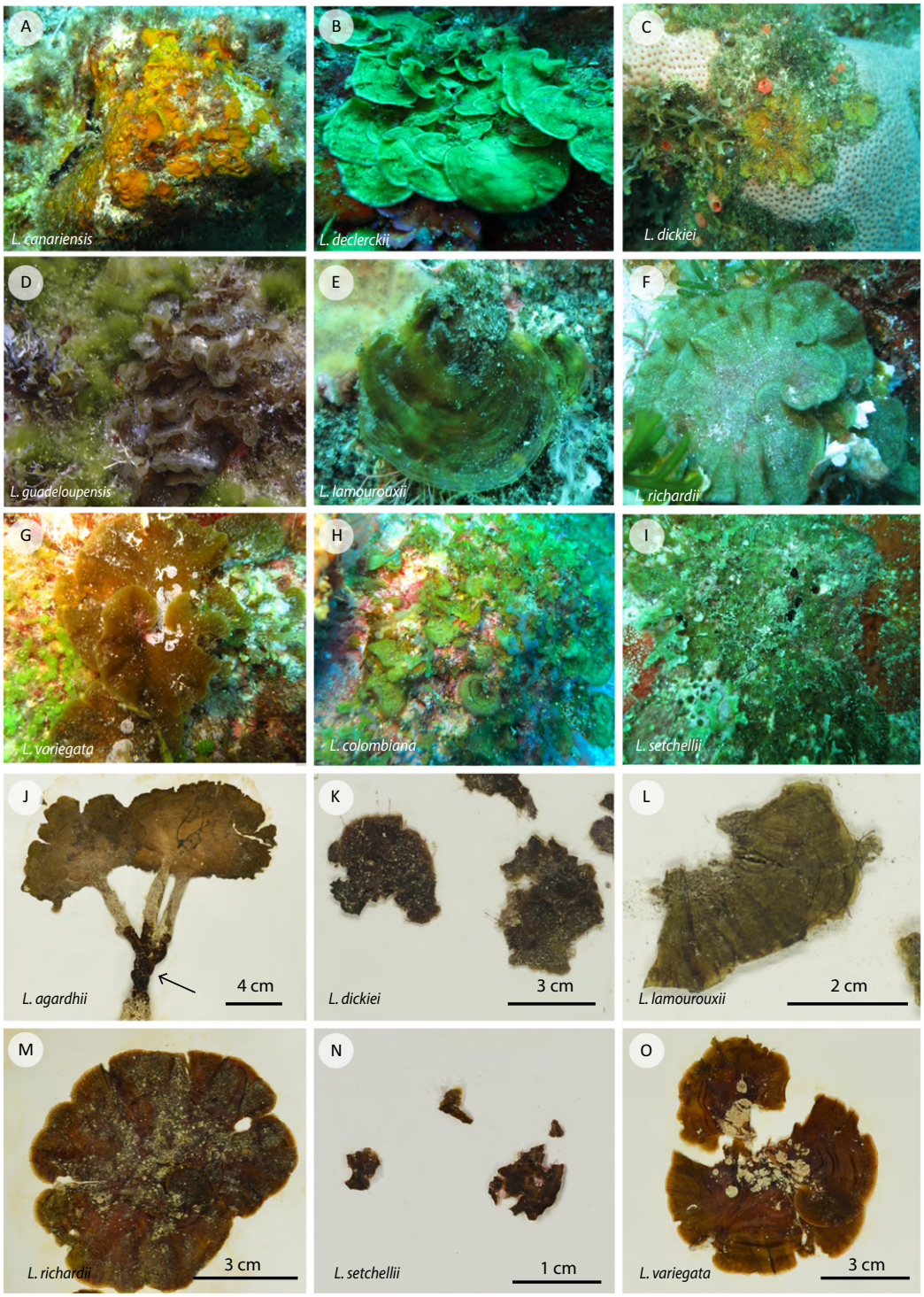


FIG. 3. Habit photographs of some *Lobophora* species from the Greater Caribbean and herbarium pictures. *Lobophora canariensis* from Saint Lucia, voucher CP15460 (A); *L. declerckii* from Saint Lucia, voucher CP15434 (B); *L. dickiei* sp. nov. from Martinique, voucher CP15086 (C); *L. guadeloupensis* from Curaçao, voucher CWV0822 (D); *L. lamourouxii* sp. nov. from Saint Vincent, voucher CP15164 (E); *L. richardii* sp. nov. from Martinique, voucher CP15127 (F); *L. variegata* from Saint Martin, voucher CP15730 (G); *L. colombiana* from Bequia, voucher CP15268 (H); and *L. setchellii* sp. nov. from Saint Vincent, voucher CP15174 (I). Photographs of holotype of new species and of *L. variegata* from Saint Martin: *L. agardhii*, voucher CP15811 (J); *L. dickiei*, voucher CP15473 (K; the black arrow shows *L. dickiei* at the base of *Avrainvillea nigricans*); *L. lamourouxii*, voucher CP15166 (L); *L. richardii*, voucher CP15127 (M); *L. setchellii*, voucher CP15174(N); and *L. variegata*, voucher CP15729 (O). [Color figure can be viewed at wileyonlinelibrary.com]

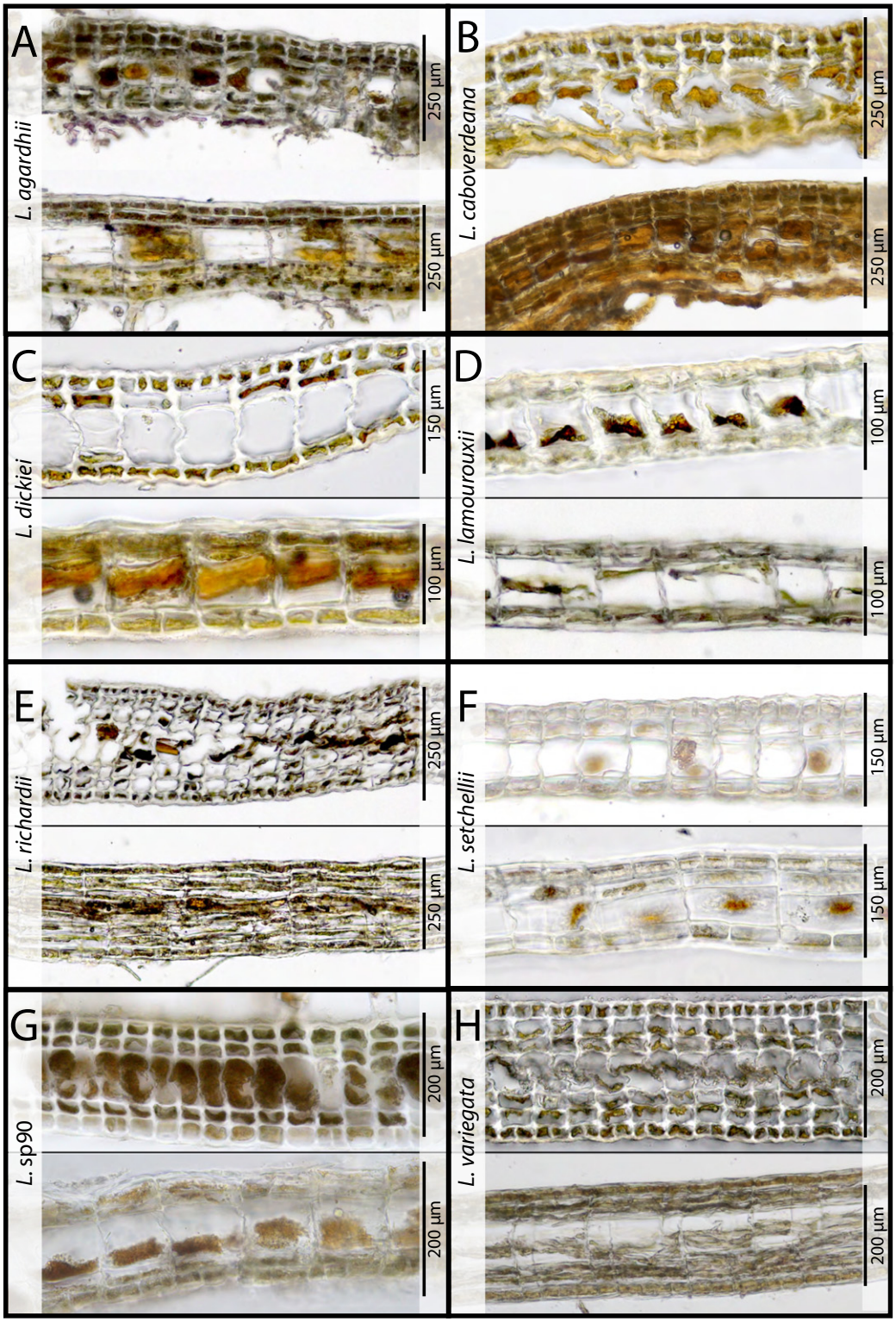
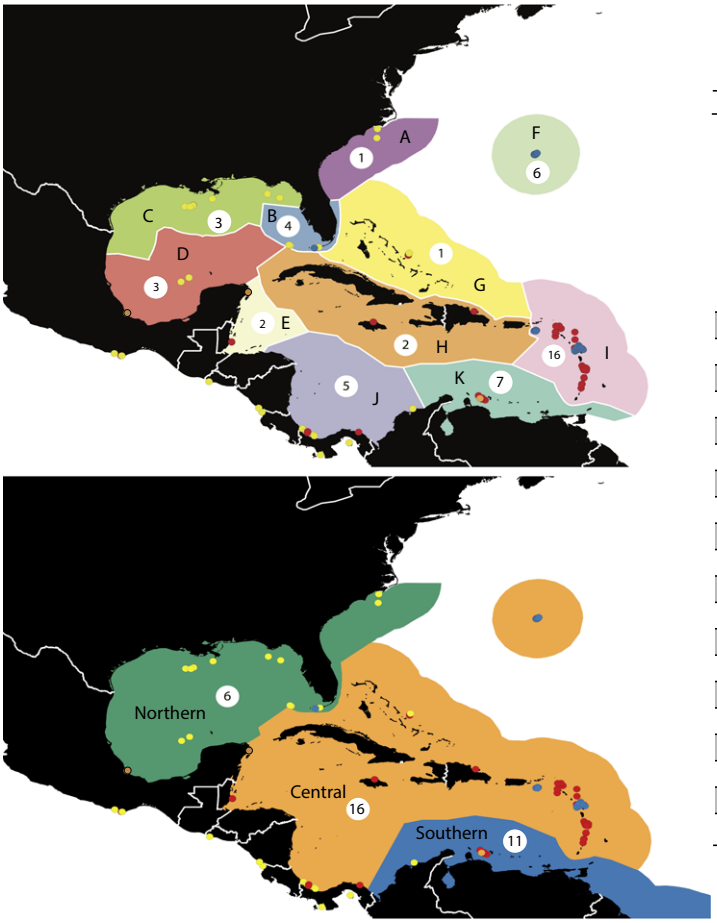


FIG. 4. Transverse (up) and longitudinal (down) sections of thallus of new *Lobophora* species from the Greater Caribbean. *L. agardhii* sp. nov. from Saint Martin, voucher CP15811 (A); *L. caboverdeana* from Bequia, voucher IRD11180 (B); *L. dickiei* sp. nov. from Martinique, voucher CP15473 (C); *L. lamourouxii* from Saint Vincent, voucher CP15164 (D); *L. richardii* from Martinique, voucher CP15127 (E); *L. setchellii* sp. nov. from Saint Vincent, voucher CP15174 (F); *L.* sp90 from Saint Vincent, voucher CP15183 (G); and *L. variegata* from Saint Martin, voucher CP15729 (H). [Color figure can be viewed at wileyonlinelibrary.com]



# specimens				63				182					144		
				Northern				Central					Southern		
	Eastern Pacific	Indo-Pacific	Eastern Atlantic	Carolinian (A)	Floridian (B)	N. Gulf of Mexico (C)	S. Gulf of Mexico (D)	Western Caribbean (E)	Bermuda (F)	Bahamian (G)	Greater Antilles (H)	Eastern Caribbean (I)	Southwest Caribbean (J)	Southern Caribbean (K)	Total
L. aghardii									●			●			2
L. caboverdeana			●									●			1
L. canariensis			●						●			●	●	●	4
L. colombiana												●	●		2
L. crispata													●		1
L. declerckii					●		●	●	●		●	●	●		7
L. delicata			●			●			●			●			3
L. dickiei												●			1
L. dispersa		●	●	●	●	●	●					●	●		6
L. guadeloupensis												●		●	2
L. lamourouxii												●		●	2
L. littlerorum			●						●			●			2
L. richardii												●		●	2
L. schneideri	●		●				●		●			●		●	4
L. setchellii		●										●		●	2
L. tortugensis					●	●									2
L. variegata					●			●		●	●	●			5
L. sp90												●		●	2
Total				1	4	3	3	2	6	1	2	16	5	7	
# specimens				8	9	12	34	31	26	3	7	115	18	126	

FIG. 5. *Lobophora* species diversity map per provinces (upper map) according to Robertson and Cramer (2014) and ecoregions (lower map) according to Spalding et al. (2007). The table on the right lists the presence of the 18 *Lobophora* species from the Greater Caribbean per ecoregion and provinces. [Color figure can be viewed at wileyonlinelibrary.com]

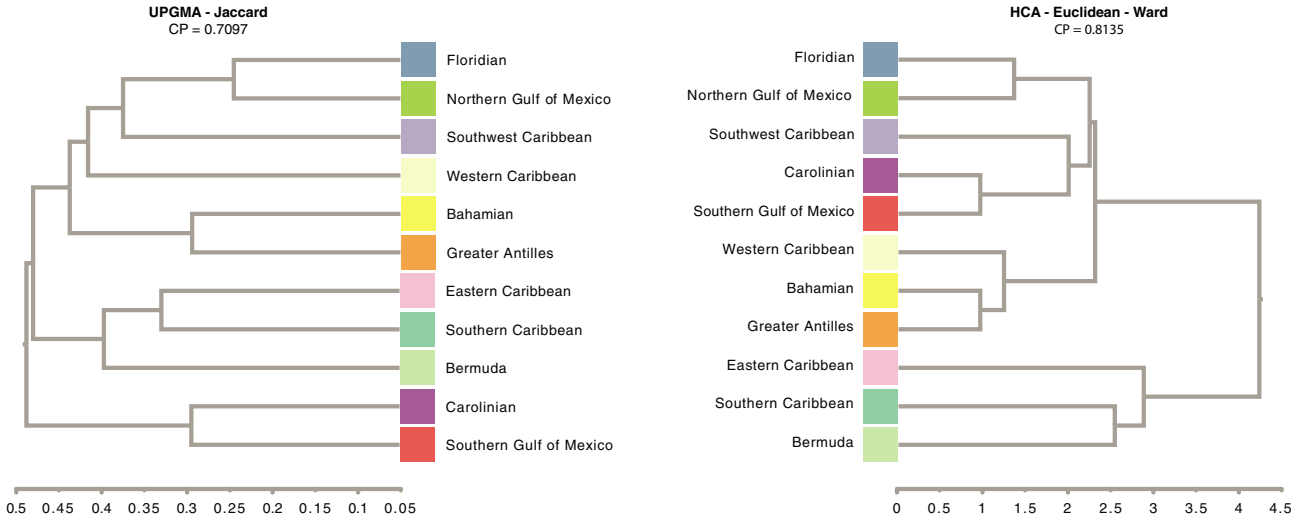


FIG. 6. Dendrograms and maps resulting from UPGMA hierarchical clustering of ecoregion (A) and provinces (B) species assemblages based on similarity matrix computed with Jaccard coefficient for *Lobophora*. [Color figure can be viewed at wileyonlinelibrary.com]

TABLE 4. Comparison of morphological and ecological features of the Greater Caribbean *Lobophora* species.

	Morphology	Habitat	Depth	Exposition	Substrate	Grazing intensity	Abundance
L. agardhii sp. nov.	Crustose	Sand bottom	0–8	N/A	Rock, seaweed	N/A	Low
L. canariensis	Crustose/ Decumbent	Coral reef	0–36	Medium–Low	Rock	N/A	Low
L. caboverdeana	Crustose	*Sargassum* bed	0	High	Rock, seaweed	N/A	Low
L. colombiana	Decumbent	Coral reef	0–20	Medium–Low	Rock	N/A	N/A
L. crispata	Fasciculate/ Stipitate	Coral reef	1–20	N/A	Rock	N/A	N/A
L. declerckii	Conk-like/ Decumbent	Coral reef	12–36	Low	Rock	Medium	High
L. delicata	Procumbent	Coral reef	0–14	Low	Rock	N/A	Low
L. dickiei sp. nov.	Crustose/ Procumbent	Coral reef	5–20	N/A	Dead coral	N/A	Low
L. dispersa	Procumbent	Coral reef	1–90	Low	Rock, rhodolith, dead coral	N/A	High
L. guadeloupensis	Fasciculate	Seagrass bed	6–136	High	Rock, sand	High	N/A
L. lamourouxii sp. nov.	Procumbent	Rocky shore	5–80	N/A	Rock, CCA	N/A	N/A
L. littlerorum	Crustose	Rocky shore	0–8	High	Rock, live coral	Moderate–high	Low
L. richardii sp. nov.	Decumbent/ Fasciculate	Seaweed bed	25–30	Low	Sand	N/A	Low
L. schneideri	Fasciculate	Seagrass bed	0–12	Low	Rock	Medium	Low
L. variegata	Decumbent/ Fasciculate	Seagrass bed	8–10	Low	Rock	Moderate–high	Medium
L. tortugensis	Fasciculate	Rhodolith bed	60–90	Low	Rhodolith	Low	N/A
L. setchellii sp. nov.	Crustose/ Procumbent	Coral reef	5–20	Low	Rock, CCA	N/A	Low
L. sp90	Crustose/ Procumbent	Coral reef	10	Low	Rock	Medium	Low

CCA, crustose coralline algae.

The hierarchical analyses performed based on Spalding et al.'s (2007) 11 ecoregions do not support the biogeographic scheme proposed by Robertson and Cramer (2014) for *Lobophora,* except for within the Northern Province. The ecoregions composing the Central and Southern Provinces do not cluster together based on *Lobophora* distribution patterns. Bermuda and the eastern and southern Caribbean form a separate province; Bahamian, Greater Antilles, and western Caribbean another province (Central Province); and finally Floridian, northern and southern Gulf of Mexico, and Carolinian would form a northern province in agreement with Robertson and Cramer (2014). The placement of the southwest Caribbean comes as a surprise. Nevertheless, the unequal sampling across these ecoregions possibly explains some of these patterns, which could explain why the southwest Caribbean clusters with the Northern Province ecoregions.

With two-thirds of *Lobophora* diversity restricted to the Greater Caribbean, this region forms an isolated hotspot in the Atlantic for this genus. The rest of the Greater Caribbean diversity is mainly shared with the rest of the Atlantic. We discuss in the final section the reasons explaining this pattern.

Morphology and ecology. Previous authors recorded three main growth forms associated with the name "*Lobophora variegata*," namely, encrusting, decumbent, and ruffled (De Ruyter van Steveninck and Breeman 1987, Coen and Tanner 1989, Littler and Littler 2000). We now know that there is a continuum of morphological habits, ranging from crustose to stipitate, with each species displaying a predominant morphotype (Vieira et al. 2014, Camacho et al. 2019). We classified each species from the Greater Caribbean based on their morphology and ecology (Table 4). The morphotypes described from the Indo-Pacific are found in the Greater Caribbean, and several trends with regard to the evolutionary signal of morphological characters or habit stand out (Vieira et al. 2014).

Populations of *Lobophora* were previously reported from various habitats in the Greater Caribbean (e.g., coral reefs, mangrove, seagrass, and macroalgal beds; Coen and Tanner 1989) and at different depths from the intertidal to 135 m depth

(Schultz et al. 2015). They grow in calm to agitated waters, in low to high fish grazing zones, and on biotic and abiotic substrates. One population was reported dominating the mesophotic benthic cover in the Bahamas at 90 m (Littler et al. 1986). Similar ecological habits are found in the Greater Caribbean as in the Indo-Pacific (Vieira et al. 2014; Table 3). As previously noted, notably in Belize (Coen and Tanner 1989, Littler and Littler 2000), some morphotypes/species are associated with specific habitats (Table 4). However, while the situation in Belize may provide an example of clear habitat specialization between three doubtlessly distinct and conspicuous species, several *Lobophora* species from the Greater Caribbean adopt very similar ecological habits and largely coexist. They grow along a wide depth range, in similar habitats, under similar conditions (Table 4). Some species have greater affinities for specific habitats, but they can also be found in other habitats growing next to other *Lobophora* species. However, while several species may be found growing adjacent to each other (e.g., *L. declerckii* and *L. canariensis*), they occupy distinct niches. For example, *L. canariensis* forms small procumbent blades in shaded areas, whereas *L. declerckii* forms large shelf-like blades fully exposed to the light. Microhabitat locality allows multi-species coexistence. Furthermore, *Lobophora* species can coexist because many are extremely rare, possibly as a result of limited recruitment opportunities, which limits competition. Predation may also regulate populations of more palatable species. Other than *L. declerckii*, which can form extensive cover, intraspecific and interspecific competition is limited for most *Lobophora* species.

Lobophora is known in the Caribbean for proliferating on damaged reefs following environmental and biological disturbances, by forming dense mats over dead corals (Vieira 2020). Most *Lobophora* species are rather discrete benthic macroalgae in the Greater Caribbean ecosystems. Some species can grow basally on coral branches (e.g., *L. littlerorum* on *Porites*), but such species are sparsely distributed, and do not form extensive populations (A.H. Engelen, C. Vieira, pers. obs.). Only a few species, most notably *L. declerckii*, can cover large areas on coral reefs across the Greater Caribbean. Bloom-forming species are more likely to cause shifts from coral to *Lobophora* dominance following disturbances on reefs (Vieira 2020). In this sense, *L. declerckii* is very likely the main species concerned in *Lobophora*-coral phase shifts in the Greater Caribbean. The ecological success and the widespread distribution of *L. declerckii* may be explained by the capacity of this species to form extensive cover. Considering the ecological differences among *Lobophora* species including their ability to form blooms and to outcompete corals, future studies need to describe the taxonomy of the species of *Lobophora* (using molecular methods) that compete with corals and that are implicated in coral–algal phase shifts (Vieira 2020).

The Greater Caribbean: an evolutionary dead end?. - With no less than 11 species restricted to the Greater Caribbean (*Lobophora agardhii*, *L. colombiana*, *L. crispata*, *L. declerckii*, *L. dickiei*, *L. guadeloupensis*, *L. lamourouxii*, *L. richardii*, *L. tortugensis*, *L. variegata*, and *L.* sp90), this region of the Atlantic is characterized by a high level of endemism for the genus *Lobophora* (i.e., ca. two-thirds of the Greater Caribbean *Lobophora* species diversity). Another five species are distributed across the northern Atlantic, namely *L. caboverdeana*, *L. canariensis*, *L. delicata*, *L. littlerorum*, and *L. schneideri*. The remaining two species have a western Indo-Pacific – Atlantic distribution, *L. dispersa* (Camacho et al. 2019, Vieira et al. 2019b) and *L. setchellii* sp. nov. (Vieira et al. 2019a). Additional molecular analyses are recommended to determine whether the broad distribution of *L. setchellii*, which spans three Oceans (Atlantic, Indian, and Pacific Oceans), is the result of multiple introductions, or alternatively whether this cosmopolitan species constitutes a species complex.

Lobophora diversity in the Caribbean resulted mainly from repeated establishments at different periods by phylogenetically distant lineages (Vieira et al. 2017). These rare events of dispersal from the Indo-Pacific to the Caribbean were followed by isolation and speciation, causing a high level of endemism in this region. Given that no sister species of *Lobophora* have been identified between the eastern Pacific and the Greater Caribbean, we conclude that the formation of the Isthmus of Panama (i.e., the closing of the Central American Seaway) did not result in vicariant speciation events. It is nevertheless possible that, similarly to certain groups such as foraminifera, *Lobophora* lineages present in the eastern Pacific following the closure of Central American Seaway became extinct as a result of sea temperature decline due to increased coastal upwelling (Chaisson and Ravelo 2000, O'Dea et al. 2016). Four to five *Lobophora* diversification events occurred in the Greater Caribbean: the clades of sister species *L. variegata–L. richardii*, *L. crispata–L. guadeloupensis*, *L. schneideri–L. delicata*, and *L. lamourouxii–L. caribica*. Considering the broader distribution of the clade *L. schneideri–L. delicata* across the North Atlantic, it is possible that diversification of this clade occurred somewhere else in the North Atlantic and was followed by range expansion.

The patterns of distribution observed in the Atlantic lead us to the conclusion that the eastern Atlantic represents a subset of diversity from the western Atlantic, possibly as a result of range expansion. Similar patterns of distribution were observed in other macroalgae, for example, *Dictyota crenulata* (Tronholm et al. 2013), *Laurencia* (Hernández et al. 2017), *Halimeda* (Verbruggen et al. 2009), and *Cladophoropsis membranacea* (Kooistra et al. 1992).

The high level of endemism observed in the Greater Caribbean in *Lobophora* (~60% endemism) is also found in other Dictyotales (e.g., in *Padina* and *Dictyota*; Tronholm et al. 2013, Silberfeld et al. 2014). The inclusion of molecular data may explain why these numbers contrast with the generally low level of endemism characterizing the Greater Caribbean based on public databases (30% endemism; Costello et al. 2017), and thus stresses the importance of using molecular taxonomic approaches to accurately assess levels of endemism.

CONCLUSIONS

For more than 200 years, phycologists incorrectly assigned the morphological and ecological diversity of the genus *Lobophora* to a single species. Here we add to the growing body of evidence that there are numerous species, and that the Greater Caribbean accounts for at least 18, including 11 endemic species. While some parts of the Greater Caribbean deserve further attention, for example, the Bahamas, Greater Antilles (e.g., Cuba), western part of the Gulf of Mexico, and the western Caribbean, we have gained a better perspective on *Lobophora* diversity, ecology, and distribution within this region. The increasing number of molecular and geographic studies on *Lobophora* makes this brown algal genus a good candidate model for biogeographic and evolutionary studies in the future. Finally, this study illustrates how sampling based on DNA identification is reshaping biogeographic patterns, as we know them.

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Camacho, O., Fernández-García, C., Vieira, C., Gurgel, C. F. D., Norris, J., Freshwater, D. W. & Fredericq, S. 2019. The systematics of *Lobophora* (Dictyotales, Phaeophyceae) in the western Atlantic and eastern Pacific oceans: eight new species. *J. Phycol.* 55:611–24.

Chaisson, W. & Ravelo, A. 2000. Pliocene development of the east-west hydrographic gradient in the equatorial Pacific. *Paleoceanography* 15:497–505.

Coen, L. & Tanner, C. 1989. Morphological variation and differential susceptibility to herbivory in the tropical brown alga *Lobophora variegata*. *Mar. Ecol. Prog. Ser.* 54:287–98.

Costello, M. J., Tsai, P., Wong, P. S., Cheung, A. K. L., Basher, Z. & Chaudhary, C. 2017. Marine biogeographic realms and species endemicity. *Nat. Commun.* 8:1057.

De Ruyter van Steveninck, E., & Breeman, A. 1987. Deep water populations of *Lobophora variegata* (Phaeophyceae) on the coral reef of Curaçao: influence of grazing and dispersal on distribution patterns. *Mar. Ecol. Prog. Ser.* 38:241–50.

De Ruyter van Steveninck, E., Kamermans, P. & Breeman, A. 1988. Importance of physical and biological processes in structuring tropical intertidal populations of *Lobophora variegata* (Phaeophyceae). *Mar. Ecol. Prog. Ser.* 44:77–84.

Edgar, R. C. 2004. MUSCLE: multiple sequence alignment with high accuracy and high throughput. *Nucleic Acids Res.* 32:1792–7.

Godínez-Ortega, J. L., Cabrera, L. I., Garcia-Sandoval, R., Wynne, M. J., Olivares-Rubio, H. F., Ramirez-Garcia, P. & Granados-Barba, A. 2018. Morphological and molecular characterization of *Lobophora declerckii* and *L. variegata* (Dictyotales, Ochrophyta) on the Atlantic coast of Mexico. *Phytotaxa* 382:57–73.

Hernández, O. E., Sentíes, A., Dreckmann, K. M., Cassano, V. & Fujii, M. T. 2017. Species diversity and biogeographical patterns of *Laurencia* sensu stricto (Rhodophyta) in the Atlantic Ocean. *Hidrobiológica* 27:301–14.

Kooistra, W. H., Stam, W. T., Olsen, J. L. & van den Hoek, C. 1992. Biogeography of *Cladophoropsis membranacea* (Chlorophyta) based on comparisons of nuclear rDNA ITS sequences. *J. Phycol.* 28:660–8.

Lê, S., Josse, J. & Husson, F. 2008. FactoMineR: an R package for multivariate analysis. *J. Stat.* 25:1–18.

Littler, D. S. & Littler, M. M. 2000. *Caribbean reef plants. An identification guide to the reef plants of the Caribbean, Bahamas, Florida and Gulf of Mexico.* Offshore Graphics Inc., Washington, DC, 542 pp.

Littler, M. M., Littler, D. S., Blair, S. M. & Norris, J. N. 1986. Deep-water plant communities from an uncharted seamount off San Salvador Island, Bahamas: distribution, abundance, and primary productivity. *Deep-Sea Res. Pt. I.* 33:881–92.

O'Dea, A., Lessios, H. A., Coates, A. G., Eytan, R. I., Restrepo-Moreno, S. A., Cione, A. L., Collins, L. S., De Queiroz, A., Farris, D. W. & Norris, R. D. 2016. Formation of the Isthmus of Panama. *Sci. Adv.* 2:e1600883.

Robertson, D. R. & Cramer, K. L. 2014. Defining and dividing the greater Caribbean: insights from the biogeography of shorefishes. *PLoS ONE* 9:e102918.

Schultz, N. E., Lane, C. E., Le Gall, L., Gey, D., Bigney, A. R., De Reviers, B., Rousseau, F. & Schneider, C. W. 2015. A barcode analysis of the genus *Lobophora* (Dictyotales, Phaeophyceae) in the western Atlantic Ocean with four novel species and the epitypification of *L. variegata* (J.V. Lamouroux) E.C. Oliveira. *Eur. J. Phycol.* 50:1–20.

Silberfeld, T., Bittner, L., Fernández-García, C., Cruaud, C., Rousseau, F., Reviers, B., Leliaert, F., Payri, C. E. & De Clerck, O. 2014. Species diversity, phylogeny and large scale biogeographic patterns of the genus *Padina* (Phaeophyceae, Dictyotales). *J. Phycol.* 49:130–42.

Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdaña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A. & Lourie, S. A. 2007. Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. *Bioscience* 57:573–83.

Sun, Z., Hanyuda, T., Lim, P. E., Tanaka, J., Gurgel, C. F. D. & Kawai, H. 2012. Taxonomic revision of the genus *Lobophora* (Dictyotales, Phaeophyceae) based on morphological evidence and analyses *rbc*L and *cox*3 gene sequences. *Phycologia* 51:500–12.

Thiers, B. 2020. *Index Herbariorum: A global directory of public herbaria and associated staff.* New York Botanical Gardens Virtual Herbarium, New York, NY, US Available at: http://www.givd.info.

Tronholm, A., Afonso-Carrillo, J., Sansón, M., Leliaert, F., Fernández-García, C. & De Clerck, O. 2013. Taxonomy of the *Dictyota ciliolata–crenulata* complex (Dictyotales, Phaeophyceae). *Phycologia* 52:171–81.

Tyberghein, L. 2012. Evolution, diversity and niche dynamics of seaweeds. Ph.D. dissertation, Ghent University, Ghent, 185 pp.

Verbruggen, H., Tyberghein, L., Pauly, K., Vlaeminck, C., Nieuwenhuyze, K. V., Kooistra, W. H., Leliaert, F. & De Clerck, O. 2009. Macroecology meets macroevolution: evolutionary niche dynamics in the seaweed *Halimeda*. *Global. Ecol. Biogeogr.* 18:393–405.

Vieira, C. 2020. *Lobophora*–coral interactions and phase shifts: summary of current knowledge and future directions. *Aquat. Ecol.* 54:1–20.

Vieira, C., Aharonov, A., Paz, G., Tsiamis, K., Engelen, A., Einav, R. & De Clerck, O. 2018. Diversity and origin of the genus *Lobophora* in the Mediterranean Sea including the description of two new species. *Phycologia* 58:163–8.

Vieira, C., Camacho, O., Sun, Z., Fredericq, S., Leliaert, F., Payri, C. & De Clerck, O. 2017. Historical biogeography of the highly diverse brown seaweed *Lobophora* (Dictyotales, Phaeophyceae). *Mol. Phylogen. Evol.* 110:81–92.

Vieira, C., Camacho, O., Wynne, M. J., Mattio, L., Anderson, R., Bolton, J. J., Sansón, M. et al. 2016. Shedding new light on old algae: matching names and sequences in the brown algal genus *Lobophora* (Dictyotales, Phaeophyceae). *Taxon* 65:689–707.

Vieira, C., De Clerck, O., Millet, L. & Payri, C. E. 2019a. Description of 10 new *Lobophora* species from the Bismarck Sea (Papua New Guinea). *Phycol. Res.* 67:228–38.

Vieira, C., D'hondt, S., De Clerck, O. & Payri, C. E. 2014. Toward an inordinate fondness for stars, beetles and *Lobophora*? Species diversity of the genus *Lobophora* (Dictyotales, Phaeophyceae) in New Caledonia. *J. Phycol.* 50:1101–19.

Vieira, C., Henriques, F., D'hondt, S., Neto, A. I., Almada, C. H., Kaufmann, M., Sansón, M., Sangil, C. & De Clerck, O. 2019b. *Lobophora* (Dictyotales) species richness, ecology and biogeography across the North-eastern Atlantic archipelagos. *J. Phycol.* https://doi.org/10.1111/jpy.12956.

Supporting Information

Additional Supporting Information may be found in the online version of this article at the publisher's web site:

Figure S1. Phylogenetic tree of *Lobophora* species using maximum likelihood method based on *cox*3 sequences. Values shown at each node represent bootstrap supports. Two species from the Greater Caribbean were not identified in our study, *L. crispata,* for which no *cox*3 sequences are available, and *L. tortugensis* indicated by a star in the tree.

Table S1. Information on the sampling campaigns and countries.

Table S2. Information on the *Lobophora* specimens collected in the Greater Caribbean.