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LOBOPHORA (DICTYOTALES) SPECIES RICHNESS, ECOLOGY AND BIOGEOGRAPHY ACROSS THE NORTH-EASTERN ATLANTIC ARCHIPELAGOS AND DESCRIPTION OF TWO NEW SPECIES[1]

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The brown alga *Lobophora* (Dictyotales, Phaeophyceae) is an important macroalga in the North-eastern Atlantic archipelagos (i.e., Macaronesia). Notably in the Canaries it can dominate benthic assemblages. While the genus has been the subject of several ecological studies in the Canaries, no study has yet been conducted to assess species-level diversity of *Lobophora* in Macaronesia. We reassessed the diversity of *Lobophora* in Macaronesia, reporting the presence of seven species (*L. caboverdeana* sp. nov., *L. canariensis*, *L. dagamae* sp. nov., *L. delicata*, *L. dispersa*, *L. littlerorum*, and *L. schneideri*). *Lobophora* spp. from Macaronesia are morphologically and ecologically distinguishable. In the Canaries, *L. schneideri* dominates the photophilic assemblages from the intertidal to 20-30 m depth. *Lobophora dagamae* sp. nov. grows in less illuminated shallow habitats, and replaces *L. schneideri* from 30 to ~80 m. *Lobophora canariensis* also has a wide vertical distribution, from the intertidal to deep waters, while *L. delicata*, *L. dispersa* and *L. littlerorum* grow in shallow waters. The dominance of species with an upright habit versus prostrate or crustose species may be mediated by the pressure of herbivores. Four species have an amphi-Atlantic distribution: *L.*

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***littlerorum*, *L. canariensis*, *L. delicata*, and *L. schneideri*. *Lobophora schneideri* and *L. delicata* are furthermore distributed in the Mediterranean Sea. By sampling a pivotal region in the Atlantic, this study significantly improves our knowledge of *Lobophora* biogeography in the Atlantic Ocean. Macaronesia constitutes a species–poor region for *Lobophora* where no diversification events occurred, and a region of overlap between the Greater Caribbean and the Indo-Pacific.**

Key index words: **barcoding; *cox*3; Macaronesia; phylogeny; molecular taxonomy**

Abbreviations: **_cox_3, mitochondrial encoded cytochrome c oxidase III gene; DNA, deoxyribonucleic acid; *psb*A, chloroplast encoded photosystem II protein D1; *rbc*L, chloroplast encoded ribulose-1,5-biphosphate carboxylase**

Located between 14° N and 39° N, 32° W and 13° W, the Macaronesian biogeographic region (i.e., North-eastern Atlantic archipelagos) lies along a latitudinal gradient of ~ 2850 km. Macaronesia comprises four archipelagos, the Azores, Madeira, the Canary, and Cape Verde Islands (Fig. 1). All islands are of volcanic origin and have emerged from the ocean basin at various points in time. Ocean currents, notably the Azores and Canary currents (branches of the North Atlantic current) link these archipelagos creating a route for the spread of marine coastal organisms from North to South. In addition, the North Equatorial current and counter-current and the Mauritanian current directly affect the Cape Verde archipelago (Arístegui et al. 2009). Latitudinal changes in sea surface temperature (SST) can exceed 6°C (Table 1). Colder and mesotrophic waters surround the Azores. In Madeira and western Canaries the waters are oligotrophic, while the eastern Canaries are slightly affected by Northwest African upwelling. In contrast, Cape Verde Islands have nutrient–enriched waters because of the strong upwelling plume from the coast of Senegal and Mauritania (Hoepffner et al. 2014).

Seaweed assemblages vary drastically along this latitudinal gradient, with communities dominated by cold-temperate taxa in the northernmost archipelago of the Azores, a mixture of species with colder and warmer affinities in Madeira and the Canaries, and a dominance of tropical taxa in the southernmost Cape Verde Islands (Sangil et al. 2018). The Dictyotales Bory de Saint-Vincent (Phaeophyceae), apart from the crustose coralline algae, are the dominant macroalgae in Macaronesia. *Lobophora* is one of the most ecologically important genera, though important differences in abundance exist between and within archipelagos (Sangil et al. 2018). *Lobophora* populations colonize rocky substrates from the intertidal to deep subtidal, at least to 80 m depth (C. Sangil, pers. obs.). In the Canary Islands and Madeira, *Lobophora* frequently dominates and monopolizes shallow subtidal macroalgal assemblages. There, growth and size of *Lobophora* populations are strongly controlled by the grazing of the sea urchin *Diadema africanum* (Sangil et al. 2011). Urchin barrens replace *Lobophora* communities in places where overfishing has allowed the demographic burst of *D. africanum* (Sangil et al. 2012). While the genus has been the object of several ecological studies in this region, no comprehensive taxonomic study has yet been conducted in Macaronesia assuming until 2016 that individuals of *L. variegata* constituted all the populations studied. In 2016, *Aglaozonia canariensis* was transferred to *Lobophora* (as *L. canariensis*; Vieira et al. 2016), thus bringing the number of documented species in the Canary Islands to two. A recent study showed that the Mediterranean Sea accounted only three *Lobophora* species including one obvious lessepsian migrant (*L. lessepsiana* Vieira et al. 2018). In contrast, the Greater

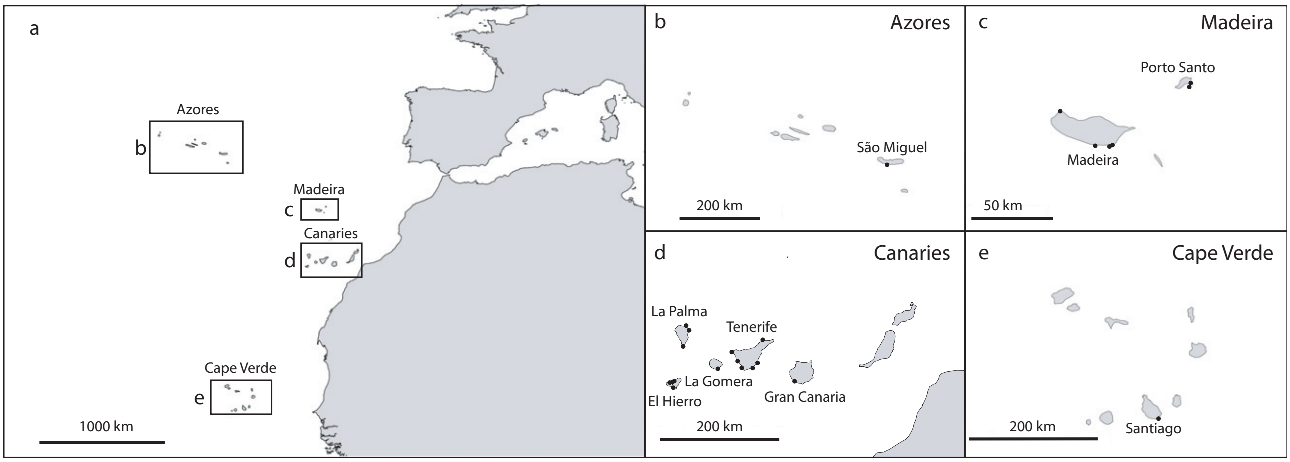


FIG. 1. Map of sampling localities in the Macaronesian archipelagos (a). Sampling was performed in the Azores (b), Madeira (c), Canaries (d), and Cape Verde (e).

TABLE 1. Summary of the geographic position, oceanographic conditions and richness of herbivores in the Macaronesian archipelagos (see Sangil et al. 2018 for references).

	Azores	Madeira	Canaries	Cape Verde
Latitude	39.72 to 36.92N	33.10 to 32.40N	29.41 to 27.63N	17.21 to 14.80N
Longitude	−31.79 to −24.77W	−17.26 to −16.27W	−18.16 to −13.33W	−25.36 to −22.66W
SSTmin	15.39–16.40°C	17.47–18.14°C	18.06–19.87°C	21.82–23.51°C
SSTmean	18.42–19.46°C	20.30–21.10°C	20.22–22.14°C	23.95–24.90°C
Water	Mesotrophic	Oligotrophic	Oligotrophic	Mesotrophic
Productivity	Nitrate 1.2–1.6 μmol·L^{-1} Chl *a* 0.16-0.29 mg·m^{-3}	Nitrate 0.67–0.73 μmol·L^{-1} Chl *a* 0.11-0.16 mg·m^{-3}	Nitrate 0.56–0.68 μmol·L^{-1} Chl *a* 0.12-0.18 mg·m^{-3}	Nitrate 1.39–1.850 μmol·L^{-1} Chl *a* 0.25-0.39 mg·m^{-3}
Herbivores	Poorly diversified 3 urchins species 5 fish species	Poorly diversified 4 urchins species 5 fish species	Poorly diversified 4 urchins species 5 fish species	Diversified 5 urchins species 11 fish species

Caribbean stands as the diversity hotspot for the genus *Lobophora* in the North Atlantic with 18 species and a high level of endemism (Vieira et al. 2017, unpublished, Camacho et al. 2019). This study focused on Macaronesia to improve our understanding of diversity and biogeography of the genus *Lobophora* in a pivotal region in the Atlantic. To reassess the species diversity of *Lobophora*, we conducted a wide-ranging molecular-based taxonomic study across the Macaronesian archipelagos, documented Macaronesian *Lobophora* species ecology and analyzed how these species relate among archipelagos and to other Atlantic regions.

MATERIALS AND METHODS

Taxon sampling. Sampling was performed in the four archipelagos (i.e., Azores, Madeira, Canary, and Cape Verde Islands). Specimens of *Lobophora* were collected by SCUBA and snorkeling from 15 localities in five (El Hierro, La Palma, La Gomera, Tenerife, and Gran Canaria) of the seven Canary Islands; from six localities in Madeira; from Lagoa, Ilha de São Miguel, in the Azores; and from Quebra Canela, Praia, Santiago in Cape Verde Islands. A total of 114 sequences were generated from the Canary Islands, 77 sequences from Madeira, 70 from Azores and 15 from Cape Verde Islands (Table S1 in the Supporting Information).

Ecological, molecular and morphological analyses. During field sampling, notes were made of ecological conditions, algal coverage and growth habit of the *Lobophora* specimens collected.

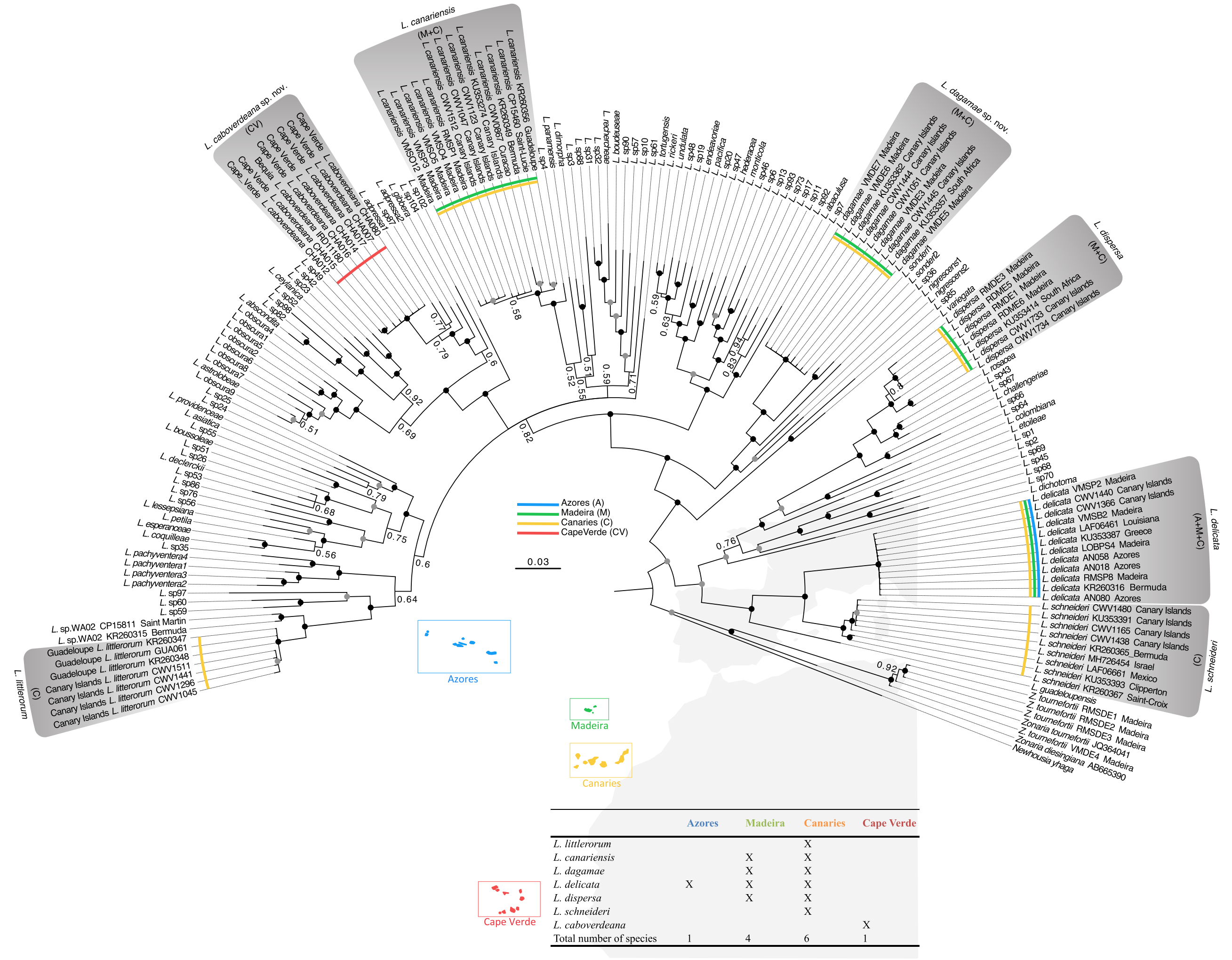
Total genomic DNA was extracted from tissue samples dried in silica gel using the cetyl-trimethyl ammonium bromide extraction method. DNA sequences were generated from the mitochondrial encoded cytochrome c oxidase III gene (*cox*3) shown to be an excellent barcode marker for the genus (Vieira et al. 2014, 2016), and in addition the chloroplast encoded ribulose-1,5-biphosphate carboxylase (*rbc*L) and the photosystem II protein D1 (*psb*A) genes for the newly described species. The sequences were added to the data sets from Schultz et al. (2015), Vieira et al. (2016), and Camacho et al. (2019) and aligned using MUSCLE (Edgar 2004). Phylogenetic trees were reconstructed using Bayesian and maximum likelihood methods based on the three markers following Vieira et al. (2016) for the three markers. Morphological observations of *Lobophora* specimens included analyses of the habit (general appearance, growth form, size and color of the thallus) and internal structure following Vieira et al. (2014). Longitudinal and transverse sections were made by hand of the middle portions of the thallus. Field photographs were taken with a digital camera (Nikon D7000; Nikon Corporation, Tokyo, Japan), and microscopic images were captured using a Fujifilm X10 digital camera attached to a Leica DM500 (Leica Microsystems, Wetzlar, Germany) microscope. Voucher specimens were dried as herbarium exsiccate and deposited in either BR (Herbarium of the Botanic Garden Meise, Belgium) or TFC (Herbarium of the University of La Laguna, Canaries), in some cases, specimens were preserved in a 4% formaldehyde solution with seawater for anatomical examination.

RESULTS

Phylogenetics trees generated by Bayesian inference and maximum likelihood analyses based on *cox*3, *pbs*A and *rbc*L markers resolved the Macaronesian sequences in seven distinct clades that were previously documented (Figs. 2, S1–S5 in the Supporting Information). These clades are not restricted to Macaronesia. Five clades correspond to *L. canariensis*, *L. delicata*, *L. schneideri*, *L. dispersa*, and *L. littlerorum* C.W.Schneider, N.E.Schultz & L.Le Gall; and two correspond to previously reported but undescribed lineages: *L.* sp37 and *L.* sp89 (Vieira et al. 2016, unpublished). A total of one, four, six and one species of *Lobophora* were identified in the Azores, Madeira, Canaries, and Cape Verde, respectively (Fig. 2).

Lobophora species from Macaronesia are morphologically distinguishable. The habit, in terms of general appearance, growth form, size, and color of the thallus allows identifying the different species (Fig. 3; see dichotomous key below). In particular, there are four different growth forms: erect, decumbent, prostrate and crustose. *Lobophora schneideri* is characterized by its erect ruffled thallus; *Lobophora dagamae* sp. nov. and some specimens of *L. canariensis* show a decumbent morphotype; both *L. delicata* and *L. dispersa* exhibit prostrate blades; and *L. littlerorum, L. caboverdeana* sp. nov. and some thallus of *L. canariensis* are crustose. Other habit characteristics inherent to each species are shown in the identification key (see below). The clear differentiation of habit among species makes it possible to show that some commonly grow very close to each other in the same habitat, as can be seen in Figure 4.

The internal vegetative morphologies of all species examined clearly presented the generic criteria



	Azores	Madeira	Canaries	Cape Verde
L. littlerorum			X	
L. canariensis		X	X	
L. dagamae		X	X	
L. delicata	X	X	X	
L. dispersa		X	X	
L. schneideri			X	
L. caboverdeana				X
Total number of species	1	4	6	1

FIG. 2. The phylogenetic tree of the genus *Lobophora* based on Bayesian method, generated with MrBayes v3 (Ronquist and Huelsenbeck 2003), and based on *cox*3 sequences. The values shown at each node represent posterior probabilities. Full support (posterior probabilities = 1) is indicated in black and high support (posterior probabilities > 0.95) is indicated in gray. [Color figure can be viewed at wileyonlinelibrary.com]

of *Lobophora*: multilayered thallus composed of an outer cortex and inner medulla with the central layer of medullary cells being distinctly larger. However, certain differences are also observed between the species in relation to the number of cell layers and the cell morphology (Fig. 5, Table 2). *Lobophora caboverdeana* sp. nov. is the thickest Macaronesian species (170–215 µm), which sets it apart from the other two encrusting species *L. canariensis* (80–112 µm) and *L. littlerorum* (95–140 µm). *Lobophora delicata* (48–65 µm) is the thinnest species and is characterized by translucent blades, which distinguishes it from the other prostrate species. We provide a formal description for the two undescribed species.

Taxonomic results. ***Lobophora caboverdeana* sp. nov. C.W.Vieira, C.H.Almada**

Figures 3c, 5, a and b, 7f

Description: Thallus fan shaped, up to 5 cm wide and 4 cm tall, rugose surface, coarse and rigid predominantly crustose, greenish-brown to dark yellow-brown. Thallus firmly attached to the substratum across the whole of the ventral surface by rhizoids. Thallus composed of single-cell–layered medulla, three- to four-cell–layered cortex on the dorsal and ventral sides. The thallus is 170–215 µm thick and composed of 7–9 cell-layers. The species is distinguished from the sympatric species by its crustose habit and thick thallus. Mitochondrial–encoded *cox*3 sequence = GenBank accession MN190399-MN190413; chloroplast–encoded *rbc*L and *psb*A sequences MN190600-MN190603 and MN190596-MN190599.

Geographic distribution: Bequia, Cape Verde

Holotype: CHA002, collected 26 November 2018, deposited in the Herbarium of the Botanic Garden Meise, Belgium (BR).

Habitat: Found growing strongly attached to the bedrock in intertidal rock pools.

Etymology: The species is named after the type locality, Cape Verde Islands.

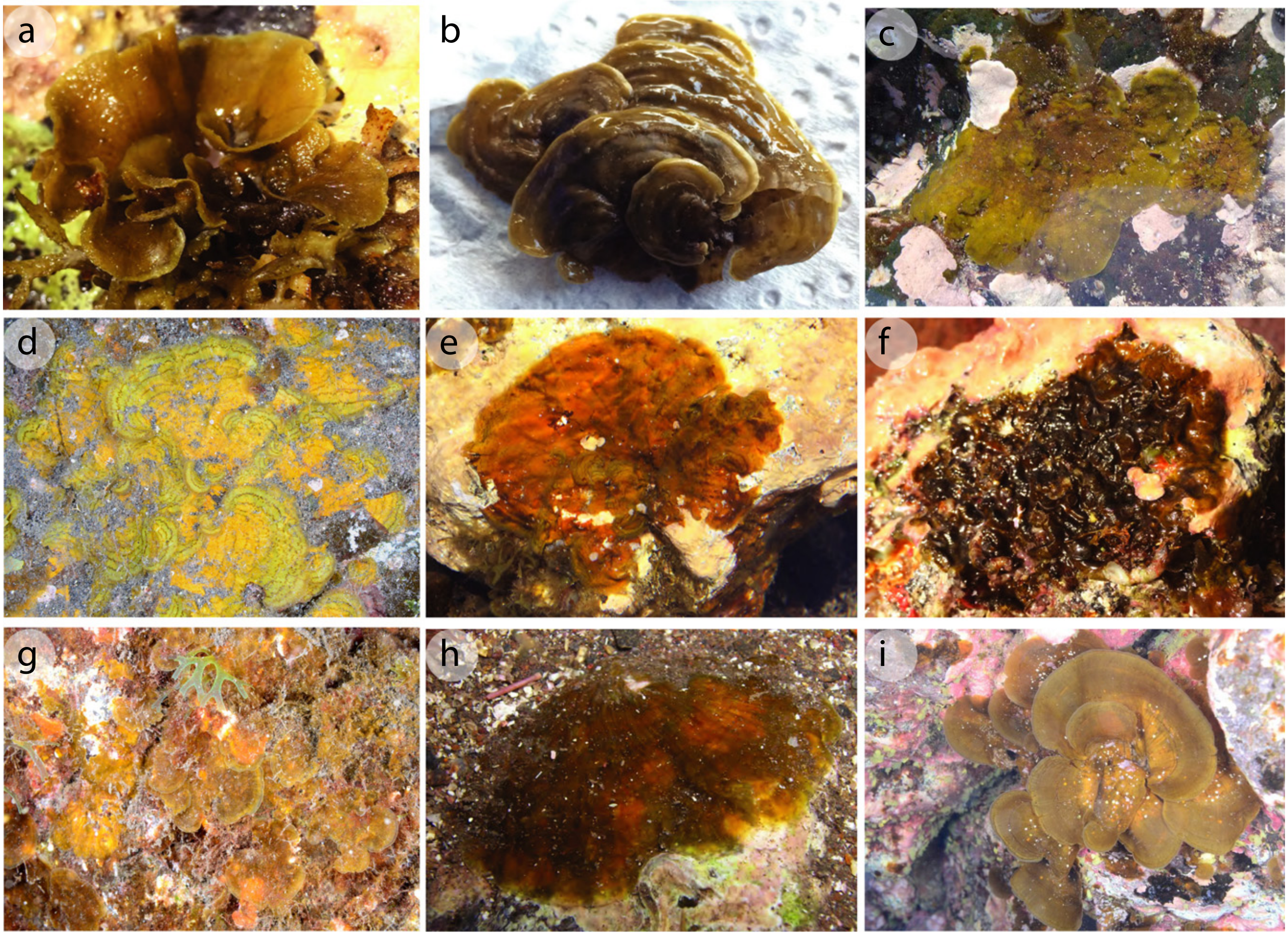


FIG. 3. Close-up photographs of *Lobophora* species, in situ or ex situ, from Macaronesia. *Lobophora schneideri* in Tenerife, Canary Islands (a); *L. dispersa* in Tenerife, Canary Islands (b); *L. caboverdeana* sp. nov. in Cape Verde (c); *L. canariensis* in El Hierro, Canary Islands (d, e); *L. littlerorum* in El Hierro, Canary Islands (f); *L. delicata* in Tenerife, Canary Islands (g) and in Madeira (h); *L. dagamae* sp. nov. in Tenerife (i). [Color figure can be viewed at wileyonlinelibrary.com]

Specimens: CHA002, CHA003, CHA004, CHA006, CHA007, CHA008, CHA009, CHA010, CHA012; CHA014, CHA015, CHA016, CHA017, CHA080, CHA081 collected 26 November 2018, Quebra Canela, Praia, Santiago, Cape Verde, *leg.* C. H. Almada. CP15294 collected 28 April 2015, West Cay, Bequia, *leg.* C. Payri.

***Lobophora dagamae* sp. nov. C.W.Vieira**

Figures 3i, 5, k and l, 7d

Description: Thalli in dense erect blades, medium to dark brown. Fronds composed of several lobes, stipitate, anchored, up to 4 cm wide and 4.5 cm tall, rugose surface, brown in color with white margin. Thalli attached to bedrock by a discrete holdfast. Margin entire. Thallus composed of single-cell–layered medulla, three- to four- and three-cell–layered cortex on the dorsal and ventral side, respectively. The thallus is 95-173 μm thick and composed of 7 cell-layers. The species is distinguished from the sympatric species in having darker brown thalli with basal mound of hairs. Mitochondrial-encoded *cox*3 sequence = GenBank accession MN190333-MN190333, MN190464-MN190468; chloroplast-encoded *rbc*L and *psb*A sequences KU353155- KU353156 and KU352861-KU352862.

Geographic Distribution: Canary Islands (Spain), Madeira (Portugal), South Africa

Holotype: CWV1444, collected 08 March 2017, deposited in the Herbarium of the Botanic Garden Meise, Belgium (BR).

Habitat: Mostly found growing on the vertical side of bedrock in shaded areas.

Etymology: The species is named after the Portuguese explorer Vasco da Gama, because the species distribution in western Indo-Pacific and in Macaronesia reminds the route followed along the coast of Africa via Tenerife and the Cape Verde Islands by this explorer.

Specimens: CWV1444, CWV1445, collected 08 March 2017, Charco Azul, El Hierro, Canary Islands, *leg.* C. Vieira; CWV1588, collected 09 March 2017, Tacoron, El Hierro, Canary Islands, *leg.* C. Vieira.

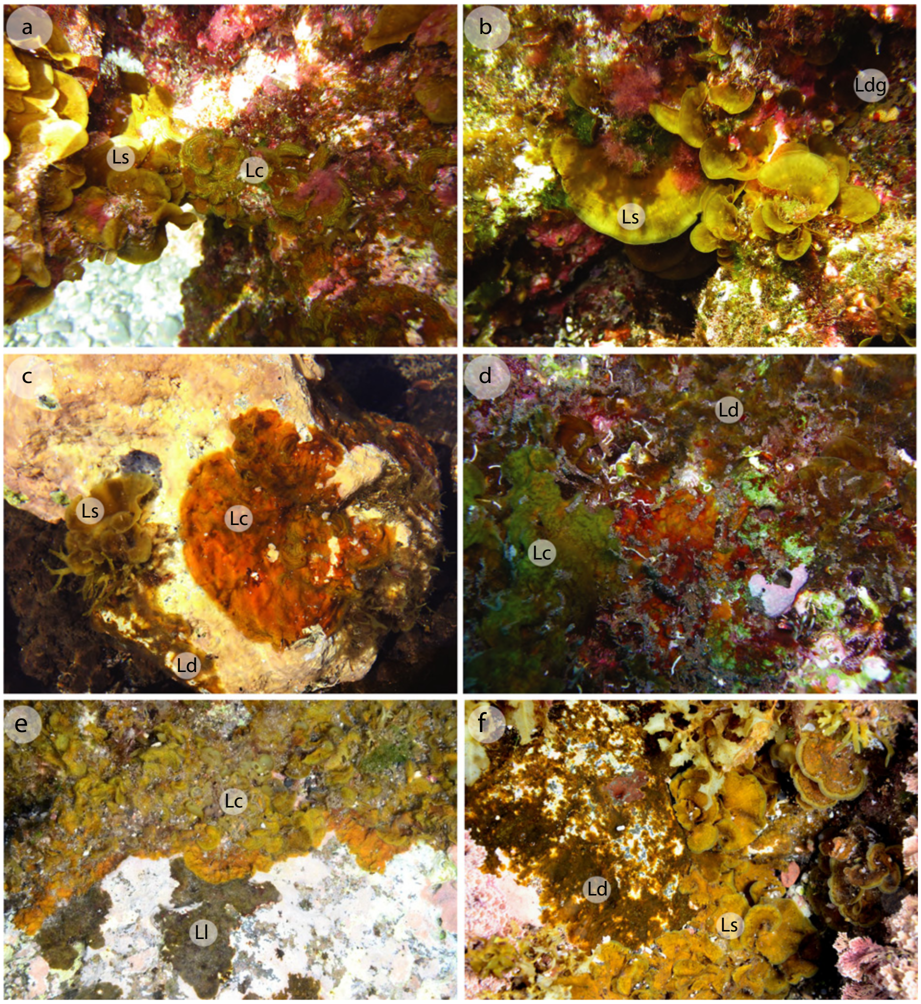


FIG. 4. In situ photographs showing sympatric *Lobophora* species competing for space in Tenerife, Canary Islands. Lc: *L. canariensis*, Ls: *L. schneideri*, Ldg: *L. dagamae* sp. nov., Ld: *L. delicata*. [Color figure can be viewed at wileyonlinelibrary.com]

DISCUSSION

Diversity. This is the first wide–ranging taxonomic sampling of the genus *Lobophora* in Macaronesia, with a more thorough effort performed in the Canary Islands and Madeira. We report the occurrence of seven species (Table S2 in the Supporting Information), of which five were previously described from the Mediterranean Sea or western Atlantic Ocean (*L. canariensis, L. delicata, L. dispersa, L. littlerorum* and *L. schneideri*). Two species are described here, *L. dagamae* sp. nov. and *L. caboverdeana* sp. nov. We did not find genuine *L. variegata* in Macaronesia, providing additional evidence that the latter species is most likely restricted to the Caribbean Sea. Except for the sister species *L. delicata* and *L. schneideri*, the Macaronesian species do not form a monophyletic clade. The North-eastern Atlantic, including the Mediterranean Sea, is thus far less diverse than the North-western Atlantic (i.e., Greater Caribbean), which accounts at present 18 species (Vieira et al. unpub. data). Causes potentially explaining why this region is less diverse than the Greater Caribbean are further discuss below.

Distribution. The *Lobophora* species documented in this study are not restricted to Macaronesia (Fig. 6). Their distributions extend across the Atlantic (*L. caboverdeana* sp. nov., *L. canariensis*, *L. delicata*, *L. littlerorum*, *L. schneideri*) and to the western Indo-Pacific (*L. dagamae* sp. nov., *L. dispersa*). *Lobophora delicata* and *L. schneideri* have a northern amphi-Atlantic distribution, including the Mediterranean Sea (Vieira et al. 2018). *Lobophora schneideri* is furthermore present in the eastern Pacific in Clipperton Island, probably as a result of human–mediated dispersal (Vieira et al. 2018). *Lobophora canariensis, L. caboverdeana* sp. nov. and *L. littlerorum* have a northern amphi-Atlantic distribution but are absent from the Mediterranean Sea. *Lobophora dagamae* sp. nov. is distributed in the eastern Atlantic and in the western Indo-Pacific (South Africa and Madagascar; Vieira et al. 2016). Finally, *L. dispersa* and *L. caboverdeana* sp. nov. are present across the Atlantic and also in the western Indo-Pacific (Vieira et al. 2016). Similar distribution patterns were observed in other macroalgae, e.g., *Dictyota crenulata* (Tronholm et al. 2013), *Laurencia* (Hernández et al. 2017) *Halimeda*

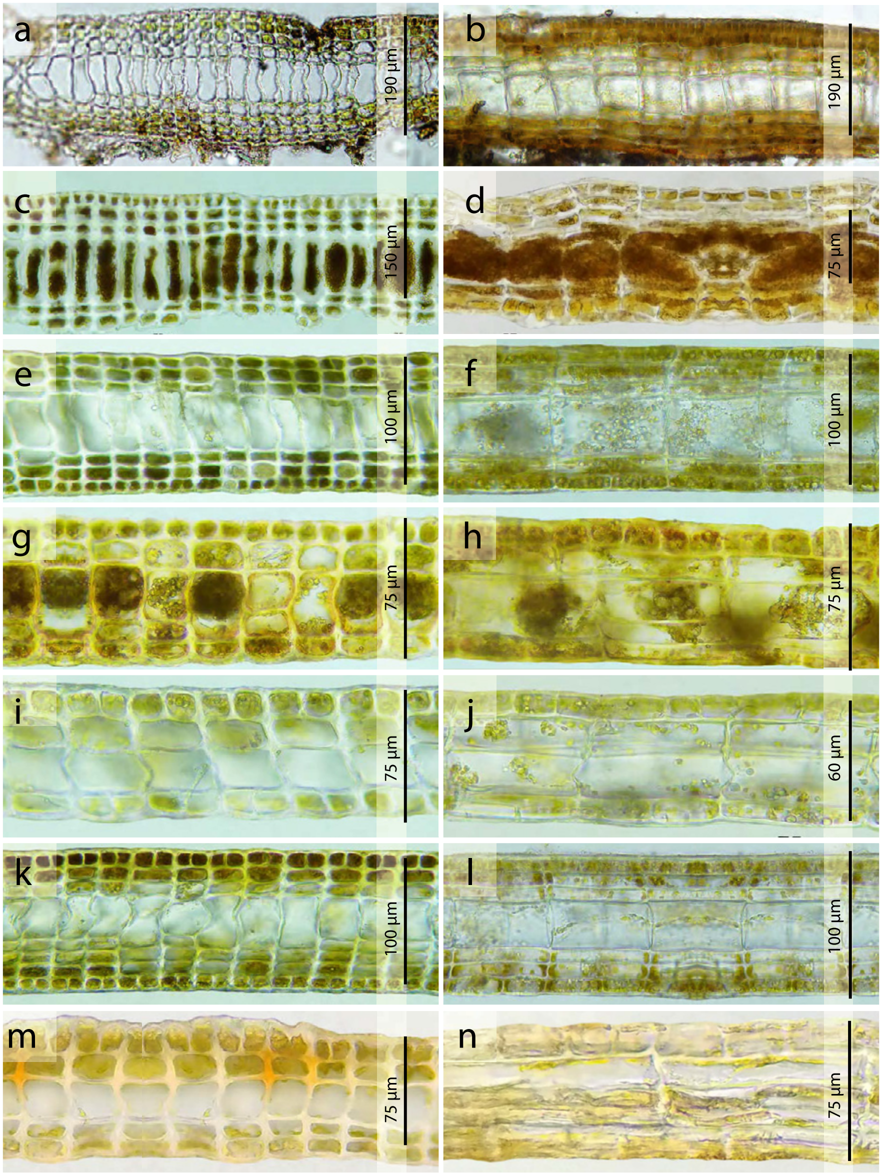


Fig. 5. Transverse (a, c, e, g, i, k, m) and longitudinal (b, d, f, h, j, l, n) sections of thallus of *Lobophora* species from Macaronesia. *Lobophora caboverdeana* sp. nov. from Santiago, Cabo Verde, voucher CHA002 (a, b); *L. dispersa* from El Médano, Tenerife, Canary Islands, voucher TFC Phyc 7579 (c, d); *L. schneideri* from Punta del Hidalgo, Tenerife, Canary Islands, voucher TFC Phyc 15810 (e, f); *L. littlerorum* from Punta del Hidalgo, Tenerife, Canary Islands, voucher TFC Phyc 15809 (g, h); *L. delicata* from Punta del Hidalgo, Tenerife, Canary Islands, voucher TFC Phyc 15807 (i, j); *L. dagamae* sp. nov. from Punta del Hidalgo, Tenerife, Canary Islands, voucher TFC Phyc 15812 (k, l); *L. canariensis* from Punta del Hidalgo, Tenerife, Canary Islands, voucher TFC Phyc 15808 (m, n). [Color figure can be viewed at wileyonlinelibrary.com]

(Verbruggen et al. 2009), and *Cladophoropsis membranacea* (Kooistra et al. 1992). The presence of these *Lobophora* species in the Macaronesian archipelagos likely resulted from range expansions from the Greater Caribbean or the Indo-Pacific. In this regard, Macaronesian archipelagos consist of a region of range overlaps for *Lobophora* species, which present wide distributional ranges.

Between the two better–sampled archipelagos (Canaries and Madeira), the Canary Islands displayed the highest species diversity, with six species (Fig. 2). *Lobophora schneideri* and *L. littlerorum* were absent from Madeira. Two species were restricted to one archipelago, *L. littlerorum* in the Canary Islands and *L. caboverdeana* sp. nov. in Cape Verde. Although data are not yet available, personal observations allow us to state that probably a better sampling in Cape Verde will show that the local *Lobophora* species are different from the other Macaronesian archipelagos.

Low diversity. Unpublished data (Vieira, C., Morrow, K. M., D'Hondt, S., Camacho, O., Engelen, A. H., Payri, C. & De Clerck, O., unpub. data) concluded that 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. The low diversity and the lack of apparent endemism of the genus *Lobophora* within the Macaronesian archipelagos may also be linked to niche conservatism and habitat filtering. Admitting that the presence of the *Lobophora* species in Macaronesia resulted from range expansion, the donor regions (i.e., Greater Caribbean and Western Indo-Pacific) were

TABLE 2. Comparison of morphological characters among species of *Lobophora* from Macaronesia.

	L. canariensis	*L. caboverdeana* sp. nov.	*L. dagamae* sp. nov.	*L. delicata*	*L. dispersa*	*L. littlerorum*	*L. schneideri*
Thickness							
Average	102 ± 8	183.7 ± 13.7	132.0 ± 32.7		131.8 ± 17.2		167.0 ± 8.6
Min–Max	80–112	170–215	95–173	48–65	114–164	95–140	156–180
Number of cells							
Average	5.0 ± 0.0	8.3 ± 0.6	7.0 ± 0.0		7.2 ± 0.4		6.9 ± 0.3
Min–Max	5	7–9	7	3–4	7–8	5–6	6–7
Number of dorsal cells							
Average	2.0 ± 0.0	3.9 ± 0.3	3.1 ± 0.3		3.2 ± 0.4		3.0 ± 0.0
Min–Max	2	3–4	3–4	2	3–4	2–3	3
Number of ventral cells							
Average	2.0 ± 0.0	3.3. ± 0.5	3.0 ± 0.0		3.0 ± 0.0		2.9 ± 0.3
Min–Max	2	3–4	3	1	3	2	2–3
Medulla length							
Average	79 ± 12	70.0 ± 5.0	62.0 ± 7.8		82.0 ± 8.4		117.2 ± 13.3
Min–Max	60–100	65–75	55–75		70–90	60–80	106–140
Medulla height							
Average	45 ± 6	60.0 ± 7.1	36.3 ± 4.1		45.6 ± 9.8		68.4 ± 8.1
Min–Max	30–54	50–75	30–43	20–34	34–60	38–40	60–80
Medulla width							
Average	33 ± 4	37. 0 ± 6.3	23.5 ± 2.2		22.4 ± 2.6		27.6 ± 2.6
Min–Max	30–40	30–50	20–25	25–29	20–26	32–46	24–30
Dorsal height							
Average	30 ± 3	70.7 ± 5.3	50.4 ± 21.4		45.6 ± 7.8		50.4 ± 3.1
Min–Max	26–34	30–80	30–80		40–60		44–56
Ventral_height							
Average	27 ± 3	53.0 ± 9.6	41.8 ± 12.8		40.6 ± 1.9		48.2 ± 4.8
Min–Max	20–32	40–70	27–58		38–44		40–56
Thallus							
Growth-form	Crustose to decumbent	Crustose	Crustose to procumbent	Crustose, procumbent, decumbent	Procumbent	Crustose	Ruffled
Color	Orange-brown	Light-brown	Light-brown	Translucent light green	Light to dark brown	Green to brown	Light green
References	Vieira et al. (2016)	This study	This study	Camacho et al. (2019)	This study	Schultz et al. (2015)	Vieira et al. (2018)

significantly warmer than the recipient region (except for Cape Verde). Accordingly, only a subset – those already adapted to colder parts of the donor regions – of the species that dispersed to Macaronesian archipelagos managed to tolerate the relatively lower temperatures (habitat filtering on an ecological scale) or to adapt to colder temperatures (niche conservatism). In fact, within the northern Macaronesian archipelagos (excluding Cape Verde), the sea surface temperature ranges from 16 to 23°C. In contrast, in the Caribbean the average sea surface temperature is ~27°C, thus significantly warmer, and varies as little as 3°C throughout the year. Among the amphi-Atlantic species, three (i.e., *L. delicata*, *L. dispersa* and *L. schneideri*) present warm-temperate affinities in the Greater Caribbean (Vieira, C., Morrow, K. M., D'Hondt, S., Camacho, O., Engelen, A. H., Payri, C. & De Clerck, O., unpub. data), thus supporting the idea that species already adapted to colder temperature had higher chances to expand to northern Macaronesian archipelagos. This is also the case for *L. dagamae* sp. nov., which expanded from the temperate South-western Indo-Pacific (South Africa and Madagascar).

Alternatively, the relative young geological age of these volcanic islands could explain the patterns of diversity observed in Macaronesia. The first island of the Azores, Santa María, emerged 8.12 Mya. The oldest island in Madeira, Porto Santo, emerged some 14 Mya, and in the Canary Islands Fuerteventura began rising ~ 60 Mya. The easternmost islands of Cape Verde (Sal, Maio, Boavista, Santiago) emerged 25 to 15 Mya. The Macaronesian archipelagos are, therefore, much younger than the Western part of the North Atlantic. Colonization opportunities may, nevertheless, have been possible from 60 Mya through the oldest islands, which are presently submerged, i.e., seamounts (Fernández-Palacios et al. 2011), but on remote and limited number of islands. While *Lobophora* colonized the Atlantic from the early Paleogene (Vieira et al. 2017) the western and eastern North Atlantic regions did not present equal evolutionary opportunities. Accordingly, the present low diversity observed within the North-eastern Atlantic region, characterized by the absence of endemism, may be the result of more recent colonization events from the Greater Caribbean and the western Indo-Pacific.

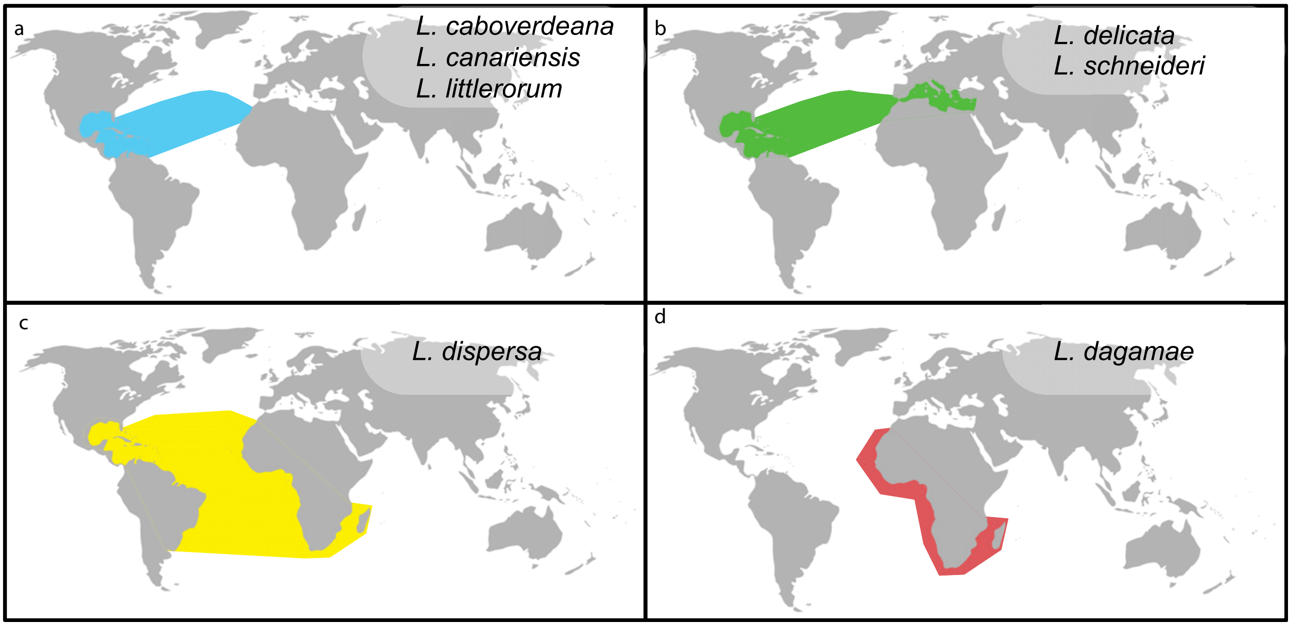


FIG. 6. Distribution maps. Distribution of *Lobophora caboverdeana*, *L. canariensis* and *L. littlerorum* (a); *L. delicata* and *L. schneideri* (b); *L. dispersa* (c); and *L. dagamae* sp. nov. (d). [Color figure can be viewed at wileyonlinelibrary.com]

Ecology. The relative benthic cover of *Lobophora* varies drastically between archipelagos and even islands. Coverage of *Lobophora* species is generally quite low across archipelagos. An exception is found in the western Canary Islands, characterized by low herbivore populations, especially the sea urchin *Diadema africanum*, and warm and oligotrophic waters (Sangil et al. 2014a), where dense macroalgae assemblages are observed year long (Fig. 7, a and b). Herbivores and temperature have been documented as the main factors involved in the abundance of *Lobophora* in the Macaronesian archipelagos. In the coldest waters of Azores only *L. delicata* was found. *Lobophora delicata* is a photophilic species that grows from the intertidal to shallow subtidal, although in the Azores it has a scarce cover and other dictyotaleans such as *Zonaria tournefortii* outnumber it in abundance (Sangil et al. 2018). In the central archipelagos of Madeira and Canaries, *Lobophora* species are the potential dominant species in rocky bottom communities. Nevertheless, the effect of overfishing has decimated the fish predator populations of *Diadema africanum* and as a result the populations of this urchin have increased disproportionately transforming the subtidal macroalgal beds to urchin barrens (Hernández et al. 2008). Only in the northern coast of the islands where wave exposure prevents grazing by *D. africanum* or in the western Canary Islands where the human pressure is less, *Lobophora* beds dominate and even monopolize subtidal landscapes (Sangil et al. 2014a). Following massive mortality events in *D. africanum* in the last decade (Clemente et al. 2014), *Lobophora* populations are recolonizing the sea bottoms in Madeira and the Canary Islands (C. Sangil, F. Henriques, C. Vieira, pers. obs.). High herbivore pressure is a natural condition in the warmest waters of Cape Verde. Although in this archipelago *D. africanum* does not present high-density populations, there are great populations of herbivore fishes, such as surgeons, scarids and damselfishes, which control the development of any noncrustose macroalgae including the species of *Lobophora* (Sangil et al. 2018).

The highest diversity of *Lobophora* is found in the intertidal pools and the shallow subtidal, where different species share the same habitat. In the Canary Islands, all species except for *L. dispersa*, were observed growing next to each other in the same habitat, indicating a high level of competition for space. Its own niche may nevertheless characterize each species. *Lobophora schneideri* is the most common species in the Canary Islands (C. Sangil, M. Sansón, C. Vieira, pers. obs.). By its characteristic ruffled growth form, *L. schneideri* is easily recognized growing from the intertidal to 20 m depth forming abundant beds (Fig. 7, a and b). The ability to form large populations is apparently an inherent trait of this species, since comparable beds were documented in the eastern Mediterranean Sea (Israel; Vieira et al. 2018). *Lobophora schneideri* might also be present in Madeira (Ferreira et al. 2018). *Lobophora dagamae* sp. nov., characterized by a stipitate thallus, is also a very abundant species in the Canary Islands. It grows in shallow waters on vertical surfaces or low illumination habitats as a sciaphilic species, replacing *L. schneideri* from 20 to 80 m depth where it can form dense beds between black corals (*Antipatharia*). *Lobophora canariensis* is also quite

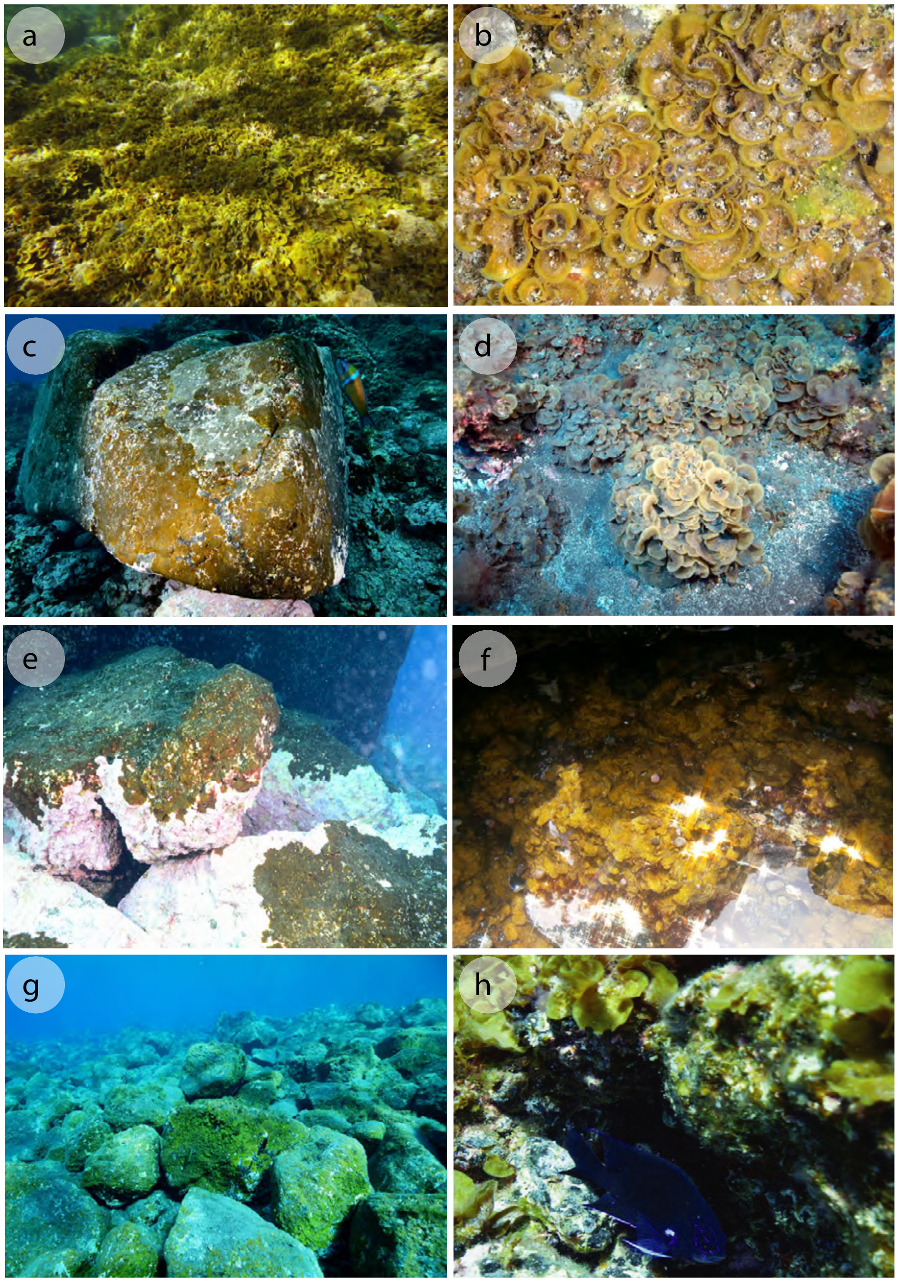


FIG. 7. Habitat photographs of *Lobophora schneideri* meadow in El Hierro, Canary Islands (a, b); *L. delicata* in La Palma, Canary Islands (c); *L. dagamae* sp. nov. in La Palma, Canary Islands (d); *L. littlerorum* in La Palma, Canary Islands (e); *L. caboverdeana* sp. nov. in Cape Verde (f); *L. canariensis* growing on boulders in El Hierro, Canary Islands and farmed by the Canary damselfish in the midst of *L. schneideri* meadow, picture courtesy of Jan Ranson. [Color figure can be viewed at wileyonlinelibrary.com]

common in the Canary Islands (Fig. 7g), although it is a rather discrete species forming small patches. It grows in a wide bathymetric range from the intertidal to 40-50 m depth. This species is characterized by two morphotypes. The crustose morphotype consists of large orange-green encrusting thin blades speckled with dark brown-olive colors, and the prostrate morphotype consists of smaller and decumbent light-green blades also speckled with dark brown-olive colors (Fig. 3, d and e). This species and other crustose *Lobophora*, such as *L. littlerorum* and *L. delicata*, are common in *D. africanum* barrens (Sangil et al. 2014b). In addition, *L. canariensis* was observed being cultivated by the Canary damsel, *Similiparma lurida*, within *L. schneideri* dominated assemblages in the Canary Islands (C. Vieira, pers. obs.; Fig. 7h), and by another species of damselfish (*Abudefduf taurus*) within *L. declerckii* dominated assemblages in Curaçao (C. Vieira, pers. obs.). The damsel fishes remove *L. schneideri* or *L. declerckii* from a small area and allow *L. canariensis* only to grow where the latter develops decumbent thalli. In some habitats, *L. canariensis* is most abundant in the Canary damsel territory. It is not known why the damselfishes specifically cultivate this less common species instead of *L. schneiderii* or *L. declerckii.*

Lobophora delicata is also common in the Canary Islands growing next to other species, forming crustose to prostrate somewhat transparent blades light green in color. It grows mainly on walls and large boulders in shallow waters. Similarly as in the Greater Caribbean, *L. littlerorum* forms dark and narrow crusts growing in shaded areas, underside of rocks or even below *L. schneideri* blades. Found in the Canary Islands and Madeira, *L. dispersa* forms prostrate undulated blades, and grows in shallow and highly wave–washed habitats or in shaded areas. Finally, *Lobophora caboverdeana* sp. nov. was observed attached to the bedrock forming dense patches in shallow waters in Cape Verde.

KEY TO THE SPECIES OF *LOBOPHORA* IN NORTH-EASTERN ATLANTIC

1.	Blades crustose, tightly adhering to rock over entire ventral surface	2
1'.	Blades prostrate to erect	4
2.	Blades light green to orange speckled with dark brown and olive colors	***L. canariensis***
2'.	Blades dark green or brown in color	3
3.	Blades dark green in color and thick (170 – 215 μm)	***L. caboverdeana***
3'.	Blades uniformly dark brown in color	***L. littlerorum***
4.	Blades prostrate, thin, smooth or undulated	5
4'.	Blades erect or decumbent but not adhering over entire ventral surface	6
5.	Blades smooth, light green in color, somewhat transparent	***L. delicata***
5'.	Blades undulated, brown in color	***L. dispersa***
6.	Blades erect ruffled with basal mound of hair, light to dark green in color	***L. schneideri***
6'.	Blades decumbent	7
7.	Blades light green to orange speckled with dark brown and olive colors	***L. canariensis***
7'.	Blades flat with basal mound of hairs, light to dark brown in color	***L. dagamae***

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CONFLICT OF INTEREST

The authors have no conflict of interest to declare.

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Supporting Information

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

Figure S1. The phylogenetic tree of the genus *Lobophora* based on Maximum Likelihood method, generated with RAxML v8 (Stamatakis 2014), and based on *cox*3 sequences. The values shown at each node represent bootstrap supports.

Figure S2. The phylogenetic tree of the genus *Lobophora* based on Bayesian method, generated with MrBayes v3 (Ronquist and Huelsenbeck 2003), and based on *psb*A sequences. The values shown at each node represent posterior probabilities.

Figure S3. The phylogenetic tree of the genus *Lobophora* based on Bayesian method, generated with MrBayes v3 (Ronquist and Huelsenbeck 2003), and based on *rbc*L sequences. The values shown at each node represent posterior probabilities.

Figure S4. The phylogenetic tree of the genus *Lobophora* based on Maximum Likelihood, generated with RAxML v8 (Stamatakis 2014), and based on *psb*A sequences. The values shown at each node represent bootstrap supports.

Figure S5. The phylogenetic tree of the genus *Lobophora* based on Maximum Likelihood, generated with RAxML v8 (Stamatakis 2014), and based on *rbc*L sequences. The values shown at each node represent bootstrap supports.

Table S1. Collection details of the specimens from Macaronesia studied here and in Vieira et al. (2016) with GenBank accession numbers of the mitochondrial (*cox*3) and chloroplast (*psb*A, *rbc*L) gene sequences.

Table S2. Distribution of *Lobophora* species in the Macaronesian archipelagos.